

## **How primate brains vary and evolve**

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**Studies of brain evolution tend to focus on differences across species rather than on variation within species. A new study measures and compares intraspecific variation in macaque and human brain anatomy to explore the effect that short-term diversity has on long-term evolution.**

Evolutionary neuroscience focuses on diverse aspects of variation that are particularly relevant to human and nonhuman primate brain evolution. Plenty of studies have compared the evolution of total brain size and of the size of certain brain regions in different species. Very few studies, however, have measured and compared variation within species, which is commonly considered the raw material for evolution: the more variable a population is, the more options natural selection will have to choose from. Therefore, we can expect that increased variation within species will go hand in hand with rapid evolution. Conversely, there can be reasons to expect the opposite relationship: perhaps a high level of variation will hamper evolution because many

individuals will show trait values that will substantially differ from optimal values. Of course, selection can influence intraspecific variation as well: it can reduce it when certain traits are substantially more advantageous than others, or increase it when environments are also variable. Because of the lack of relevant comparative data, the exact relationship between human brain variation and evolution, certain aspects of which seem to have occurred at a particularly fast pace [1], is currently unknown.

In a recent publication in *Cerebral Cortex*, Croxson and colleagues [2] address this topic, testing the hypothesis that the human brain is more variable than the brain of other primates and this has facilitated and sped up brain evolution in our species. Their study quantifies and compares variability in human and macaque brains using structural magnetic resonance imaging (MRI) scans. To do so, they produce species-specific templates and measure the deformations required to match each individual to their corresponding template. They separate their analyses into those corresponding to grey matter and white matter, and they use several analytical approaches and visualization tools to compare cortical regions, assessing differences between hemispheres.

As compelling as the reasoning laid out in their paper is, Croxson and colleagues' results are unexpectedly unclear. Once size variation is removed from analyses, overall human brains are not particularly more variable than macaque brains. It seems, however, that patterns of variation may differ in both species, with evolutionarily recent association areas being more variable in humans. These results, however, are also less clear than I would have expected: while a positive association between variability and evolutionary expansion is observed in the temporal lobe, such an association is not found (or it is extremely weak and not consistent across hemispheres)

in the parietal and the frontal lobes, which are also involved in higher cognitive functions (Figure 1).

So, how can build upon these results? Firstly, increasing sample size, which amounts only to 10 individuals per species in Croxson and colleagues' study, would be important to more accurately reflect intraspecific variation. Secondly, the comparison of only two species is necessarily very limited because it does not allow for an unequivocal clarification of the traits that are human-specific versus those that are macaque-specific. Assembling relatively large samples of *in vivo* MRI scans of nonhuman primates is painfully difficult, but an effort to increase these samples may very well pay off and show a clearer-cut scenario. Indeed, there are some resources that can be easily added to this study and to other similar ones. For example, numerous chimpanzee MRI scans are now available to researchers world-wide through the National Chimpanzee Brain Resource (<http://www.chimpanzeebrain.org/>). Other researchers have studied relatively large samples of capuchin monkeys [3], vervet monkeys [4] and olive baboons [5]. Although still very limited, the comparison of these different groups would help clarify possible evolutionary trends in patterns and levels of variability across major anthropoid primate groups. In addition, the study of endocranial anatomy based on cranial collections can prove useful. Although endocasts are only partially informative with respect to neuroanatomy, cranial collections are diverse and plentiful, and they can provide valuable information regarding overall and lobe-specific levels of neuroanatomical variation [6]. The study of endocranial anatomy will even allow for the study of intraspecific variation and its effect on the diversification of fossil lineages. Intraspecific variation in other key macro-, microstructural and molecular traits, including cytoarchitectural

boundaries and gene expression, is expected to influence evolutionary change and can be studied in collections of post-mortem brains.

Another crucial point that can be further explored is the origin of neuroanatomical variation. Recent quantitative genetic studies have shown that human neocortical variation is more heavily influenced by environmental factors than chimpanzee variation [7]. This result seems to be associated with human's unparalleled behavioral flexibility and with our enhanced capacity for social and cultural learning [8]. Although comparisons with other species are again needed, several lines of evidence indicate that this increased plasticity in brain organization is a human-specific evolved trait [9]. Measuring variation over different ontogenetic stages can help confirm this point by revealing the way that anatomical diversity is accumulated through development. If the origin of brain variation is predominantly environmental, this will have important functional implications regarding the formation of neural circuitry and its behavioral outputs. If the origin of brain variation is genetic, however, this will be reflected in the tempo and mode of evolution. Needless to say, both genetic and environmental factors can play important roles and interact in complex ways.

Croxson and colleagues' study has very nicely set the stage to explore the relationship between short-term variation and long-term evolution in primate brains. While their study does not provide all the answers, it certainly poses some fascinating questions that can help us move forward: Are there species-specific differences in levels of variation? Do more variable species evolve faster or slower than less variable species? Are brain areas involved in complex functions universally more variable than primary areas? What is the functional significance of anatomical

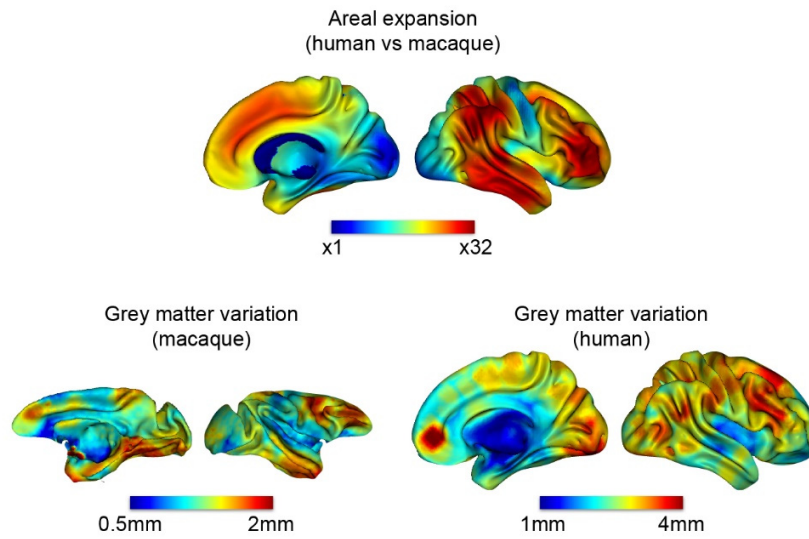
variation? A narrow focus on human neuroscience or on a few model species is very unlikely to help us clarify these issues. Rather, a synergic combination of complementary research approaches and data sharing initiatives will be essential to advance in our understanding of these fundamental aspects of brain evolution in humans and other primates.

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**Figure 1. Evolutionary expansion versus variability in macaques and humans.** Macaque-to-human areal expansion map showing the brain regions undergoing the strongest evolutionary expansion in humans (top). Distribution of grey matter variability in macaques (bottom-left) and humans (bottom right). Croxson and colleagues' results indicate a relatively high and significant positive association between areal expansion and grey matter variability in the human temporal and limbic lobes, a significant negative association in the occipital lobe, and no clear association (low and/or not significant correlation) in the frontal and parietal lobes. Macaque and human brains are not to scale. Different parts of the figure have been modified, with permission, from refs. [2,10].