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# Remarkable but Not Extraordinary: The Evolution of the Human Brain

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My object in this chapter is solely to shew that there is no fundamental difference between man and higher mammals in their mental faculties.

CHARLES DARWIN, *THE DESCENT OF MAN*, CHAPTER 2<sup>1</sup>

IN 1871, twelve years after making waves in science and society at large with *On the Origin of Species*, Darwin visited, in *The Descent of Man*, a lingering question his previous work had opened, only to leave unanswered: How far were his general conclusions about the descent of species through modification applicable to humans, if at all?

His start to Chapter 2, “Comparison of the Mental Powers of Man and the Lower Animals,” left no doubts that his answer was “all the way.” The putative mental continuity between humans and other species was a piece of evidence as fundamental to establishing Darwin’s case for human evolution as was the far easier to demonstrate physical continuity. But in 1871, there was not much to argue for (or against) any similarity between human and nonhuman behavior, much less between the

neurobiological underpinnings of mental capacities of humans and other species.

If only Darwin could have known in the late nineteenth century what a then newly born science, neuroscience, would reveal over the coming 150 years. Neuroscience originated with anatomists, physiologists, and physicians who were already at work at the time of Darwin's writing of *Descent*, and who over the next few decades became more and more interested in systematically tracing the makings of the mind to the workings of the brain.

In 1863, French physician Paul Broca had described, before members of the Anthropological Society of Paris how language was disrupted by lesions to the frontal lobe on the left side of the human brain. That confirmed Prussian anatomist Franz Gall's views that different parts of the brain had different functions in generating the mind<sup>2</sup>—much as the various organs of the body were already known to have separate, if inter-related, roles in supporting life.

It is easy to understand how, compared with some obvious similarities between humans and other species in bodily shape and overall organization, the mental powers characteristic of humans would appear strikingly different from those of other species and thus cast doubt on any proposition that humans descended from some “lower form.”<sup>3</sup> Descent presupposes gradation, and by the late 1800s, any transition between an apelike form and the modern European men carrying out such studies seemed outlandishly sudden, not to say impossible. There were too many “missing links,” and not just in the fossil record. How could the seemingly extraordinary human intellectual faculties possibly arise from a brain so like those of so many other species, only larger?

Curiously, over most of the 150 years since Darwin's *Descent*, neuroscience has addressed that fundamental question of how mammalian brains are generated and organized in *similar* ways across species, from mouse to human, while simultaneously harnessing expectations and theories of human exceptionality. Evolutionary conservation across mammalian brains and bodies—the very foundation that allows clinical and neuroscience research to use mice, rats, cats, rabbits, dogs, pigs, and

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monkeys as laboratory surrogates for humans (and to some extent even chicks, fruit flies, and worms)—has coexisted with the suspicion that deep, deep down, the human species is different where it matters the most: its brain. Darwin would have been befuddled, I think, at how his legacy could at the same time be embraced (humans evolved, like any other species) and disputed (for surely human evolution must be distinguished by some unique set of events and features)—and by the same individual scientists.

Of course, if the human foreigner is easily and unmistakably singled out in a band of our closest living relatives, chimpanzees, and not just because she is the only one cloaked in fabric, it is because various features *do* differ between the species. But that was exactly Darwin's point: that over time and generations, species that once were one and the same retain some similarities while still becoming more and more different in other ways. The question that mattered for Darwin in Chapter 2 of his *Descent of Man* was not whether human mental faculties belonged with the former (the similar) or the latter (the different) but whether human intellectual faculties, clearly "superior" to those of "lower animals,"<sup>4</sup> differed only in degree from the intellectual faculties of other species, or also in kind. It is a question that would have remained restricted to metaphysics and science fiction—for how could one get into another animal's mind to know it?—if not for the cunning and persistence of a legion of scientists.

