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Beyond Cortex: The Evolution of the Human Brain

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Human evolution has been marked by a striking increase in total brain volume relative to body size. While a prominent and characteristic feature of this volumetric shift has been the disproportionate expansion of association cortex across our evolutionary lineage, descent with modification is apparent throughout all neural systems in both human and nonhuman primates. However, despite evidence for the ubiquitous and complex influence of evolutionary forces on brain biology, within the psychological sciences the vast majority of the literature on human brain evolution is entirely corticocentric. This selective focus has contributed to a flawed theoretical framework in which the evolution of association cortex is viewed as an isolated process, removed from the rest of the brain. Here, we review our current understanding of how evolutionary pressures have acted across anatomically and functionally coupled networks, highlighting the diverse set of rules and principles that govern human brain development. In doing so we challenge the systemic mischaracterization of human cognition and behavior as a competition that pits phylogenetically recent cortical territories against evolutionarily ancient subcortical and cerebellar systems. Rather, we propose a comprehensive view of human brain evolution with critical importance for the use of animal models, theory development, and network-focused approaches in the study of behavior across health and disease.

Keywords: brain evolution, cerebral cortex, subcortical, association cortex, network neuroscience

The Evolution of the Human Brain

The human cerebral cortex is widely viewed as the "crowning development of the neomammalian brain" (MacLean, 1972), vastly expanded relative to other nonhuman primates and disproportionately occupied by distributed networks of association regions that support our more complex and elaborated mental processes (Rakic, 2009; Reardon et al., 2018). Consistent with this conceptual bias, our modern understanding of human cognition within the psychological sciences is largely built upon a corticocentric literature that exclusively focuses on the evolutionary forces that underlie the emergence of additional cortical areas and associated regional expansion (Felleman & Van Essen, 1991; Preuss & Goldman-Rakic, 1991; Rakic, 2000, 2009; Sherwood et al., 2008). Conversely, subcortical and cerebellar structures are commonly seen as evolutionarily stagnant, isolated from the "higher" functions of the brain, responsible for base instinctual desires, and subservient to cortical regulation through a rigid top-down hierarchy (Parvizi, 2009). As a consequence of this fragmented understanding of brain evolution, our field biases the interpretation of cross-species work fundamental to progress in the brain sciences and engages in theory development that is often removed from scientific evidence.

The view that psychological processes and brain biology reflect a rigid evolutionary hierarchy with prefrontal executive functions at the "top" has infested both the empirical literature and associated theory development in psychology and neuroscience. Here, we challenge this scalar conceptualization of human evolution, which places aspects of the brain on discrete points that ascend along some sort of one-dimensional *anthropocentric* axis (see Appendix). In doing so, we review the current scientific consensus on how evolutionary processes have influenced the anatomical and functional systems that make up the human brain, discussing associated biological constraints and providing select examples within cortical, subcortical, and cerebellar systems. Critically, the purpose of this paper is not to provide exhaustive or complete coverage of the voluminous literature on brain evolution in vertebrate mammals, as thorough treatments of this topic are available elsewhere (Butler & Hodos, 2005; Shepherd, 2017; Striedter, 2005). Rather, from our perspective as psychologists and neuroscientists, we seek to provide organizing principles for framing and synthesizing this diverse and active area of research, so that theoretical development can be facilitated for the study of human behavior across both health and disease.

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Man's (Cortex's) Place in Nature

The oldest known primate fossils are approximately 55 million years of age, with our earliest primate ancestors potentially diverging from other placental mammals during the Cretaceous period, over 80 million years ago (Tavaré et al., 2002). The brains of vertebrate mammals contain many specialized systems, each with its own dissociable, but partially interlinked, evolutionary history. As primates evolved, the *hominin* lineage has experienced multiple events that have increased brain size, culminating in a rapid volumetric expansion across the ~25 million years that separate us from macaques and the ~6 million years since our divergence from chimpanzees and bonobos, our closet living primate relatives (Hill et al., 2010; Kaas, 2008). Among animals, absolute brain and body sizes characteristically share a predicable *allometric* relationship (Jerison, 1955). In modern humans, however, the brain is about fivefold larger than would be expected in a typical vertebrate mammal. Although all primates exhibit a disproportional enlargement of *neocortex*, relative to absolute brain volume, this evolutionary expansion is most evident in the increased surface area of the cerebral cortex in humans (Finlay & Darlington, 1995; Hill et al., 2010; Kaas, 2004; Wei et al., 2019). Notably, this scaling is not uniformly distributed throughout the cortical sheet (Finlay & Darlington, 1995). Although the basic organization of the primary sensory and motor areas that comprise unimodal cortex emerged early in the course of vertebrate evolution (Suryanarayana et al., 2020), as brain sizes have increased in primates the evolutionary enlargement of the cortical mantle has been preferentially localized within spatially distributed aspects of the prefrontal, temporal, and parietal cortices that fall between the primary and secondary sensory systems (Figure 1A, B; Buckner & Krienen, 2013; Krubitzer & Kahn, 2003). Of note, these expanded cortical territories occupy the "association centers" that Paul Flechsig theorized to underpin higher cortical functions and complex associative processing (Flechsig, 1896). In contrast to unimodal sensory areas, which possess a more serial, hierarchical pattern of feedforward/feedback connectivity (Felleman & Van Essen, 1991), association cortex is marked by a complex noncanonical circuit organization (Goldman-Rakic, 1988). The expansion of this form of circuit across hominin evolution is hypothesized to support the parallel and reentrant processing necessary for the formation of complex network relationships. For instance, allowing for certain networks to bias the function of other networks in hierarchical (Badre & D'Esposito, 2009), interacting (Spreng et al., 2013), and time varying (Reinen et al., 2018) configurations. The extent to which this neocortical expansion may be expected under allometric brain growth patterns common to primates or is reflective of an extraordinary feature of human evolution remains unresolved (Finlay, 2019; Herculano-Houzel, 2012; Marino, 2006; Semendeferi et al., 2002). As one example, while the rapid enlargement of cortical association networks has been an important locus of genetic changes in human evolution (Wei et al., 2019), recent evidence suggests the presence of shared mechanisms for size-dependent patterning of the cortical sheet within species of primates. This includes spatial convergence of cortical remodeling and areal scaling throughout evolution, development, and across individuals within a species as a function of population-level variability in brain size (Reardon et al., 2018).

Critically, the expansion of the human brain does not proceed without limit, rather it is held in check by a interrelated set of biological bounds including the energetic and metabolic costs necessary to support brain functions (Roth & Dicke, 2005), wiring costs (Assaf et al., 2020; Zhang & Sejnowski, 2000), and the restricted space available in the human skull (Striedter, 2006). The necessary compactness of brain circuitry is, in part, enabled by cortical folding patterns (Mota & Herculano-Houzel, 2012; Zilles et al., 2013) theorized to arise from mechanical tension along axons, dendrites, and glial processes over the course of development (Tallinen et al., 2016; Van Essen, 1997). These biological limits are balanced against the adaptive benefits of an increase in brain size and associated shifts in cognitive capacity, which can facilitate flexible responses to buffer individuals against environmental stressors (Sol et al., 2007) and support complex, multiindividual, social interactions (Dunbar & Shultz, 2007). Beyond these broad shifts in cortical anatomy, a host of other specializations have occurred in the make-up of human brain tissue throughout the evolution of our species, including the presence of novel cell populations, altered molecular cascades, developmental stages, and wiring paths (Krienen et al., 2019; Rakic, 2009; Sherwood et al., 2012; Somel et al., 2013). Even within brain structures whose volumes are relatively conserved across species, these evolutionary innovations can have profound functional consequences (Herculano-Houzel, 2012; Katz & Harris-Warrick, 1999; Kim et al., 2017), a critical facet of neurobiology we highlight in subsequent sections.

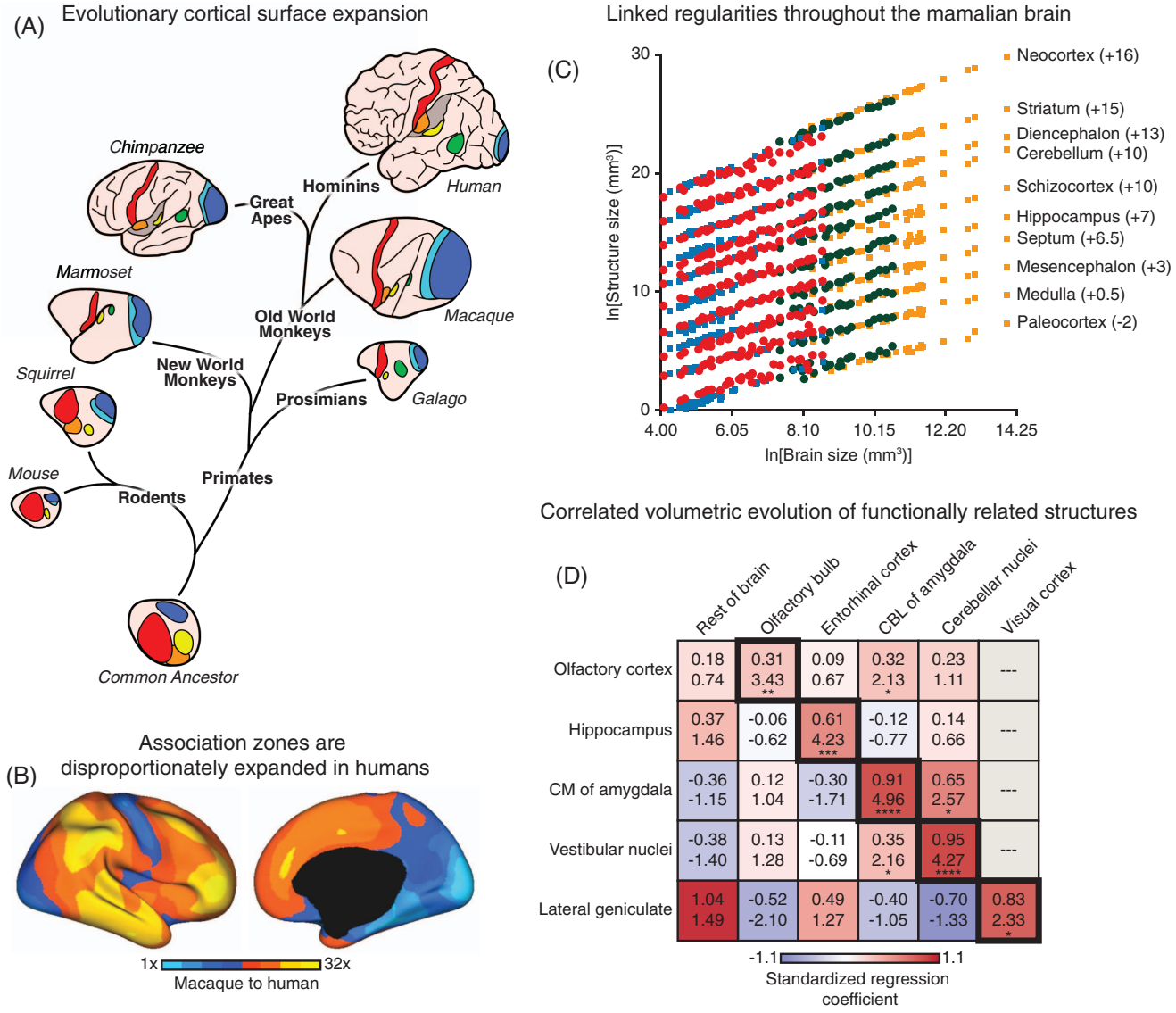
The Coordinated Structure of Brain Evolution

