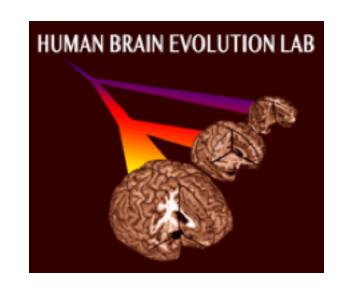


Functional Correlates of Structural Asymmetries in the Human Brain

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- Humans are much more strongly right-handed than other apes.
- Handedness may be associated with language lateralization.
- Is handedness reflected in human brain asymmetry (and therefore possibly fossil brain endocasts)?

Introduction:

The human brain is both structurally and functionally asymmetric. However, there have been relatively few studies assessing both structural and functional asymmetries in the same subject population. One behavioral asymmetry of particular interest to human evolution is handedness, which is much more pronounced at the population level in humans than in other species. It has been postulated that this may be related to the evolution of tool manufacturing and use, as well as language. The development of tool use may have selected for lateralized cognitive and motor functions that provided a foundation for the later left-lateralization of speech and language in humans (Bradshaw 1993).

Analyses of fossil hominin endocasts have revealed anatomical asymmetries that are assumed to reflect asymmetries in underlying brain regions. Handedness has been shown to be associated with brain petalias (the greater protrusion of the right frontal and left occipital lobes), the motor cortex, and the planum temporale (Amunts et al. 1996, Foundas et al. 1995) but its association with other structural areas of the brain have not been extensively investigated. Knowing the extent to which neuroanatomical asymmetries in different regions of the brain are associated with handedness will allow better assessment of handedness in fossil specimens. Using the MRI scans of 71 healthy, female subjects we assessed the degree of association between handedness and structural asymmetry. Interesting areas of association include the hand region of the motor and somatosensory cortexes, planum temporale, fusiform gyrus, and Broca's area.

Materials and Methods:

71 female subjects consisting of 36 sibling pairs were recruited (mean age = 23.2 years, age range 18-43). Magnetic Resonance Imaging (MRI) was performed on each subject. Handedness was measured using the Oldfield handedness inventory (Oldfield, 1971). Scores indicated that 5 subjects were left-handed and 66 were right-handed.

- A left-right reversed version was created of each scan
- Each left-right reversed image was morphed into the corresponding original image, creating a distortion map using the Advanced Normalization Tools package (ANTs)
- Jacobians (log transformed) were calculated on each voxel of each of the distortion maps. Jacobians are localized scaling coefficients that indicate how much each voxel of the left-right reversed image needs to be expanded or shrunk to match the original scan
- The Jacobian maps for each individual were then morphed into an averaged template and then a standardized template brain (MNI 152)
- A linear mixed effects (lme) model with Jacobian values and handedness as fixed effects, and sib pairing as a random effect (to control for family relatedness), was used to assess the degree of association
- t-values of the lme fixed effect of handedness on Jacobian values were mapped
- p-values of the lme fixed effect of handedness on Jacobian values were corrected for multiple comparisons using False Discovery Rate and mapped

Results:

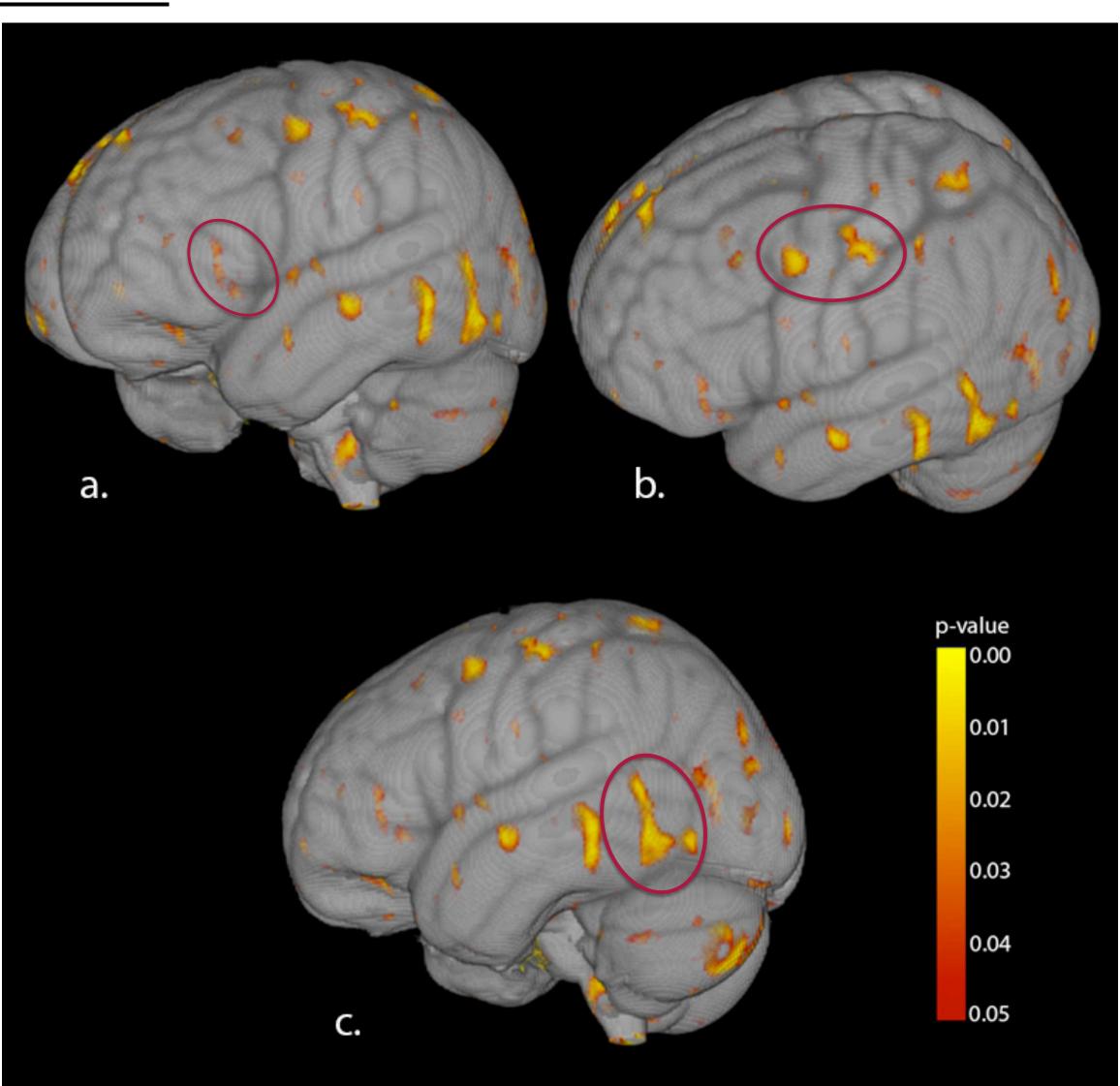


Figure 1. Areas of the brain surface where the degree of asymmetry is most strongly associated with handedness (p<0.05 uncorrected) **a**. Brodmann's area 45 (Pars Triangularis of Broca's Area) **b**. hand region of the motor and somatosensory cortexes **c**. fusiform gyrus.