I'd like to make clear that, Darwin's arguments notwithstanding, the exact answer to the question of whether human brains and mental functions differ in degree or in kind from those of other animals is actually irrelevant for the purposes of establishing whether or not modern humans descend from some relative shared with great apes. That has by now been amply and solidly determined by decades of work by paleontologists, archaeologists, primatologists, geneticists, biochemists, and biologists. So much accumulated evidence makes it today an undisputed fact that humans in their modern incarnation—size, shape, and all—did not exist on the planet as recently as half a million years ago, just as it is known that splendid triceratops and velociraptors once roamed the Earth but now only modest-size birds serve as reminders of

their existence. What persists as *hypothesis* is the narrative of precisely *how* that happened.

Still, it is an interesting point: whether human brains and therefore their minds differ from those of other primates, and even other mammals, in kind or simply in degree. It is an important one, too, and for more than philosophical reasons or self-serving hubris. If the human brain is essentially made in the image of other primate brains, as Darwin submitted, then much insight is to be gained into our own humanity from studying and understanding other fellow primates and their ways and behaviors. If the human brain is mostly just a large primate brain, and we understand how a primate brain is both similar and different from a rodent brain, then there is plenty to be learned by studying the brains of mice and rats, which develop in three weeks, not forty, and then mature, age and die in the tractable space of two years, not eighty, which makes much of human-relevant research feasible within the lifetime of individual researchers. And once mental functions can be mapped onto brain circuits, then understanding the evolution of the mind becomes a much less ethereal task, for reconstructing the evolutionary history of the brain can offer direct insights into what mental functions are or were available to different brains, living or dead.

Neuroscience has learned much in these 150 years about how the brain is organized and how it generates the mind, and these insights have informed the comparison between the “intellectual faculties”<sup>5</sup> of humans and other species. Whereas it is likely that the brains of insects, mollusks, and vertebrates appeared independently in evolution (even if organized by many of the same genes), all vertebrates and their brains are solidly rooted together, forming one large genealogical tree that descends from the same common and exclusive pool of ancestors. I will stick to the brains of vertebrates here, although, as it turns out, many of the most basic principles of brain structure and function are applicable across the board: organization in loops, spontaneous activity modulated by the senses, and associative connections that create complexity, flexibility, and the ability to reference the self.

The first principle is that all nervous systems, in all animals with one such system, are organized as closed loops that feed signals from the

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body to the brain and take signals from the brain back to the rest of the body. The former are conveyed through the senses; the latter, through nerves to muscles and viscerae, including glands, which make changes to the body—changes that then immediately circle back to the brain through the senses. The important part about the loop arrangement is that there is no beginning, middle, or end to signal trafficking in the nervous system. Every sensation can lead to an action; every action leads to a sensation. The loop becomes active as it forms and only silences in death.

Reflex movements, recognized in the nineteenth century,<sup>6</sup> are a type of action that occurs through the simplest of loops: those formed directly between a sensory surface and the muscles that move it. The loop is short and simple, and reflex actions are so named because they quickly and stereotypically “bounce back” from the nervous system directly or indirectly to the body part of origin—a finger being pulled back after touching a hot stove, for example. If there is a triggering stimulus, the reflex action always occurs and always in the same way.

Reflexes were already known to scientists and physicians in Darwin’s time and were recognized as “basic units” of behavior. Herbert Spencer, and then Charles Sherrington, famously proposed that behavior was a series of coordinated reflex actions chained together, one right after the other.<sup>7</sup> This was an influential view that steered many lines of research well into the late twentieth century, until two discoveries rocked the field. One was Sten Grillner’s demonstration that neurons form circuits that can generate patterned behavior, such as rhythmic swimming, walking, or breathing, but that patterned behavior could happen in the absence of patterned sensory input.<sup>8</sup> All it takes is a steady signal that turns the entire circuit on. Increasing or decreasing the strength of that steady signal suffices to modulate the behavior, turning a walk, for instance, into a trot and then into a gallop.