The corticocentric view of human brain functions has a long intellectual history, in part motivated by the widespread belief that evolution consists of a linearly progressive pattern, from fish and amphibians, through reptiles, birds, and then mammals. This incorrect evolutionary model echoes the hierarchical ranking of animals based on an Aristotelian notion of an approach toward a perfect form, with humans at the top (Figure 2A). In the late nineteenth and early twentieth centuries neuroanatomists extended these "Scala Naturae" arguments to anatomical structures within a species, proposing that neocortex reflects a recent evolutionary innovation in mammals that is layered on top of a phylogenetically primitive ancestral brain (Butler & Hodos, 2005). At this time, luminaries like Ludwig Edinger posited that cerebral subdivisions are distributed in a manner that reflects their progressive ascension from lower order primitive processing capabilities to higher order cognitive functions (Edinger & Rand, 1908). Within this framework, the evolved and "rational" cortex sits astride the brain with subcortical systems playing a subservient role in cognition and behavior (7). A view point that was perhaps most famously popularized by Paul MacLean when he theorized the presence of a *triune* brain in primates, which he speculated emerged along three core evolutionary patterns (reptilian, paleomammalian, and neomammalian; MacLean, 1990). Here, the striatal complex was thought to reflect a major aspect of the reptilian forebrain, often referred to as the "lizard brain" in popular culture, while the limbic system was paleomammalian in origin. Conversely, the frontal lobes were believed to represent the pinnacle of brain evolution as they emerge from the telencephalon, which at the time was thought to be the most phylogenetically recent aspect of the neuroaxis (but see Briscoe & Ragsdale, 2019).

The triune brain and similar scalar theories regarding primate brain evolution, mirror many of the historic arguments centered

Figure 1

Linked Evolutionary Regularities Are Evident Throughout the Mammalian Brain

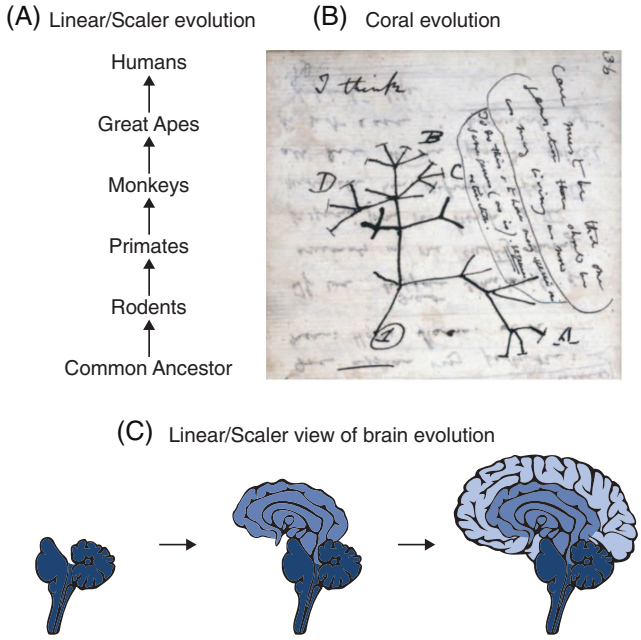


Note. (A) Extant primates possess a greater percentage of the cortical mantle that falls between primary and secondary sensory systems relative to other placental mammals. Here, primates are displayed relative to rodents and the theorized organization of cortical fields in the common ancestor of placental mammalians (adapted from "Nature versus nurture revisited: An old idea with a new twist," by L. Krubitzer and D. M. Kahn, 2003, *Progress in Neurobiology*, *70*(1), pp. 33–52. https://dx.doi.org/10.1016/S0301-0082(03)00088-1). Brains are not drawn to scale. Dark blue, primary visual area; light blue, secondary visual area; green, middle temporal visual area; yellow, primary auditory area; red, primary somatosensory area; orange, secondary somatosensory area. (B) Association cortex territories are disproportionately expanded in humans relative to nonhuman primates. Estimated evolutionary cortical expansion between an adult macaque and the average human adult is displayed on the lateral and medial cortical surfaces (data from Hill et al., 2010). Colors reflect the scaling value required to match the size in the human brain. For macaques, a continuous surface estimate of expansion was derived from 23 distributed landmarks. (C) Linked regularities are present throughout the evolution of mammalian brains. Sizes of 10 brain subdivisions from 131 species plotted as a function of total brain sizes. Orange squares, simians; green circles, prosimians; red circles, insectivores; blue squares, bats. Sizes are plotted as a function of total brain size on natural logarithmic scales. Arbitrary constants are used to visually separate the plots are listed in parentheses following each subdivision (adapted from "Linked regularities in the development and evolution of mammalian brains," by B. L. Finlay and R. B. Darlington, 1995, *Science*, *268*(5217), pp. 1578–1584. https://dx.doi.org/10.1126/science.7777856; see also, Reep et al., 2007). (D) Volumetric evolution in primates is correlated across functionally related brain structures. Contrasts in the volume of each structure in the left column were regressed on volumes of structures in the top row (data from Barton & Harvey, 2000). Values in each cell reflect standardized regression coefficients (top), *t*-values (bottom). Significant results suggest joint evolution of the two structures in question, independent of change across the other structures in the same row. Predicted relationships are indicated by the bold boxes. Scale bar reflects standardized regression coefficients. CM = centromedial complex; CBL = cortico-basolateral complex; entorhinal cortex includes subiculum.

* $p \leq .05$. ** $p \leq .01$. *** $p \leq .001$. **** $p \leq .0001$.

Figure 2

Aristotelian Scalar and Darwinian Coral Views of Evolution



Note. (A) The incorrect linear/scalar view of evolution. Reminiscent of Aristotle's "Scala Naturae" and subsequent "Great Chain of Being" models for organizing the natural world. Here, species are ranked within fixed positions, with those higher along the chain considered to be evolutionarily advanced relative to the species below. (B) Darwin's initial sketch of an evolutionary tree, from his First Notebook on Transmutation of Species (1837). Diverging lines reflect branching descent producing new varieties as species diverge from one or more common ancestors through the continued action of evolutionary forces along each branch. Reproduced by kind permission of the Syndics of Cambridge University Library. (C) Incorrect linear/scalar view of brain evolution in humans. In this case, it is assumed that as new vertebrate species arose, evolutionarily novel brain structures were simply laid on top of existing phylogenetically ancient systems.

around speciation through natural selection, or the process through which populations evolve to become distinct species. While a substantial portion of his contemporaries viewed evolution as a progressive scalar process, Darwin understood that speciation does not produce linear scales, rather it results in family trees, bushes, or corals due to the continued action of evolutionary forces on each distinct branch (Figure 2B; Darwin & Barrett, 1987; Striedter, 2006). Yet, while scalar arguments are now antiquated amongst evolutionary biologists, these same biases still remain pervasive in within some sectors of psychology and neuroscience. For example, the first *amniotes* evolved from amphibian ancestors ~340 million years ago. However, despite clear evidence indicating that the *synapsid* ancestors of mammals diverged at the beginnings of amniote life, evolving separately from *sauropsid* forebearers of reptiles and birds (Shedlock & Edwards, 2009), the erroneous idea that primate cortex consists of a new layer stacked atop an ancestral reptilian brain is still widely held by many modern psychologists (Figure 2C). Even independent of MacLean's theory, the unilinear/scalar view of evolution is often applied unevenly throughout the brain, with cortical systems miscast as phylogenetically recent and simply enveloping evolutionarily conserved subcortical territories. While much of the foundational work in this area is from a period when scientific methods were limited to gross volumetric estimates, largely relying on endocasts of extinct species, there is now ample evidence for progressive differentiation across all brain systems throughout our evolutionary lineage (Striedter, 2005).

The preferential expansion of prefrontal cortices and associated cognitive functions, for example "higher-order" executive, cultural, or social capacities in humans (Donald, 1991; Dunbar & Shultz, 2007), are often viewed as being directly/specifically selected for through natural selection. As eloquently worded by Stephen Jay Gould in 1979, through this view "an organism is atomized into 'traits' and these traits are explained as structures optimally designed by natural selection for their functions" (Gould & Lewontin, 1979). However, it is not sensible to argue that all of biological variation can be explained solely in terms of Darwin's law of natural selection down to the individual component parts that make up a living whole, independent of associated developmental and functional constraints (Montgomery et al., 2016). Core to our understanding of brain evolution is the degree to which the evolutionary adaptation of one brain system, for instance a circumscribed aspect of association cortex, might occur in isolation. This reflects part of a broader historical debate in evolutionary biology regarding the extent that evolution through natural selection can freely influence the form of a given species. Indeed, one of the most puzzling questions across the neurosciences is how novel cortical territories emerge through evolutionary pressures to become integrated with and impinge upon the brain's existing network architecture. During prenatal brain development, for instance, mammals produce an overabundance of cells, of which only a subset eventually survive to reach a mature stage (Rakic, 2009). The determination of which neurons will persist is a competitive process where immature cells vie for appropriate innervation targets and supplies of trophic factors (Yuan & Yankner, 2000). This process of neuronal overpopulation and subsequent elimination optimizes brain connectivity as neurons that are not fully integrated within local circuits are pruned to help to ensure stable network function (Pfisterer & Khodosevich, 2017). Consistent with these regional circuit-level relationships, perhaps the most striking feature of brain evolution is the presence of strong volumetric associations within developmentally linked and functionally coupled systems, and the general absence of such tight bonds between systems (Barton & Harvey, 2000; Finlay et al., 2001). How such relationships emerge remains an open question and several hypotheses have been put forth regarding the cause of allometric scaling among brain components. By one view, these linked regularities arise through general constraints imposed by the action of evolutionary processes on shared developmental programs, a process termed "concerted" evolution (Finlay & Darlington, 1995). An alternate, but not mutually exclusive, possibility is that the brain evolves in a "mosaic" manner, or the hypothesis that natural selection may act on individual behaviors, selectively impacting associated brain systems in a manner that maintains functional correspondence (Barton & Harvey, 2000; see also, Striedter, 2006).

As with other complex biological systems, brains are organized and modified through coordinated interactions across multiple scales, from genes and molecules through cells, circuits, networks, and behavior that unfold in a dynamic manner across development. Given these constraints, it should be expected that brains will

change, at least in part, as a covarying whole and subcortical structures will reflect the changes in the cortical areas with which they share connections according to conserved scaling relationships. In line with these assumptions, the theory of concerted evolution posits that conserved patterns of brain scaling across structures evolve through global alterations to the duration of neurogenesis, with any evolutionary change in brain anatomy or function linking with coordinated changes across the entire system (Finlay & Darlington, 1995; Finlay & Uchiyama, 2015). This model hypothesizes that allometric relationships between brain components, even functionally unrelated ones, emerge as the end result of the highly preserved order of neurogenesis across species (Workman et al., 2013), which is most evident in the disproportionate expansion of late developing structures like association cortex in humans. However, while neocortex exhibits the steepest slope of expansion, distinct allometric scaling profiles are apparent for each brain structure (Figure 1C; Finlay & Darlington, 1995). These data indicate continuity of brain structure sizes across both orders (insectivores, bats, primates) and suborders (simians and prosimians). Indeed, with the exception of the olfactory bulb which is uniformly smaller in primates relative extant nonprimate mammals (Heritage, 2014), the presence of such linked regularities can by leveraged across species with remarkable precision to predict the size of individual structures relative to total brain size (Finlay & Darlington, 1995). As such interregional correlations should be impossible if brains were to evolve through a purely mosaic manner, it is highly likely that developmental cascades constrain evolutionary changes in neural systems.

