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Original publication

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Evolution of brain lateralization: a shared hominid pattern of endocranial asymmetry is much more variable in humans than in great apes
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Questions and answers

Why is human brain asymmetry interesting?

Language, handedness and other typically human cognitive and behavioral abilities are predominantly processed in one of the two brain hemispheres. Functional lateralization is related to morphological brain asymmetry – small differences between the left and right hemisphere. Brain asymmetry in humans, our closest living and our extinct relatives is therefore interesting and informative about the evolution of human cognitive abilities.

Are there any ideas about the evolution of human brain lateralization?

A large body of work using diverse methodologies from multiple scientific fields have investigated brain lateralization and asymmetry as well as related behavioral features like language and handedness. Based on fossil endocasts (brain imprints in the neurocranial bones) of our ancestors, it has been suggested that the emergence of a modern human-like brain asymmetry pattern coincides with the emergence of early stone tools in the archaeological record. Several hypotheses have therefore linked the evolution of functional brain lateralization (hemispheric specialization) with morphological brain asymmetry, tool use, right-handedness, gestural and finally spoken language. Based on magnetic resonance brain scans, it has been proposed that non-directed, random asymmetry is elevated in humans as compared to chimpanzees and that this is a sign of increased brain plasticity in humans.

What is an endocast and how does it relate to the brain?

An endocast is an imprint that the brain leaves on the internal surface of the bony braincase (the endocranium). Given the tight interactions between the cranial bones and the brain during growth, it approximates the size and outer shape of the brain. Sometimes, it replicates brain convolutions and blood vessels that left impressions into the endocranial bones. However, it doesn’t tell us about internal brain structures like neural connections between brain regions. Since the brain itself does not fossilize, endocasts are regularly used to study brain evolution in extinct species, for example in Neanderthals.

How does an endocast arise, how is it generated?

Sometimes natural endocasts develop during fossilization when the bony braincase is filled with sediments after the brain has already decayed. Endocasts can also be generated artificially. For the latter, there is a traditional approach where molding material is applied to the inside of the bony braincase to obtain a negative cast of the endocranial surface, which is a positive cast of the outer brain surface including its surrounding tissues like meninges. Today, this is usually done in a computer environment using a digital copy of the cranium based on computed tomographic (CT) scans. Thereby, the crania are not harmed during casting and results can be visualized in relationship to the cranium.

Why study comparative brain asymmetry based on endocasts?

To learn about the uniqueness of human brain asymmetry, we can study the brains of our closest living relatives, the great apes. However, brain data of chimpanzees and especially of gorillas and orangutans are rare. Previous studies therefore were left with comparisons of humans to chimpanzees only. On the other hand, crania of chimpanzees, gorillas, and orangutans are readily available in museum collections and can be used to generate endocasts. While endocasts provide only partial information about brain morphology (see above), the usage of endocasts allows to broaden the comparative framework beyond human-chimpanzee comparisons. This is important to be able to find out which asymmetry features are human-specific as opposed to specific to chimpanzees.

What kind of brain asymmetry is visible on endocasts?

The so-called Yakovlevian torque of the human brain is observable and well-described on endocasts. This asymmetry pattern includes a more backwards projecting left hemisphere (a left occipital petalia) in combination with a more forward projecting right hemisphere (a right frontal petalia). This is related with an asymmetry of the lateral fissure and the central sulcus that can be only observed on endocasts if the relevant brain convolutions left impressions in the endocranial bones. While this pattern is prevalent in humans, a few individuals do not show it or show the opposite. Interestingly, this directional asymmetry is correlated with right-handedness. Furthermore, Broca’s cap on endocasts (corresponding to Broca’s area) is morphologically asymmetric. Asymmetry in this area that is important for speech production conforms to the functional lateralization of language and speech. Endocasts of great apes have been described as being asymmetric as well but previous studies did not find a clearly directed, population-wide pattern like the one in humans.

What is directional and fluctuating asymmetry?

The left occipital and right frontal petalias combination (see above) is shared in most human individuals. Such a directional asymmetry pattern common in a population is thought be under strong genetic control and probably related to specific brain functions. The left and right hemisphere can further vary in each individual adding to the population-wide prevalent pattern to different degrees and in different directions and thereby might obscure the directional pattern of the population. This fluctuating asymmetry is thought to result from individual developmental variation (developmental instability) and might also be interpreted as sign of developmental plasticity.

How does the quantification of shape asymmetry work methodologically?

We used geometric morphometrics based on three-dimensional coordinates of homologous measurement points called landmarks instead of more traditional measurements like distances and volumes. Doing so, we can quantify and compare not only size differences between the left and right side, but also which parts of the left side are differently shaped than the right side and which local asymmetries are correlated with other local asymmetries. Furthermore, we used multivariate statistics to investigate directional and fluctuating asymmetry patterns, or in other words the most prevalent asymmetry pattern in each species as well as the variation around it.

What did we find in the new study?

First, humans are not more asymmetric than great apes as expected based on previous studies on humans and chimpanzees only. Instead, chimpanzees are on average less asymmetric than humans, gorillas and orangutans. Second, the proportion of directional asymmetry is smaller in humans than in great apes. Third, the pattern of directional asymmetry is very similar in humans, chimpanzees, gorillas, and orangutans, contradicting the idea that the combination of left occipital and right frontal petalias is unique to humans. Furthermore, this pattern includes differential projections of the temporal poles and the cerebellar lobe. Fourth, this shared pattern is less directed in humans and different local asymmetries are less correlated than in great apes. In other words, human individuals are much more variable around the directional pattern than great apes.

What do our findings mean for the ideas about the evolution of human brain lateralization?

As we found a shared asymmetry pattern in humans, chimpanzees, gorillas, and orangutans, morphological asymmetry that has been interpreted previously as typical for human brains can no longer be linked directly to human-specific hemispheric specialization such as handedness or language. It evolved not only in humans but far earlier. Instead, our findings suggest that this ancestral morphological brain asymmetry was co-opted in humans for lateralized cognitive abilities related to typical human behaviors. This suggests that this asymmetry pattern in endocasts of fossil hominins should not be used as a proxy for the evolution of human-like functional lateralization such as right-handedness and language capabilities, without additional archaeological evidence. The magnitude of random asymmetry (fluctuating asymmetry) on top of the directed pattern suggests that humans and great apes have comparable levels of developmental instabilities or developmental plasticity. On the other hand, humans are much more variable in the pattern of asymmetry, showing less correlation of different local asymmetries. This probably reflects increased functional and developmental modularization of the human brain that may be adaptative.