Even more transformative was the growing recognition in the 1990s that the brain is dominated by “ongoing activity”: spontaneous variation in how excitable different neurons are at any moment, variation that suffices to turn circuits on and off independently of sensory input.<sup>9</sup> The ongoing, internally generated activity can spread among neurons and

circuits, and take on patterns in space and time that mimic those elicited by the senses. For instance, for a person with eyes closed in a dark room, the image of a loved one on a sunny or rainy day can come to mind. Such internal activation of sensory representation constitutes the basis of memory recall, imagination, and dreaming.<sup>10</sup> Starting in the late twentieth century, then, there was growing recognition that animals and their brains are not necessarily confined to their present environment and circumstances. Neurons were upgraded from mere transistors in a circuit to autonomous units that could generate patterns of their own. Sensory input from the environment was downgraded from master controller of behavior to a modulator that interfered with the ongoing activity of the brain and thus nudged or even pushed behavior this way or that way but was neither necessary nor sufficient to cause behavior, except for those truly reflexive actions. In this scenario, mental activity, however defined, must be something that brains can generate spontaneously, depending on how their loops are organized, and to a degree that is in some proportion to how complex these loops are. And if it turned out that those neuronal loops and circuits in the brain were organized in similar ways across species, then the inevitable conclusion would be that the minds that those brains can generate must not differ terribly in kind, just as Darwin hypothesized.

As it turns out, vertebrate brains are much more similar to than they are different from one another in how their neuronal loops are organized into circuitry. All of them have simple, direct loops between body and hindbrain or spinal cord that suffice to generate reflex actions, such as adjustments in blood pressure, blood flow to the organs, automatic movements of the eyes that track objects, or small corrective movements that maintain body posture. Those loops are connected to circuits in the hindbrain—the part of the brain connected to the spinal cord—that integrate sensory information and ongoing activity and feed it back onto the outgoing neurons in the lower loops. These hindbrain circuits are the unsung heroes of behavior, those structures that effectively, ultimately, control whether one is awake, asleep, or somewhere in between; when one starts walking, breaks into a gallop, or stands still; when breathing stops and swallowing, talking, or singing happens

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instead; where eyes and ears are directed; how much blood pressure rises or drops; what digestive enzymes are secreted and in what amounts.

These hindbrain loops, in turn, are subject to the influence of yet other loops—ones they establish with the cerebral cortex. The cerebral cortex is a structure formed almost all the way up in the neural tube that gives rise to the nervous system in early development, posterior only to the part of the brain that controls all glands in the body: the hypothalamus. Just as the hypothalamus is the master of all things secreted in the body, the cerebral cortex, by virtue of its connections with all other loops that operate the body, has control, or at least influence, over all actions of the nervous system that are executed by those lower loops. Even the cerebral cortex is subject to modulation by other loops, such as the basal nuclei and cerebellum, which make actions smooth and fluid and keep sensory surfaces stable and ready for what is expected to come.

Within the cortex itself there are even more loops, such as those that bring information together from all the senses into the hippocampus and back to the cortex. New memories are formed as the hippocampus weaves together sensory associations that become written into the circuitry of the brain. Without memory, every animal would be forever stuck in the present, doomed to reacting to stimuli and asking the same questions over and over again. With memories, animals gain a past, and with the ability to evoke the past to make plans, they gain a future. Other parts of the cerebral cortex, especially the prefrontal loops, generate representations of those plans and associate them with information from the senses on the current context, position, and situation of the individual. With these associative cortices, behavior gains complexity. A key function of these particular cortical loops, for instance, is executive control: the capacity of going beyond simply responding to the present reality as assessed through the senses by modulating behavior according to internal reasoning and plans. Yet other cortical loops form the default-mode network, which allows referencing actions and sensations to a self anchored in the body, and the social network, which allows the cortex to represent others and their feelings and intentions, and thus allow behavior of the individual to take others into consideration.

