

The Skinny on Brains: Size Matters

By Jon H. Kaas, Ph.D.

Editor's Note: This article is the second of two that addresses the development of the human brain. Last month's article, "The Evolution of Human Capabilities and Abilities," focused on neurons, the basic information-processing units of the nervous system. This month's article examines the evolution of the neocortex, a part of the cerebral cortex concerned with sight and hearing in mammals, regarded as the most developed part of the cortex.

Compared to other mammals, one cannot help but be impressed with the abilities of humans to imagine things, ponder the past and future, communicate through speech and writing, and understand the mental states of others. Humans are also capable of a deep understanding of the physical properties of materials and objects that can be used as tools or for building; they have the ability to recognize and know countless other people, and to interact and cooperate for the greater good. We are culturally adaptive to the extent that we occupy most of the ecosystems on earth. And if that's not impressive enough, we are planning to inhabit a space station on Mars.

Individual humans are highly variable in what they know and what they can do, as evidenced by athletes, musicians, scholars, writers, and architects. The best business leaders probably do not know how to farm and vice versa. All these varied and profound abilities depend on our brains—and especially our expansive neocortex.

Our understanding of how our brains execute these impressive abilities is fragmentary. Nevertheless, we are rapidly learning the ways in which brains vary across the classes (taxa) of mammals, and how these differences allow for human abilities.

The distinctive features of human brains emerged and further differentiated as our ancestors evolved, especially over the last two million years, with the modern human brain reaching its current potential perhaps as long as 200,000 years ago. Here, we consider brain features that are enhanced compared to those of other mammals, and likely account for our unique abilities.

Size Matters

Obviously, having a larger brain must present some advantages to compensate for its huge metabolic cost and long developmental time. As brain size is relatively easy to measure, there is a long history of research relating brain size to cognitive and other mental abilities,¹ and meaningful correlations have been produced repeatedly.²

The range of brain sizes across mammals is huge, ranging from the tiny shrew (0.06-3.0-grams) to the African elephant (4,600-grams).² As a general rule, mammals with small brains have limited behavioral abilities, while those with large brains have greater cognitive and mental capacities.

The spectrum across primate species, while less than that of all mammals, is also significant, ranging from the smallest primate brain of the appropriately named mouse lemur—roughly 1.5 grams—to the largest of primate brains, the human brain of 1,200 to 1,400 grams or more. The mouse lemur is well adapted to varied habitats in Madagascar, but its behaviors resemble those of the house mouse more than those of the human.

A more useful comparison may be with chimpanzees, our closest relatives, whose brains of around 340 grams are roughly one-quarter the size of ours. Chimpanzees are clearly very intelligent and have visual and other sensory abilities that match or perhaps exceed those of humans. Although they cannot produce speech, some chimpanzees can learn the meanings of symbols for objects and acquire an understanding of hundreds of English words. They are, however, severely limited in the cognitive abilities involved in using tools or instruments to retrieve and acquire food. Compared to humans, they are also limited in their ability to infer or understand what others know.

But there are reasons to be cautious about assuming that brain size is the whole story. Brain size correlates with body size; oftentimes even within a species. As body size is determined by both genetic and environmental factors, body and brain sizes tend to be smaller in females of our species, and in members of cultures less exposed to modern fast foods. In the past, this led scholars to underestimate the mental abilities of women and individuals reared on fewer calories.

In addition, some mammals (especially primates) and birds do better than expected for their brain sizes. The question is why the relationship between brain size and behavior generally holds—and when it doesn't, why not?

Neurons vs. the Neocortex

A modern understanding of the number of neurons in brains, or parts of brains, of various vertebrates comes from the recent studies of Suzana Herculano-Houzel (author of last month's [Cerebrum article](#)) and her research team.⁴ If larger brains have more computational capacity, and the basic computational unit of the brain is the neuron, the total number of neurons in the brain should correlate better than brain size with brain functions, especially if brain size does not fully predict numbers of neurons.

