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Human brain evolution

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Abstract

Although we share evolutionary history with other primates, examples of apparent cognitive and behavioral discontinuity between humans and other species abound. Neuroanatomical and molecular differences that distinguish the human brain are evident at several levels of organization. Changes in overall anatomy include an increase in absolute and relative brain size. In addition, there may be novel parietal lobe areas in humans that are involved in processing of evermore fine-grained visuospatial information. Modifications in microstructure, such as the distribution patterns and morphology of neurons and glial cells are also significant. Finally, changes in expression of both mRNA and proteins reflect increased energy consumption and plasticity. All together, these brain specializations, when coupled with cultural forces, shaped the evolution of human cognition.

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> *Nevertheless the difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind*
> ~ Darwin, 1871

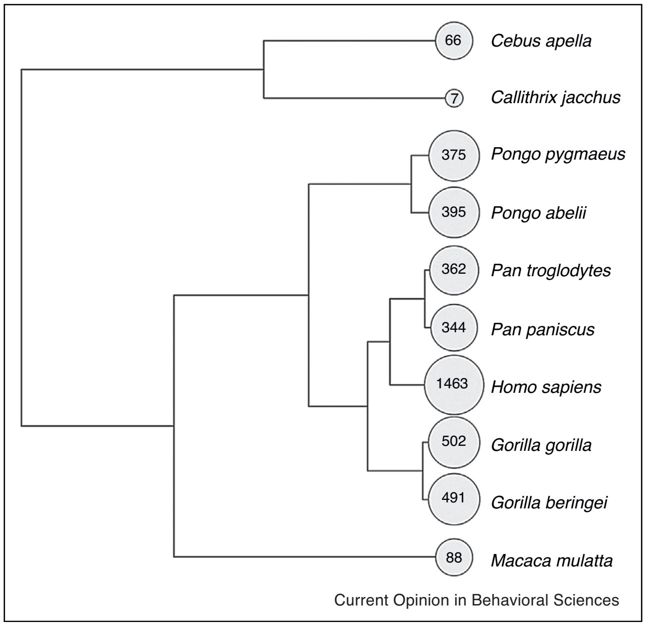
Following Darwin, the study of human cognition has been properly placed within an evolutionary context. To understand the human mind – how we acquire, process, store, and act on information from the environment – we have to know the long history of our species and the selective pressures that shaped our ancestors. One way of doing this is to compare the differences and similarities among extant species in cognitive processes and the neuroanatomical structures that underlie them. This approach requires understanding the phylogenetic relationships among species to infer the evolutionary changes that occurred in the past. Because the great apes (the primate group that includes chimpanzees, bonobos, gorillas, and orangutans) are the closest living relatives of modern humans, they are an essential basis for comparison. Indirect as it is, the comparative method is one of the most powerful tools we have available, as brains and cognition do not fossilize. Indeed, comparative analysis has provided important insights into the evolution of human behavior and cognition. It has been observed that many behaviors previously thought to be uniquely human are actually present in other species as well, sometimes even to a greater degree (*i.e.*, eusociality in *Hymenoptera*). Tool-making and use, for example, are not restricted to our species alone. When Jane Goodall reported tool-making in chimpanzees, Louis Leakey famously replied: “Now we must redefine ‘tool’, redefine ‘man’, or accept chimpanzees as humans” [1].

Yet, examples of apparent cognitive and behavioral discontinuity between humans and other species abound. Our syntactically rich language, ability to understand the mental states of others, capacity to make complex tools, and propensity to generate and manipulate symbols are exceptional [2]. What are the possible evolutionary changes in brain structure that allowed these faculties? Here, we offer a brief overview of the evolution of the human brain and the likely neuroanatomical changes associated with our species’ distinctive cognitive abilities. These changes occurred at several levels of brain organization, providing the neuroanatomical hardware for the origin of human behavior and cognition.

Primates are a very diverse group of mammals of nearly 500 living species that includes lemurs, lorises, tarsiers, New World monkeys, Old Word monkeys, and apes. Most comparative neuroanatomical research has focused on a tiny fraction of this variety, concentrating on a few primate model species, including common marmosets (*Callithrix jacchus*), capuchin monkeys (*Cebus apella*), rhesus macaques (*Macaca mulatta*), and chimpanzees (*Pan troglodytes*) [3]. Our closest living relatives are the chimpanzees and the bonobos, with whom we share a last common ancestor dated to about 6–8 million years ago [4] (Figure 1).

