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Asymmetry of the Modern Human Endocranium

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Introduction:

Details of hominin brain evolution are typically inferred from endocasts. However, very little research has been done to ***quantifiably*** establish the relationship between an endocast and its corresponding brain. This study investigates this relationship using asymmetry of the **entire** endocranial surface. As the modern human brain is structurally asymmetric, the results of this study allow for a direct comparison of this characteristic between the two surfaces. In addition, because evolutionarily interesting aspects of behavior, such as handedness and language processing, are organized asymmetrically in the brain, it is of great interest to know whether these same asymmetries can be seen on the endocranial surface.

The main objective of this study was to use geometric morphometrics to determine relative shape differences between the left and right hemispheres of the modern human endocranium, in order to better characterize the relationship between the endocranial surface and brain surface of modern humans. This study is unique in that it examines the entire endocranial surface, rather than just a subset of anatomical landmarks.

Main Questions:

1. Where is the modern human endocranium asymmetric and what is the variance at those locations?

2. Does the endocranial asymmetry of modern humans correspond to the brain asymmetry of modern humans?

Materials and Methods:

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).
- For each specimen, 29 fixed landmarks and 5 curves (red circles in Fig. 1) were digitized on bony structures of the endocranial surface. These landmarks were primarily used as reference points for the placement of the surface semilandmarks and not for the description of endocranial asymmetry.
- A mirrored version of each specimen's endocast was created (Meshlab). The fixed and curve landmark coordinates for each specimen were also mirrored across the y-axis by multiplying the x-coordinate by -1.
- Surface semilandmarks (green circles in Fig. 1) were then placed on each specimen's original and mirrored endocast (Geomorph package in R).
    - A template of 860 roughly equidistance surface semilandmarks was digitized on one specimen's original endocast (*buildtemplate* function of Geomorph).
        - The *buildtemplate* function placed the surface semilandmarks on the endocranium using an algorithm described in Gunz et al. (2005) and Mitteroecker and Gunz (2009).
    - The template of surface semilandmarks was then warped to each specimen's original and mirrored endocasts (*digitsurface* function of Geomorph). Based on the location of the fixed landmarks and curve semilandmarks, *digitsurface* placed the same number of surface semilandmarks in the same location as the template on each endocast.
        - The *digitsurface* function down samples each surface model, registers the template file with the specimen using a generalized procrustes analysis, and uses a nearest neighbor algorithm to match the location of each endocast's surface semilandmarks with the template's surface semilandmarks (Adams et al., 2015).
- A generalized procrustes analysis was performed (*gpagen* function of Geomorph). All of the specimens' original and mirrored landmark and semilandmark configurations were superimposed, scaled, and rotated until the corresponding coordinates of all endocasts were aligned as closely as possible.
    - In order to optimize their location, the semilandmarks on the curves and surfaces of each endocast were slid along their tangent directions, or planes, by minimizing the Procrustes distance between the template and target specimens.
- The curve and surface semilandmarks of each endocast were then fixed and to ensure correct measurement of asymmetry, each specimen's pair of endocasts (original and mirrored) were individually Procrustes aligned to each other (*gpagen*).

Data Analysis:

Overall Asymmetry Value (Figure 2):

- The Procrustes distance was measured between each specimen's original and mirrored endocast landmark configurations, producing a value that describes the overall amount of asymmetry for that specimen (Ventrice, 2011). The Procrustes distance is the square root of the sum of squared distances between all of the corresponding landmarks of two shapes, in this case between the original and mirrored endocasts of each specimen. The Overall Asymmetry Value revealed which specimens are the most and least asymmetric, as well as the variation in amount of asymmetry.

