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Asymmetry of Language-Related Areas on Modern Human Endocasts: contradictory evidence via non-rigid diffeomorphic registration

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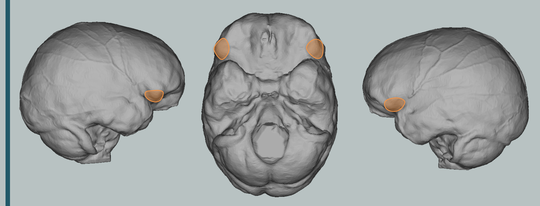
Background:

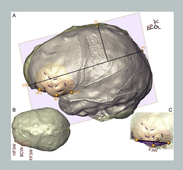
Details of hominin brain evolution are typically inferred from endocasts (casts of the internal surface of the skull). The Broca's cap region (protrusion of the orbital portion of the inferior frontal gyrus) on endocasts is particularly interesting because of its supposed location overlying brain regions that are relevant to aspects of language production. Previous research claims that in modern humans, Broca's cap is asymmetric in size with the left side larger than the right, matching the asymmetry of Broca's area and potentially telling us something about the presence of language (Holloway et al. 2005, Broadfield et al. 2001).



Example of a modern human endocast. Orange ovals indicate the location of Broca's Cap.

However, the majority of previous research on Broca's cap (and endocasts in general) has been **qualitative** (i.e. feeling 'bumps', visually deciding size differences) rather than **quantitative**. The limited quantitative research that has been done has typically used a method called Geometric Morphometrics (GM). GM is the analysis of shape using 2- or 3-D Cartesian geometric coordinates.

A recent GM study (Balzeau et al. 2014) found right Broca's Cap to be larger than the left in modern humans, although the left tends to look more 'globular' (thus biasing visual analysis). However, these results are based on the location of only 3 landmarks.



The goal of this research is to quantitatively measure the asymmetry of modern human endocasts, Broca's cap in particular, to test prior claims. Previously, when a fossil endocast was found to have a leftward Broca's cap asymmetry, it was claimed that it appeared to resemble modern human morphology, but this might not be the case.

Initial Study:

I previously investigated overall endocranial asymmetry using quantitative methods. The main objective of the study was to use geometric morphometrics to determine relative shape differences between the left and right hemispheres of the modern human endocranium. This study was unique in that it was the first study to ***quantitatively*** examine asymmetries of the ***entire*** endocranial surface, rather than just a subset of anatomical landmarks.

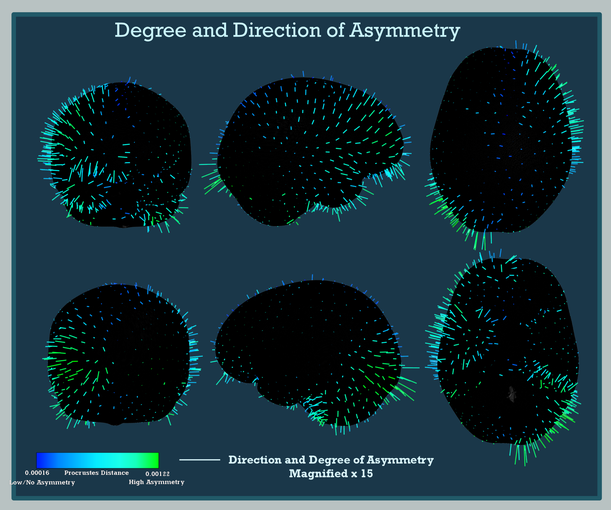
The results (see below) also found a rightward asymmetry of the Broca's cap region, however it was unclear if it was just an artifact of the overall petalial asymmetry of the frontal lobe or a true rightward asymmetry.

Current Study:

The current study investigates right-left endocranial asymmetries using non-rigid diffeomorphic mapping methods originally developed for registering fMRI data (via ANTs). Unlike my initial study, this method allows us to see ***local*** shape and size changes.

Initial study using Geometric Morphometrics

"Asymmetry of the Modern Human Endocranium"
Master's Thesis at University College London



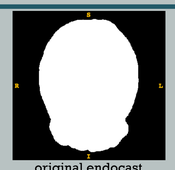
Vectors are drawn between the mean mirrored endocast's surface semilandmarks and the mean original endocast's surface semilandmarks and plotted on the mean original endocast shape. The directions of the vectors indicate the direction of asymmetry at that landmark (magnified by 15 for easier visibility) and the color indicates the degree of asymmetry.

