

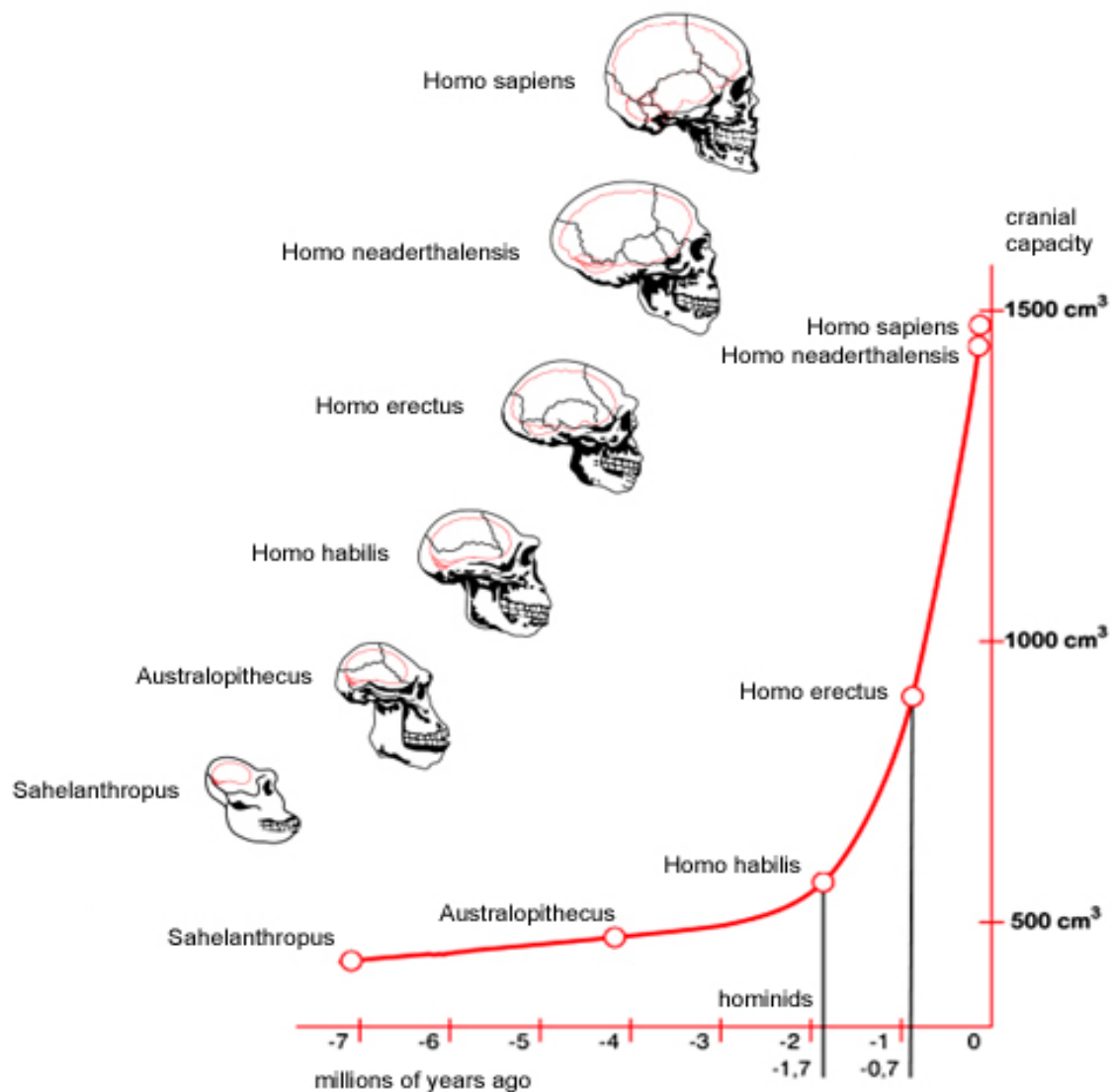
Evolutionary Emergence and Possible Adaptive Functions of Cortical Expansion and  
Resultant Encephalization in Modern *H. sapiens*

Rainer Karcher

## Encephalization Factor And Evolutionarily Trends

Given the vast range of specialized behaviors distinguishing anatomically modern humans from other primates, one might expect an equally pronounced departure in cerebral organization. In fact, the brains of anthropoid primates average twice in size that which would be expected of a given nonprimate mammal of equal body size (Deacon 1997). Further, the weight of the human brain averages 1400g, approximately three times (Sherwood *et al.* 2008) the size of the great apes. There does appear to be a strong correlation between human intelligence and neuroanatomical expansion, and a number of explanations have been offered to account for this pronounced anatomical deviance from other primates.