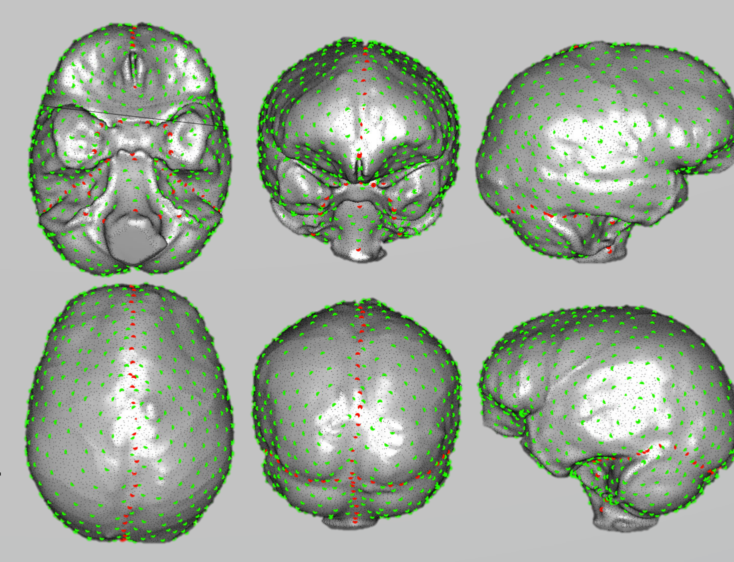

Figure 1. 860 surface semilandmarks (green) were placed on each specimen's original and mirrored endocasts using the location of the fixed landmarks and curve semilandmarks (red).

Degree of Asymmetry (Figure 3 and 4):

- The Procrustes distance was also measured between each corresponding landmark of the original and mirrored endocast pairs to determine which specific landmarks were asymmetric. The mean and standard deviation of the Procrustes distance between each landmark pair was calculated and used to describe where and to what degree the modern human endocranium is asymmetric, as well as the variation of those asymmetries. Note that the Procrustes distance is the same on both sides and does not show the direction of asymmetry (this is because the left side of the original endocast is identical to the right side of the mirrored endocast and vice versa).

Direction of Asymmetry (Figure 5):

- In order to determine the direction of asymmetry, the mean shapes of the original and mirrored endocasts were created through the estimation of the average landmark coordinate configuration for each set of endocasts (*mshape* function of Geomorph). The shape differences between the mean shape of the original endocasts and the mean shape of the mirrored endocasts were plotted (MATLAB) by drawing vectors from the landmarks of the mean mirrored endocast to the corresponding landmarks of the mean original endocast. The direction of the vectors illustrates the mean direction of asymmetry and the color refers to the degree of asymmetry.

Results:

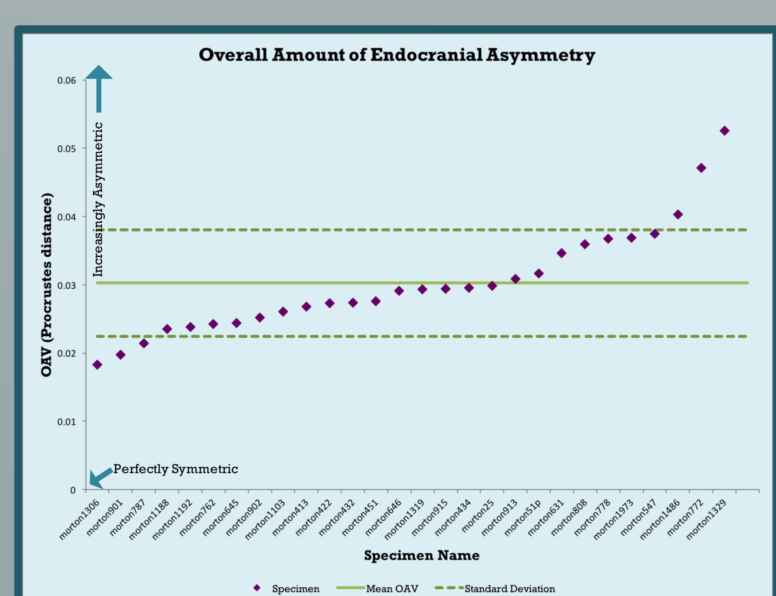

Figure 2. Plot of the Overall Asymmetry Value for each specimen. Mean OAV = 0.03025364, standard deviation = ±0.0078129