Compared to other primates, humans have very large brains. Weighing approximately 1400 g, our brains are roughly three times larger than those of other great apes and also significantly larger than expected for a primate of our body size. Fossil evidence of the cranial capacity of our direct ancestors indicates gradual increase in brain

Figure 1



Phylogenetic tree of primates.
Phylogenetic relationships among the great apes and other primate species mentioned. The numbers indicate endocranial volumes (in cm^3, rounded to the nearest whole number) and the size of the circles shows the natural log transformation of the endocranial volumes to demonstrate the diversity in brain size of the primate species. Data from Refs. [5,6].

size early in hominin evolution with a period of more accelerated growth within the last 2 million years [7]. Brain size enlargement in human evolution was undoubtedly important for increasing overall information processing capacity through greater numbers of neurons and synaptic connections. However, brain expansion all on its own cannot adequately explain the specific cognitive faculties of our species for several reasons. Many species, including non-primates such as elephants and whales, have brains larger than ours (although with perhaps fewer neocortical neurons) and yet do not approach the cognitive sophistication of humans. Moreover, species may be comparable in brain size yet differ dramatically in behavior and social skills. Chimpanzees and bonobos, for example, have similar brain size but differ in temperament and social behavior. Lastly, there is about 1000 g normal range of variation among modern humans in brain mass, however all are capable of commanding language and display other human-specific capacities. Therefore, much of the answer probably lies in changes to brain development, neuroanatomical reorganization, and modifications at the molecular level. It is likely that evolutionary changes at these levels, and not solely absolute brain size or total number of neurons, better explains species differences in cognition.

The increase in human brain size is due mostly to expansion of the neocortex [8], particularly heteromodal association regions of the frontal, temporal, and parietal lobes. Some evolutionary changes to human association cortex have involved differential enlargement of regions that are homologous in other primates [9]. Notably, many regions of the prefrontal cortex have been shown to be homologous between humans and other great ape and monkey species, including Broca's language areas (areas 44/45) (Friederici, 2016). Some of the changes to human association cortex, however, might comprise differentiation of novel and functionally distinct areas that perform increasingly fine-grained information processing. For example, data suggest that, compared to rhesus macaques, human intraparietal sulcus (IPS) includes three additional motion-sensitive areas dedicated to processing of three-dimensional form in relation to motion [10]. As a result, human parietal lobe includes more regions dedicated to processing of shape compared to that of rhesus macaques. Addition of these and other parietal areas likely enhanced processing of visual and somatosensory information necessary for complex manipulative abilities required for tool manufacture and use [11,12]. Determination of whether these parietal areas are truly unique to the human brain will require comparative studies with great apes. Nevertheless, this possibility is supported by evidence from fossil endocranial morphology showing that one of the most distinguishing features of modern humans is a more bulging parietal region compared to Neandertals and other hominins [7]. Using combined functional and structural MRI data from the Human Connectome Project, a recent study identified some 180 distinct cortical areas in the human brain based on variation in cortical thickness, myelination, and connectivity patterns [13••]. This number far exceeds estimates of the number of areas for other primates [14], although such an approach for parcellation has not yet been conducted with brains of non-human species.

A point of disagreement has been the relative size of the frontal lobes and different prefrontal cortical areas in humans versus other primate species. Regions of the prefrontal cortex play a significant role in language, planning, decision-making, working memory, and other higher-order cognitive functions. Some have argued that change in the absolute and proportional size of the prefrontal cortex is tightly correlated with corresponding changes in other brain areas [15,16], while other analyses show that human prefrontal cortex is enlarged beyond what would be predicted from primate brain scaling trends [17,18]. Regardless of these scaling predictions, it is striking that direct comparisons of various cytoarchitecturally-defined cortical areas in humans and chimpanzees show that frontopolar cortex (area 10), Broca's area (areas 44/45), and the anterior insular cortex are about six times larger in humans, whereas the primary