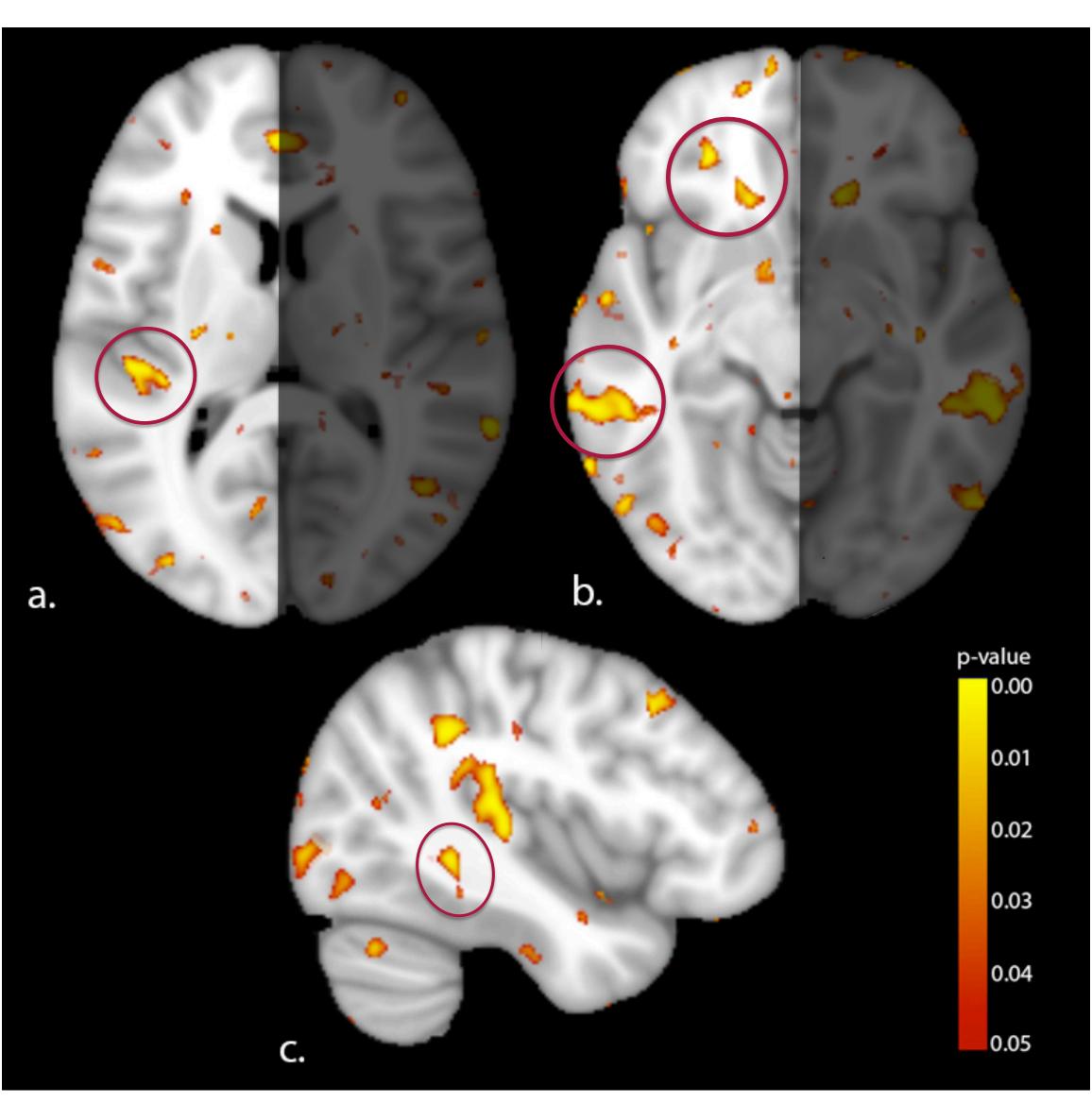


Figure 2. Internal areas of the brain where the degree of asymmetry is most strongly associated with handedness (p<0.05 uncorrected), highlighting: **a**. planum temporale **b**. middle temporal and orbitofrontal **c**. white matter of Wernicke's area (likely including the arcuate fasciculus)

A word on statistical significance:

None of the p-values of the Ime fixed effect of handedness on Jacobian values survived the False Discovery Rate correction for multiple comparisons. However, because many voxels are not truly independent (e.g., because of proximity and shared anatomy and function), False Discovery Rate may not be appropriate. Further statistical analysis using another method may be needed to better assess the significance of these associations.

Conclusions:

Significant associations were found between degree of asymmetry and handedness.

Interesting regions include:

- Several areas in the occipital lobe petalia, frequently used to suggest handedness
- Broca's area (Brodmann's area 45) speech and language area, typically functionally lateralized to the left hemisphere
- Hand region of the motor and somatosensory cortexes
- Middle temporal lobe surface (fusiform gyrus) –
 involved in word and face recognition and semantic
 categorization
- Planum temporale speech and language area,
 typically functionally lateralized to the left hemisphere
- Orbitofrontal (grey and white) social processing and risk/award assessment
- Middle temporal lobe surface including underlying white matter – object identification and/or language association
- White matter deep to Wernicke's Area likely extension of the arcuate fasciculus

Summary of key findings:

- Asymmetries in modern human brains appear to be associated with handedness
- Many of the areas where asymmetry is associated with handedness are also associated with language function
- These results suggest it may actually be possible to infer handedness from asymmetries in fossil brain endocasts

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