Standard Deviation of the Mean Degree of Asymmetry of Each Landmark

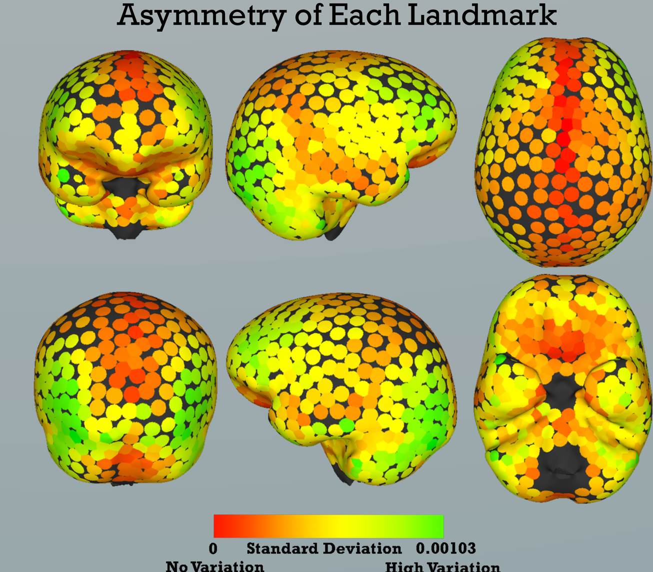

Figure 3. Standard deviation of the surface semilandmarks plotted on the mean original endocast shape.

