Evolutionary and Developmental Issues in Cognitive Neuroscience

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Glossary

Diffusion tensor imaging (DTI) – A magnetic resonance imaging (MRI) technique that measures water diffusion through biological tissues. This noninvasive method can be used to visualize white matter tracts in the brain.

MRI morphometry – An analytic approach to structural MRI data analysis that enables the comparison of the size and shape of specific brain structures, for example, at different ages or across different species.

Ontogeny – The development of an organism from the fertilized egg to its mature form.

Phylogeny – The evolutionary development of a species.

Theory of mind – The ability to attribute mental states – beliefs, intents, desires, pretending, knowledge, and so on – to oneself and others, and to understand that others have beliefs, desires, and intentions that are different from one's own.

Most cognitive neuroscience research to date has focused on the relationships between the brain and behavior in the human adult. We can gain additional insights into these relationships by considering how this finely tuned organ came to be, both from an evolutionary and a developmental perspective.

The tradition of linking evolution and development together dates back to 1866 to the well-known 'biogenetic law' of Ernst Haeckel: "Ontogeny recapitulates phylogeny." For Haeckel, ontogeny and phylogeny were two aspects of the same process. The biogenetic law was discredited long ago as a general principle of biology. It assumes that evolution acts only at the endpoints – that is, adult stages – of development, whereas evolution can, and does, modify organisms at every stage of development. The process of development is not merely a series of architectural changes that are required to yield the mature organism: the intervening organizations have to be functionally viable in the social and ecological contexts in which immature animals find themselves.

There are, however, other reasons to consider development and evolution together. One reason is that evolutionary changes are modifications of developmental programs – a concept explored in evolutionary developmental biology, a field commonly known as 'evo-devo.'

Saying that evolution involves changes in the genome really does not tell us much by itself. To make meaningful contact with the organism and its life history, it is important to consider genetic changes in the context of development. For example, building a bigger brain could entail adding more neurons or, alternatively, increasing connectivity and synapse number while maintaining neuron number. We know that all neocortical neurons are generated early in development. Thus, increasing brain size by adding more neurons would require changing gene activity early in development. Tinkering with the genome at this early stage could have a variety of secondary effects, both positive and negative, such as extending the life span. In contrast, enlarging the brain by increasing synapse number could be effected by changing the actions of genes expressed later in development, even as late as adulthood. There may be a bias toward modifications late in development, given that modifications early in development could have deleterious effects that extend across the rest of the life span.

Second, both developmental and evolutionary researchers explore the relationship between variations in brain structure and variations in brain function. Stemming directly from Darwin's doctrine of continuity, there is a strong tradition in the neurosciences and psychology that the brain and mind of humans differ only quantitatively from those of our relatives. As Darwin put it, the differences are matters of degree and not of kind. Darwin's doctrine of continuity does not fit well with our modern understanding of evolutionary change, but it remains popular – in part because it serves as a rationale for viewing model animals as simplified versions of human beings. Yet, humans are not simply macaque monkeys with additional components or layers of complexity – macaques and humans are both specialized endpoints of evolutionary history, each having changed in particular ways since their divergence about 25 million years ago. Increasingly, experimental psychologists are embracing significant species differences in psychological organization, although there is still a lack of consensus about the nature of human cognitive specializations, as discussed below.

Similarly, in development, children are often – but overly simplistically – viewed as simplified versions of adults. Infants exhibit certain behaviors that are adaptive

at their stage of life, but that are no longer needed later in life, such as grasping and suckling reflexes. Infants also exhibit cognitive capacities that adults do not; they can discriminate subtle phonetic differences, even between sounds that are not used to distinguish between words in their native language – a capacity that allows them to learn language readily. Adolescents, too, are not merely adults with diminished capacity. They exhibit, strongly, reward-driven behavior and high levels of novelty seeking – behaviors that maximize the potential for learning. Such behaviors are associated with tangible risks, however, and after a period of exploration and learning during the teen years, it might make sense to curb these exploratory tendencies to a certain extent.

In summary, comparative studies show that while there are many similarities between humans and other animals, in particular other primates – which is expected because we do share common ancestors – there are also important differences. These differences are manifested not only in the highest-order cognitive and behavioral functions, but also at a variety of levels of organization and a variety of points in development. On the flipside, developmental studies do provide evidence of emerging levels of complexity from infancy to adulthood, but at each stage of development we are adapted to our particular circumstances.

