Review

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The evolution of distributed association networks in the human brain

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The human cerebral cortex is vastly expanded relative to other primates and disproportionately occupied by distributed association regions. Here we offer a hypothesis about how association networks evolved their prominence and came to possess circuit properties vital to human cognition. The rapid expansion of the cortical mantle may have untethered large portions of the cortex from strong constraints of molecular gradients and early activity cascades that lead to sensory hierarchies. What fill the gaps between these hierarchies are densely interconnected networks that widely span the cortex and mature late into development. Limitations of the tethering hypothesis are discussed as well as its broad implications for understanding critical features of the human brain as a byproduct of size scaling.

A speculative hypothesis

Our ancestors advanced tool use, evolved language, and achieved complex social order during the past 3 million years. From one perspective, that is a lot of time for drift and selection to mold a new species. Changes in gene frequencies and adaptive mutations can arise rapidly in isolated populations. From another perspective, it is unexpected given the trajectories of closely related primate species. To anchor this point, consider the divergent evolution of the common chimpanzee and the bonobo over the past 1–2 million years. These two great apes became genetically isolated from one another when the Congo River formed allowing distinct phenotypes to evolve over a short time period [1]. Bonobos display a matriarchal social order that differs from the aggressive alpha male-dominated society of the chimpanzee [2,3]. Chimpanzees use primitive tools to extract food in the wild, whereas

Glossary

Allometric evolution (within the context of brain evolution): evolutionary changes in one brain component that are predicted by changes in whole-brain size or by changes in another brain component. The relationship can deviate from isometric scaling, meaning that one component differs to a greater degree than the other, but the two components must show a predictable relationship.

Association cortex: portions of the cerebral cortex that do not fall within primary sensory or motor projection areas. The term was popularized by Flechsig (1896) to identify regions of cortex that function as integration or association centers for more complex or elaborated mental processes.

Australopiths: an early, extinct hominin genus discovered in Africa that walked upright but possessed brains only slightly larger than those of apes.

Canonical circuit (canonical macrocircuit): a network of brain areas characterized by dense local connectivity between areas and a serial, hierarchical flow of information across areas. Such networks link incoming sensory information to the development of a motor response or action.

Default network: a set of brain regions more active when people rest passively compared with when they focus on features of the external environment. The network is also active when people remember, think about the future, or engage in other forms of internal mentation, leading to the hypothesis that the network is important to advanced forms of cognition including the ability to mentally imagine oneself in alternative scenarios.

Encephalization: brain size that exceeds the size predicted by body mass. Across species, most variation in brain size is predicted by body mass. The ratio of actual brain size versus the predicted brain size from body mass is known as the encephalization quotient. Humans have the highest encephalization quotient among mammals.

Hierarchical organization: organization by which connections between areas facilitate ascending (forward) information flow and are often paired with reciprocal (descending) feedback connections. Information is successively transformed and elaborated at each step in the hierarchical sequence. Note that the term hierarchical as used here to describe anatomical connection patterns differs from other (but related) forms of hierarchical control that refer to how certain networks control other networks (e.g., [59]).

Hominin: humans and extinct human ancestors that are more closely associated with the human line of evolution than with chimpanzees and other apes.

Hominids: humans, the great apes (chimpanzees, gorillas, orangutans), and their extinct ancestors.

Mosaic evolution (within the context of brain evolution): evolutionary changes in one brain component without simultaneous changes in another brain component. Also called modular evolution.

Noncanonical circuit: network organization in which widely distributed regions possess connections that do not conform to a sequential sequence of feedforward and feedback relationships; rather, they tend to be reciprocally connected with multiple violations for simple feedforward/feedback connectivity and share common targets and inputs that are distributed across the brain.

Spandrel (in evolutionary biology): a characteristic or feature that was not the product of direct adaptive selection, but rather emerged as a side effect of direct pressure on some other feature.

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bonobos do not [3]. Differences in brain structures exist between the two species that may be important to social behaviors [4], but these differences pale in comparison with the expansion of the life cycle, social organization, and cognitive abilities that emerge in hominins over a slightly longer time frame [5].

Given the quick pace of change observed in the hominin lineage, we are left with a puzzle: how did brain networks that underlie extraordinary human capabilities evolve so rapidly? A large part of the explanation must lie in the brain expansion that separates us from our ape cousins (Box 1). The human brain is more than triple the size of the chimpanzee brain [6]. Fossil evidence suggests that this increase occurred over roughly the time period when our ancestors advanced their extraordinary abilities [7], but not necessarily in lock step with the exact timing of behavioral and cultural achievements (Box 2). Key genetic events also occurred that may interact with or cause brain expansion in hominins (e.g., [8–15]; see [16] for discussion).