In a series of important studies, Herculano-Houzel determined the number of neurons in the 19 orders or taxa of mammals with brains of different sizes. While her research focuses on neurons, we will focus on a part of the brain called the forebrain, and especially the neocortex, which is the structure that is most important in cognition. For most orders of mammals, increased neocortical size is not matched by an equivalent increase in neuron number: a doubling of cortex leads to something less than a doubling of neurons. Instead, neurons tend to get bigger as the cortex gets bigger, except in primates.

In primates, the relation of brain size to numbers of neurons is constant, i.e. the scaling is isometric. This is much like Alice in *Alice in Wonderland*: as Alice shrinks to a much smaller size or grows much larger, the proportions among her parts remain the same. In primates, this is the case for the brain in general and for the neocortex in particular, as increased brain size is mainly in the cortex. As cortex doubles in size, the number of neurons doubles. In humans, the cortex makes up more than 80 percent of the brain mass, and has roughly 16 billion neurons, more than any other mammal, including elephants and cetaceans with much larger brains.

The great number of cortical neurons in human brains reflects the exceptional cognitive abilities of humans. However, as Herculano-Houzel points out, this greater number of neurons is exactly what would be predicted from primate brain scaling laws. Although the human cortex has the number of neurons predicted from cortical size for primates, the result makes humans unique among mammals overall by having more neurons in cortex than non-primates with even larger amounts of cortex. This is important because the number of neurons in the cerebral cortex correlates better with cognitive abilities than with absolute cortical size or cortical size relative to body size.⁵

The studies of neuron numbers in brains, and parts of brains, reveal two other important points. First, birds are very successful vertebrates. Their brains are small, yet they appear to have high levels of cognitive abilities. Within the nearly 11,000 species of birds, cognitive abilities are especially high in the Corvidae family of birds (jays, ravens, crows, and magpies) and parrots. These species also have relatively larger forebrains than other birds. In addition, all birds have forebrains that are more densely packed with more small neurons than the forebrains of mammals, even primates with somewhat larger brains.⁶ Thus, for both primates and birds, neuron number better predicts cognitive abilities than forebrain size.⁶

Second, the cerebellum is a part of the brain that contains most of the brain's neurons.⁴ While the cerebellum has been implicated in cognitive functions, it is predominantly concerned with motor control, which occurs without conscious effort and depends on huge numbers of very small neurons. Because neurons are so densely packed, the size of the cerebellum does not keep pace as the neocortex gets larger. However, the numbers of neurons in the two regions tend to remain proportional.

This relationship suggests that the specialized functions of the neocortex and cerebellum are aligned in some manner, but that cognitive functions are more closely tied to the former rather than the latter. The elephant brain, three times larger than the human, has nearly 98 percent of its neurons in its cerebellum, but only one third the number of cortical neurons as humans. This disproportion indicates that the relation of cortical-to-cerebellar neurons is not necessarily fixed,⁴ and supports the above conclusion about the relative importance of the two areas in cognition.

But the number of neurons in the cortex does not fully explain human abilities, either. For example, why did Neanderthals, with brains as big as ours and as many neurons, become extinct while we have populated the earth? And how can human children treated for epilepsy by having much of the right cerebral hemisphere removed, grow up to be highly functional adults?

Cortical Structure

The neocortex of mammals is subdivided into functionally specialized zones. Korbinian Brodmann, a German neurologist in the early 20th Century who became famous for parsing the cerebral cortex into 52 histologically distinct regions (known as Brodmann areas), considered these areas to be functional equivalents of the organs of the body, such as heart, lung, and kidney.⁷ While this definition has proven useful, it has been difficult to identify and delimit such cortical areas.