Below, we provide a brief overview of current topics in evolution and development that relate to higher-order cognitive functions and the brain regions that support them, given that these are the functions for which the cross-species and developmental differences are most salient. We first consider ideas about the evolution and development of behavior, then brain anatomy, and finally brain function.

Comparative and Developmental Psychology

There have been several efforts to characterize the nature of the differences between humans and the great apes – chimpanzees, bonobos, gorillas, and orangutans – the animals most closely related to us. Tomasello and colleagues, for example, see the differences mainly in terms of the elaboration of social cognition in humans, as compared to cognition related to the physical world. Povinelli and colleagues, on the other hand, see a deeper distinction involving capacities for abstract representation that cuts across the social/physical distinction. For the latter view, what is uniquely human is the emergence, during childhood, of symbolic systems, including language as well as the ability to represent unseen causes and abstract categories.

The idea that language is a human specialization is no longer highly controversial. Additionally, humans, but not nonhuman primates, understand physical interactions of objects in terms of abstract or unobservable causes or relations – a way of understanding the world known as 'folk physics.' Similarly, humans understand the knowledge states of other individuals – so-called 'theory of mind' – which is another example of how we understand the world in terms of abstract causes or relations. Povinelli and colleagues have argued that chimpanzees (1) do not understand that other individuals – or they themselves – possess minds and (2) do not understand how minds work. Thus, for example, chimpanzees do not understand that one has to have certain kinds of perceptual experiences to possess certain kinds of knowledge. In contrast, starting around 4 years of age, children performing the Sally–Anne test begin to demonstrate understanding of what knowledge others have access to.

Humans have the ability to extract abstract relationships between multiple mental representations. This ability, referred to as 'relational reasoning,' allows us to represent higher-order relationships between sets of mental representations. Analogical reasoning is a form of relational reasoning that involves abstracting a relationship between familiar items and applying it to novel representations. Forming analogies allows us to determine general principles from specific examples, and to establish connections between previously unrelated pieces of information. Analogical thought is an important means by which cognition develops. For example, children use analogies to learn new words and concepts by association with previously learned information. Penn, Holyoak, and Povinelli have argued that nonhuman primates lack the ability to integrate multiple mental relations, an ability that is considered a key component of human cognition.

Comparative and Developmental Neuroscience

Comparative Neuroanatomy

Human brain evolution is remarkably poorly understood, although it is beginning to yield its secrets to modern comparative studies. It is clear that evolution affected the human brain at many levels of organization, from the molecular biology of neurons to patterns of long-range cortico-cortical connectivity. Moreover, human evolutionary specializations are not limited to brain regions that are usually associated with higher-order cognitive functions. There are, for example, differences in the morphology and biochemistry of neurons in anterior cingulate area 24, a limbic region implicated in the affective regulation of behavior. Additionally, there are cellular and modular organizations of primary visual cortex that may be reflected in changes in the response properties of higher-order visual cortex. Thus, human specializations

are observed at the cellular level even in terms of basic visual processing.

Brain Size and Proportions of Lobes and Regions

The most conspicuous and well-known specialization of the human brain, however, is its remarkable size. Our closest relatives are chimpanzees, and average adult-human-body size is only slightly larger than that of a chimpanzee; yet, our brains are about 3 times larger: chimpanzee brains average a little less than 400 cc, while human brains average approximately 1400 cc. Most of the difference reflects an expansion of the neocortex and its associated white matter in human evolution. Although the human and chimpanzee lineages diverged some 6–7 million years ago, paleontological evidence indicates that most of this increase in brain size occurred over the last 2 million years, a point at which hominins may have begun to incorporate large amounts of animal flesh in their diet.

Traditionally, this large increase in size was thought to reflect the addition of tissue to the classical higher-order association regions, not only including the prefrontal cortex, but also the temporal and parietal association regions. The conclusion that prefrontal and other higher-order cortical regions disproportionately expanded in humans has more recently been challenged by Semendeferi and colleagues. Using MRI morphometry, they reported that the relative proportions of the cerebral mantle occupied by the frontal, parietal, and temporal lobes are about the same in humans and great apes, despite the much larger absolute size of the human brain. It must be remembered, however, that prefrontal cortex is not the same as frontal cortex: the frontal lobe contains motor and premotor cortex, in addition to prefrontal cortex. Similarly, the parietal and temporal lobes contain primary somotosensory and auditory areas, respectively, as well as association cortex. As it happens, the sizes of the primary, sensory, and motor areas in humans are, in absolute terms, very similar to those of great apes, while the association cortical regions are vastly larger in humans. Comparisons of sensory versus association nuclei of the thalamus yield similar results. Thus, the available evidence supports the classical conclusion that humans underwent an enormous evolutionary expansion of association cortex, although it is important to note that the evidence comes mainly from a handful of very old studies.