A contrary, but not wholly incompatible theory focuses on region-to-region mosaicism, or the presence of complex interdigitated patterns that change at the level of the functional systems (Barton & Harvey, 2000). This is idea that natural selection and associated evolutionary pressures can differentially influence the size, cellular composition, or molecular processes of distinct brain systems, independent of evolutionary change in other structures. Indeed, the patterns of covariance among components of mammalian brains closely correspond to their anatomical and functional connectivity (Barton & Harvey, 2000; Whiting & Barton, 2003). This is evident when considering gross volumetric estimates across avian and mammalian species (Barton & Harvey, 2000; Iwaniuk et al., 2004), as well as when examining subnuclei (Barton, 2007; Whiting & Barton, 2003), genetic influences on cortical structure (Grasby et al., 2020), the relations linking anatomical projections and connectivity patterns on cell transcriptomes (Kim et al., 2020), and spatial variation in cellular composition or profiles of gene transcription (Anderson et al., 2018, 2020). While these data suggest that functional, and not just developmental constraints, could drive allometric scaling between brain components, the mosaic hypothesis does not rule out the possible influence of developmental cascades. Rather, proponents of this theory hold that when observed, developmental integration will reflect the product of selection to maintain functional correspondences (Montgomery et al., 2016).

A commonly held misconception of the mosaic hypothesis is that it explains only unique adaptations in discrete structures, for example the residual variation in the volume of a given brain region that persists after accounting for overall brain size. If this were the case, in this strict form it might be misperceived to be consistent with traditional scalar views of brain evolution. However, the hypothesis is not that mosaic evolution simply acts upon individual components of the brain in a fully isolated manner, but rather that it shapes functionally connected systems as a coordinated whole (Figure 1D). Structures linked by important functional and anatomical connections covary in size, even after accounting for the effects of size change in other brain systems (the neocortex, diencephalon, mesencephalon, cerebellum, and medulla). Mosaic evolution is detectable even at this anatomically crude level, as structurally and functionally linked systems show significantly correlated volumetric evolution (Barton & Harvey, 2000). This is evident, for example, in the relationship between association cortex and the dorsal thalamus in primates, where coevolution is hypothesized to have resulted in disproportionate cortical expansion and associated functional specialization of novel thalamic subfields (Halley & Krubitzer, 2019), reflecting the presence of both concerted and mosaic processes. Additional support has emerged from studies of primate cortico-cerebellar systems where the neocortex, cerebellum, and intermediate nuclei display strongly correlated structural metrics ranging from increased neuron quantities through changes in overall volume (Barton & Harvey, 2000; Smaers et al., 2018; Whiting & Barton, 2003). Thus, it is reasonable to assume that the process of human brain evolution was not restricted to isolated patches of neocortex, but rather concerted functions mediated by more distributed brain networks, supporting the view that spatially distributed processes should serve as the target of empirical study and focus for theory development (Barton & Venditti, 2013; Hanson et al., 2014).

Brains evolved under a host of functional and structural constraints, having to accommodate multiple, often opposing requirements. Importantly, neither the proponents of concerted or mosaic evolution advocate for pure forms of their theories and it is widely acknowledged that both developmental and functional constraints influence the evolution of neural systems. Accordingly, it is perhaps best to consider mosaic evolution as occurring within the context of conserved developmental patterns. Certainly, there is evidence for the contribution of both mosaic and concerted evolution across species (Montgomery et al., 2016; Striedter, 2005) and much of the current debate is centered on the degree to which evolutionary forces may be constrained by conserved developmental cascades or functional relationships (Box 1).

Linked Regularities Across Brain Systems

One of the most pervasive assumptions about human brain evolution is that the vast expansion of the cerebral cortex occurred in isolation, removed from the rest of the brain. For instance as reflected in the overwhelming corticocentric focus in current neuroscience research on cognitive functions (Parvizi, 2009). Above, we highlighted both evolution theory and developmental data demonstrating that this belief is without foundation. Next, we detail examples of descent with modification across subcortical and cerebellar brain systems that have been traditionally miscast as phylogenetically ancient. In doing so we focus primarily on mammalian, in particular hominid, brain evolution (for a discussion of hominid relative to invertebrate, reptilian, and avian evolution see Striedter, 2006). Critically, the selected brain systems are not meant to be exhaustive, rather we hope to highlight the reciprocal connectivity between cortical and subcortical structures, detailing how the evolution of aspects of association cortex, including their

emergent psychological and cognitive functions, can be best understood in the context of distributed networks throughout the brain.

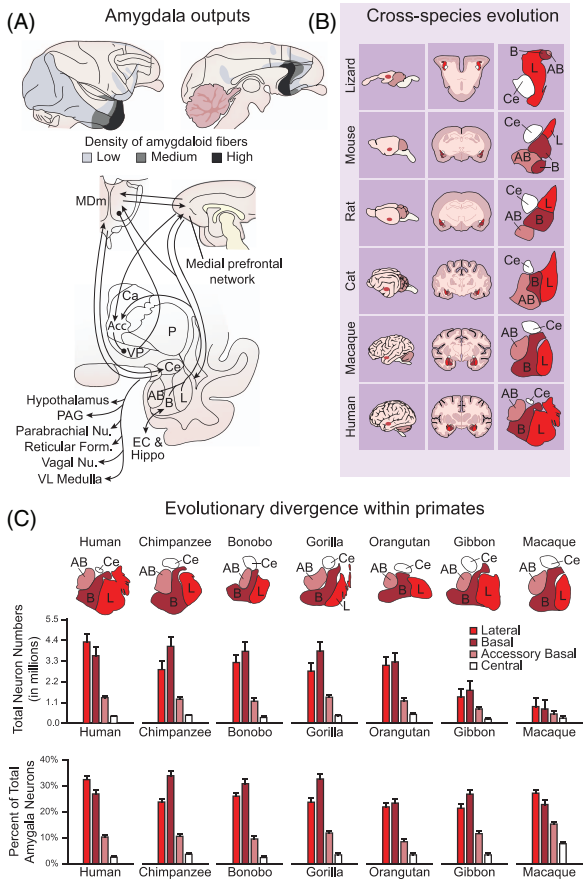
Amygdala

A shared property of all living creatures is the capacity to detect and respond to survival relevant threats and opportunities in the environment (LeDoux, 2012). The associated responses can encompass behaviors involved in defense, the preservation of energy and nutritional supplies, homeostatic processes including the regulation of body temperature and fluid balance, and reproductive drives. These survival mechanisms are present in single-cell organisms, such as bacteria, which have the capacity to retract from harmful chemicals and to accept chemicals that have nutritional value (Macnab & Koshland, 1972). However, in multicell organisms the processes allowing for the detection of, and coordinated response to, changes in the environment must be represented internally. Although the evolutionary conservation of core systems across species is often discussed in terms of somato/motor and sensory cortices, there is considerable evidence in amniote vertebrates for a broadly shared circuitry underlying survival functions such as defense responses to unconditioned and conditioned stimuli in the environment (LeDoux, 2012; Martínez-García et al., 2002). In mammals, a central component in this reactive machinery is the amygdala, a collection of nuclei situated in the temporal lobe.

Named for the almond shape of the basal nucleus (Burdach, 1822), the amygdala was first recognized as a distinct brain region by Karl Friedrich Burdach near the turn of the nineteenth century. The primate amygdaloid complex contains at least 13 separate nuclei, each with unique patterns of connectivity and function (Brabec et al., 2010; Pape & Paré, 2010; Sah et al., 2003; Figure 3). These subnuclei are commonly clustered into three primary divisions: (a) the deep-seated basolateral (BLA) complex composing of the lateral nucleus, basal nucleus, and accessory basal nucleus, (b) the superficial cortical nucleus and nucleus of the lateral olfactory tract, and lastly, (c) a centromedial group comprising the medial and central nuclei (CeA; Price, 1987; Sah et al., 2003; Tyszka & Pauli, 2016). In brief, multisensory information from the external environment is first received by the amygdala via projections to the lateral nucleus from both the thalamus and sensory cortices, it is transmitted to the BLA and the adjacent CeA. The BLA conveys information to cortical regions, although this process is heavily regulated by excitatory projections from cortex (Janak & Tye, 2015) and through associated intercalated cells which can gate basolateral–central amygdala impulse transmission (Milad & Quirk, 2012). The central nucleus then plays a key role in the modulation of autonomic and endocrine responses for a host of visceral functions (LeDoux, 2000, 2012). For instance, the expression of hard-wired, automatic, defensive reactions ranging from freezing behavior through hormonal release during Pavlovian fear conditioning in rodents critically depends on the CeA.

Avian, mammalian, and reptilian brains have diversified across hundreds of millions of years of expansion and independent evolution. Yet despite their varied evolutionary lineages, and heterogeneous embryological origin, the amygdala has been theorized to possess a common histochemical and connectomic organization, reflecting a functional system in the telencephalon of amniote vertebrates (Martínez-García et al., 2002). This supports the notion that, in some form, the structures within the

Figure 3
Evolution of the Amygdala Across Species



Note. (A) Schematic of amygdala circuits in a macaque involving the basal ganglia, cortex, hypothalamus, and brainstem. The aspects of cerebral cortex that receive axonal projections from the amygdala are displayed as dark, medium, and lightly shaded areas reflecting the density of amygdaloid fibers (adapted from "Neurocircuitry of mood disorders," by J. L. Price, and W. C. Drevets, 2010, Neuropsychopharmacology, *35*(1), pp. 192–216. https://dx.doi.org/10.1038/npp.2009.104). Acc = accumbens; AB = assessory basal; B = basal; Ca = caudate; Ce = central, EC = entorhinal cortex; form = formation; hippo = hippocampus; L = lateral; MDm = mediodorsal nucleus of the thalamus; Nu = nuclei; P = putamen; PAG = periaqueductal gray; VL = ventrolateral; VP = ventral pallidum. (B) Amygdala subnuclei vary across species contingent on the degree of connectivity with aspects of cortex and other noncortical structures. An enlarged image of the lateral, basal, accessory basal, and central subnuclei of the amygdala are displayed next to the corresponding coronal section from the brains of a lizard (proposed homologies from Martínez-García et al., 2002), mouse, rat, cat, macaque, and human. (C) Amygdala subnuclei vary across different primate species. Images of amygdala subnuclei are displayed from the brains of a human, chimpanzee, bonobo, gorilla, orangutan, gibbon, and macaque. Bar graphs display the average number amygdala neurons (top) and percent of total neurons (bottom) in lateral, basal, accessory basal, and central subnuclei of the amygdala across species (adapted from "Neuronal populations in the basolateral nuclei of the amygdala are differentially increased in humans compared with apes: A stereological study," by N. Barger, L. Stefanacci, C. M. Schumann, C. C. Sherwood, J. Annese, J. M. Allman, J. A. Buckwalter, P. R. Hof, and K. Semendeferi, 2012, *The Journal of Comparative Neurology*, *520*(13), pp. 3035–3054. https://dx.doi.org/10.1002/cne.23118). Error bars reflect standard error. Illustrations are not drawn to scale.

