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Is Broca's cap really larger on the left in modern humans?: Contradictory evidence via non-rigid diffeomorphic mapping methods

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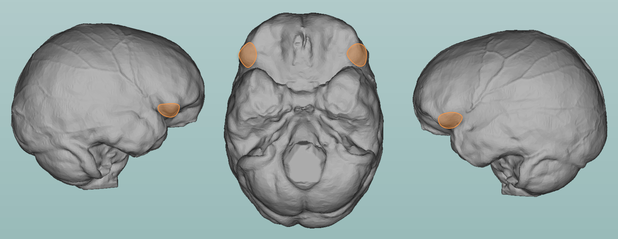
Background:

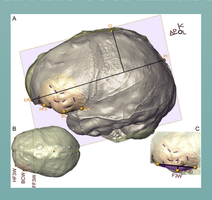
Details of hominin brain evolution are typically inferred from endocasts (casts of the internal surface of the skull). The Broca's cap region (protrusion of the orbital portion of the inferior frontal gyrus) on endocasts is particularly interesting because of its supposed location overlying brain regions 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 (a langage area of the brain) 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 and Broca's cap in particular, to test prior claims.

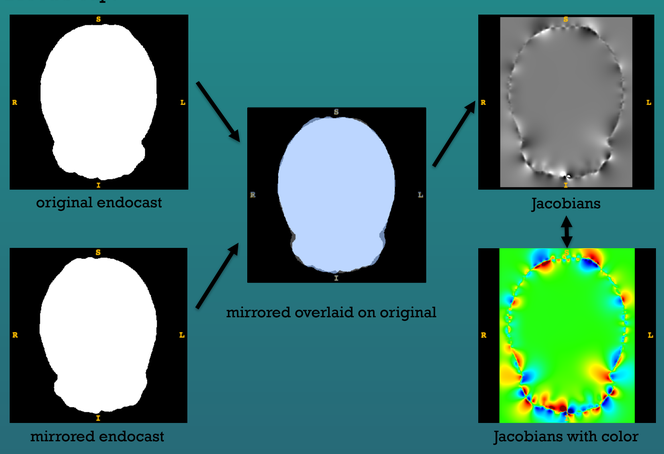
The current study investigates right-left endocranial asymmetries using non-rigid diffeomorphic mapping methods originally developed for registering MRI data (via ANTs). This method allows us to see detailed local shape and size changes.

Sample:

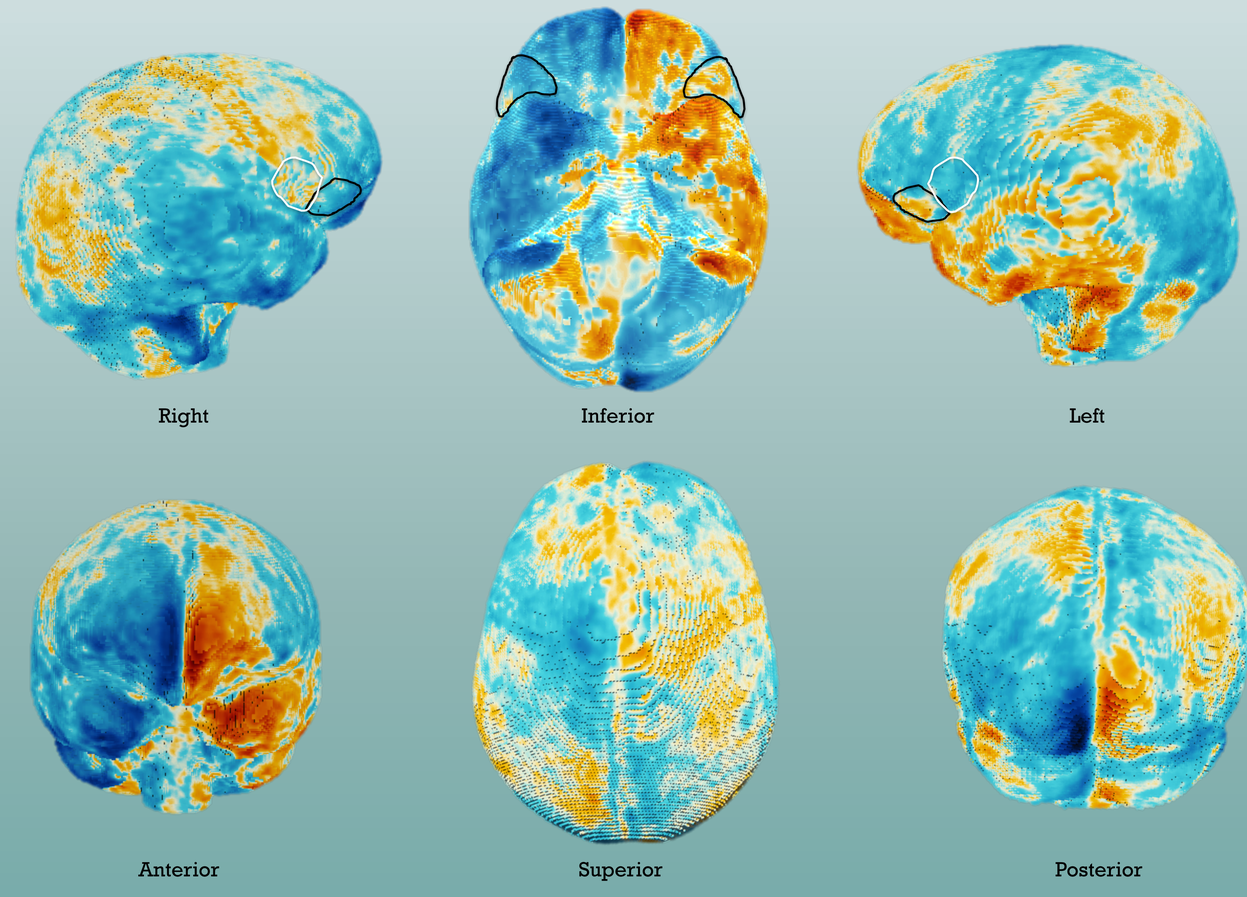
- High resolution computed tomographic (CT) scans of crania from 100 adult modern human specimens, including 50 males and 50 females ranging from 25 to 30 years of age (Open Research Scan Archive, Monge and Schoenemann (2011)).

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.
- Advanced Normalization Tools (ANTs) software (stnava.github.io/ANTs/) 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 and corrected for multiple comparisons (FDR) 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.



Mean Asymmetry of 100 Modern Human Endocasts



Black outline indicates Broca's cap
White outline indicates possible Broca's Area

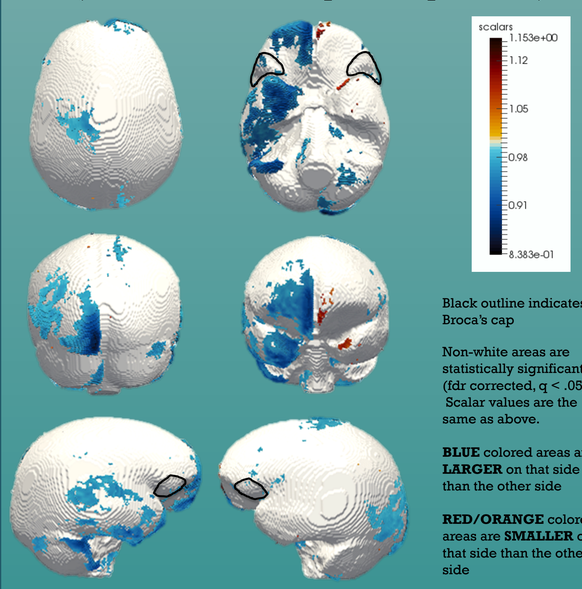
Scale:

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 colored areas are **LARGER** on that side than the other side

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

Statistically significant areas of asymmetry (corrected for multiple comparisons).