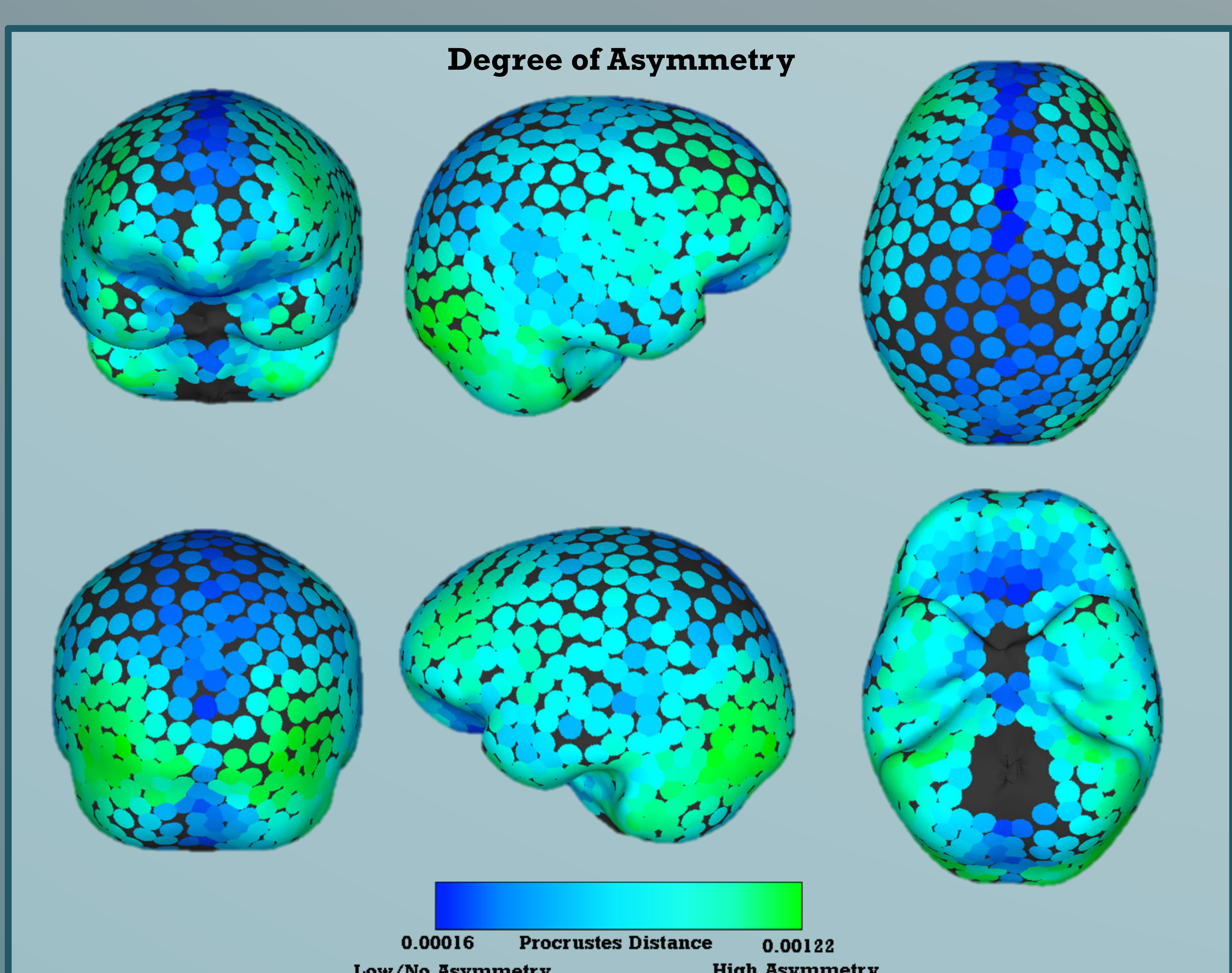

Figure 4. The surface semilandmarks are plotted on a 3D model of the mean original endocast shape and colored to indicate the mean degree of asymmetry at that landmark. Note: direction of asymmetry is not indicated in this figure.