amygdaloid complex were present in the brain of ancestral *tetrapods* (Moreno & González, 2007). Importantly however, the presence of a common system does not suggest perfect evolutionary conservation. While only a limited set of volumetric analyses have targeted the evolution of the amygdala and other limbic structures (Armstrong, 1990; Barger et al., 2014; Barton et al., 2003; Stephan, 1983; Vilensky et al., 1982), a prominent theory postulates differential conservation across amygdala subdivisions (Moreno & González, 2007). Here, the cortico-medial region is classified as "evolutionarily primitive," given its connections with the olfactory system. Conversely, the BLA complex is considered to be "evolutionarily newer," as reflected in predominant coupling with the neocortex, in particular evolutionarily expanded aspects of medial prefrontal cortex and sensory association areas, as well as other subcortical structures like the hippocampus (Amaral & Price, 1984; Janak & Tye, 2015). Consistent with the presence of volumetric relationships linking functionally coupled brain structures, especially those sharing major axonal interconnections (Barton & Harvey, 2000), amygdala subnuclei vary in cellular composition across species contingent on the degree of connectivity with aspects of cortex, and as a function of ethological need. Although the cortical projections to the amygdala are similarly organized across rodents and primates (McDonald, 1998), both afferent (Supèr & Uylings, 2001) and efferent connections with neocortex (Amaral & Price, 1984; Catani et al., 2003; Iwai & Yukie, 1987) are markedly less prominent in rats (Krettek & Price, 1977). In line with the expansion of the fiber bundles and associated cortical territories across our evolutionary lineage, the subnuclei of the BLA are preferentially expanded in human and nonhuman primates (63%–69% of total amygdala volume) than in rats (Sprague-Dawley rats; 28% of volume; Chareyron et al., 2011). Conversely, the relative volume of the centromedial compartment is comparatively similar across species (Chareyron et al., 2011), possibly due to its principal connections with autonomic and brainstem circuits. Across primates, it has additionally been observed that the BLA is marked by differential expansion of its discrete subnuclei in humans, with the lateral nucleus undergoing a disproportionate increase in volume compared to the basal nucleus (Barger et al., 2007), suggesting that variability in volumetric reorganization may be influenced by interconnections with associated brain structures (Figure 3A).

Brains vary in characteristics other than size. Evolutionary changes cannot solely be defined by the study of any single morphologic metric in isolation (Healy & Rowe, 2007) and the volume of a structure does not explicitly reflect the distribution of associated cell types that are vital to the effective functioning of the nervous system, especially between remotely related species (Herculano-Houzel et al., 2007). As one example, comparative work examining neuron counts across human and nonhuman primates have revealed increased cellular density in humans, concentrated within the lateral nucleus of the amygdala (Barger et al., 2012) which shares dense connections with the regions of temporal cortex that are preferentially expanded, as compared to nonhuman primate species. Moreover, the proportion of neurons within the human lateral nucleus is almost 60%, far greater than estimated by allometric trends based on nonhuman primate data (Barger et al., 2012; Sherwood et al., 2012), making for a remarkable magnitude of expansion in this region of subcortex.

The evolutionary divergence of amygdala subnuclei in primates, relative to rodents, is coupled with the increased presence of neuropil suggesting heightened dendritic arborization and a greater number of glial cells relative to neurons (Chareyron et al., 2011; Rai et al., 2005). This cytoarchitectonic profile is further amplified in the human amygdala, when compared to nonhuman primates and rodents (Hamidi et al., 2004; Schumann & Amaral, 2005). Interestingly, this likely reflects a general feature of larger brains, for instance following the pattern of reduced neuron/glia ratio in the frontal cortices of primates (Friede & Van Houten, 1962; Sherwood et al., 2006) as well as Broca's area (Schenker et al., 2008), and the face area of the primary motor cortex (Sherwood et al., 2003). The proportional decrease in neuron density is functionally relevant and hypothesized to link with greater intrinsic and extrinsic interconnectivity (Chareyron et al., 2011). Critically, cell specific alterations and associated differences in receptor composition between the rodent and human brains may explain the lack of general neuromodulatory responses across species. For example, relative to rodents, primates display increased diversity of Gamma aminobutyric acid $(GABA)_A$ receptor subunit expression in the amygdala, potentially accounting for distinct reactions to GABAergic agents (Stefanits et al., 2018). Taken together, convergent evidence suggests greater complexity of amygdala circuitry in primates. More importantly, given the diversity of evolutionary patterns across a multitude of neural components, it is necessary to recognize that no single factor, such as local tissue volume, can fully account for brain evolution. Going beyond volumetric alterations to incorporate multiple levels of biological analyses will contribute toward a more comprehensive understanding of structural and cellular variation in brain architecture.

Cortico-Striato-Thalamic Circuits

The cerebral cortex is tiled with a complex mosaic of densely interconnected yet spatially distributed functional networks. Rather than operating in isolation, the cortex works in concert with subcortical structures including the basal ganglia and thalamus to orchestrate and execute affective, cognitive, and motivated motor behaviors (Alexander et al., 1986; Haber, 2016). Associated projections extend across the cerebral cortex, providing an anatomical skeleton that enables a hub-like exchange of information, with spatially distant nodes of distributed cortical networks converging to communicate with common basal ganglia and thalamic subnuclei. Broadly, in both human and nonhuman primates, cortico-striato-thalamic pathways can be thought of as comprising functional loops, through which associative, sensorimotor, and limbic information are processed in parallel (Alexander et al., 1986). While early work often focused on the prominent role of these pathways in motor functions, such as the planning, initiation, and execution of movement (Albin et al., 1989), their coordinated function also underpins cognitive and emotional processes including decision-making, goal-directed behavior, and reward-based learning (Haber, 2016). Given space constraints, we specifically focus on evidence for divergent evolution within two structures and their associated circuitries, namely, the striatum and the thalamus.

Striatum

The striatum serves as the main receptive center of the basal ganglia receiving wide-ranging connections that extend across cortex (Alexander et al., 1986; Haber & Knutson, 2010; Haber et al., 1995; Parent & Hazrati, 1995). Afferent projections to the striatum are derived from three major sources: (a) massive and topographic input from the cerebral cortex; (b) input from the thalamus; and (c) and input from the brain stem, principally from dopaminergic cells. Cortical and thalamic projections extend from anterior to posterior striatum in longitudinal zones (Selemon & Goldman-Rakic, 1985), with ventromedial striatum receiving projections primarily from limbic (ventral medial and orbital frontal) cortex, central striatum from association cortex, and dorsolateral striatum from sensory–motor-related areas (Alexander et al., 1986; Parent & Hazrati, 1995). More complex projection patterns, including interdigitated and overlapping terminal fields, are also present (Selemon & Goldman-Rakic, 1985). The striatum then sends ascending projections back to cortex via the pallidal complex, substantia nigra, and thalamus, forming a series of parallel, but overlapping circuits (Alexander et al., 1986; Haber et al., 1995, 2006; Haber & Knutson, 2010; Parent & Hazrati, 1995).

A wealth of studies have probed the functionalities of the striatum and its subdivisions, yet volumetric work directly examining the striatum in the context of human evolution remains scarce (but see, Stephan et al., 1981). All vertebrates possess a striatum, containing a nucleus accumbens, and globus pallidus or pallidum (Marín et al., 1998), and many organizational similarities exist within the basal ganglia of reptiles, birds, and mammals (Striedter, 2005). Yet, while broad cell groupings and connections are shared, the manner in which information flows through the basal ganglia is distinct across animal classes. In amphibians, for example, the striatum mainly receives sensory input from the dorsal thalamus, whereas in reptiles, the sensory input emerges from the dorsal ventricular ridge (Guirado et al., 2000), which shares putative homologies with mammalian cortex (Briscoe & Ragsdale, 2018). Conversely, as mammals diverged from the sauropsid lineage, the cortical sheet progressively became the primary target of basal ganglia circuitry (Reiner et al., 1998; Smeets et al., 2000). Put simply, the basal ganglia did not evolve as a single unit. One prominent example is the presence of multiple levels of compartmental organization (i.e., the striosome and matrix) that distinguishes mammalian striatum from the laminar cerebral cortex (Haber & Gdowski, 2004). Given the increase in the number of cortical neurons and development of cortico-striatal and corticofugal fibers enabling extensive inputs from the cortex, it has been proposed that this compartmentalization of the striatum, exclusive to mammals, emerged in parallel with the evolutionary expansion of the cortex (Hamasaki & Goto, 2019).

Broad spatial patterns of gene expression and associated cell-type distributions show strong correspondence within limbic and somato/motor cortico-striato-thalamic functional networks (Anderson et al., 2018, 2020), a profile of network associated expression that is evolutionarily conserved in human and nonhuman primates. However, ~9% of brain expressed genes have dissociable developmental expression trajectories in rhesus monkeys and humans (Bakken et al., 2016) and recent studies have turned to examining the molecular and cellular associates of evolutional variation along phylogenetic branches. Notably, a rare and molecularly heterogeneous class of interneurons expressing dopamine biosynthesis genes tyrosine hydroxylase (TH+) and DOPA (3,4-dihydroxyphenylalanine)decarboxylase (DDC) is enriched in both the human striatum and neocortex relative to nonhuman African apes (Sousa et al., 2017). These genes, encoding for neurotransmitter biosynthesis enzymes and receptors, are neuromodatory in nature and alterations in these expression patterns likely impact the overall function of the corresponding neural circuits. Relatedly, emerging evidence shows an abundance of a unique striatal interneuron type in primates without a homologous cell-type counterpart in the mouse striatum, cortex, thalamus, or hippocampus (Krienen et al., 2019). These interneurons account for an estimated 30% of interneurons in the human and the marmoset striatum, suggesting a clear evolutionary divergence in striatal cytoarchitecture between primates and rodents.