The evolutionary enlargement of the human brain could have had a number of effects on the internal organization of the brain. Many researchers have followed Brodmann in concluding that the human brain has cortical divisions (areas) that are not present in smaller-brained primates. Therefore, for example, his human map contains areas 44 and 45 – which collectively constitute a large part of Broca's area – in the human frontal lobe, areas that are missing in his monkey maps. This is intuitively appealing, since one might expect that humans evolved new cortical areas to support novel human functions. The truth of the matter would seem to be more complicated, however: there is reasonable (if not definitive) evidence that homologs of Broca's and Wernicke's language areas exist in nonhuman primates, their lack of language notwithstanding. One might argue, more generally, that the expansion of cortex in human evolution should be accompanied by the addition of new cortical areas, since larger-brained mammals typically have more cortical subdivisions than smaller-brain mammals, but we currently lack the detailed and reliable cortical maps for humans and great apes that would allow us to definitively identify homologous areas across species and determine whether humans possess areas that nonhuman primates lack. The example of language cortex should, however, prompt us to take seriously the idea that human brain evolution was not simply an add-on process, but that it also involved modifying preexisting structures to support novel functions.

There is, in fact, evidence that the evolution of language involved physical changes in the brain other than the addition of new areas. Buxhoeveden and colleagues have described differences in the size and spacing of cortical microcolumns between the left and right Wernicke's areas of humans, differences not observed in chimpanzees or macaques. Recently, Rilling and colleagues used diffusion tensor imaging (DTI) to compare the organization of white matter pathways that interconnect Wernicke's and Broca's areas in humans, chimpanzees, and macaques. In humans, it has long been supposed that Wernicke's and Broca's areas are linked by a specific fiber bundle, the arcuate fasciculus. Using DTI, Rilling and colleagues found that the arcuate fasciculus of humans, but not chimpanzees, carries fibers from a broad region of middle and inferior temporal cortex, ventral to Wernicke's area, which are known to represent word meaning.

The advent of DTI, which enables the noninvasive tracking of fiber pathways, is a landmark in comparative neuroscience. For the first time in the history of neuroscience, it is possible to directly compare the connectivity of the human brain to that of chimpanzees and other nonhuman primates, and to explore how evolution reorganized the system of white matter fascicles that bind cortical areas into higher-order neurocognitive systems. It seems likely that the arcuate fasciculus findings will be the first of many demonstrations of evolutionary specializations of human brain connectivity.

Of course, fiber organization and long-range cortical connectivity, as important as they are, represent just one level of brain organization. As noted above, evolutionary specializations of the human brain have now been

documented at finer levels of organization, such as micro-architectural organization of neuronal groups and the biochemical and morphological characteristics of different cell types. Evidence from recent comparative genomic studies points to the possibility of rather profound differences in the organization of the molecular machinery that regulates cerebral energy metabolism and the formation and stabilization of synapses.

There remain major unanswered questions in our understanding of human brain evolution. For example, while it seems likely that the genetic program regulating the generation of neurons in embryonic life was modified in human evolution, we do not know which genes were involved. Moreover, it has been argued that human post-natal development is not simply a stretched-out version of ape development, but also includes uniquely human pre-adult developmental stages. We know very little about the genetic and neurodevelopmental correlates of such changes. There is, as noted above, evidence from gene-expression studies suggesting that energy metabolism and synaptic biology of adult human cortex were modified in human evolution; what are the psychological counterparts of these changes? Finally, we still know very little about the nature of changes in the large-scale regional organization and connectivity of human cerebral cortex that support distinctively human higher-order cognitive functions.

Fortunately, we now have methods, such as DTI and various molecular techniques, that – in the context of comparative studies – will enable us to progress on these fundamental questions about human nature. Unfortunately, comparative studies have historically not enjoyed very strong support from funding agencies, and the US government recently decided to end support for its chimpanzee facilities. Without the ability to compare humans to chimpanzees, our closest relatives, our ability to understand what it is about our minds and brains that make us human will be severely compromised.