Increased encephalization – the degree to which an organism's cerebral mass outweighs that which is expected proportionally to its body mass – owing largely to cortical expansion, has been ostensibly vital to the evolution of the modern human brain. Given this dramatic increase in brain mass relative to other anthropoid primates, it is widely speculated that these significant changes occurred after the hominin lineage departed from its last common ancestor with the great apes. The current fossil record indicates that since the last common ancestor, the hominid lineage has experienced gradually sloping increases in cranial capacity which were sometimes accompanied by overall body mass increase (Sherwood *et al.* 2008). However, beginning with *H. erectus* roughly 1.8 million years ago, hominids began experiencing brain mass expansion at a greatly accelerated rate of increase (Sherwood *et al.* 2008), the anatomical yield of which is apparent today.



*Evolutionary increases in cranial capacity among species in the hominid lineage; image adapted and translated from Le Journal duNet, "Volume cérébral des Hominidés" (see References for full citation).*

In an ideal world, evolutionary study of the human brain could be traced by sifting through the lineage of hominid predecessors via purely archaeological means.

The unfortunate reality, however, is that unlike other adaptive features in human evolution – such as the rise of habitual bipedalism (Sherwood *et al.* 2008), or adoption of tool use, which offer hard tissue evidence – soft tissues and behavioral innovations cannot fossilize. Thus, there is no definitive fossil record for brain development. As direct paleontological support in this case is extremely limited, potential evidence must usually be carefully reconstructed through the use of endocranial casts, known as endocasts, from hominid skull dimensions in the existing paleontological record. While quite useful, these casts present only an impression of the gross morphological features of the brain once contained by the cranium's original owner, and much information cannot be inferred decisively, such as the subject's neuroanatomical organization or irrelevant behavioral traits. However incomplete, these records comprise the only existing evidence of temporal development in brain morphology and hominid behavior (Sherwood *et al.* 2008), allowing researchers a crucial glimpse into the adaptive interplay between these two variables.

### **Adaptive Advantages and Selective Pressures for Encephalization**

As any significant morphological modification over the course of evolution is generally assumed to have conferred adaptive advantages, we must infer that the accelerated increase in brain size found in *H. erectus*, relative to its hominin predecessors, implies a marked evolutionary advantage. The development of certain skills (e.g., foraging for food, spatial memory) have been found dependent upon the volumes of specific features of neuroanatomy, whereas many other capabilities characteristic of hominid behavior are at present thought to be related to overall volume of the cortex, while not necessarily to the size of any one area of the

cortex (Breedlove *et al.* 2010). For instance, hemispherical asymmetries have been observed in endocasts of hominids from the Pliocene onward, and such features in modern humans are functionally integral to capabilities such as language, attentional direction, emotional regulation, and musical capacity (Blumenberg 1983). On the whole, the evolutionary development of certain behavioral trends may have been contingent upon cortical expansion (Breedlove *et al.* 2010) and hemispherical specialization, however minimal. Finlay and Darlington (1995) made the observation that the regions of the hominid brain which underwent the most drastic evolutionary modifications are those which develop relatively late in an individual's life, such as neuronal density within the cortex. Likewise, the brain regions developing earlier in life are less pronounced in size than those which emerge later in development. This suggests that the heightened degree of encephalization in the case of the hominid brain might be attributed to positive selection for prolonging stages of neuroanatomical growth, as a single genetic mutation which prolonged the latter stages of development – particularly, neurogenesis and widespread formation of synaptic connections in the cortex – might yield an enlarged cortex, relative to other gross neuroanatomical features (Breedlove *et al.* 2010).

