Endocast asymmetry in pongids assessed via non-rigid deformation analysis of high-resolution CT images

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Abstract

Human brains are asymmetrical, both in structure and function. The extent and pattern of asymmetries on the endocranial surfaces of pongids and humans, and how they might match expectations from published studies of their actual brains, is ultimately important for understanding what fossil endocasts might be able to tell us about the brains of these creatures, thereby potentially informing us about their behavior. Gross neuroanatomical asymmetries (known as petalias) favoring the right frontal and left occipital regions of the brain are common in humans, and are reasonably common in pongids. However, the combination of right frontal and left occipital petalias in the same specimen appears to be absent (or extremely rare) in pongids. The behavioral significance of this difference is unclear, but it is suggestive of a possible anatomical marker of evolved behavioral abilities in hominids.

Published studies of endocranial petalias have typically used only a few measurements to quantify hemispheric differences. We applied a method in which a series of virtual endocasts are morphed into their respective mirror images. The degree to which left and right hemispheres mismatch is then measured at each point on the endocranial surface. Statistical population assessments of left-right asymmetry using this method will be described for analyses of 10 *Pan troglodytes*, 9 *Pan paniscus*, 12 *Gorilla gorilla*, 11 *Pongo pygmaeus*, and 11 *Homo sapiens* endocasts. The extent and pattern of human endocranial asymmetries consistently differ from pongid endocranial asymmetries will be demonstrated, and functional implications of these differences will be discussed.

Background

Human brains are functionally asymmetric, with specific types of processing tending to be done in (lateralized to) one hemisphere more than the other. Language is one important species-specific behavior that is lateralized in this way (e.g., Broca's and Wernicke's language areas are localized to the left hemisphere of most (but not all) people. The strong bias towards right-handedness (left-hemisphere dominance) may also be related to language, and may have its origins in stone tool manufacturing (it has been suggested that early stone tools show signs of right-handedness; Toth 1985). Human brains are morphologically asymmetric, presumably reflecting these functional asymmetries. Morphological asymmetries of the brain appear to be reflected in asymmetries of the endocranial surface. Quantifying endocranial asymmetry may allow us to assess the likelihood of functional asymmetries of fossil hominids. Sambungmacan 3 appears to have a larger protrusion in the region of Broca's area ('Broca's cap') for example (Broadfield et al. 2001; Figure 1)

Early work on endocranial asymmetry focused on petalias (protrusions on one side larger than the other). The behavioral significance of petalias is not known but it is assumed to be related to functional asymmetries of brain function. Human endocasts appear to be more asymmetrical than ape endocasts in a specific way: they are more likely to show the combination of both left occipital and right frontal petalias than are those of other apes (Holloway and and de la Coste-Lareymondie 1982; Figure 2).

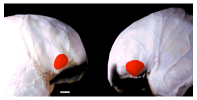

Figure 1: Apparent asymmetry of 'Broca's cap' of the endocast of Sambungmacan 3 (Broadfield et al. 2001)

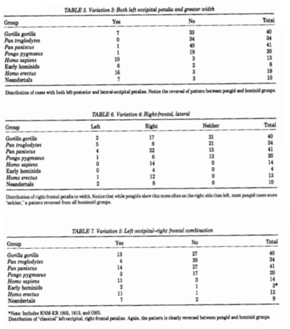

TABLE 5. Variation 3: Both left occipital petalia and greater width

Group	Yes	No	Total
Gorilla gorilla	7	33	40
Pan troglodytes	0	34	34
Pan paniscus	1	40	41
Pongo pygmaeus	1	19	20
Homo sapiens	10	3	13
Early hominids	6	2	8
Homo erectus	16	3	19
Neandertals	7	3	10

Distribution of cases with both left-posterior and lateral-occipital petalias. Notice the reversal of pattern between pongid and hominid groups.

TABLE 6. Variation 4: Right-frontal, lateral

Group	Left	Right	Neither	Total
Gorilla gorilla	2	17	21	40
Pan troglodytes	5	8	21	34
Pan paniscus	4	22	15	41
Pongo pygmaeus	1	6	13	20
Homo sapiens	0	14	0	14
Early hominids	0	4	0	4
Homo erectus	1	12	0	13
Neandertals	2	8	0	10

Distribution of right-frontal petalia in width. Notice that while pongids show this more often on the right side than left, most pongid cases score "neither," a pattern reversed from all hominoid groups.

TABLE 7. Variation 5: Left occipital-right frontal combination

Group	Yes	No	Total
Gorilla gorilla	13	27	40
Pan troglodytes	4	30	34
Pan paniscus	14	27	41
Pongo pygmaeus	3	17	20
Homo sapiens	11	3	14
Early hominids	2	1	3*
Homo erectus	11	1	12
Neandertals	7	2	9

*Note: Includes KNM-ER 1805, 1813, and OH5.
Distribution of "classical" left-occipital, right-frontal petalias. Again, the pattern is clearly reversed between pongid and hominid groups.

Figure 2: Original petalial data from Holloway and and de la Coste-Lareymondie (1982)

Recently, morphing techniques have been applied to the comparison of endocranial shape in general (e.g., MacLeod et al. 2003), left-right asymmetries in human vs. chimpanzee brains (Gilissen 2001; Figure 2 below), and male vs. female human brains (Falk et al. 2005). The present study applies these techniques to the study of endocranial asymmetries.

