16

Phylogeny and Ontogeny in Human Neuroscience

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Abstract

Currently we do not have a really good idea about what is special about the human brain and how this has led to uniquely human behaviors. To progress forward, we first need to ignore appeals to authority (e.g., Darwin) and accept that mammalian brains are not simply differently sized versions of the same thing. This does not mean that there are not commonalities between the brains of mammalians and other taxonomic groups, but that the only way to identify meaningful similarities and differences is through a comparative approach that looks at a number of different species. This chapter argues that two other lines of investigation are important in comparative neuroscience. First, investigating development will help to solve how evolution finds the same or different solutions. Homologous or convergent developmental trajectories reveal the constraints (or the lack of constraints) on how the brain reaches an adaptive solution. Second, investigating the body and its biomechanics will reveal how the structure of the body generates both constraints and advantages for the nervous system. Understanding the evolution of the human brain requires a comparative understanding of how it develops and operates in concert with the body.

What Is Special about the Human Brain?

We know a lot about the human brain, but oddly enough, we do not know a lot about what makes it special (Preuss 2000b). As a result, there is no well-developed theory of how our brain generates behavior, unique or otherwise; that is, we lack clear ideas regarding the distinctive characteristics of the human brain that would illuminate how and why human behaviors may be similar or different from the behavior of a monkey, a rodent, or any other animal. One potential explanation for this is that we have wrong ideas about the nature of brain evolution, and perhaps this is Darwin's fault. Darwin argued that the neural differences between humans and other animals were not of kind but of degrees; that is, he argued in effect that all brains were the same, just

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differently sized (Darwin 1888). Thus, our ideas about brain evolution may be faulty because most neuroscience research has focused on the human brain, along with a few animal species (mice, rats, and macaque monkeys) whose brains are treated as uniformly structured, miniaturized versions of the human brain (Preuss 2000b).

To understand what it means to be human, it is essential to understand how our brains and behaviors evolved. The origins of the human brain and how it shapes (and is shaped by) our behavior are largely mysterious for two reasons. First, there are few ways to reconstruct ancestral human behaviors as no records of behavior (beyond stone tools, perhaps) have been preserved. Thus, for instance, we have no idea what Neanderthal vocalizations sounded like or whether word-like utterances were strung together syntactically by them. Second, soft tissues such as the brain and muscles do not fossilize, and the hominid fossil records of skulls and skeletons that we do have are woefully incomplete and representative of only a very few individuals. As such, an understanding of the origins of the human brain and behavior must resort to the comparative method: Understanding what it means to be human requires comparing our brains and behaviors to those of other extant species. With any behavioral and/or neuronal phenotype that two closely related species share, it can be inferred that their last common ancestor also exhibited that phenotype—the phenotype is *homologous*. Conversely, any behavioral and/or neuronal phenotype that two distantly related species share (i.e., a phenotype that is unlikely to be shared by a common ancestor) would be an instance of *convergent evolution*. In this manner, the comparative method reveals the behavioral and biological traits of extinct ancestors and helps us identify behavioral and neural homologies, species-unique capacities, and/or products of convergent evolution.

The Few Things We Know about the Human Brain Are Special

Using the comparative approach, we have a handful of findings regarding what makes the human brain different from the brains of other animals. Our brains are much bigger than expected for our body size (Jerison 2012). Along with this overall increased size, evidence suggests that, over the course of human evolution, association areas in the neocortex grew disproportionately relative to primary sensory areas (Sherwood et al. 2008). For example, our prefrontal cortices are larger than expected when compared to other primates, although, as noted by Preuss (2000b), this finding is complicated by the different criteria that have been used to define "prefrontal" or "frontal" cortex across studies (Brodmann 1912; Blinkov and Glezer 1968; Semendeferi et al. 1997). Within cortical areas, we also see human specializations. For example, human primary visual cortex has modified magnocellular pathway components in layer 4—modifications that are absent in apes and monkeys—suggesting changes

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in how visual information was processed over the course of human evolution (Preuss et al. 1999).

