**Brain Evolution**

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The human brain is where human nature lives. So, for at least a century, most researchers have viewed brain size expansion as the central mystery of human evolution – far more important than the evolution of upright walking, round buttocks, opposable thumbs, hairless bodies, long head hair, thick penises, everted lips, male beards, female breasts, pointy chins, or skin color. Brain size in our lineage tripled in the last two million years, from a chimp-sized average of about 450 cc, around 2 million years ago. Brain size increased in several steps from those early Australopithecines to Homo erectus to archaic Homo sapiens to anatomically modern humans, reaching its current size of about 1,250 cc by around 150,000 years ago (Pearson, 2004; Rightmire, 2004). Different brain areas scaled up fairly proportionally (Finlay et al., 2001), though there was some disproportionate expansion of neocortex (Oxnard, 2004), especially prefrontal white matter (Schoenemann et al., 2005). This fairly rapid, prefrontal-biased brain size expansion suggests a functional expansion of behavioral capacities, driven by directional (more-is-better) selection.

The question is: what selection pressures drove brain size upward in our ancestors? Selection pressures can be parsed in different ways. There are different modes of selection: natural versus sexual selection, ecological versus social selection, simple optimization versus coevolutionary arms races, selection for practical adaptations versus selection for costly signals. There are different types of competition across species (with pathogens, parasites, predators, and ecological rivals) and within species (arms races between parents and offspring, males and females, dominants and subordinates). There are different levels of selection: gene, individual, group, species.

Every possible mode, type, and level of selection has been identified as a possible cause of human brain expansion by someone, somewhere. Craig Stanford argues big brains are for hunting big game (Stanford & Bunn, 2002). Robin Dunbar (2005) argues they’re are for managing complex social relationships in hunter-gatherer bands. Andrew Whiten and Richard Byrne argue they’re for manipulating and deceiving band-mates (Whiten & Byrne, 1997; Byne & Corp, 2004). Mark Flinn argues they’re for attaining ecological dominance through social competition (Flinn et al., 2005). Robert Boyd and Peter Richerson (2005) argue they’re for learning cultural innovations with group survival payoffs. I argue they’re for attracting sexual partners (Miller, 2000). How can we distinguish which selection pressures were probably most relevant? Whenever we have too many plausible theories, it helps to add some empirical constraints.

First, brains are so costly that they could not have grown bigger without directional selection favoring some behavioral capacities that required a size increase. The fitness benefits of bigger brains had to exceed the fitness costs of bigger brains. These costs include energy, obstetric problems, and psychopathology. The human brain is about 2% of body mass and .05% of body cell-count, but consumes about 20% of the body’s calories (24 watts out of about 120 watts at rest) and 15% of its oxygen. Also, it is hard for human females to give birth to big-brained babies – birth complications are much more common than among other apes, and human infants must be born several months premature (compared to a normal ape-development schedule) to fit through the birth canal. Finally, big human brains are prone to dramatic behavioral malfunctions at much higher rates than observed in great apes, such as schizophrenia, depression, anxiety disorders, obsessive-compulsive disorders, autism, religiosity, and runaway consumerism. It is important to distinguish between adaptations that reduced the relative costs of big brains – such as higher paternal investment (Kaplan et al., 2000), or more meat-eating that allowed a smaller, cheaper gut (Aiello & Wells, 2002) – versus selection pressures that increased the benefits of big brains. Cost-minimizers may have been necessary but not sufficient for brain expansion.

Second, the human brain seems computationally excessive compared to what would be needed for any well-specified cognitive task. The 20 billion neurons in the human cerebral cortex can perform, very roughly, about one quadrillion (1015) computational operations per second. Suppose a chimp-sized brain can only perform a third this many – say, 330 trillion, using perhaps 7 billion cortical neurons. The chimp-sized brain suffices for a highly adaptable, creative, social primate, capable of complex emotions, tool-making, social intelligence, and moral intuition. The quandary is this: what evolutionary problems are too complex to be solved by the chimp brain’s 300 trillion operations per second, but can be solved by the human brain’s one quadrillion operations per second? Artificial neural network models rarely require more than a few thousand units (simulated neurons) to solve ‘complex’ computational problems such as recognizing a few hundred distinct human faces, or a few thousand words from a speech stream. The human brain seems like computational over-kill.

Third, it is not enough to identify some behavioral task that sounds computationally difficult but ancestrally useful, because almost all such tasks are already solved by many species of smaller-brained animals. Complex ‘extended phenotypes’ (animal architecture and tools) are constructed by spiders, termites, weaverbirds, bowerbirds, beavers, and chimpanzees (Hansell, 2005). Complex social intelligence is shown by hyenas, wolves, elephants, dolphins, whales, baboons, and great apes (De Waal & Tyack, 2003). Complex social foraging for diverse, transient food sources is shown by many species, from pigeons to lions (Giraldeau & Caraco, 2000). Less well-known examples are even more puzzling. The common honeybee *Apis mellifera* does complex, socially coordinated foraging using a 6-lobed brain totaling 0.139 cubic millimeters (Haddad et al., 2004). Our brains are about 9 million times larger, so even a typical 40,000-bee colony survives with 1/200th the aggregate brain volume of a human. A worker bee weighs about 80 milligrams, so the colony’s total bee-weight is about 3.2 kilograms, or 1/20th of a human. Why do we need 10 times as much brain per body mass as a bee colony?