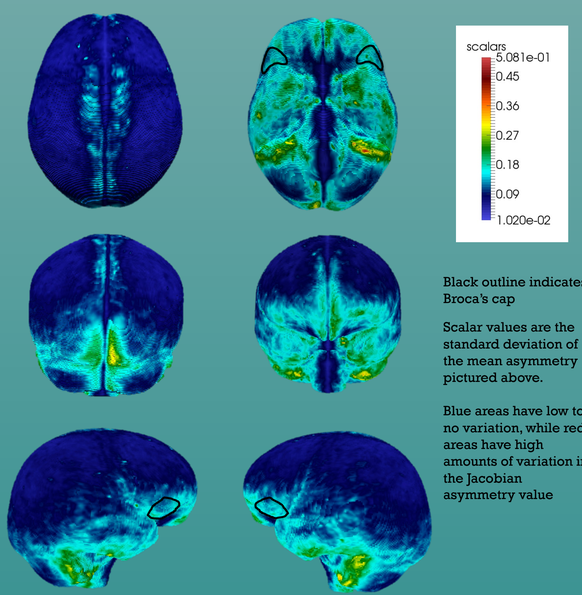
Black outline indicates Broca's cap

Non-white areas are statistically significant (fdr corrected, $q < .05$). Scalar values are the same as above.

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

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

Standard deviation of the mean asymmetry



Black outline indicates Broca's cap

Scalar values are the standard deviation of the mean asymmetry pictured above.

Blue areas have low to no variation, while red areas have high amounts of variation in the Jacobian asymmetry value

Number of endocasts out of subset (N=28) with:

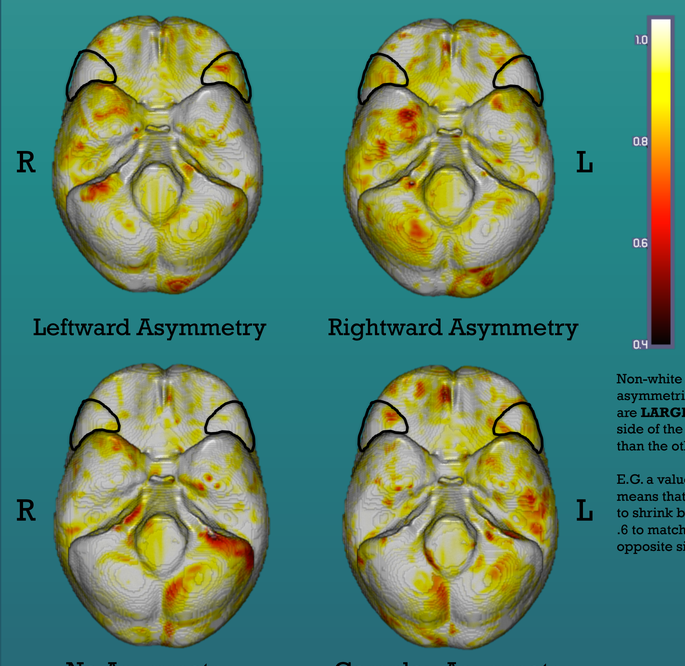
Leftward Asymmetry:
5 (18%)

Rightward Asymmetry:
16 (57%)

No Asymmetry:
2 (7%)

Complex Asymmetry:
5 (18%)

Examples of individual patterns of asymmetry shown on the average endocranial surface



Non-white areas are asymmetric areas that are **LARGER** on that side of the endocast than the other side

E.G. a value of .6 means that area needs to shrink by a factor of .6 to match the opposite side.

Discussion:

- **Broca's cap is an average of ~5% larger on the right hemisphere compared to the left hemisphere.** This is contradictory to previous qualitative reports of a leftward asymmetry in modern humans, but supports the quantitative results of Balzeau et al. 2014.
- **The discrepancy between qualitative and quantitative analyses of endocasts suggests that we must reevaluate previous assumptions about endocranial morphology.** These results especially cast doubt upon the assertion that Broca's cap asymmetry is related to language lateralization of the brain.
- However, there is an area that is superior and posterior to Broca's cap that is an average of ~3% larger in the left hemisphere than the right. This area is anatomically closer to Broca's area of the brain and suggests that is still could be possible to see language related asymmetries on the the endocranial surface.

References:
Balzeau, Antoine, et al. "Variations in size, shape and asymmetries of the third frontal convolution in hominids: Paleoneurological implications for hominin evolution and the origin of language." Journal of human evolution 76 (2014): 116-128.
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.
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Monge J, and Schoenemann PT. 2011. The Open Research Scan Archive (Orsa): A massive open-access archive of research quality computed tomography (CT) scans. Pleistocene Databases: Acquisition, Storing, Sharing 4:61-67.

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