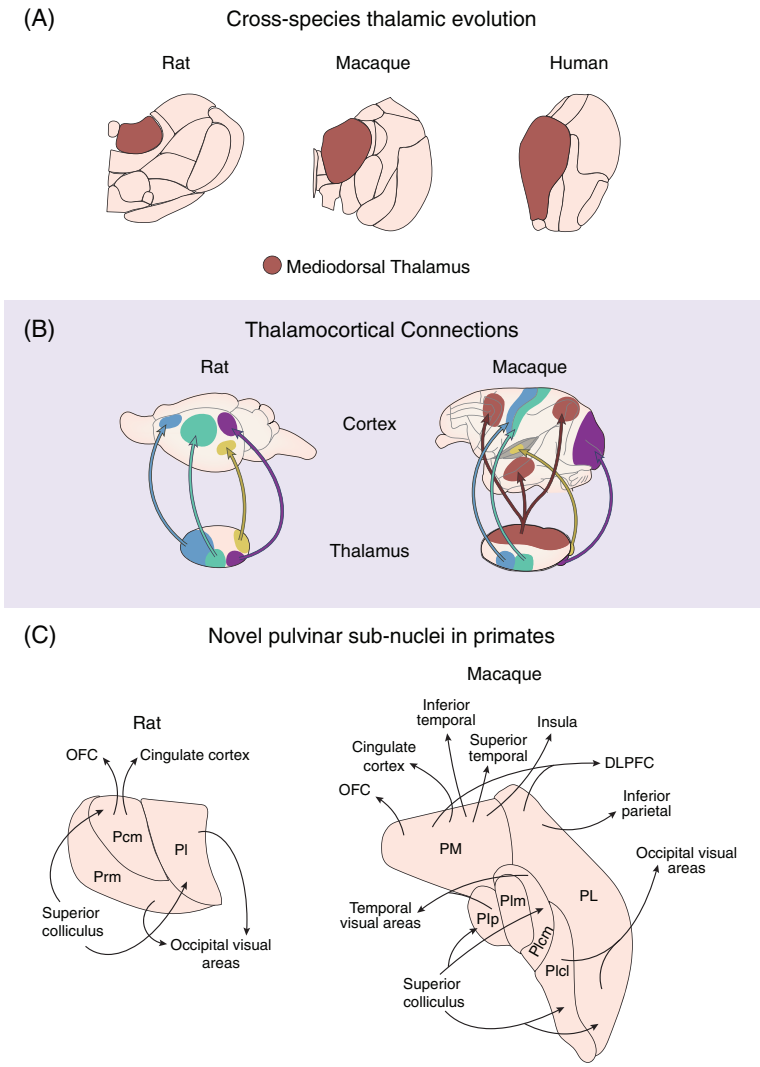
Thalamus

Classically regarded as the central sensory and motor relay station of the brain, the thalamus is a multinucleated structure that facilitates the reciprocal communication of signals between subcortical, cerebellar, and cortical regions through a distributed profile of anatomical connections (Schmahmann & Pandya, 2008; Theyel et al., 2010). Thalamic afferents sculpt both the boundaries and internal structure of emerging primary sensory areas across development (Pons et al., 1991). With the exception of olfaction, all sensory information passes through the thalamus prior to reaching the cortex, lending to the widespread view amongst psychologists of it as an evolutionarily primitive structure. Counter to this conceptualization, comparative work has illustrated the progressive differentiation and independent elaboration in thalamic nuclei along phylogenic branches (Butler, 2008; Halley & Krubitzer, 2019). Although rudimentary patterns of thalamocortical and corticocortical connections are present across species, possibly emerging from a common ancestor, more intricate connectivity motifs have arisen in conjunction with cortical expansion and supplementation of new thalamic fields in some lineages (Krubitzer & Disbrow, 2008). For instance, as reflected from early mammals such as monotremes, marsupials, and rodents through eutherian (placental) mammals and primates (Krubitzer, 2009; Krubitzer & Disbrow, 2008), or in the absence of a six-layered cortex and descending cortical input to the thalamus in reptiles (Pritz, 2015).

The composition of thalamic nuclei and potential for associated homologies across tetrapods is a matter of intense debate (Butler, 2008). The thalamic complex can be broadly divided into three primary clusters, of which the dorsal thalamus, including the mediodorsal nucleus, serves as a connectional hub to multiple-distributed cortical association areas (Figure 4; Selemon & Goldman-Rakic, 1988). Perhaps unsurprisingly, this region has experienced the greatest expansion in vertebrates, especially primates (Baldwin et al., 2017). This is evident across subnuclei of the dorsal thalamus, for example, the lateral geniculate nucleus and the pulvinar, which are particularly enlarged in primates who rely heavily on visual input (Barton, 1998, 2004; Grieve et al., 2000). Although vertebrate mammals broadly possess a pulvinar complex comprised of two to three subnuclei, in primates six or more additional subnuclei have been identified, which are not evident in rodents (Jones & Rubenstein, 2004; Kaas & Lyon, 2007). Intriguingly, cross-species gene expression data from mice and monkeys indicate that while homologous nuclei exhibit shared transcriptional profiles across

Figure 4

Evolution of the Thalamus and Thalamocortical Connections Across Species



Note. (A) The dorsomedial nucleus (red) of the thalamus is displayed in a rat, macaque, and human. Across human and nonhuman primates, association nuclei comprise the largest proportion of the thalamus (Krienen & Buckner, 2017). Here, mediodorsal thalamus reflects both medial magnocellular and lateral parvocellular nuclei. (B) Thalamocortical connections in rodents and macaques. Sensory thalamic nuclei project to primary sensory areas in the neocortex. In rodents, primary and secondary sensory areas occupy large swaths of the cortical sheet. In primates, association nuclei such as the dorsomedial nucleus send and receive projections from association regions distributed across the cortical mantle. Updated from Krienen and Buckner (2017). (C) Organization of the pulvinar and its subdivisions in rats and macaques (adapted from "The evolution and functions of nuclei of the visual pulvinar in primates," by M. K. L. Baldwin, P. Balaram, and J. H. Kaas, 2017, *The Journal of Comparative Neurology*, *525*(15), pp. 3207–3226. https://dx.doi.org/10.1002/cne.24272). In primates the pulvinar it is architecturally distinct from other mammals, possessing additional subdivisions relative to nonprimate species. In rats, nuclei displayed include the Pcm = caudal medial pulvinar; Pl = lateral pulvinar; Prm = rostral medial pulvinar. In primates, figure displays the PL = lateral pulvinar; Pip = posterior inferior; PIm = middle inferior; PIcm = central medial nuclei; PM = extending into portions of the medial pulvinar. Other divisions include the central lateral inferior, PIcl = a large central nucleus located anterolaterally within the inferior pulvinar; Pic = a more medial nucleus, PIm which extends dorsally into the regions of the superior or medial pulvinar as well as the lateral PI "shell" (PLs, PLs-l). OFC = orbital frontal cortex; DLPFC = dorsolateral prefrontal cortex. Illustrations are not drawn to scale.

species, primate-specific gene expression patterns are evident in the pulvinar (Jones & Rubenstein, 2004). Cortical connections with the pulvinar complex are topographically organized in partially overlapping zones (Shipp, 2003). Reflecting a diffuse map of the cortical sheet, these reciprocal cortico-pulvino-cortical circuits broadly mirror the organization of direct cortico-cortical connections.

Large-scale association networks share common thalamic input from the medial pulvinar nucleus, which is preferentially expanded in primates (Armstrong, 1981). This connectivity motif suggests that that association networks can be recruited through shared aspects of thalamus, highlighting a regulatory role for cortico-thalamic connections in the formation and maintenance of functional assemblies across the cortical sheet (Breakspear, 2017; Shipp, 2003). For instance, in humans (Garrett et al., 2018; Shine et al., 2019) and nonhuman primates (Baxter, 2013), medial thalamic nuclei play a key role modulating large-scale brain dynamics and distributed cortical processing during periods of increased cognitive complexity (Bell & Shine, 2016). Unfortunately, the processes through which thalamocortical connections may guide the development of association cortex remain to be determined. Suggesting the presence of a scheduled maturation in the development of thalamic projections to unimodal and association cortices, functional connectivity between the thalamus and somatomotor cortex is evident in human neonates, while connectivity between the thalamus and association networks does not emerge until the first year of life (Alcauter et al., 2014).

The patterning of a given patch of cortex, as indexed by distinct gene expression profiles, is intimately linked with its connectivity to thalamus, which in turn is influenced by associated constellations of projection neuron subtypes (Greig et al., 2013). In rodents, for example, *Lmo4* and *Bhlhb5* are expressed in postmitotic neurons and guide the input of sensory information from the thalamus and development of associated corticofugal pathways (Joshi et al., 2008; Kashani et al., 2006). Intriguingly, *Lmo4* may be further specialized in humans, as reflected in differential expression across the right and left hemispheres in human embryos, which likely influences aspects of left–right asymmetry (Sun et al., 2005). Further, there is evidence for a class of migratory neurons and associated migratory pathway exclusive to human primates (Letinic & Rakic, 2001). Here, retroviral labeling in slices of embryonic human brain tissue have revealed that populations of cells originating from the telencephalic ganglionic eminence migrate to become GABAergic interneurons in the dorsal thalamus, preferentially the medial dorsal and pulvinar nuclei. To date, the presence of this pathway has not been demonstrated in either rodent or nonhuman primates (Letinic & Rakic, 2001). These data raise the intriguing possibility that human thalamus recruits a supplementary class of neurons from the neighboring, mitotically-active ganglionic eminence in a bid to accommodate the increased axonal input from the rapidly enlarging neocortex (Buckner & Krienen, 2013; Rakic, 2009). As such, understanding the role of thalamic association nuclei in the protracted development and wiring of spatially removed aspects of cortex will be key to determining how areal identity is differentially acquired across species (Greig et al., 2013).

Cerebellum

At the turn of the twentieth century the cerebellum was conceptualized by Charles Sherrington to serve as the "head ganglion of the proprioceptive system" (Sherrington, 1952), reflecting its position atop the spinal cord. Consistent with this framing, until recently the cerebellum was primarily known for its prominent role in planning, execution, and regulation of motor actions, such as those related to eye-hand coordination in primates. All vertebrate brains have a cerebellum, with the possible exception of hagfish (Larsell & Jansen, 1967; Nieuwenhuys et al., 1998). While seminal work from the 1980s provided extensive evidence linking aspects of human cerebellum (i.e., dentate nucleus) to association cortex (Leiner et al., 1986), suggesting differential expansion in primates relative to other species (Leiner, 2010), the cerebellum has been traditionally considered to be evolutionarily conserved and primitive. More recently, this view has been challenged by a renewed focus on the role of cortico-cerebellar circuits in a range of cognitive functions (Buckner, 2013; Ramnani, 2006; Rapoport et al., 2000; Wagner et al., 2019), psychiatric conditions (Schmahmann et al., 2007), and clear evidence of cerebellar specialization across hominid evolution (Barton, 2012).

The cerebellum is primarily connected to the cerebral cortex through two polysynaptic circuits (Schmahmann & Pandya, 1997). Cortical inputs synapse in the pons and then cross over to the contralateral cerebellum. The output channel emerges from deep cerebellar nuclei, projecting first to the thalamus, and then back to cortex. Distinct cerebellar regions are connected to separate cortical territories, forming a complex yet topographically organized network structure. Broadly, with the exception of primary visual cortex, in humans the fraction of the cerebellum dedicated to each cortical network mirrors that network's spatial coverage across the cortical sheet (Buckner, 2013; Buckner et al., 2011). Reflecting a pattern of correlated evolution, as brain size increased from rodents through nonhuman and human primates, the cerebellum disproportionately increased in volume at a rate second only to the preferential scaling of cerebral cortex (Finlay & Darlington, 1995). These data are consistent with neuronal counting work demonstrating relatively fixed cellular scaling rules linking the numbers of neurons in the cerebellum and cerebrum across species (Herculano-Houzel, 2012). In line with the theory that the basal ganglia, the cerebellum and the cerebral cortex constitute an integrated functional network (Carta et al., 2019), the dentate nucleus in the cerebellum reflects a source of dense polysynaptic projections to the striatum (Bostan & Strick, 2018). While basal ganglia output to the thalamus targets different aspects than those from the cerebellum (Percheron et al., 1996), the two circuit motifs influence many of the same cortical territories.