Brodman characterized the cortical landscape on the assumption that differences in regional function are reflected by differences in structural specialization. He accordingly based his depictions of brain areas on variations of neurons within structures. Today we more reliably divide the cortex into areas of likely functional significance with an array of staining procedures that reflect both structural and functional differences among neurons.⁸ In addition, we define sensory and motor areas using functional maps of sensory inputs or motor outputs, patterns of cortical and subcortical connections, and imaging of cortical activation patterns. Agreement across such methods provides the strongest evidence for a specific area's existence.

The number of cortical areas clearly varies across mammals, increasing with brain and neocortex size. Those with small brains and little neocortex may have 20 or fewer.⁹ Primates may range from 50 areas or less in those with smaller brains and less neocortex, to 200 or more per cerebral hemisphere in humans.^{9,10}

We know much less about the cortex of other large-brained mammals such as whales and elephants, but cortical architecture suggests that they have far fewer cortical areas than humans. The human brain, nearly uniquely, adds to the total number of its functional areas by differently specializing corresponding parts of each hemisphere. We have areas for language, for example, in the left cerebral hemisphere, and areas for visuospatial and attentional abilities in the right.¹⁰

Humans also have or share a sub-areal organization in some areas of the cortex that increases processing capacity.¹¹ As an example, primates divide primary visual cortex, V1, into two sets of cortical columns of neurons, one of which processes information about color and contrast, and the other selective for specific orientations of edges in visual stimuli.

More structural and functional divisions of cortical layers in primates, especially in humans, may offer more ways of increasing processing capacity. The six primary layers of cortex in all mammals create functionally distinct channels. In primates, sublayers within are further specialized. And a subdivision of one of these layers in primary visual cortex appears to be specialized differently in humans than in other primates.¹³

Overall, humans probably exceed all other mammals in numbers of cortical areas. This creates more and longer processing streams, and more interactions between streams. Sensory information and memories can be evaluated and processed more extensively, and in more different ways, in human brains. As cognitive psychologist Steve Pinker has emphasized, the neural computations at each processing step may be rather simple, but a series of these steps can result in complex outcomes.¹⁴

Human Uniqueness

In humans and other mammals, neurons vary structurally and also in the neurotransmitters and receptors they use to communicate with one another. Such features allow neurons to function differently and promote specialization.¹⁵

Neurons may be more varied in humans than in other primates and most other mammals. Structurally, our most common type of neuron is the pyramidal cell, which varies considerably in the size of the cell body and of its dendritic arbor (which receives electrochemical messages from neighboring neurons). A large cell body reflects the need to sustain a long, thick axon (to transmit a message), or a widespread dendritic arbor, or both. A small cell body is usually paired with a small dendritic arbor and a short, thinner axon. Neurons with large arbors usually receive small numbers of synaptic inputs from many sources and integrate these inputs. Those with small arbors usually are powerfully activated by just a few input axons and are good at preserving information for distribution and further use.

The smallest neurons, located in sensory areas of some primates, respond to only a few axons from neurons in the brain's thalamus, and then relay those messages only to nearby neurons.

Neurons that transmit inhibitory messages, which constitute 20 to 25 percent of all cortical neurons, are typically also small.

One class of inhibitory neurons, the double bouquet cell, is found in the cortex of primates but not in other mammals. Von Economo neurons, large, spindle-shaped cells with a simple dendritic arbor, were thought to be present in only a few cortical areas in only humans and certain apes, but have more recently been observed in other mammals with large brains. Overall, primate brains appear to have more specialized and unusual neuron types, and this variety may contribute to brain function, especially in humans.

Some cortical areas are noteworthy in having neurons with specialized features. Thus, primary sensory areas often have a thick layer that is densely packed with small neurons. In monkeys, apes, and humans, these neurons are especially small. In addition, the pyramidal neurons of these primates are smaller than in other cortical areas. Overall, neurons in this area are packed three-to-four times more tightly than in most of the rest of the cortex.¹⁶

Thus, the large primary visual area of primates, especially humans, is well designed to preserve and distribute details of the visual image. Yet primary visual cortex has some neurons specialized to integrate information. A scattering of very large pyramidal neurons known as Meynert cells, have widespread basal dendrites that gather information over a large expanse of cortex. They send information related to visual motion and change over thick, long, rapidly conducting axons to more distant parts of the brain.

