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. Perusal potentially informing us about their behavior. Gross neuroanatomical asymmetries (known as petalias) causing 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, 1 Pongo pygmaeus, and 11 Homo sapiens endocasts. The extent and pattern of human endocranial petalias consistently differ from pongid endocranial petalias 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 humans (e.g., Broca’s and Wernicke’s language areas are localized to the left hemisphere). However, this is not the case in pongids and chimpanzees, with both species having functional areas that are not lateralized to a particular hemisphere. The strong bias towards right-handers (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-handers. Toth 1985). Human brains are morphologically asymmetric, presumably reflecting these functional asymmetries. Morphological asymmetries of the brain appear to reflect in asymmetries of the endocranial surface. Quantitative 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: Apparent asymmetry of ‘Broca’s cap’ of the endocast of Sambungmacan 3 (Broadfield et al. 2001)

Recently, morphing techniques have been applied to the comparison of endocranial shape with strong bias towards right-handers (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-handers. Toth 1985). Human brains are morphologically asymmetric, presumably reflecting these functional asymmetries. Morphological asymmetries of the brain appear to reflect in asymmetries of the endocranial surface. Quantitative 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).

Early work on endocranial asymmetry focused on petalias (protrusions on one side larger than the other). The behavioral significance of this is not known but it is assumed to be related to functional asymmetries of brain function. Human brains 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 (Howell and de la Coe-Lareymondie 1982; Figure 2).

Figure 2: Original petal data from Holloway and de la Coe-Lareymondie (1982)

Methods

High resolution 3D scans were obtained from 49 specimens:

- 10 Pan troglodytes
- 9 Pan paniscus
- 12 Gorilla gorilla
- 1 Pongo pygmaeus
- 11 Homo sapiens

The non-human primate endocasts were high-resolution scans of lateral/epiproctor endocasts made by Ralph Holloway. The homo endocasts were obtained in 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 defined such that this mid-sagittal 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 as 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: local, non-rigid morphing to further refine the mapping to the atlas

This results in a set of vector maps which describes, 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 each point comparison 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.

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 the atlas is larger than the specimen at that location. Suppose, for example, a Jacobian of 2 means that twice the size in the atlas.

Because Jacobians are computed for each computed map in the atlas, these results in a detailed map of the scaling information — unique to each specimen at each point on the atlas.

6) To compare left-right asymmetries, Jacobian maps for each individual were left-right reversed. Because the atlas was constructed from maps that were mapped by assessing differences between the normal and left-reversed Jacobian maps which overlap exactly. Comparisons are made between (natural) log transformed Jacobsians, because they are symmetric about 0 (the natural log of 0 = −∞; the natural log of 1 = 0; the natural log of 2 = ln 2 = .69)

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

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 petal 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
- Hominid 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.

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Literature Cited


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