Comparative volumetric analyses harnessing data from both extant and fossil species have identified a preferential increase in size of the cerebellum relative to the rest of the brain in apes compared to other mammalian lineages (Barton & Venditti, 2014; MacLeod et al., 2003; Miller et al., 2019; Smaers et al., 2018), in particular the lateral output nucleus of the cerebellum (the dentate), the deep cerebellar nuclei with the most profuse connections to the cortex (Leiner, 2010). In humans, relative to great apes, the ventral dentate, preferentially interconnected with prefrontal cortex, is disproportionately larger than the motor cortex linked dorsal dentate (Matano, 2001). Further, the fractions of cerebellar volume occupied by Crus I and Crus II, modules that are connected with the prefrontal cortex, are proportionally larger in humans compared to chimpanzees and capuchins (Balsters et al., 2010). Converging evidence from structures that project to Crus I and Crus II, such as the principal olive (Herrero et al., 2006), reveal selective enlargement in monkeys compared to cats (Bowman & Sladek,

1973) with a progressive trend of volumetric increases from prosimians to humans (Matano, 1992). The profile of volumetric expansion in humans, is also reflected in the segmentation of cerebral peduncle white matter fibers on the basis of their origins in the cerebral cortex (Ramnani et al., 2006). In macaques, for example, fibers linked with the cortical motor system occupy the greatest proportion of the cerebral peduncle, while a relatively small proportion of fibers are linked to prefrontal cortex. Conversely, in humans, the largest proportion of fibers are not from the cortical motor areas, but rather the prefrontal cortex.

Consistent with the observed volumetric differences across species, histological analyses of the cerebellum in humans and rodents across multiple stages of development have revealed the presence of divergent developmental patterns (Haldipur et al., 2019; Hashimoto & Hibi, 2012). Although the cerebellum is one of the first brain structures to differentiate in the neural tube, it is one of the last to mature after birth (Wang & Zoghbi, 2001; White & Sillitoe, 2013). This developmental period is prolonged in primates, relative to other mammals, extending from 3 weeks postnatal in mouse though 2 years in humans. The cerebellum emerges from the dorsal region of the posterior neural tube along the midbrain/hindbrain boundary. Two core germinal zones generate the cells that comprise the cerebellum. Cells that develop into the deep cerebellar nuclei and Purkinje cells arise from progenitors in the ventricular zone, while cerebellar granule neurons are derived from progenitors in the rhombic lip. The rhombic lip of the cerebellum persists over a prolonged developmental period in humans relative to rodents, after which it undergoes structural alterations to create a progenitor pool which is absent in other species, including nonhuman primates (Haldipur et al., 2019). Suggesting cerebellar reorganization is predicated on developmental patterning, the later developing lateral cerebellum displays an increased rate of evolutionary expansion in primates relative to earlier developing aspects of the medial cerebellum (Smaers et al., 2018).

The evolutionary divergence in cerebellar volumes and associated developmental processes are reflected across biological scales. For instance, across anthropoid primates, protein coding genes implicated in cerebellar development exhibit as much evidence for positive selection as those associated with cortical development (Harrison & Montgomery, 2017). Additionally, microRNAs (miRNAs) play a key role in the posttranscriptional regulation of gene expression (Cannell et al., 2008) and embryonic development (Ivey & Srivastava, 2015). Suggesting the fundament importance of miRNA in the process of developmental remodeling, most miRNA genes are highly conserved among primates in terms of both sequence and expression (Liang & Li, 2009). Yet, out of the hundreds of expressed miRNAs in primate brains, approximately ~11% diverged significantly between humans and chimpanzees and ~31% between human and macaque evolutionary lineages (Hu et al., 2011). One of these miRNAs, miR-184 is abundantly present in human prefrontal cortex and cerebellum, relative to nonhuman primates, and has been established to play an important role in neural stem cell proliferation (Liu et al., 2010). Although data conclusively establishing the contribution of phylogenetically recent patterns of miRNA regulation in human-specific phenotypic adaptations is lacking, this work exemplifies the presence of evolutionary divergence in miRNA mediated regulation of gene expression among humans, chimpanzees, and rhesus macaques across both cortex and cerebellum.

Toward a Comprehensive View of Brain Evolution

The principles that govern human brain evolution remain one of the most important and fascinating topics across the brain sciences. The preceding sections highlight select aspects of this vast literature, demonstrating the presence of species-specific patterns of evolution within both cortical and noncortical systems. Yet, despite this converging evidence, our field has largely neglected this body of work. Consistent with this incomplete conceptualization of brain evolution, much of the modern empirical work in psychology and neuroscience rests on a theoretical scaffolding exclusively focused on the cerebral cortex (Parvizi, 2009), suggesting that "human-specific" capacities such as higher-level cognition, consciousness, mentalizing, and morality are limited to, and fully dependent, upon associated areal expansion. The problematic effects of this theoretical bias are evident throughout the literature, contributing to the systemic mischaracterization of basic properties of brain functioning across species and the neglect of fundamental aspects of brain evolution in vertebrate mammals.

It is important to note that the arguments we raise are not meant to criticize research on the functional properties of the cortical sheet or theories regarding the importance of association cortex mediated functions for complex cognition. Certainly, there is overwhelming evidence in support of these positions. However, a primary goal of any field of scientific study is not simply to provide evidence in response to the questions we pose regarding structure of the world around us, but perhaps more fundamentally, to conduct informed research that is built upon the current state of our scientific understanding. As scientists, we do not operate in a historical vacuum. Rather, we inherit the arguments put forth by our intellectual predecessors and the theoretical scaffolding we use to construct our research programs is heavily biased by the echoes of their prior work. Here, the pervasive misrepresentation of human cognition and behavior as a competition between phylogenetically recent cortical territories and evolutionarily conserved subcortical and cerebellar systems is still widely held across the field and persistent enough to raise concerns. A fascinating and important topic, which is explored in final sections, is how to best correct for this existing cortical bias to incorporate our modern understanding of human evolution throughout the brain sciences.

The Road Ahead

Over the past several decades, convincing arguments have been made for a shift away from a largely cortical focus on the study of brain functions (Barton, 2012; Parvizi, 2009, 2012) and the development of biologically plausible theories of behavior constructed through careful consideration of our evolutionary history (Cisek, 2019; Holmes & Patrick, 2018; LeDoux, 2012). The field's current divergence from the empirical bedrock and limitations of the resulting theoretical approaches have been articulated many times, yet corticocentric views of human evolution and associated reductionist models of brain functioning remain remarkably prevalent. This cortical focus is further reinforced by existing methodologies in human neuroscience which have limited signal-to-noise ratio for examining subcortical contributions to cognition or a focus on surface-based analytic approaches. These collective observations illustrate several key points. First, discarding a scalar conceptualization of human brain evolution will have clear implications for the

interpretation of the cross-species work that is fundamental to progress in the neurosciences. Second, push–pull and dual process models centered on dichotomous or strictly hierarchical interactions linking cortical and noncortical systems are at best vague approximations that are loosely tied to actual brain biology. Third, it is imperative that we adopt a network-based perspective on brain evolution that incorporates both cortical and noncortical systems. However, doing so will require a broad field-wide shift from the study of the specialization or segregation of brain functions in isolated regions toward an analytic framework that targets functional integration (and improved sampling methods for subcortical and cerebellar functions), working to characterize how signals covary across spatially distinct territories throughout the brain (Sporns, 2014).

Interpretation of Cross-Species Work

The complex and distributed nature of brain evolution presents clear implications for the interpretation and the translation of cross-species research. Without question, the tenuous connections linking seemingly analogous behaviors across human and animal models have been subjected to pointed critiques over the years (e.g., Hyman, 2012), perhaps most frequently in the study of psychiatric illness where both mechanistic insights and novel therapeutic agents remain elusive (Box 2). Yet, a fundamental and often neglected facet in these debates is the tendency for researchers to carry forward the very same methodological and intellectual biases when working to translate neurobiological discoveries across species. Here, outside of cortex, homologies are often broadly assumed, and it is frequently taken for granted that one species can faithfully represent the neurobiological properties of another.

It is highly unlikely that organisms separated by millions of years of independent and divergent evolution will recapitulate all of the salient features of human behavior or share perfect correspondence with respect to the underlying biological cascades. While broad components of brain biology may be preserved across species, the principled evaluation of results from a given animal model is inextricably tied to the extent consistent functions are present within the targeted system or level of analyses. To properly link discoveries across model organisms and to then leverage this information to understand human brain functioning, one must consider each species' unique biology and ethological niche. As one example, the recent development of large-scale sequencing technologies, the emergence of whole-brain transcriptional atlases, and a cultural shift toward open access data have enabled the multiscale study of genetic, cellular, and molecular associates of human brain organization (Arnatkevičiūtė et al., 2019). Yet, with the possible exception of rare syndromes caused by highly penetrant mutations, the hurdles for translating genetic discoveries from animal models to humans remain daunting. Recent work in human genetics has established the polygenetic nature of common psychiatric illnesses (Anttila et al., 2018) and brain anatomy (Grasby et al., 2020), identifying hundreds of allelic variants that contribute to phenotypic variance. Although animal models are needed to dissect the associated discoveries, the presence of gene homologies between a given model organism and humans does not ensure the direct translation of results. In part, this is due to the vastly different impacts when comparing knockout/knockdown models in nonhuman animals with naturally occurring allelic variation in humans as well as inherent cross-species differences, such as levels of transcription, underlying cell distributions, and the distinct structure of gene regulatory networks.

As a field we have been repeatedly led astray by the anthropomorphization of animal behavior and the mistaken assumption of neurobiological homologies. Without doubt animal work is critical for understanding the fundamental rules that govern brain biology, driving progress in the study of core neurobiological mechanisms ranging from the molecular cascades that underpin brain development, cellular proliferation, and synapse formation through the basic properties of neural circuit function. However, as we work to translate these discoveries to humans, we cannot assume that subnuclei, underlying cellular composition, connectivity motifs, or associated computations are consistent across species with divergent *ethology*. Of note, these interpretive issues have been amplified by the dwindling diversity of species studied in modern neuroscience laboratories, as the field has converged on the use of a few model organisms (Yartsev, 2017). Fundamental to understanding the functional outcomes of evolutionary divergences across species is the study of a diverse set of animal models, pioneered by the field of neuroethology. Furthermore, interpretations must consider the similarities and differences in brain anatomy—for example, the presence of granular prefrontal cortex in the primate brain, but not in the rodent brain; flat versus sulcal brains (even among primate species); differences in sulcal and gyral subdivisions; and anatomical biases dictated by dominant sensory and motor faculties. Such anatomical differentiations support the use of a nonhuman primate bridge between research findings in rodents and humans for successful identification and translation of the underlying mechanisms of brain functioning. In the absence of meticulously cataloged discoveries from comparative research, we risk misinterpreting results that may be species-specific, for instance in human clinical trials for treatment and drug development.