Oddly enough, humans do not seem to possess any unique cortical areas relative to other Old World primates, at least when brain areas are defined using cytoarchitectural criteria (Zilles et al. 1995; Preuss 2000b; Petrides and Pandya 2002). For example, though humans alone possess linguistic abilities, macaques and apes share with humans homologous cortical areas located in what is defined as the language-related Broca (Deacon 1992; Petrides et al. 2005; Schenker et al. 2010) and Wernicke regions (Galaburda and Pandya 1982; Spocter et al. 2010). Similarities notwithstanding, connectivity between ventral motor and inferior parietal regions (a pathway known in humans as the arcuate fasciculus) is nevertheless quite different between humans, chimpanzees, and macaques (Rilling et al. 2008). In humans, the terminations of the arcuate fasciculus connect the superior, middle, and inferior gyri of the temporal lobe with the following frontal regions: ventral premotor cortex, pars opercularis, pars triangularis, and middle frontal gyrus. Examination of the same pathway in the chimpanzee revealed extensive frontal terminations similar to humans, but the terminations in the middle and frontal temporal gyri were much less numerous. In macaques, these temporal lobe terminations were entirely absent.

While there is evidence of human brain specializations such as those described above, we have no idea how such neural differences relate to behavior. It is typically assumed, for example, that the overall larger size of the human brain must (somehow) confer our uniquely human behaviors, such as language. Such facile ideas are easily dismissed. For instance, some microcephalic patients—whose brains are about the size of a chimpanzee's brain (i.e., one third the size of a normal human brain)—are able to produce language, within limits (Dobyns 2002; Allen 2009). How is this possible if brain size is of primary importance to language function? We should be careful not to be lulled into adopting the notion of the "cerebral rubicon" (Allen 2009)—the idea that once the size of our ancestral human brains reached some threshold, our cognitive abilities increased disproportionately giving us our uniquely human behaviors.

When comparing brains and behaviors of different species with humans, it is crucial to note that while comparative studies may reveal that rats, mice, and/or macaques share some phenotypes with humans, this does not mean that these species *are* the last common ancestors. Yes, of course, that should be obvious. What I mean is that we sometimes forget that a macaque monkey, for instance, does not by itself represent what a primate ancestral to humans would be like. This is because each extant species followed its own evolutionary trajectory for millions of years, yielding its own species-specific behavioral and neural specializations. Roughly speaking, the split between the evolutionary lineages that led to rodents versus primates occurred 90 million years ago. So, rats and mice have been evolving their own specializations in parallel with humans for that many years. Similarly, the lineages leading to marmoset monkeys (a New

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World primate) and macaque monkeys versus humans separated 40 million and 25 million years ago, respectively. As a result, each primate species has a number of shared neural phenotypes with humans and other primates as well as a number of differences (Preuss 2009).

Taking Development Seriously

We must always keep in mind that human behavior and neurobiology are products of phylogenetic as well as ontogenetic processes (Gould 1977). Evolution acts on developmental processes to produce adult phenotypes. Changing developmental trajectories is the only way to evolve phenotypic changes. By comparing developmental processes, we can thus compare more deeply the similarities or differences across species (Schneirla 1949; Deacon 1990; Finlay et al. 2001). A similar behavioral phenotype across two species may arise through different or identical developmental processes (i.e., exhibit multiple realizability), and different developmental trajectories *could* suggest entirely different neural mechanisms, even though the behaviors seem the same.

