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The grammar of mammalian brain capacity

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ABSTRACT

Uniquely human abilities may arise from special-purpose brain circuitry, or from concerted general capacity increases due to our outsized brains. We forward a novel hypothesis of the relation between computational capacity and brain size, linking mathematical formalisms of grammars with the allometric increases in cortical–subcortical ratios that arise in large brains. In sum, i) thalamocortical loops compute formal grammars; ii) successive cortical regions describe grammar rewrite rules of increasing size; iii) cortical–subcortical ratios determine the quantity of stacks in single-stack pushdown grammars; iv) quantitative increase of stacks yields grammars with qualitatively increased computational power. We arrive at the specific conjecture that human brain capacity is equivalent to that of indexed grammars – far short of full Turing-computable (recursively enumerable) systems. The work provides a candidate explanatory account of a range of existing human and animal data, addressing longstanding questions of how repeated similar brain algorithms can be successfully applied to apparently dissimilar computational tasks (e.g., perceptual versus cognitive, phonological versus syntactic); and how quantitative increases to brains can confer qualitative changes to their computational repertoire.

1. Brain growth shows surprisingly few signs of evolutionary pressure

Different animals exhibit different mental and behavioral abilities, but it is not known which abilities arise from specializations in the brain, i.e., circuitry to specifically support or enable particular capacities. Evolutionary constraints on brain construction severely narrow the search for candidate specializations. Although mammalian brain sizes span four orders of magnitude [1], the range of structural variation differentiating those brains is extraordinarily limited.

An animal's brain size can be roughly calculated from its body size [2], but much more telling is the relationship between the sizes of brains and of their constituent parts: the size of almost every component brain circuit can be computed with remarkable accuracy just from the overall size of that brain [1,3–5], and thus the ratios among brain parts (e.g. cortical to subcortical size ratios) increase in a strictly predictable allometric fashion as overall brain size increases [6,7] (Fig. 1).

These allometric regularities obtain even at the level of individual brain structures (e.g., hippocampus, basal ganglia, cortical areas). There are a few specific exceptions to the well-documented allometric rule (such as the primate olfactory system [8]), clearly demonstrating that at least some brain structure sizes *can* be differentially regulated in evolution, yet despite this capability, it is extremely rare for telencephalic structures ever to diverge from the allometric rule [4,6,7,9]. Area 10, the frontal pole, is the most disproportionately expanded structure in the human brain, and has sometimes been argued to be *selected* for differential expansion, yet the evidence has strongly indicated that area 10 (and the rest of anterior cortex) are nonetheless precisely the size that is predicted allometrically [6,7,10,11].

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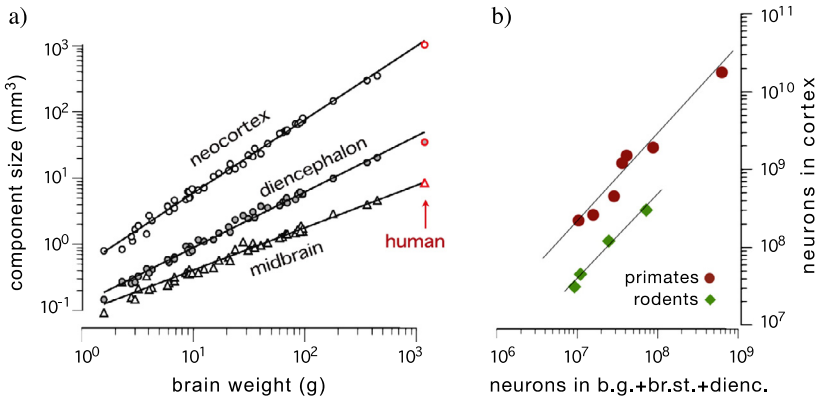

Fig. 1. Allometric relations among brain parts. (a) Distinct brain components grow at different fixed rates as brain size increases. Shown are the sizes of brains and components in primates. The slope of neocortical increase is greater than 1; neocortex becomes disproportionately enlarged in big brains, in an allometrically highly predictable fashion. Notably, human brains are no exception. (b) Corresponding increases in numbers of neurons accompany cortical size increase, again increasing predictably and allometrically. Shown are cortical neurons vs. the sum of neurons in basal ganglia (b.g.), brain stem (br.st.), and diencephalon (dienc.).

These findings inexorably lead to the remarkable conclusion that, with few exceptions, brains do not choose which structures to differentially expand or reconfigure [4,6,11–15]. The same allometric relations recur for all the primary components of the mammalian forebrain (telencephalon), and the same recurring circuit motifs, large and small, are repeated throughout the brain [16,17]. The resulting truly-notable uniformity holds across orders of mammals (along with distinct variants seen within different subgroups such as rodents versus primates [7]).

These unexpectedly powerful allometric constraints strongly suggest that novel specialized circuits may not be the explanation for novel abilities in human brains (such as syntax). Rather, this may be an instance in which a quantitative change (increased brain size) results in a qualitative one (uniquely human abilities): simply adding more of the same computational units creates new competencies. Such instances are rare but far from unknown (e.g., in evolution, and in economies of scale). A few specific well-studied computational mechanisms exhibit the ability to yield qualitative changes arising from size changes. These include bifurcation systems [18–21], and formal grammars [22–24].

The necessary implication would be that telencephalic computational operations are constrained to the set of those few mechanisms that do yield qualitatively different outcomes simply via quantitative change. We will show that there already are biologically grounded, bottom-up simulation and analytic studies that have strongly implicated formal grammars as the emergent mechanisms from telencephalic operation.

Again, we emphasize that it is not yet known whether some uniquely human cell types, or genetic innovations, or anatomical conformations, have the power to give rise to uniquely human abilities. It remains possible that new discoveries will identify mechanisms with the requisite power to explain novel human abilities. But we posit that it is not at all unreasonable to also search for explanations in the other direction: mechanisms by which new uniquely human abilities could arise purely from the rigid allometric increase in brain-body ratio and cortical–subcortical ratio. Rather than neglect this possibility, we take it as a serious contending hypothesis, and deliberately explore its potential implications.

2. Derivation of computations of thalamocortical and cortico-hippocampal circuits

Computational modeling of neural circuits has led to the identification of algorithms that may be carried out by particular anatomical systems in mammalian telencephalon.

Extensive bottom-up modeling work [14,25–28] began with simulations of physiological operations occurring in the anatomical circuitry of thalamocortical loops. Every cortical region is connected to thalamic regions by both afferent and efferent projections [29–31]; Table 1 contains a brief précis of the simulated physiological steps occurring in thalamocortical circuitry reported by Rodriguez et al. [25].

Many cortical areas receive only nonspecific (matrix), but not topographic (core), projections from thalamus; in these regions, outputs of superficial cortical layers become topographically-organized input to middle and superficial layers of downstream regions, whose deep layers send reciprocal feedback to the originating superficial layers [32–37]. This cortico-cortical organization, together with the cortico-thalamic matrix loops that occur throughout cortex [38], have been hypothesized to subserve corresponding functions [14,39–43].

The resulting studies have strongly suggested characterizations of two constituent algorithms of thalamo-cortico-cortical operation: i) categorization of objects by similarity, and ii) chaining objects into sequences; pseudocode algorithms for these are presented in Table 2 (from [25]).

The output of a given cortical area becomes input (both divergent and convergent) to other, downstream, regions, as well as receiving feedback from them. Producing categories and sequences, in cortico-cortical succession, yields sequences of