How might a large brain enable complex cognitive functions? One possibility is that the human brain possesses more computational capacity because it has a large number of neurons – estimated at 86 billion neurons using modern cell-counting techniques [17]. Other large-brained mammals, such as whales and elephants, radiate from ancestors that had reduced neuronal densities. The

Box 1. The evolutionary road to the human brain's expanded cerebral cortex

The hominin brain grew rapidly over the past 3 million years in a primate lineage that had already experienced multiple events that increased brain size (Figure I depicts hominin brain evolution estimated from fossil endocasts, with labels for representative individuals from major species). The most significant determinant of our large brain size is that we are large animals: absolute brain size scales allometrically with body size [148]. After factoring out body weight, which accounts for as much as 85% of the total variance in brain size across mammalian species, the human brain is about five times larger than one would expect for a typical mammal [149,150]. Primates generally have disproportionately larger brains for their body size than other mammals (quantified as the encephalization quotient). This relative size difference is present at early embryonic stages, suggesting an ancient evolutionary event that shifted a greater proportion of the embryonic precursor cells to commit to a neuronal lineage ([151], data interpreted in [152]; see also [153]). Differences across primate suborders hint at other major evolutionary events including a step increase in brain size in monkeys (e.g., macaque and squirrel monkey) relative to prosimians (e.g., lemur). The acceleration over the past several million years probably derives from a distinct mechanism. Chimpanzees and humans have roughly the same body size and share a common ancestor about 5–7 million years ago. The early phases of brain development for chimpanzees and humans are conserved, with a similar proportion of the total body size devoted to the brain. At late phases, the brain continues to grow relative to the body in humans but stops earlier in chimpanzees, leading to a relative brain size expansion [152] (see also [154,155]). An interesting feature of brain scaling is that brain enlargement disproportionately expands some brain structures more than others. The cerebral cortex in mammals has the most privileged position in brain growth. A key contributor to disproportionate cortical expansion is constraints from embryonic development [135]. Cerebral cortex progenitor cells are the last to be born among different neuronal pools. Because embryonic development is temporally stretched in large-brained mammals, the cerebral progenitor pool continues to divide for the longest period and forms the largest cell pool. This 'late equals large' developmental feature causes the cerebrum to have the greatest relative size increase. The cerebral surface area is $\sim$120 cm^2 in the macaque and a remarkable $\sim$960 cm^2 in the highly gyrified human brain [25] (see also [156]).

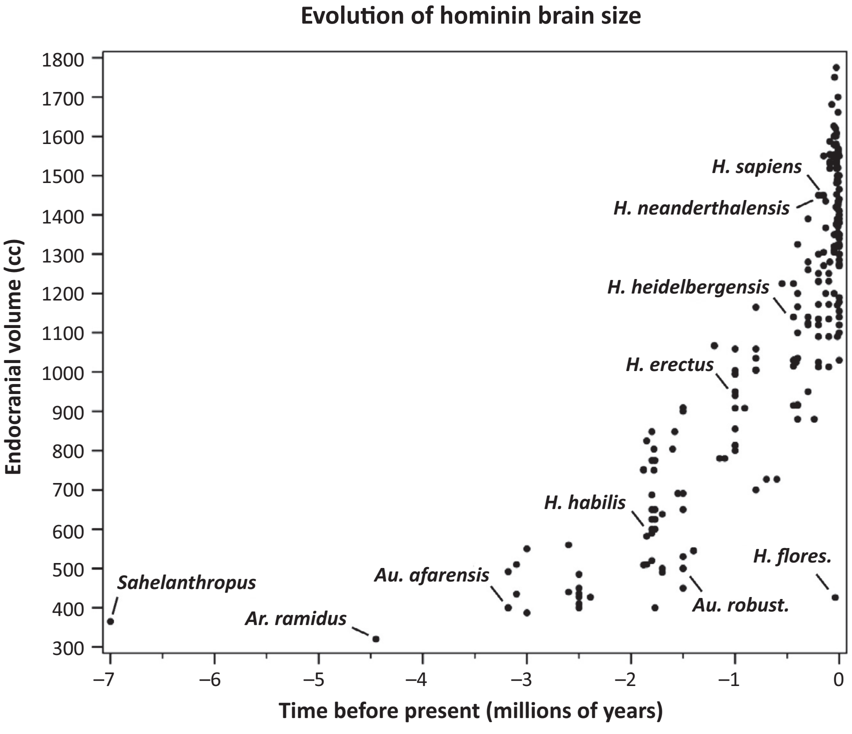

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Figure I. Hominin brain evolution estimated from fossil endocasts.