Sample:

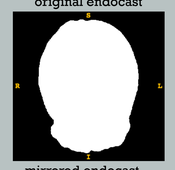
- High resolution computed tomographic (CT) scans of crania from 28 adult modern human specimens, including 14 males and 14 females ranging from 25 to 30 years of age (Open Research Scan Archive, Monge and Schoenemann (2011)).

Methods:

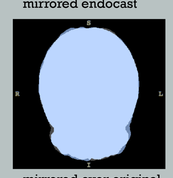
- Virtual endocasts were extracted from CT scans using two- and three-dimensional semi-automated segmentation (Avizo 7.0).
- Endocast images were mirrored and aligned.
- ANTs software was used to diffeomorphically map the mirrored endocasts back into the original endocasts, creating transformation maps that indicated where voxels from the original endocast image map to voxels on the mirror image.
- Jacobians were then calculated at each voxel on the transformation maps. Jacobians are unit-less measures that quantify how much larger or smaller a point in space in the mirror image is compared to the corresponding point in the original image.
- The Jacobian values were visualized on each endocast to determine individually the direction of asymmetry around Broca's cap.
- The average Jacobian value for Broca's cap was determined by morphing each endocast and it's Jacobian map to an averaged template created using ANTs. T-tests were run on each voxel to determine statistical significance.
- Broca's cap was defined on each endocast and the Jacobian values were used to determine the direction of the asymmetry of the voxels within Broca's cap.