The series of genetic mutations culminating in the current anatomical state of the brain were likely to have precipitated complex structural reorganization in the cortex, resulting in developmentally modified patterns of neuron specialization differentiation, variations in dendritic and synaptic interconnectivity, axon fiber and glial cell density per volume of cortical tissue, and frequency rate of axon fiber myelination (Parker and Gibson 1979). Much progress has been made in the identification of the genetic components responsible for cortex expansion over the course of hominid evolution (Bradley 2008). Since the last common ancestor in the

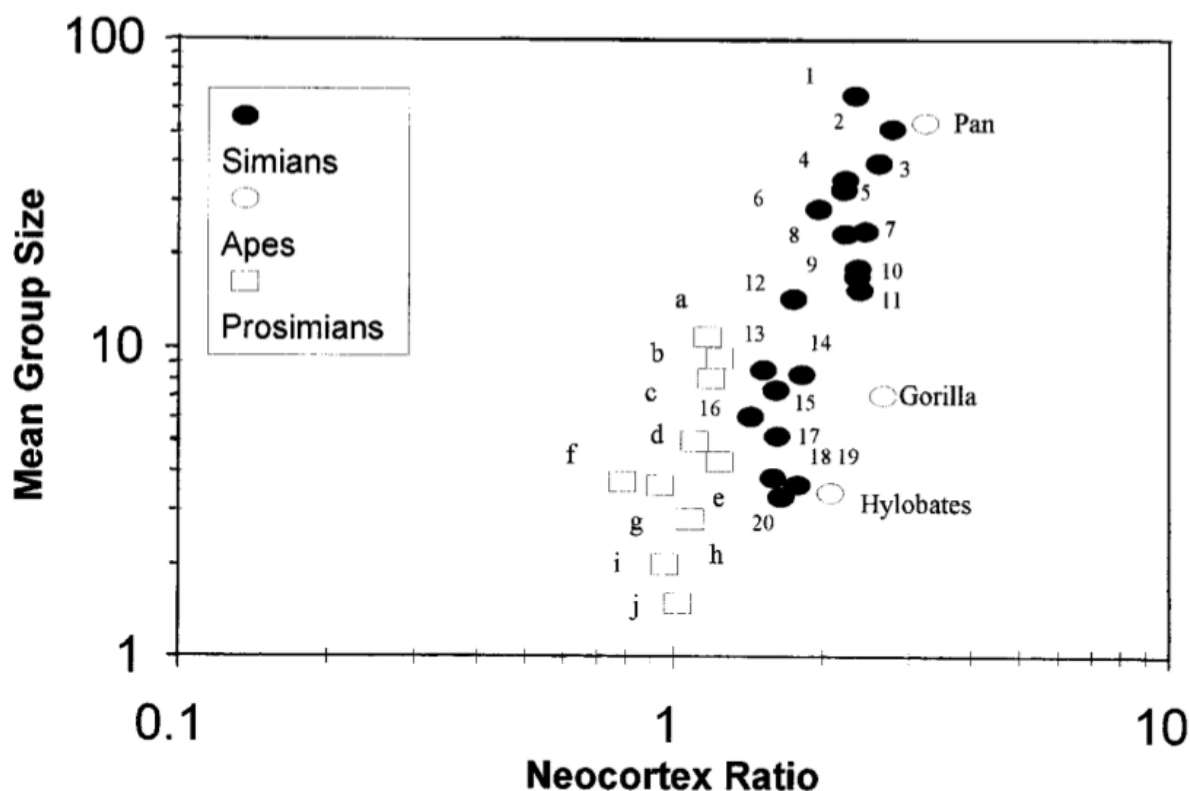
hominid lineage, evidence has risen of positive selection for several genetic factors which are known to act in cell cycle regulation (Sherwood *et al.* 2008), most notably genes involved in mediation of apoptosis, or programmed cell death, of neural cells. These suggested modifications regarding cell division, functional differentiation, and regional migration and manifestation of neural cells, may account for the human brain's deviation in growth trajectory (Sherwood *et al.* 2008) and increased encephalization from that which is found in most nonhuman primates. A growth trend in human brain development which favors minimal development of the cranium (e.g., delaying bone hardening and plate fusion in the skull until after birth) is vital to this increase of encephalization (and the entailed cortex expansion) in modern humans. Also, at present, the average width of the human pelvis cannot accommodate prenatal skull hardening or significant increases in encephalization. As the neural-synaptic associations within the cortex are developed incompletely at birth, they remain quite malleable throughout much of infancy, allowing social immersion (Sherwood *et al.* 2008) and a boundless expanse of environmental stimuli to mold synaptic formation at a rate as yet unrivaled at any other stage in the human lifespan.