Corticocentric Views on Evolution and Push–Pull/Dual Process Models

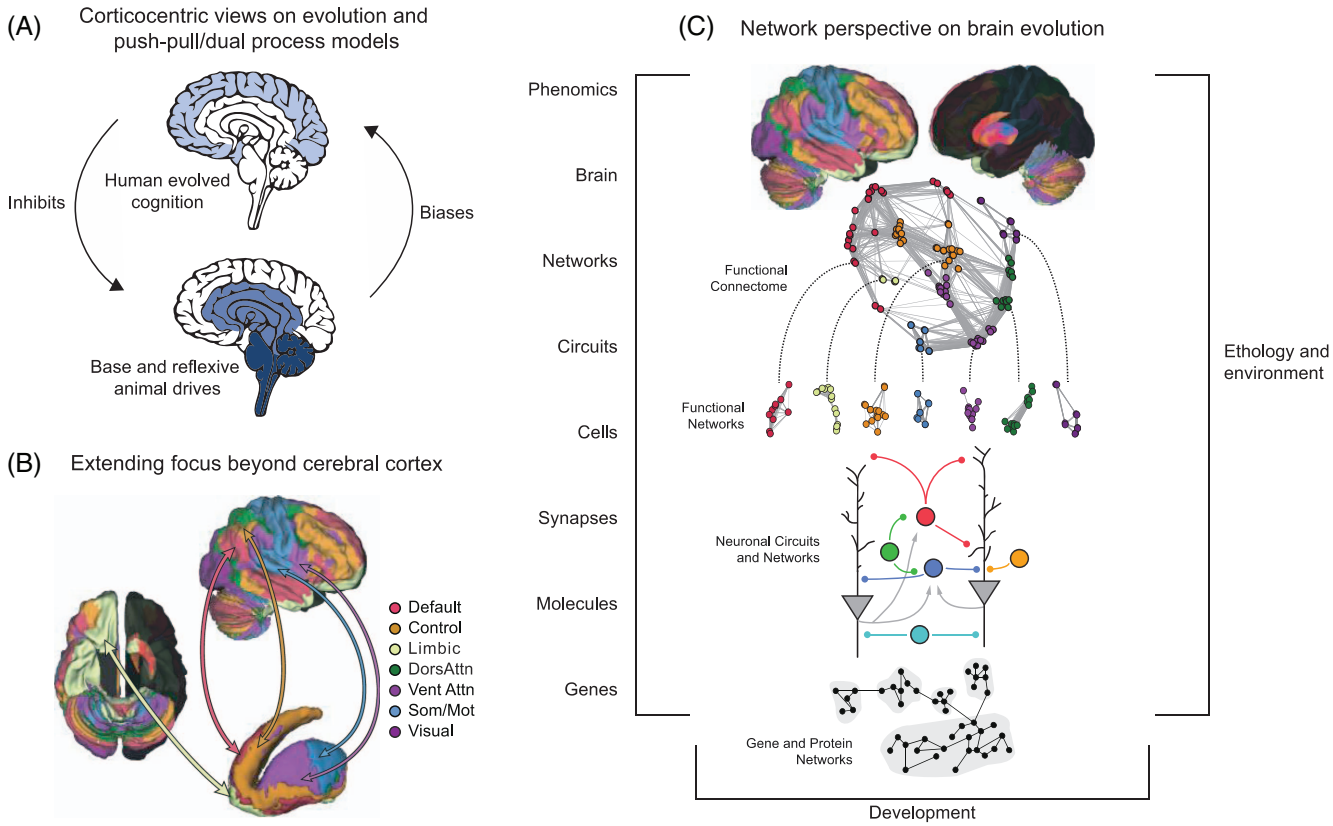
> When ideation rises into perception, there is, physically, a stronger discharge of the same nervous arrangements of the higher, so that the middle and then the lowest centers are overcome—J. Hughlings Jackson (Jackson, 1884).

The idea that human-specific complex cognitive abilities are exclusively linked with the rapid evolutionary expansion of association cortex has become a central tenet in modern psychology. This has led to a myopic focus on the study of cortex when examining "higher functions" of the brain or searching for human-specific capabilities and a nearly complete disregard of relevant subcortical processes (Parvizi, 2009). This theoretical stance is in sharp contrast to the clear evidence of pervasive brain-wide evolution and the presence of distributed and mutually embedded functional circuitry linking cortical and noncortical territories (Miller & Clark, 2018; Pessoa, 2014). However, this dichotomous view of brain function is still widely held, and likely as a direct consequence, the literature is littered with push–pull and dual process models hypothesizing that disinhibited behavior emerges when maladaptive prefrontal functioning releases subcortical regions to respond in their innate way (Figure 5A).

The theorized division of labor distinguishing phylogenetically recent cortical territories from evolutionary stagnant subcortical and

Figure 5

Toward a Network Perspective on Brain Evolution and Functioning



Note. (A) Schematic representation of a biologically implausible push–pull or dual process model for studying brain functioning. Here, cognition and behavior is conceptualized as a competition between deliberative "higher-level" executive functioning and innate/reflexive noncortical systems. (B) The integrated network architecture of cortex, cerebellum, and striatum is displayed on the lateral and ventral surfaces of the left hemisphere/cerebellum and striatum (adapted from "Gene expression links functional networks across cortex and striatum," by K. M. Anderson, F. M. Krienen, E. Y. Choi, J. M. Reinen, B. T. T. Yeo, and A. J. Holmes, 2018, *Nature Communications*, *9*(1), Article 1428. https://dx.doi.org/10.1038/s41467-018-03811-x). Here, a complex connectional motif is evident, reflecting the combination of signals across spatially distant cortical and noncortical territories. Network solution from Yeo et al. (2011). DorsAttn = dorsal attention; Som/Mot = somato/motor; VentAttn = ventral attention and salience; Control = frontoparietal control network. (C) Schematic representations of the network structure across biological levels, from genetic and cellular processes through large-scale functional systems. At the base of the figure, gene and protein networks are depicted as a graph in which individual processes are shown as nodes and process–process interactions as edges connecting the nodes. From there cellular circuit motifs emerge, up through the formation and maintenance of large-scale networks distributed in an interdigitated manner throughout the brain (adapted from "The myth of optimality in clinical neuroscience," by A. J. Holmes and L. M. Patrick, 2018, *Trends in Cognitive Sciences*, *22*(3), pp. 241–257. https://dx.doi.org/10.1016/j.tics.2017.12.006). Readers should note that feedforward/feedback relations also link across the levels, while associated processes vary as a function of developmental stage and interactions with the environment.

cerebellar regions has been present since the earliest circuit models of cognition and emotion (MacLean, 1990; Papez, 1937). A view of brain organization as a hierarchical and dichotomous order between cortical and subcortical structures that harkens back to classic Victorian notions of disinhibition advocated by John Hughlings-Jackson (Jackson, 1884; Parvizi, 2012) and dual process theory as proposed by William James (James, 1890), and still remains firmly entrenched in our modern scientific discourse. This is evident, for instance, in theories regarding natural instincts versus rational thought and free will, affect versus cognition, model-based versus model-free learning, and reflexive versus deliberate responding. Nearly ubiquitous to these models is a dichotomy between automatic versus controlled processes, between cortical and noncortical functions. However, such a clean separation between "higher" and "lower" functions is artificial, outside the primary sensory systems initial transmission of incoming sensory information. Simply put, one processing stage does not exist without the other (Parvizi, 2009) and associated behaviors emerge through the coordinated function of an integrated system (Parvizi, 2012). The continued and pervasive use of push–pull models is problematic, not just because this framework mischaracterizes the functional organization of the human brain, but chiefly because they perpetuate a binary view of human nature. One where human expanded aspects of cortex wage an eternal struggle against base, reflexive, and innate animalistic drives from primitive noncortical systems.

Critically, it is difficult to disentangle programs of research that incorporate these dichotomous and hierarchical models as simplified, although biologically implausible, heuristics for understanding

brain functions from research that takes such two system theories at face value. This is evident in clinical psychology and psychiatry, where cortical disinhibition is frequently theorized to account for pathological behavior that is contextually inappropriate or in cognitive neuroscience where results outside of cortex are often ignored or only mentioned in passing. Research in both neuroscience and psychology has been ill-served by the dichotomization of concepts like affect and cognition into distinct and competing processes. At times, successful model development may be driven by observed relationships in the data, rather than integration of underlying biological knowledge. However, the observations we make are limited by breadth of our existing scientific paradigms and associated questions we pose. Here, more often than not, modern dual process models of human cognition and behavior still suffer from variable degrees of corticocentric myopia, both in the empirical literature they draw from as well as their theoretical underpinnings. A complementary theoretical approach, which we advocate for here, involves the construction of network-based models that use a priori knowledge of brain evolution to gain insight into species-specific differences.

The careful consideration of evolutionary divergences across species is critical given that a precise definition of "higher-level" human cognition remains unclear and an increasing number of studies have revealed neural correlates of associated functions outside the cortex. In vertebrates there is a common presence of large-scale connectional systems involving the midbrain, hypothalamus, thalamus, basal ganglia, and amygdala (Pessoa et al., 2019). Here, the process of evolution has resulted in a complex functional tapestry, where new circuits are continually woven into existing systems producing complex interactive relationships that stretch across the entire brain (Miller & Clark, 2018). The association and integration of information processing are basic features of the vertebrate brain and the large degree of crosstalk between cortical and noncortical systems suggests that human cognition and behavior cannot be cleanly carved into two distinct systems (Pessoa et al., 2019; Rmus et al., 2021). Work in rodents, as one example, has revealed causal functions of subcortical areas, such as the ventral tegmental area, amygdala, and thalamus, in regulating seemingly complex behaviors involving decision-making and social interactions (Anderson, 2016; Chen & Hong, 2018; Proulx et al., 2014; Russo & Nestler, 2013). Moreover, though fewer in number, existing studies in nonhuman primates demonstrate a core role of subcortical areas, such as the ventral tegmental area, striatum, and amygdala, in behaviors requiring learning and decision-making (Baxter & Murray, 2002; Chang et al., 2013; Gangopadhyay et al., 2021; Schultz, 1997). The role of subcortical areas in cognitive functions is certainly not limited to nonhuman animals. For instance, recent work has revealed increased activation of intermediate and rostral portions of lateral and ventrolateral periaqueductal gray (PAG) columns in humans is modulated by cognitive load (Kragel et al., 2019). Further, there is compelling evidence that the human cerebellum is engaged in a wide array cognitive tasks (King et al., 2019). These data suggest that executive functioning and cognitive control are not solely mediated by activity in the cortex, but that noncortical structures traditionally studied through the lens of autonomic regulation also play a crucial role in "higher-order" processes.

Above we illustrated how a community of scientists can be biased by historical arguments to rely on deceptively simple models that distort our understanding of brain organization. Recent empirical work and converging evidence across our evolutionary lineage calls for a more nuanced conceptualization of human brain functioning. These data have important implications for research on the functional architecture of human and nonhuman animal brains. Given strong evidence for the universal influence of evolutionary forces throughout the brain and the reciprocal anatomical and functional relationships linking cortical and noncortical structures, theoretical and analytic approaches that consider the brain's complex network structure are clearly warranted (Bassett et al., 2018) and likely closer to the functional principles that guide brain evolution, development, and organization.

Network Perspective on Brain Evolution and Associated Theory Development

One key conclusion from the voluminous literature reviewed above is that cortical, subcortical, and cerebellar systems are not wholly distinct in terms of evolution, development, or function but instead their interactions and relationships are deeply embedded in the organizational fabric of the brain. Evolution has imbued vertebrate brains with a complex connectional motif, affording the combination of signals across spatially distant cortical and noncortical territories. The distributed and tightly interdigitated nature of this functional architecture motivates programs of research that consider the brain as a multiscale system composed of complex networks of cells, local circuits, subnuclei, and cortical patches encompassed within broader large-scale network ensembles. The study of the association and integration of information cascading through this multiscale neuronal architecture can provide information on homologous or divergent aspects of neurobiology across species that is inaccessible through classic approaches that focus on single regions or isolated patches of cortex (Pessoa et al., 2019).