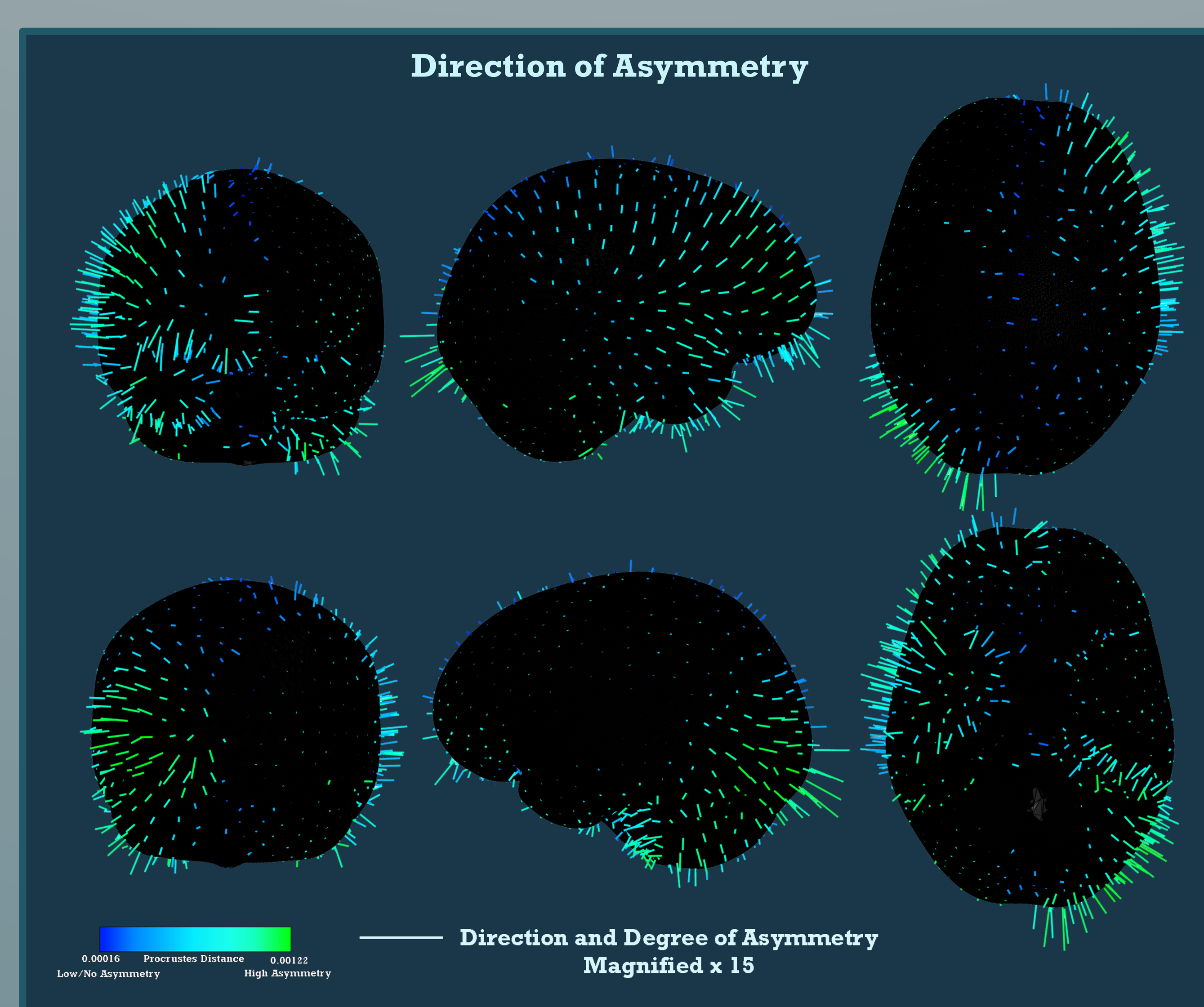

Figure 5. Vectors are drawn between the mean mirrored endocast's surface semilandmarks and the mean original endocast's surface semilandmarks and plotted on the mean original endocast shape. The direction of the vectors indicates the direction of asymmetry at that landmark (multiplied by 15 for easier visibility) and the color indicates the degree of asymmetry.

Conclusions:

1. Where is the modern human endocranium asymmetric and what is the variance at those locations?

- **Petalias and Yakovlevian Torque** (Figure 6):
    - Frontal lobe: extends more anteriorly, laterally, and superiorly in the right hemisphere than the left, including the right temporal lobe and as far back as the right parietal.
    - Occipital lobe: extends more posteriorly, laterally, and inferiorly in the left hemisphere than the right and below the transverse sulcus to include the left cerebellum.
    - The superior and inferior extensions are not as frequently discussed in the literature as the width and anterior-posterior distribution.
    - Standard deviations were highest for the landmarks involved in the petalial pattern of asymmetry, suggesting that the degree and direction of this pattern is not completely consistent.

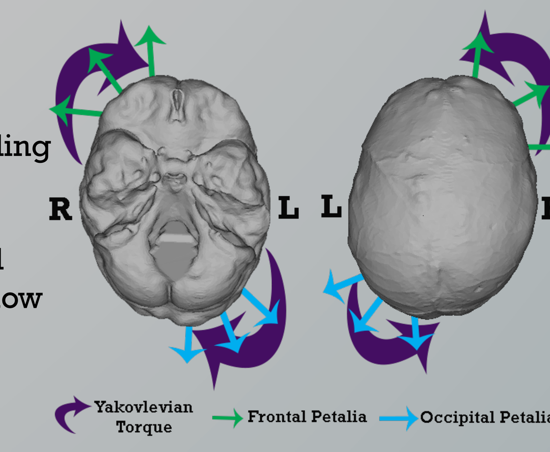

Figure 6. An example of the right frontal and left occipital petalias and Yakovlevian torque on the endocranial surface of one of the specimens used in this study.