Growing a Big Brain

Since brain size seems to be the obvious feature that distinguishes our brain from other species, let us start there. In terms of mass and neuronal numbers, the human brain appears to be a scaled-up version of a primate brain (Herculano-Houzel 2009). Although it is not exceptional in terms of its cellular composition, the human brain contains as many neuronal and nonneuronal cells as would be expected of a primate brain this size. In terms of absolute numbers of neurons, however, the human brain contains more neurons relative to other primates. It is through developmental processes that it achieves this difference. For example, the genesis of cortical neurons during primate development (including humans) is distinguished from mouse development by the appearance of a novel zone of cell proliferation known as the outer subventricular zone; this zone contains an additional population of neuronal stem cells that contribute to the increased size of primate neocortices relative to other mammals (Lui et al. 2011; Dehay et al. 2015). Another link between development and evolution, as it relates to brain size, is evident in the analysis of genes related to the nervous system. A number of studies have revealed that there are genes in the nervous system which show unique patterns of evolution in the primate lineage leading to humans (e.g., Kouprina et al. 2004; for a review, see Gilbert et al. 2005). Mutations in some of these genes lead to congenital microcephaly (Mochida and Walsh 2001; Dobyns 2002). This suggests that they may have a role in defining the most distinguishing characteristic of the human brain: its size.

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Development Timing

Often in contemporary comparative studies, the behavioral capacities of *adult* nonhuman animals are compared with those observed in human infants, with the guiding assumption being that similar behaviors would indicate the same underlying neural processes. Indeed, whole research programs devote much effort to comparing the behavioral capacities of adult monkeys or apes to those of developing humans (e.g., Egan et al. 2007; Herrmann et al. 2007). Unwittingly, I have also participated in this line of thinking. For example, my colleagues and I showed that adult Old World monkeys are able to match species-specific faces to voices (Ghazanfar and Logothetis 2003; Jordan et al. 2005); the implicit assumption in our work was that this is homologous to the ability of human infants to do so (Kuhl and Meltzoff 1982; Patterson and Werker 2003; Jordan and Brannon 2006). One possible source for thinking this way may have come from the elegant, pervasive, tenacious but ultimately incorrect idea that "ontogeny recapitulates phylogeny" (Gould 1977). Under this scenario, the human infant goes through stages of development that reflect all human ancestors (Haeckel 1866). In other words, the human infant brain must go through a stage that represents a "primitive" adult monkey brain; any uniquely human behavioral and neural capacities are "added on" after that stage (in evolutionary biology, this is referred to as "terminal addition"). We are left with the "triune" brain theory, which holds that new neural circuits get added on to a "reptilian brain" to generate mammalian behaviors (MacLean 1990). The validity of "ontogeny recapitulates phylogeny" and its attendant ideas (e.g., terminal addition, the triune brain theory) have been debunked many times as it relates to behavioral development (Medicus 1992). Consider this vivid debunking example: The coqui frog, found and heard all over Puerto Rico, skips the tadpole stage: it bypasses the "fish" stage in the "ontogeny recapitulates phylogeny" scenario during development and emerges from the egg as a fully formed but diminutive frog (Callery and Elinson 2000). Ontogeny does *not* recapitulate phylogeny.

The fundamental problem with making claims about homologous behaviors is the possibility that similar behavioral capacities may be mediated by different developmental processes. This alternative scenario is possible because brain development follows different trajectories in animals relative to humans, particularly with regard to timing. Old World monkey infants, for instance, are neurologically precocial relative to human infants. At birth, the rhesus monkey brain is heavily myelinated whereas the human brain is only moderately myelinated (Gibson 1991). Likewise, in the rhesus monkey, sensorimotor tracts are heavily myelinated by 2–3 postnatal months, whereas in humans they are not myelinated until 8–12 months of age. These facts suggest that postnatal myelination in the rhesus monkey brain is about three to four times faster than in the human brain (Gibson 1991; Malkova et al. 2006). Although the rate is different, the spatiotemporal sequence of myelination (and other indices of

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brain growth) along different neural pathways is the same between monkeys and humans (Clancy et al. 2000; Kingsbury and Finlay 2001) and generally coincides with the emergence and development of species-specific motor, socioemotional, and cognitive behaviors (Antinucci 1989; Konner 1991). Finally, in terms of overall brain size at birth, Old World monkeys are among the most precocial of all mammals (Sacher and Staffeldt 1974): ~65% of their brain size is present at birth compared to only ~25% in human infants (Sacher and Staffeldt 1974; Malkova et al. 2006). Thus, human infants are born altricial relative to most other primates (Portmann 1990), due most likely to a maternal inability to provide necessary energy requirements to the developing fetus (Dunsworth et al. 2012).