The primary motor cortex in humans and other primates is also characterized by very large pyramidal neurons in layer five, which are especially large in humans. These Betz cells summarize a lot of information and activate motor neurons in the brainstem and spinal cord over thick, long axons. Other pyramidal neurons in the primary motor cortex (M1) are also large and summarize many inputs, while the small neurons are almost totally missing. M1, especially in humans, is thus specialized for summing information from many sources, as the final cortical location for producing actions.

Primates also have a unique part of the prefrontal cortex, a dorsolateral region known as the granular prefrontal cortex.¹⁷ As the name suggests, it is distinguished by a layer of small granular neurons, a feature that would preserve input information. Yet, it also has large pyramidal neurons in another layer, implying an integrating function. Thus, this region of the cortex, unique in primates and expanded in humans, appears to have both information-preserving and summing functions in different layers of cortex, much like the primary visual cortex.

Human Benefits

Much of motor performance is controlled by subcortical centers in the brainstem and spinal cord. Early mammals got along fine without primary motor and premotor cortical areas, as do present-day monotremes and marsupials. For early mammals, cortical motor control was mainly from somatosensory areas. In primates, somatosensory areas include areas that contribute projections to subcortical motor centers.

Cortical motor and premotor areas apparently arose with the emergence of placental mammals, and they have been modified, expanded, and multiplied in their various branches. Although cortical sensory areas also have motor functions, they and motor areas are organized differently. Sensory maps are “topographic,” preserving the relationship among sensory receptors, while motor maps are “fractured” or “mosaic,” closely grouping neurons that contribute to cooperative movements of body parts. This more advanced organization in placental mammals appears to provide advantages in mediating and guiding motor behavior.

Specializations of motor and premotor cortical areas add to human motor abilities. Perhaps the most notable ability that humans have as a result of motor and premotor cortical specialization is a high level of conscious control over our vocal apparatus, which allows us to speak fluently. Another innovation has been a specialized part of the primary motor cortex deep in the central sulcus (the brain fissure that separates the parietal lobe from the frontal lobe and the primary motor cortex from the primary somatosensory cortex) that provides motor control of individual fingers.

Most primates have this capacity to a limited extent. But the skillful finger movements needed to play the piano, type, or use tools depend on a part of the motor cortex that sends more

projections directly to synapse on the motor neurons that activate muscles that move the digits—a distinctively human arrangement. While macaque monkeys have such direct projections from a "new" part of the primary motor cortex,¹⁹ this direct projection is likely proportionately and absolutely greater in humans. Another way that motor and premotor cortex areas have been modified and expanded in humans concerns the subdivision of these areas into patches of neurons or "domains" for specific, functionally relevant behaviors.

The Dorsal Stream Action System

All mammals have two cortical visual systems, a dorsal one to guide actions and a ventral one for object identification. This concept stems from studies in the 1960s²⁰ from which it became apparent that the two visual systems involve complementary paths from the retina through different brain areas.

In many mammals, the two systems function somewhat independently, allowing these animals to retain many visual abilities even after primary visual cortex lesions. In primates and especially in humans, however, the ventral object identification pathway to the inferior temporal lobe has been greatly enhanced and is totally dependent on the primary visual cortex for information. This enhancement allows us to recognize thousands of faces, an ability that promotes complex social systems.

The dorsal system provides visual inputs to the posterior parietal cortex to help in the selection and guidance of functionally relevant actions, but in primates the source of the visual information likewise comes predominantly from connections with the primary visual cortex. Thus, a lesion of the primary visual cortex, especially in humans, renders both systems sub-functional, and the visual abilities that remain may be no more than "blindsight" (the ability of people who have visual cortex lesions to respond to visual stimuli that they do not consciously see).