The idea that connections among cells, circuits, and larger networks are crucial for brain function has been a central thread in modern neuroscience, this theoretical framework has developed in parallel with classic lesion or localized methods for examining brain functions. Locationist perspectives assume that a given behavior or cognitive process will be supported through distinct biological mechanisms, reflected as a sort of natural kind that resides within a specific brain region. Conversely, network neuroscience adopts methods and analytic approaches that examine multiple sets of elements within a functional system or "network" (Bassett et al., 2018; Sporns, 2014). Brain networks can be examined across multiple scales, from cytoarchitectonic, metabolic, or gene regulatory cascades through the broad functional patterns that link across patches of cortex and subcortical nuclei (Figure 5). Critically, network-based methods that examine cognitive architectures comprised of multiple components should be viewed as a complement to traditional locationist approaches that focus on the discrete elements of a neurobiological system. As one example, functional Magnetic resonance imaging (MRI) based parcellation approaches have been widely utilized to study the spatial organization of large-scale functional networks through the joint analyses of data across vast numbers of individuals (Eickhoff et al., 2018). The topography of these population-based network solutions is closely coupled to cognitive function, and a strong correspondence has been observed linking the spatial structure of intrinsic functional connectivity MRI (fcMRI) and extrinsic (task-evoked) networks of the human brain (Cole et al., 2014; Crossley et al., 2013). More recently, methods

from network science are expanding in new directions, going beyond descriptive accounts of network topology and toward the study of brain dynamics, phenotypic prediction, the impact of focal perturbations on network structure, and research that spans diverse neurobiological systems (e.g., gene expression, cytoarchitecture, and in vivo brain functioning; Bassett & Sporns, 2017; Bassett et al., 2018).

The methods of network neuroscience provide a principled way to synthesize data across biological scales, integrating diverse aspects of brain functioning from both cortical and noncortical systems. However, to date, when applied in humans these approaches have primarily focused on the cerebral cortex. Although there are some notable exceptions (Buckner et al., 2011; Choi et al., 2012; Hwang et al., 2017; Ji et al., 2019; Tian et al., 2020), in instances where subcortical structures are included in network-based analyses they are often done so in an anatomically coarse manner that lacks the granularity necessary to examine discrete subnuclei, while the cerebellum is for the most part entirely neglected. This is compounded by the fact that many modern in vivo methods for interrogating brain functions in humans are not well suited for the study of subcortical structures (e.g., electroencephalography or magnetoencephalography, near-infrared spectroscopy, optical imaging, and transcranial magnetic stimulation). Even in MRI, the current dominant approach for studying brain functioning in humans, data processing pipelines are heavily biased to cortex as evident in the use of corticocentric methods to place individuals in a standard stereotaxic, or common, physical space for further analyses and a limited focus on the detailed examination of the multinucleated subcortical structures.

At present, only a limited subset of published reports have incorporated noncortical regions into large-scale network descriptions of human brain functioning and behavior. Indeed, the lack of research focusing on unified whole-brain network parcellations has contributed to a fundamental knowledge gap in the field, particularly when considering the study of "human specific" behaviors or the comparison of network properties across species. The inclusion of noncortical projection systems into analyses of network-level connectivity would dramatically alter our models of the brain's computational landscape (Pessoa, 2014), shifting it to more accurately reflect the underlying biological constraints. It is clear that data from whole brain network-level approaches will be needed to complement and complete our current corticocentric understanding of the evolution of the human nervous system. To accurately model how information flows and is integrated across a spatially distributed network architecture we need to establish the topographic organization of the brain, taking into account our current understanding of evolutionary divergences and homologies across species. Ultimately, there are likely a host of useful spatial resolutions depending on the particular scientific question. Here, a multiscale whole-brain approach may add to our understanding of the network mechanisms that underpin brain structure and function in the context of human brain evolution.

Conclusion (Lessons Learned)

This review provides a conceptual framework and call to shift our research agenda away from a largely cortical focus on the study of human brain functions. A deeper knowledge of the principles of evolution gives us insight into the role of the brain in shaping human behavior and cognition, providing the opportunity to study how species-specific neurobiological changes may have emerged across our lineage. The literature presented here suggests the clear need to move beyond the widely held conceptualization of human cognition and behavior as a competition that pits phylogenetically recent cortical territories against evolutionarily ancient subcortical and cerebellar systems. The focus on the neocortex as the principal area of change in human and nonhuman primate brain evolution has been excessive and may have been largely misguided, emphasizing the need for ethologically mindful comparative studies to go beyond the analysis of individual patches of cortex. Rather, the field should replace this "corticocentric myopia" (Parvizi, 2009) with an integrated view that incorporates the evolution of developmental cascades, cellular composition, neuroanatomical structure, and distributed functional networks/systems throughout the brain (Whiting & Barton, 2003).

Box 1
Brain Evolution and Developmental Patterns

It is not sensible to argue that all of biological variation can be explained solely in terms of natural selection down to the individual component parts that make up a living whole. Populations evolve in a manner that is subject to other principles or laws, including developmental and/or physical constraints (Gould & Lewontin, 1979; Striedter, 2006). Central to our understanding of neurodevelopment is the radial unit hypothesis, which postulates that cortical formation begins when proliferating cells in the ventricular zone of the telencephalon undergo a series of symmetrical divisions, creating a thin sheet of radial columns (Rakic, 2009). Over the course of primate evolution increasing cell divisions and/or survival rate within the ventricular zone is theorized to have contributed to the enlargement of the cortical mantle. The heightened number of radial columns allows for swaths of the developing cortical plate to untether from the molecular gradients and early activity cascades that bias the formation of sensory hierarchies (Buckner & Krienen, 2013), providing the opportunity for novel connectivity patterns to emerge. Critically however, noncortical inputs are important drivers of cortical arealization. For instance, a pathway has evolved in human primates through which neurons from the telencephalic ganglionic eminence migrate to form interneurons in the medial dorsal thalamus and pulvinar (Letinic & Rakic, 2001). Suggesting that the maturation of the embryonic protomap into its adult form may be only accomplished in tandem with specific thalamocortical innervations (Krienen & Buckner, 2017; O'Leary & Sahara, 2008), thalamic inputs have been found to regulate the specialization of cortical areas (Antón-Bolaños et al., 2019; Lokmane et al., 2013). Of note, the presence of shared progenitor pools are not specific to thalamus, both cortical and striatal interneurons possess a common developmental origin, arising from progenitor cells within the ventral forebrain (Marín & Rubenstein, 2003). Critically, the question of how and when spatially segregated brain systems come to wire to together remains unresolved, as does the role of primate specific evolutionary expansion and reorganization in associated subcortical nuclei.

Box 2

Evolution and Psychiatric Illness

A comprehensive understanding of human brain evolution can inform researchers of the potential mechanisms that may underlie psychiatric illness (genetic mutation, molecular cascade, environmental change, developmental process, etc.). Indeed, the predominant theory of the biological roots of illness lies in the emergence of intrinsic vulnerabilities within the human mind that emerged as building blocks of adaptive behavioral and cognitive function across our evolutionary lineage. Here, as with the broader neurosciences, much of the focus has been on association cortex, both historically as exemplified in the contributions of Elmer Southard (Southard, 1915), Aloysius Alzheimer (Alzheimer, 1913), and others, through the present day (Goodkind et al., 2015). Harkening back to Victorian era notions of disinhibition (Parvizi, 2009, 2012), nearly ubiquitous in modern scientific discourse is the theorized role of association cortex in directing subcortical responses, for instance the disrupted regulation of reward circuits in substance use disorders (Volkow et al., 2013) or the reflexive affective processes in anxiety and depression (Mayberg, 1997). However, the brain evolved and functions as an integrated system and the hypothesized hard separation between cortical and noncortical functions exists only in theory. Indeed, one would expect that the functions of a given patch of cortex would be inextricably tied to the connectivity with, or functioning of, associated noncortical structures. Along these lines, there is mounting evidence of impaired cortico-thalamic (Anticevic et al., 2015; Peters et al., 2016), somatosensory-motor (Kebets et al., 2019), and cerebellar functioning (Phillips et al., 2015) in patient populations. This converging literature motivates a shift from the current focus on specific structures, areas of cortex, or hierarchical relationships linking association cortex with noncortical or unimodal systems to a framework that is consistent with general evolutionary principles. Here, the field would benefit from research that seek to understand the dynamics of interregional coordination and integration within large-scale systems distributed throughout the brain and their associations with clinical presentation (Pessoa et al., 2019).

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Appendix

Glossary of Terms

Allometric Scaling

The relationship between the size of a given structure and the size of the body as a whole. Allometric equations take the general form $Y = aM^b$, where Y is biological phenotype, M is a measure of body size, and b is a scaling exponent. In allometric analyses, data are often plotted in logarithmic form so that many body sizes/species can be plotted on a single graph. This can differ from isometric scaling, where organisms maintain geometric similarity as they change in size. For instance, the relationship linking the surface area and mass of an individual's body.

Amniote

An animal whose embryo develops inside of an egg equipped with an amnion. Amniotes include synapsids (mammals) and sauropsids (reptiles and birds), as well as their evolutionary ancestors, back though their divergence from amphibians.

Anthropocentric

The view that humans are separate from nature and the central, or most important, entities in existence.

Ethology

The scientific study of animal behavior, typically under natural conditions. The treatment of behavior as an evolutionarily adaptive trait.

Hominin

A taxonomic tribe of the subfamily Homininae that includes the genus Homo (humans), the now extinct subtribe Australopithecina, the subtribe Panina, which includes common chimpanzees and bonobos, but excludes the genus Gorilla (gorillas). Homininae, or African hominids, includes two taxomonic tribes, the Hominin and Gorilla tribes.

Homology

The term homology can have a pluralistic definition depending on an author's field of study. Here, we use it to mean similarity of a given phenotype's structure, physiology, or development across different species based upon their descent from a common evolutionary ancestor.

Neocortex

Derived from the Latin "cortex," meaning bark or rind, and the Greek "neo," or new. The neocortex, or six-layered cortex, consists of the neuronal cell bodies and fibers that surround the myelinated axons in the cerebrum.

Sauropsids

A clade of amniotes, broadly equivalent to the class Reptilia ("lizard faces"), includes Aves (birds). Sauropsida is the sister taxon to Synapsida.

Scala Naturae

A concept derived from Aristotle and other Greek philosophers, expanded upon during the Middle Ages in Europe. Here, all matter and life is organized in a strict hierarchy. The chain begins with God and descends through angles, humans, animals, plants, and minerals. The higher a being is on the chain, the more attributes it is thought to possess. This includes all the attributes of the beings below it.

Synapsids

A group of animals that includes mammals and animals more closely related to mammals than to members of the amniote clade, such as reptile and birds. The nonmammalian synapsids are often referred to as stem mammals or protomammals.

Tetrapods

Defined in cladistics as the nearest common ancestor of all living amphibians and amniotes, includes surviving and extinct amphibians, reptiles, birds, and mammals.

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