This altriciality means that the human infant brain is shaped by postnatal experience to a much greater degree than other primates. Indeed, evidence suggests that even the adult human brain retains some of the plasticity that is typically exhibited in other species only in the developing brain; that is, humans evolved the capacity to maintain elevated levels of neural plasticity over a long lifetime (Bufill et al. 2011). For example, serotonergic innervation differs between adult humans, chimpanzees, and macaque monkeys, and increases in serotonin have been related to increases in plasticity. Humans and chimpanzees have a greater serotonergic innervation of the frontal cortex than macaques, suggesting selection for increased plasticity among hominoids (Raghanti et al. 2008). Moreover, genes related to synaptic plasticity increased their expression by sixfold in humans relative to chimpanzees and macaques, presumably leading to the greater synaptic density, higher synaptic turnover, and increased rates of dendritic growth found in human brains (Cáceres et al. 2003, 2006). In fact, the adult human brain has levels of gene expression that correspond to that of juvenile chimpanzees, suggesting that it evolved to retain higher levels of neural plasticity; in other words, it is "neotenic" (Gould 1977; Somel et al. 2009).

Developmental timing and species differences in the capacity to remain "plastic" may be the key to understanding the origin of at least some of our uniquely human behavioral capacities. Overall, this suggests that our brains—far more than any other species—can be molded by postnatal experience to a greater degree, not only in early life as a result of altriciality but also for longer periods even into adulthood. This is consistent with theories that link uniquely human neural structure–function relationships to the interactions between experience and neural development over the course of a lifetime (Dehaene and Cohen 2007; Anderson and Finlay 2014; Karmiloff-Smith 2015). The basic idea behind these theories is that while there are a number of evolved constraints as to how the human brain can organize itself over the course of development, experience (including cultural acquisitions such as reading and arithmetic) can exploit the human brain's plasticity to organize it in particular ways that are simply impossible in other species. The theories seem to differ in the extent to which they emphasize greater (Dehaene and Cohen 2007)

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or lesser (Anderson and Finlay 2014; Karmiloff-Smith 2015) degrees of evolutionarily related constraints. Dehaene and Cohen (2007) argue that the influence of experience is strongly constrained by an infant's domain-specific brain organization, whereas Karmiloff-Smith (2015) and Anderson and Finlay (2014) suggest that the organization of the infant's brain is a product of experience-dependent processes from the outset of its development, and thus is not constrained by preexisting organizational biases.

How Species-Typical Bodies Shape Species-Typical Brains

Typically we think of the brain's (or, more accurately, the neocortex's) job as planning future actions based on its information processing of sensory signals from the environment, followed by the generation of commands for movements based on those plans. What we forget is that the body and its species-typical structure also play an important role in this process. Different parts of the body act as filters for both incoming and outgoing signals (Chiel and Beer 1997; Tytell et al. 2011).

Every part of primate anatomy—from the head to the feet, literally—exhibits species-specific specializations (Fleagle 2013). An obvious example is the outer ear. It is extremely variable in size, shape, and mobility, even among primates, and these factors determine how each species hears. In nocturnal primates (e.g., galagos), which rely primarily on hearing to catch prey, the ears are very large (relative to head size) and mobile, with mobility conferred through a special set of muscles. In humans, the ear is small and has only limited movement. How one hears is determined by the size and shape of the ears: the ridges and valleys of the outer ear filter sounds—making some parts of the sound louder and others softer—before they hit the eardrum (Batteau 1967). Critically, which parts of a given sound get louder or softer also depends on whether the sound is hitting the outer ear from above or below; thus we learn to associate acoustic differences with the vertical location of the sound source.