- **Rightward asymmetry of Broca's cap**
    - Although Broca's cap in the right hemisphere appears more laterally located, it is possible this is an artifact of overall petalial asymmetry of the entire frontal lobe. Relative localized asymmetric protrusion of Broca's caps (e.g., favoring the left, which would be predicted based on left-lateralized language function) might be missed.
- **Four surface semilandmarks located at the anterior tip of the lateral sulcus showed a small leftward asymmetry** (Figure 7):
    - These landmarks are close to Broca's cap, but reveal more about the lateral sulcus than Broca's cap.
- **Leftward asymmetry of the anterior cerebellum**
- **Regions within the temporal lobe also displayed a rightward asymmetry** (although possibly part of the frontal petalia).
    - The temporal pole extended more anteriorly and the region corresponding to the inferior temporal gyrus extended more laterally and inferiorly in the right hemisphere.

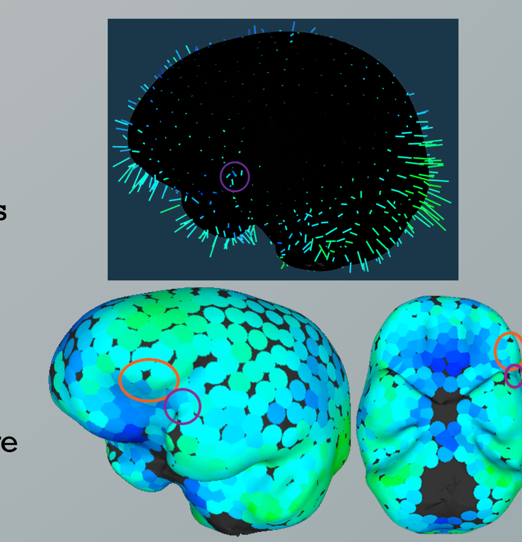

Figure 7. Location of landmarks within the inferior frontal lobe that are leftward asymmetric. Purple circle shows the location of those landmarks. Orange circle shows the location of Broca's cap.

2. Does the endocranial asymmetry of modern humans correspond to the brain asymmetry of modern humans?

- **YES.** Global asymmetries of the brain surface correspond (see Figure 8, Lancaster et al. (2003)).
    - Petalias
    - Anterior cerebellar asymmetry of the brain
    - Rightward asymmetry of the temporal lobe
- **And NO.** Smaller asymmetric regions, such as those within the motor cortex of the brain, were not visible. These may be visible when the surface is examined at a more local level (e.g. by using curvature).
- The petalias are likely the result of several smaller regions of asymmetry within the brain. Many of the areas of asymmetry found within the frontal lobe of the brain are internal and not located on the surface (Good et al., 2001, Hervé et al., 2006, Kitchell et al. in prep/2013, Luders et al., 2004, Watkins et al., 2001).
    - It is the sum of these asymmetries that leads to a large shift in the entire hemisphere and this large shift is visible with this methodology, while the small individual areas of asymmetry are not.
    - This suggests a limit to the level of detail regarding brain asymmetry that can be inferred from endocranial asymmetry

Compare With Areas Of The Brain That Are Structurally Asymmetric:

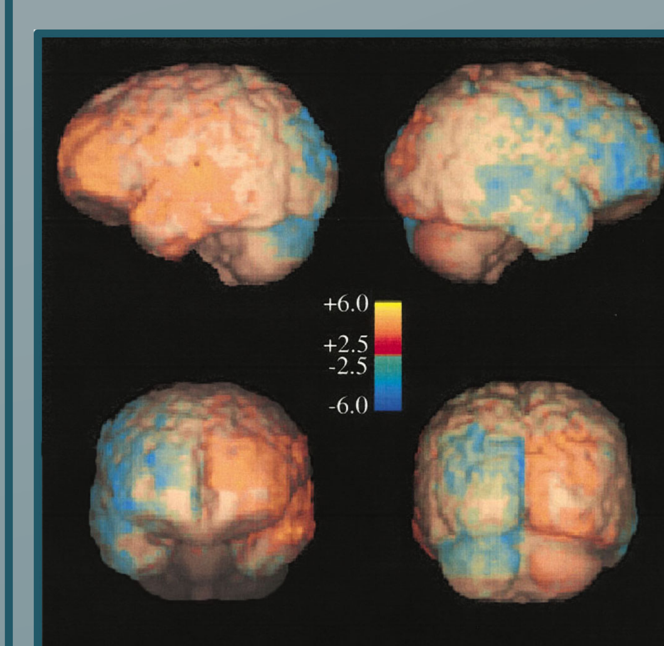

Figure 8. Surface rendering of a representative brain showing brain surface asymmetry. The brain surface is color coded to indicate inward (blue, meaning larger on that side) and outward (yellow, meaning smaller on that side) deformations needed to match the contralateral hemisphere. Left hemisphere colors are for Left-to-right analyses and right hemispheres are for Right-to-left analyses. Figure reproduced from Lancaster et al. 2003.

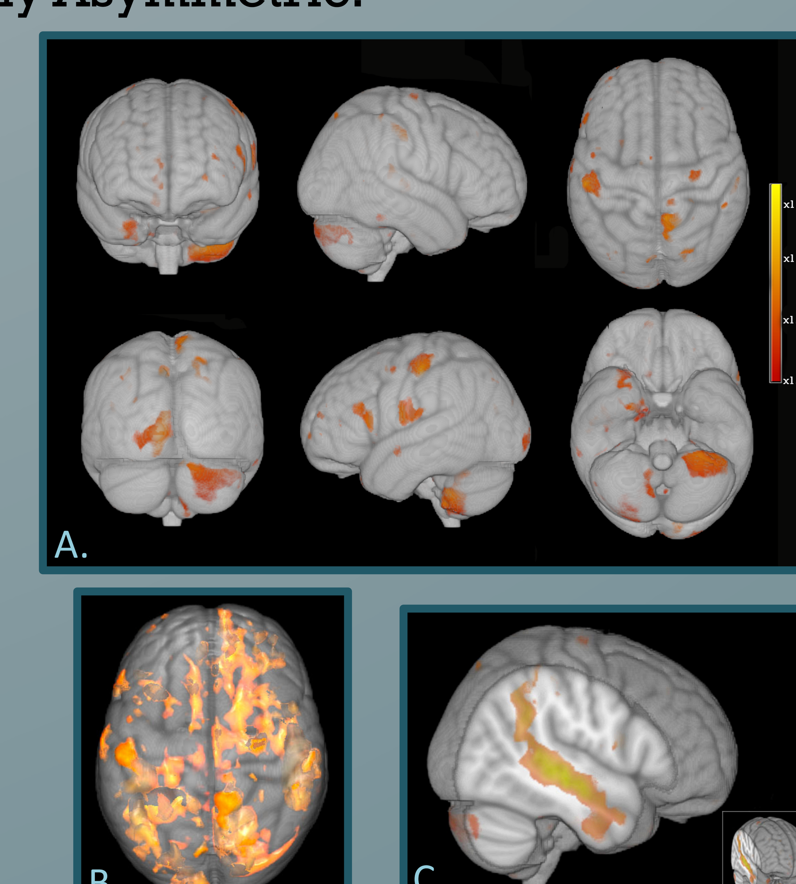

Figure 9. A. Three-dimensional rendering of the areas of cortical surface showing significant asymmetry (FDR q≤.01) (Kitchell et al. in prep/2013). The colored values indicate how much larger that area is compared to the same region in the opposite hemisphere. B. A semi-transparent view of the data in A, showing the internal areas of asymmetry. C. The data in A. cut to expose the extensive rightward asymmetry of the superior temporal sulcus.

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