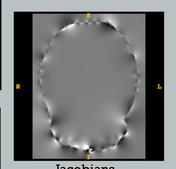
original endocast



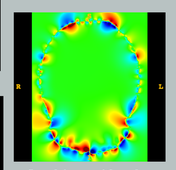
mirrored endocast



mirrored over original

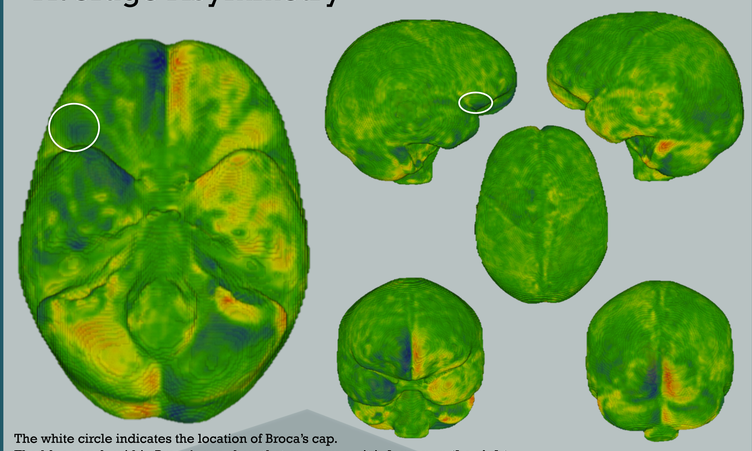


Jacobians



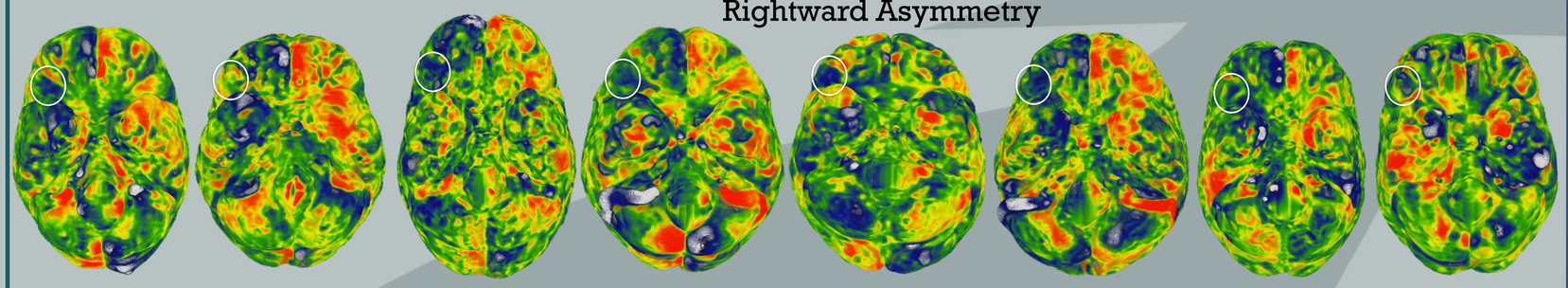
Jacobians with color

Average Asymmetry

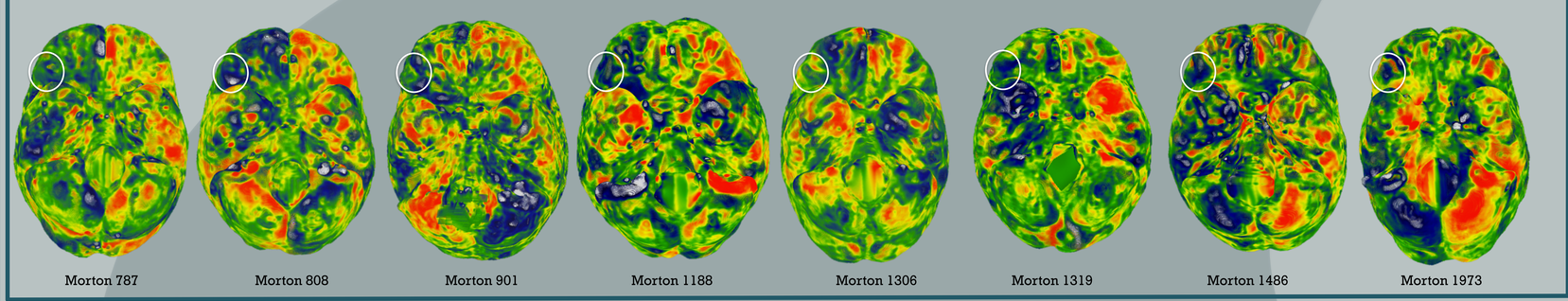


The white circle indicates the location of Broca's cap.
The blue voxels within Broca's cap show that on average, it is **larger on the right hemisphere, contradictory to previous claims.**

Rightward Asymmetry

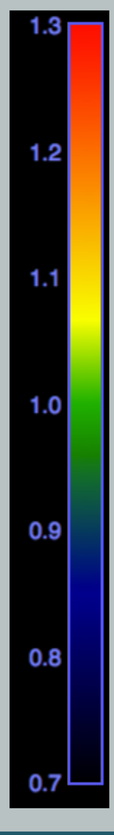


Morton 51, Morton 413, Morton 422, Morton 434, Morton 451, Morton 631, Morton 645, Morton 762

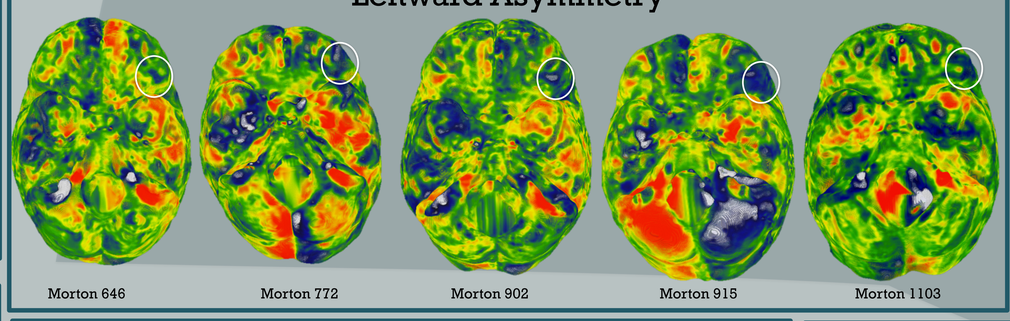


Morton 787, Morton 808, Morton 901, Morton 1188, Morton 1306, Morton 1319, Morton 1486, Morton 1973

White circle ○ indicates location of Broca's cap

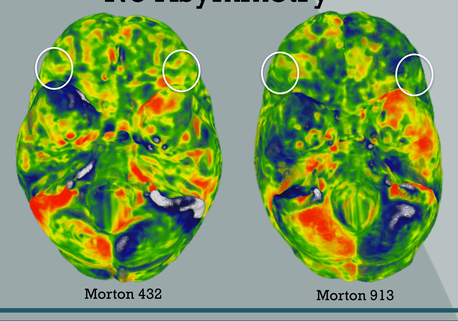


Leftward Asymmetry



Morton 646, Morton 772, Morton 902, Morton 915, Morton 1103

No Asymmetry



Morton 432, Morton 913

Scale:

Values indicate how much (%) that voxel would need to shrink (if less than 1) or expand (if greater than 1) to match the opposite side

BLUE/WHITE colored areas are **LARGER** on that side than the other side

YELLOW/RED colored areas are **SMALLER** on that side than the other side

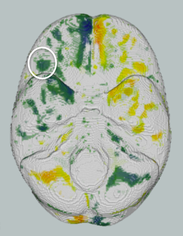
Results:

Out of 28 modern human endocasts, within Broca's Cap:

- 16 (57%) showed a **rightward** asymmetry
- 5 (18%) showed a **leftward** asymmetry
- 5 (18%) showed a **complex** (right and left) asymmetry
- 2 (7%) showed **no** asymmetry

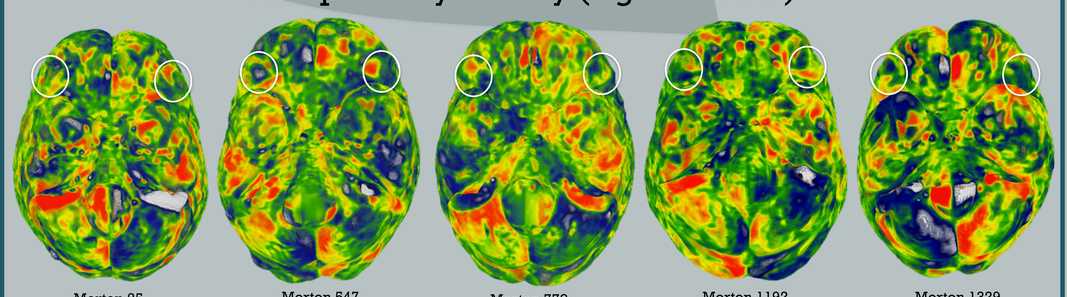
On average, Broca's cap was found to be around **10% larger on the right side** than the left side. This is contradictory to the currently held belief that the modern morphology of Broca's cap is a leftward asymmetry. Additionally, for many, the pattern of asymmetry appears to be more complicated than total rightward or leftward asymmetry.

These results suggest that we cannot rely on Broca's cap to be a reflection of Broca's area asymmetry and that we need to reevaluate current interpretations of fossil endocast asymmetry.



Statistically significant areas of asymmetry (not correct for multiple comparisons) ($p < .05$)

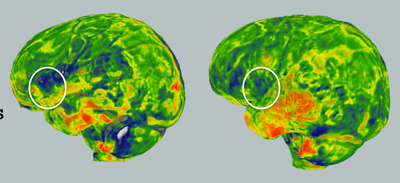
Complex Asymmetry (right and left)



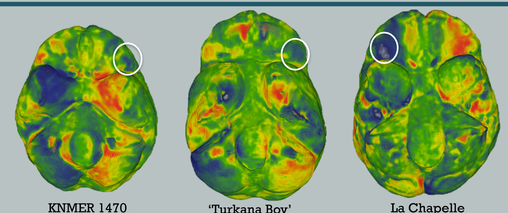
Morton 25, Morton 547, Morton 778, Morton 1192, Morton 1329

Next Steps:

- Expand the sample to include ~100 modern human endocasts
- Examine additional areas of asymmetry (perhaps over Broca's area?)
- Apply the same methods to fossil endocasts
- Compare brains and endocasts within individuals



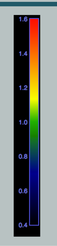
Morton 778, Morton 913



KNMER 1470
Homo rudolfensis

'Turkana Boy'
Homo erectus

La Chapelle
Homo neanderthalensis



References:

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Broadfield, Douglas C., et al. "Endocast of Sambungmacan 3 (Sm 3): a new Homo erectus from Indonesia." The Anatomical Record 262.4 (2001): 369-379.

Holloway, Ralph L., et al. "The Human Fossil Record, Brain Endocasts: The Paleoneurological Evidence, Volume 3." (2004).

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