The importance of our bodies' physical conformation to behavior and experience is reflected in how it changes and guides the nervous system during development. Continuing with the ear example, we localize sounds well as of a very young age but since our ears are still growing and changing shape, the developing brain must recalibrate itself to account for these bodily changes (King and Moore 1991). In fact, the neural circuits of the auditory system are so dependent upon the shape of the ears to guide its function that it has to wait for the body to catch up to it. Neurophysiological recordings of auditory cortical neurons in very young ferrets listening to sounds revealed that these neurons encode spatial location poorly (Mrsic-Flogel et al. 2003). The natural assumption is that the neurons are poorly tuned because they are still developing (e.g., perhaps lacking inhibitory circuits that would sharpen tuning in the auditory cortex). In actuality, however, it is because the shape of the ears (the body) is

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still developing and has not yet achieved its adult-like form. Experimentally providing the same young ferrets the ears of an adult (via virtual acoustics: delivering sounds directly in the animal's ear canals after they have been filtered by a simulated adult ear) can drive quite suddenly those auditory cortical neurons to encode sound location accurately (Mrsic-Flogel et al. 2003). Thus, in this case, the developing body is guiding the sensory functions of the nervous system, not the other way around.

The developing body also shapes motor output. Human newborns are able to make well-coordinated stepping movements when held upright, but these movements disappear by ~2 months of age (Thelen et al. 1984). While it was assumed by many that the change in stepping behavior was due solely to the developing nervous system (e.g., McGraw 1945), Thelen and colleagues hypothesized that the loss of stepping behavior was due to body growth: infants' legs typically fatten up postnatally and they do not yet have the strength to move heavier legs. To test this hypothesis, Thelen et al. (1984) submerged the infants' legs in water, effectively decreasing their mass. This resulted in the reappearance of stepping behavior and thus falsified the alternative hypothesis that neural change was necessary: change in behavior was due to changes in the body. Along similar lines, it would typically (and reasonably) be presumed that changes in vocal production over the course of development are the results of learning and, thus, changes in the nervous system. In marmoset monkeys, however, computational modeling of sensory feedback from the lungs onto central pattern generators showed that the decline in the production of context-inappropriate vocalizations could simply be the result of lung growth (a change in body morphology) without any concomitant changes in central nervous system structure (Zhang and Ghazanfar 2018). The model's predictions were tested by placing the marmoset infants in a helium-oxygen environment to effectively decrease the load on the lungs, similar to submerging human infants' legs in water to decrease their effective mass (Thelen et al. 1984). This simulated a reversal in lung growth and, as predicted, resulted in a reversion back to immature vocal behavior (Zhang and Ghazanfar 2018). The developing body can create distinct behavioral changes without the need for concomitant changes in the nervous system.

Conversely, understanding the biomechanics of the body can also be enormously useful in identifying that neural changes *were* required to generate new behaviors. For example, a precision grip is a grasping behavior that is common among Old World monkeys and apes (including humans). Such a grip allows an object to be grasped with two fingers without the use of the palm (Napier and Napier 1985). Among New World monkeys, only the cebus monkey is known to use a precision grip—an example of convergent evolution (Costello and Fragaszy 1988). The question is: What is it about the cebus monkey that allows it to produce a precision grip like an Old World primate yet unlike closely related species, such as the squirrel monkey? The answer could be due to the natural selection of the necessary hand biomechanics, neural circuitry

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changes, or both. It turns out that the hand structure of cebus and squirrel monkeys is very similar: both have thumbs that cannot rotate around a joint in the manner that an Old World primate's thumb can. It was thus assumed that neither species could perform a precision grip (Napier and Napier 1985). The fact that the cebus monkey can indeed use a precision grip suggests that its difference with other New World monkeys (or at least the squirrel monkey) is strictly brain related.