Human Brain Development

Just as a comparison of brain structure between humans and other species can provide clues regarding possible differences in mental capacity, so can it be helpful to examine how the brain changes over development. A healthy human child is born with a brain that looks remarkably like the brain of an adult, albeit 3.5 times smaller. Our brains undergo substantial structural changes during infancy and childhood. The number of synapses in the brain reaches a maximum density of about 150% that of the adult level in the first year of life, with pruning of excess synapses taking place over the rest of childhood and adolescence. Long-range projections between brain regions are established, and the axons that functionally connect these distant regions become myelinated, leading to faster neuronal transmission. By around age 9, a child's brain is approximately the same volume as that of an adult. However, upon closer examination, structural differences between these brains can still be observed.

During the second decade of life, changes in brain structure are less dramatic but still important. Cortical gray matter volume, which reflects neuronal density and the number of connections between neurons, peaks at around age 10–12, and then begins to decline. Gray matter loss occurs at different rates in different subregions of the brain. By the metric of rate of gray matter reduction, both prefrontal and parietal cortices exhibit protracted developmental time courses. During this second decade, steady increases are observed in white matter volume – which reflects myelination and increased axon thickness. Greater coherence of white matter tracts over development is associated with better performance on tasks that require interaction between regions connected by these tracts. In summary, both cortical pruning within brain regions and increased neuronal connectivity within and between regions underlie changes in brain function over development.

The finding that gray matter peaks at a different age for different brain regions shows that the brain matures in a piecemeal manner. The fact that brain development unfolds quite similarly across individuals invites the speculation that this piecemeal maturation is finely orchestrated. Indeed, as noted previously, evolutionary pressures come into play at all stages of development, such that brain function at each stage should be age appropriate.

Although brain maturation may, in broad strokes, unfold in a fairly stereotyped way, there are significant individual differences between children in brain structure and in the trajectory of brain maturation. These differences can provide insight into structure–function relationships. Interestingly, recent longitudinal work indicates that the dynamics of gray matter increases and decreases over childhood are associated with differences in intellectual ability, particularly in anterior PFC.

Developmental Functional Brain Imaging Research

The pattern of developmental changes in brain activation over childhood and adolescence has been generally characterized as a shift from diffuse to focal activation and from posterior to anterior activation. Differences are usually quantitative, with one age group engaging a region more strongly or extensively than another, but sometimes qualitative, with a shift in reliance on one set of brain regions to another.

Importantly, the precise pattern of change observed depends not only on the ages being examined and the brain region in question, but also on the task being performed during functional brain imaging. We have found

that a region may exhibit adult-like patterns of activation during middle childhood in one cognitive task, but not another. Thus, a region's cellular architecture and pattern of connections may be sufficiently developed to contribute effectively to a neural circuit underlying one task or cognitive function, but not to another. An important current and future direction for developmental neuroimaging studies, and also for comparative neuroimaging studies, is to examine developmental changes in the pathways and functional interactions between brain regions.

Conclusion

Both evolutionary and developmental approaches to cognitive neuroscience explore the differences in brain structure and function between organisms. Developmental cognitive neuroscience has focused on age-related differences in the function of a brain region or the organization of a brain network. In contrast, evolutionary neuroscience has, until quite recently, emphasized the similarities rather than differences between species, in particular between humans and nonhuman primates. Developmental and individual differences research shows us that, even within a species, there can be salient differences in structural and functional organization; it stands to reason, therefore, that differences should be observable across species.

We remain profoundly ignorant about how the human brain changed in evolution, but going by current evidence, it is clear that the human brain is not simply an enlarged monkey or ape brain: it is a different brain. Similarly, we still know relatively little about how the human brain develops and changes over the life span, but it is important to keep in mind that the adult brain is not merely the child brain with additional functions and circuits. Each stage of development must be functionally viable, and it is of interest to consider not only the adult brain as an endpoint, but also the specializations of the infant, child, or adolescent brain.

See also: Brain Evolution in Vertebrates; Brain Imaging; Human Evolutionary Genetics; Language and Communication – Brain Substrate; Neural Basis of Working Memory; Physical Cognition and Reasoning; Primate Origins of Human Behavior; Social Cognition: From Behavior-Reading to Mind-Reading.

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