Fourth, there is a peculiar disjunction between brain paleontology and brain genetics. The paleontology suggests that brain size reached close to its modern average with the evolution of anatomically modern humans about 150,000 years ago in Africa (Pearson, 2004). Since then, brain size has apparently been at a phenotypic equilibrium. However, brain size is not at a genetic equilibrium: it shows higher heritability (about .89) than almost any other human trait, with a fairly high coefficient of additive genetic variation (about 7.8) that suggests ongoing selection (Miller & Penke, submitted). Brain size also remains moderately correlated (about +.30 to +.40) with general intelligence (McDaniel, 2005; Miller & Penke, submitted; Thoma et al., 2005), and the correlation is genetically mediated (Posthuma et al., 2002). Intelligence is also correlated with body symmetry, a standard index of developmental stability and low mutation load (Prokosch et al., 2004; Thoma et al., 2005). Moreover, some brain-size-increasing alleles seem to have evolved quite recently in genes such as *Microcephalin* around 37,000 years ago (Evans et al., 2005), *APSM* around 5,800 years ago (Mekel-Bobrov et al., 2005), and some sphingolipid-related genes within the last 1,000 years (Cochran et al., in press). These findings suggest that brain size is under mutation-selection balance, with directional selection continuing to favor larger brains and higher intelligence throughout recent evolutionary history, but recurrent harmful mutations continuing to erode brain size and intelligence.

Until a few years ago, it looked like there was an equally strange disjunction between brain size expansion and techno-cultural evolution. Big human brains evolved by 150,000 years ago, yet the European archaeological record showed few behavioral innovations until the ‘Upper Paleolithic revolution’ around 35,000 years ago (Mellars, 2005), when our ancestors invaded Europe and replaced Neanderthals. However, better African archaeology has now shown that distinctly human behavioral innovations (such as stone blades, microliths, bone tools, big-game hunting, fishing, long-distance trade, pigment use, and body ornamentation) were arising throughout the Middle Paleolithic in Africa (c. 200,000 through 35,00 years ago) (McBrearty & Brooks, 2000). Thus, there is now a more consistent time-line between human paleontology and archaeology, but the archaeology remains fairly agnostic about the fitness payoffs for higher brain size.

Fifth, there are sex differences in brain size and growth pattern. Modern human brain size averages 1300 cc in males and 1180 cc in females (Miller & Penke, submitted). This 10% difference develops largely after birth, is not eliminated by ‘correcting’ brain size for body size differences (Joffe et al., 2005; Nyborg, 2005), and actually under-estimates the 16% difference in cortical neuron number (19 billion in females, 23 billion in males – Pakkenberg & Gundersen, 1997). Male brains also show more dramatic developmental changes during their later adolescence, with more gray matter pruning and white matter growth (De Bellis et al., 2001; Luders et al., 2005). Such sex differences in brain size and growth suggest that sex-blind theories of human brain expansion are unlikely to work.

Together, these five empirical constraints – high costs, computational excess, cross-species comparisons, persistent heritability, and sex differences – render some brain evolution models more likely than others. Models focused on hunting, foraging, ecological dominance, and paternal investment (e.g. Aiello & Wells, 2002; Flinn et al., 2005; Kaplan et al., 2000; Stanford & Bunn, 2002) seem best-suited to explain how we afforded the costs of big brains. They seem less compelling at explaining the fitness payoffs of big brains, since many smaller-brained species are carnivorous, omnivorous, and/or paternal.

To explain rapid expansion in a costly organ such as the brain, an evolutionary positive-feedback loop seems most appropriate. This is a common feature of all three major contenders – the social intelligence model (Byne & Corp, 2004; Dunbar, 2005; Whiten & Byrne, 1997), sexual selection model (Miller, 2000), and cultural group selection model (Boyd & Richerson, 2005). Each posits a runaway cognitive arms race – whether between individuals, sexes, or groups – that can nicely explain the high costs, apparent computational excess, and phylogentic uniqueness of the human brain. Also, each model allows some scope for costly-signaling effects (Miller, 2000b) to amplify the fitness-dependency of brain size and function, possibly explaining the persistent heritability of brain size and its correlations with general intelligence, body symmetry, and mental health (Prokosch et al., 2005; Shaner et al., 2004; Thoma et al., 2005) . Finally, insofar as hominid males always show higher reproductive variance than females, each model would also predict somewhat higher male payoffs for successful cognitive competition, and could thus explain the slightly larger male brain size and later brain maturation schedule. Thus, each of the three brain-expansion models remains empirically plausible, and awaits further research.

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