In this particular case, the neural differences may be both general organizational differences and specific ones. For instance, cortical areas 2 and 5, associated with motor planning and coordination, are very well developed in macaques, an Old World monkey, as well as in cebus monkeys (Padberg et al. 2005). In other New World primates, however, areas 2 and 5 are either absent or poorly developed. The emergence of identical cortical areas, in this case areas 2 and 5, across species (cebus and Old World monkeys) separated by a common ancestor 40 million years ago suggests that there are rather strict developmental constraints on neocortical organization (Krubitzer and Kaas 2005; Finlay and Uchiyama 2015). A specific neural difference related to the precision grip is the organization of connections from the motor cortex to the spinal cord. Cebus monkeys have extensive corticomotoneuronal terminations in the ventral horn of the spinal cord; such connections are largely absent in squirrel monkeys (Bortoff and Strick 1993). Thus, there are important differences in corticospinal projections across species that may reflect features of the sensorimotor behavior that are characteristic of that species (Lemon and Griffiths 2005).

Similarly, the production of human speech sounds has long been thought to be due to the unique anatomy and configuration of the human vocal tract. This hypothesis states that the broad phonetic range used in modern human speech required key changes in peripheral vocal anatomy during recent human evolution. For example, no nonhuman primates have ever been trained to produce speech sounds, even in chimpanzees that have been raised from birth in human homes (Kellogg 1968). This biomechanical hypothesis was widely accepted, primarily due to a seminal study which used a computer program to explore the phonetic capability of a macaque cadaver and, by extension, other nonhuman primates (Lieberman et al. 1969). New data based on X-ray images from living macaque monkeys have challenged this hypothesis (Fitch et al. 2016). This study revealed that the basic primate vocal production apparatus is easily capable of producing five clearly distinguishable vowels (e.g., those in the English words "bit," "bet," "bat," "but," and "bought") and that the phonetic range inherent in a macaque vocal tract, based on actual observed vocal tract configurations, would not impede linguistic communication *if macaques possessed human-like neural control systems* (Fitch et al. 2016). Consistent with this idea, a recent study of baboon vocalizations shows that their acoustic range is much more similar to human vowel sounds than previously thought, despite having a different vocal biomechanical configuration (Boë et al. 2017). The inability

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of nonhuman primates to speak does not reflect biomechanical limitations but rather the lack of neural circuitry to enable sophisticated vocal control.

Conclusions

At present we do not have a really good idea about what is special about the human brain and how this leads to uniquely human behaviors. To make progress in this area, we need to ignore appeals to authority (e.g., Darwin) and accept that mammalian brains are not simply differently sized versions of the same thing. These differences are not just of degree but of kind as well. Even the generic scaling laws of biological organisms would suggest that how a tiny mouse brain operates and is organized should be very different from that of a human brain (West 2017). This does not mean that there are not commonalities between them or with other species, but that the only way to identify the meaningful similarities and differences is through a comparative approach that looks at a number of different species (Preuss 2000a, b, 2009; Krubitzer and Kaas 2005), and not just in one part of the phylogenetic tree (Katz 2016b). For instance, the octopus' vertical lobe—a structure important for learning and memory—is organized in a fashion that is strikingly similar to the mammalian hippocampus (Shomrat et al. 2015). This is clearly a case of convergent evolution and suggests that there may be constraints on how a "learning and memory" structure can be assembled.

Another key to this comparative neuroscience approach is to incorporate developmental processes. We cannot assume, even in closely related species, that similarities in behavior translate to similarities in neural circuitry (Katz 2016a). Conversely, we cannot assume that distantly related species with similar behaviors exhibit those behaviors through wholly different neural mechanisms. Investigating development will help to solve how evolution finds the same or different solutions. Homologous or convergent developmental trajectories reveal the constraints (or the lack of constraints) on how the brain reaches an adaptive solution.

Finally, the body and its biomechanics are players in the evolution of behavior that are as important as the brain. The structure of the body generates constraints as well as advantages for the nervous system, and the evolution of any behavior must account for both as there is continuous feedback between the nervous system, body, and environment in any adaptive behavior (Chiel and Beer 1997). Developmental changes in the body alone can lead to radical changes in behavior. Moreover, understanding biomechanical constraints also illuminates what behavioral changes are strictly related to neurobiology differences.

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