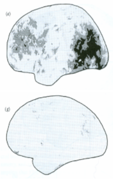

Figure 3: Average hemispheric differences in the brains of humans (top) and chimpanzees (bottom), mapped onto the left hamisphere. Darker areas indicate greater left-vs.-right differences (Gilissen 2001). Compare to Figure 5

Methods

High resolution 3D scans were obtained from 49 specimens:

10 *Pan troglodytes*, 9 *Pan paniscus*, 12 *Gorilla gorilla*, 11 *Pongo pygmaeus*, 11 *Homo sapiens*

The non-human primate endocasts were high-resolution scans of latex/plaster endcasts made by Ralph Holloway. The *Homo* endocasts were obtained from scans of crania in the Open Research Scan Archive (ORSA) at Penn. Virtual endocasts were delineated using ITK-SNAP (active contour edge-based method) by Jason Lewis (Sanford University)

Non-human scans were reformatted to .5 mm cubic voxels, human scans were reformatted to .75 mm cubic voxels (because of computational memory limits)

Processing of scans:

1) construct a perfectly symmetrical endocast target shape ('atlas') for each species. This atlas is aligned such that the midsagittal plane is perfectly aligned with the plane perpendicular to the x axis. The atlas for each species is modified from a randomly-selected endocast of that species, ensuring the atlas is close to the species' particular endocranial shape

2) calculate the curvature of the surface of the endocast at each point. This increases the information about shape available to the morphing algorithms

3) Register (align) all the curvature images from step 2 to the symmetric atlas created in step 1. This is done in two steps:
  First: affine registration (orientation of image aligned to the symmetric atlas, and isometric compression/expansion along each axis to match atlas as closely as possible)
  Second: Diffeomorphic registration: localized, non-rigid morphing to further refine the mapping to the atlas

This results in a set of vector maps which describe - for each point on the atlas - how that point needs to be modified in order to map correctly on to the corresponding point on a particular actual endocast.

Because these maps are all in the atlas 3D space, they can be easily compared, e.g.:

- differences between any two specimens (subtracting two maps)
- averages and variation among populations of specimens (averaging sets of maps, calculating SD among them at each point)
- comparisons between populations of specimens, including statistical tests

These comparisons are done voxel-by-voxel, resulting in localized descriptions of the differences/similarities at each point on the surface.

4) In order to compare specimens, it is useful to calculate the Jacobian determinants at each point (voxel). These are essentially localized scaling factors that quantify how much larger or smaller the equivalent local region is in a given specimen compared to the matching region in the atlas. Jacobians between 0 and 1 indicate that one must shrink the atlas at that location to match the specimen; a value of 1 indicates the atlas and specimen are the same size; values greater than 1 indicate one must enlarge the atlas to match the specimen (e.g., a Jacobian of 2 means that location is twice the size in the specimen that it is in the atlas).

Because Jacobians are computed for each voxel in the atlas, they result in a detailed map of the scaling information - unique to each specimen - at each point.

6) To compare left-right asymmetries, Jacobian maps for each individual were left-right reversed. Because the atlas upon which these Jacobians are mapped is perfectly symmetrical (step 1), comparing left-right asymmetries can now be done by assessing differences between the normal and left-right reversed Jacobian maps which overlap exactly. Comparisons are made between (natural) log-transformed Jacobians, because they are symmetric about 0 (the natural log of .5 = -.69; the natural log of 1 = 0; the natural log of 2.0 = +.69)

7) Paired or group t-tests can be computed for each voxel on the endocranial surface, with the pairs being normal vs. flipped shellmasked versions. These were not computed for this preliminary study due to small sample sizes

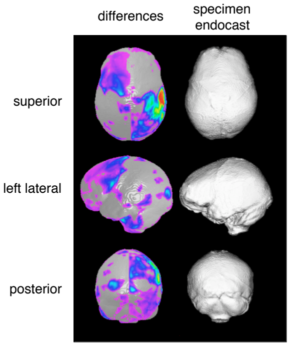

Figure 4: left-right differences for one example specimen. Colored areas indicate locations that are larger than the corresponding area in the opposite hemisphere. Color bar values are differences in natural logs of Jacobians (.3 = a scaling factor difference of 1.35, .7 = a scaling factor difference of ~2.00, 1.4 = a scaling factor difference of ~4.00, etc.)

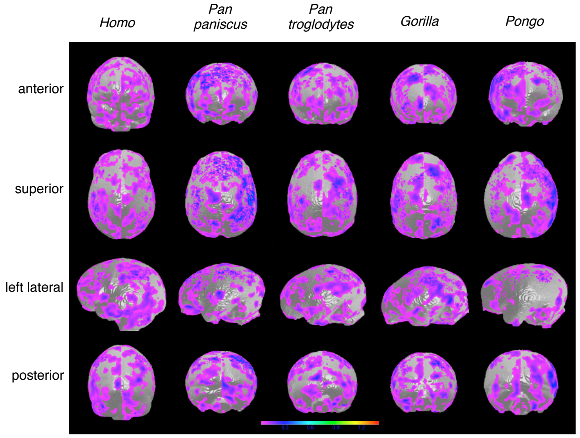

Figure 5: Average left-right differences for each species. Colored areas indicate locations that are larger than the corresponding area in the other hemisphere. Color bar values are differences in natural logs of Jacobians (.3 = a scaling factor difference of 35%, .4 = a scaling factor of difference of 50%, .5 = a scaling factor difference of 65%, etc.)

Conclusions

The relatively small sample of the present study suggests caution in interpreting results, but:

- Asymmetries do not show a simple pattern
- There is weak support for the right-frontal, left-occipital petalia pattern in humans
- Left medial and inferior temporal lobe and left lateral cerebellar regions appear to be larger in humans, to a greater extent than in apes
- Left inferior frontal area (approximating 'Broca's cap') appears larger than the right to a greater extent in humans than in apes
- Overall, *Pan paniscus* and *Pongo* appear to be the most asymmetric in this sample, though favoring the right hemisphere

Acknowledgements

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