The adaptive reason for this change in primates is not clear, but one might speculate that the growing role of the dorsal stream to the posterior parietal cortex in visually guided behavior benefited greatly from the more extensive information available from the primary visual cortex compared to information in the other path that remains important in other mammals. In humans

and many other primates, 80 percent of the projections of the retina, those concerned with producing detailed images, colors, and aspects of contrast, go to the primary visual cortex where information is distributed to both dorsal and ventral streams of cortical processing.

The newly enhanced dorsal stream projections to the posterior parietal cortex were associated with a great expansion of the posterior parietal cortex (PPC) in early primates. In these animals, the caudal part of the PPC was devoted to further visual information processing, while most of the rostral part was used to promote specific behaviors, based mainly on visual, somatosensory, and (to a lesser extent), auditory information. This cortex has been explored with electrical stimulation of the rostral part of PPC in galagos, small primitive primates from Africa. In these animals, and as found more recently in monkeys, stimulation of each of roughly eight subregions produces a different complex movement.

From lateral to medial in rostral PPC, we found subregions (or “domains”) for looking (eye movements), producing an aggressive face, protecting the face, grasping, bringing the hand to the mouth, reaching, and locomotion.²¹ These domains project to matching domains in the premotor (PMC) and primary motor (M1) cortex, where electrical stimulation produces the same movements. The functional reasons for three cortical stages is not clear, but we speculate that the PPC domains are driven by sensory inputs and that they compete with each other to relay the dominant outcome based on sensory information to PMC and M1.

We suggest that the PMC domains re-evaluate the processing outcomes from PPC with the advantage of additional information, from the prefrontal cortex, and they activate domains in the primary motor cortex accordingly. M1 domains use additional information from cingulate and supplementary motor areas and the motor thalamus to interact and produce the most appropriate action. Deactivating M1 domains renders PMC and PPC domain stimulation ineffective, providing evidence for the hierarchy of decision-making proposed above.

This dorsal stream/action system appears to have been more expanded and modified in more advanced primates. First, the arrangement of domains was rotated from a lateral-to-medial to a rostral-to-caudal cortical sequence. Second, in the evolution of modern humans, more steps were

added to the processing of visual information in the caudal PPC, and more domains added to the rostral PPC, including one for speech production and one for tool use. Likewise, the domain systems of the PMC and M1 likely have been expanded.

We emphasize the importance of this multistage expandable system because the ability to decide rapidly but carefully on the best of several alternative behaviors is especially important for humans, as their long developmental times and delayed reproduction require a long life. Given the limits of available information, some of the conclusions summarized above are speculative and open to further evaluation. Fortunately, modern neuroscience methods provide the means for a better understanding of how brains are similar and different across species, and why that matters. For now, the neural mechanisms mediating the astonishing abilities of the human mind remain incompletely understood, and this should motivate us to look further. It is an exciting time.

Bio

Jon H. Kaas, Ph.D., is Distinguished, Centennial Professor of Psychology at Vanderbilt University, where he has been since 1973. He received a B.A. from Northland College and a Ph.D. from Duke University. Kaas was elected to the National Academy of Sciences in 2000, and the American Academy of Arts and Sciences in 2001. He received the Distinguished Scientific Contribution Award from the American Psychological Association, the Karl Spencer Lashley Award from the American Philosophical Society, the George A. Miller Prize in Cognitive Neuroscience from the Cognitive Neuroscience Society in 2014, Honorary Life Member, J. B. Johnson Club for Evolutionary Neuroscience in 2014, and the Palay Award from the Journal of Comparative Neurology, 2014. He has published over 540 papers and review articles, and edited many volumes including a four-volume series "The Evolution of Nervous Systems" in 2007 and 2017. In 2009 he received the Graduate Mentoring Award from Vanderbilt University.

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