### **The Social Brain Hypothesis**

Conjectural discourse regarding selective pressures for this dramatically increased encephalization are abundant. Traditionally, it has been stipulated that brains have evolved to measure ecological information relevant to an organism's survival (Dunbar 1998) and to regulate appropriate physiological responses to these environmental stimuli. However, this argument neglects the consideration that brains are, adaptively speaking, a high-risk investment, given the

steep metabolic costs of developing and maintaining neuroanatomical features (Dunbar 1998). To illustrate this fact, the adult human brain comprises roughly 2% of the individual's total body weight, but is responsible for approximately 20% (Aiello & Wheeler 1995) of the individual's metabolic consumption. Given that this information is incongruent with the suggestion that brains are merely suited to processing ecological information, it is difficult to defend the notion that primates – especially modern humans – require an increased degree of encephalization and cortical tissue expanse to perform the same 'ecological monitoring' (Dunbar 1998) tasks as other species. An alternative hypothesis proposes that this increased encephalization and cortical tissue expansion found in primates indirectly reflects a relative increase in the complexity of social interactions and cognitive processes characteristic of this taxonomic grouping (Dunbar 1998).

Dunbar's social brain hypothesis (Dunbar 1998), is founded upon the observation of a positive correlation between large primate group populations (and a proportionally extended network of social interactivity) and enlargement of group members' cortices relative to other neuroanatomical features. Dunbar's theory postulates that cortical expansion – and thereby increased encephalization – is contingent upon the maintenance of complex interpersonal relationships, communal food sharing, shelter construction (Blumenberg 1983), and tool manufacture, all of which have positively reinforced selection for genetic markers directing the gradual expansion of cortical tissue. Consistent tool manufacture and use is still extremely limited among nonhuman primates, but all primates are quite adept within the social domain, and Dunbar's findings have continued to accrue support in the present day, as across species, nonhuman primates do exhibit a positive correlation between population size and size of the cortex in relation to other structures (Breedlove *et al.* 2010).



*Mean population size against neocortex ratio, plotted logarithmically for prosimian, simian, and anthropoid primates. Image and data credited to R.I.M. Dunbar (see References for full citation).*

## Conclusion and Future Projections

The modular expansion and reorganization of neuroanatomical tissue has comprised a majority of evolutionarily developments in the hominid brain. Recent developments, such as the controversial validation of synaptic plasticity – the capacity to process environmental stimuli and respond adaptively on a molecular scale, in a state of “ceaseless morphogenesis” (Rees 2010:152) – lead one to question how the future of human brain evolution might unfold. Making the bold assumption that *H. sapiens* persists for an additional million years, will human cortical



tissue continue expanding at a comparable rate, independent of other neuroanatomical structures, ultimately leading to an even greater degree of encephalization? Will skeletal concessions be made in obstetric interest, such as a proportional expansion of the female pelvic girdle? (Might the largely sedentary nature of modern human life remove the hard tissue barrier altogether by superseding the adaptive need of a bipedally-oriented pelvic structure? Or, for that matter, the adaptive need of larger brains?) While it is possible that future evolutionary trends in the human brain will include increased encephalization and significant expansion of cortical tissue, it is highly unlikely that these features will continue to emerge simply because there is yet room for physical expansion (Dunbar 1998). Brains are metabolically expensive, and increased encephalization factor and cortical tissue expansion will occur only when favorable selection pressures become sufficient to surpass the steep threshold (Dunbar 1998) of metabolic expense. Further, the social brain hypothesis falls short in that it emphasizes the classical view of the brain as a singular anatomical entity, without consideration for possible modular anatomical elements which may have developed contingently upon one another throughout the course of brain evolution. To this end, it is my tentative prediction that the human brain will be subject to yet more cortical expansion, but at a much more conservative rate than that which our hominid predecessors experienced, and that future evolutionarily developments will be less concerned with ever-expanding modular anatomical elements of the brain (Renfrew *et al.* 2008), but focused more acutely upon refinement of existing cerebral structures, increasing energetic efficiency, and expanding environmentally-responsive flexibility at the cellular level.

### References Cited

- Aiello, Leslie C., and Peter Wheeler. "The Expensive Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution." *Current Anthropology* 36, no. 2 (1995): 199-221. <http://www.jstor.org/stable/2744104>.
- Blumenberg, Bennett, Kurt Fristrup, Ralph L. Holloway, Kenneth H. Jacobs, and Harry J. Jerison, et al. "The Evolution of the Advanced Hominid Brain [and Comments and Reply]." *Current Anthropology* 24, no. 5 (1983): 589-623. <http://www.jstor.org/stable/2743167>.
- Bradley, Brenda J. "Reconstructing phylogenies and phenotypes: A molecular view of human evolution." *Journal of Anatomy* 212 (2008): 337-353. <http://onlinelibrary.wiley.com/doi/10.1111/j.1469-7580.2007.00840.x/pdf>
- Breedlove, S. Marc, Neil V. Watson, and Mark R. Rosenzweig. *Biological psychology: An Introduction to Behavioral, Cognitive, and Clinical Neuroscience*. 6th ed. Sunderland, MA: Sinauer Associates, Inc., 2010.
- Deacon, Terrence W. "What Makes the Human Brain Different?" *Annual Review of Anthropology* 26 (1997): 337-357. <http://www.jstor.org/pss/2952526>.
- Dunbar, Robin I.M. "The Social Brain Hypothesis." *Evolutionary Anthropology* 6, no. 5 (1998): 178-190. [http://onlinelibrary.wiley.com.libdata.lib.ua.edu/doi/10.1002/\(SICI\)1520-6505\(1998\)6:5%3C178::AID-EVAN5%3E3.0.CO;2-8/pdf](http://onlinelibrary.wiley.com.libdata.lib.ua.edu/doi/10.1002/(SICI)1520-6505(1998)6:5%3C178::AID-EVAN5%3E3.0.CO;2-8/pdf)
- Finlay, B.L. and R.B. Darlington. "Linked regularities in the development and evolution of mammalian brains." *Science* 268, (1995): 1578-1584. <http://www.jstor.org/stable/2888621>
- Le Journal duNet. "Volume cérébral des Hominidés." <http://www.linternaute.com/science/biologie/dossiers/06/0608-memoire/8.shtml>.
- Parker, Sue and Kathleen Gibson. "A Developmental Model for the Evolution of Language and Intelligence in Early Hominids." *The Behavioral and Brain Sciences* 2, no. 2 (1979): 367-407.
- Renfrew, Colin, Chris Frith, and Lambros Malafouris. "Introduction. The sapient mind: archaeology meets neuroscience" *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* 363, no. 1499 (2008): 1935-1938. <http://rstb.royalsocietypublishing.org/content/363/1499/1935>

- Sherwood, Chet C., Francys Subiaul, and Tadeusz W. Zawidzki. "A natural history of the human mind: tracing evolutionary changes in brain and cognition." *Journal of Anatomy* 212, no. 4 (2008): 426-454. <http://onlinelibrary.wiley.com/doi/10.1111/j.1469-7580.2008.00868.x/pdf>.
- Turner, Robert. "Culture and the Human Brain." *Anthropology and Humanism* 26, no. 2 (2008): 167-172. [http://www.anthrosource.net/libdata.lib.ua.edu/standardtps.aspx?doi=10.1525/ahu.2001.26.2.167&type=pdf](http://www.anthrosource.net/libdata/lib.ua.edu/standardtps.aspx?doi=10.1525/ahu.2001.26.2.167&type=pdf).