The cerebral cortex, in control of all other loops in the brain and endowed with its own internal loops, thus sits in a position that allows it to influence behavior by generating past and future, internal plans, preferences, and goals, and representing the self and others in a spatial, temporal, and cognitive context. A cerebral cortex is not strictly required for an animal to behave (in the purest sense of doing observable actions). The hindbrain handles that very well, and even human babies born without a cortex will nurse, cry, and smile. But when a cerebral cortex exists, it allows for a new level of integration of information that no hindbrain alone attains, with behavior that can be flexible and complex—never the same twice, never fully predictable from the senses.

All vertebrates possess a cerebral cortex to some degree, whether large and obvious (as in humans) or very discreet (as in fish and reptiles), layered (as in mammals) or arranged in compact chunks (as in birds). Where it has been examined, functional cortical connectivity—the layout of what structures are linked and work together—turns out to be very similar across species. Humans, like monkeys, rats, mice, and even pigeons, have cortical loops that receive copies of all information processed by the hindbrain, harbor information-processing hubs in a recognizable hippocampus and associative cortical areas, and function in tight loops with basal nuclei and the cerebellum.<sup>11</sup> Monkeys and even rats, like humans, have an anatomically and functionally recognizable self-reference network of neurons whose coherent activity supports self-awareness, anchoring the self to the body and its location. In all three species, coherent activity in this network dissolves in sleep and anesthesia.<sup>12</sup> Along with it goes human consciousness;<sup>13</sup> it is only reasonable to infer that sleeping or anesthetized mice and monkeys are unconscious for similar reasons.

There remains little to be disputed over whether brains of humans and other vertebrate species are organized in similar ways. They are, inasmuch as the same structures are recognizable and connected in similar ways. The questions that remain are questions of degree—a reality of modern neuroscience consistent with Darwin's predictions. One is: to what degree are functional brain networks really similar across humans and other species? Would their neurons be interchangeable

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across species? (To the extent that human neurons survive in mouse brains, we do know that neurons can be interchanged).<sup>14</sup> Is a pyramidal neuron in, say, the human insular cortex set up with the same ion channels, neurotransmitter receptors, and second messenger cascades as a pyramidal neuron in the mouse cortex? (Remarkably, yes: neuronal cell types are defined by very similar constellations of genes expressed in mouse and human).<sup>15</sup>

We know to expect discrete genetic differences across species—one amino acid here, maybe a small stretch over there—given the well over 50 million years that separate the last common ancestor shared by mouse and human. Such small differences may produce a small effect, none whatsoever, or maybe completely rewrite the functioning of a cell. A collection of such small differences certainly lies behind the obvious differences in appearance between humans and chimpanzees, which share an ancestor that lived only 6–7 million years ago. It seems only logical that similar small differences exist between their brains and neurons.

Indeed, the past decade has seen a surge in studies that seek and find differences between human genes and their counterparts in other species, especially in genes expressed in the brain. Curiously, the idea that the human brain must be fundamentally different from others is contrary to Darwin's reasoning and resonates instead with expectations of his contemporary Alfred Russel Wallace. But so far, no striking differences have been found that would cause radical changes of *quality* rather than gradual differences of degree. The list includes synaptic densities that are slightly higher in human brains than in mouse brains, a particular type of glial cell that is larger in the cortex of the former, and myriad genes that have been shown to impact how many neurons are generated in the brain during development.<sup>16</sup> It is unlikely that any single difference can be pinpointed as *the* difference that distinguishes the human species from any other chosen as a reference. Rather, what seems to matter most is the degree to which differences accumulate and modify the result.

Another question of degree, orthogonal to and nonexclusive of the first, regards the size of the brain networks: how many neurons com-

pose them in different species? Could differences in cognitive capabilities across species be traced to differences in the absolute numbers of neurons available for signal processing in each node of the various networks? The underlying assumption here is that neurons are the basic information-processing units of brain networks. Inasmuch as the networks are assembled in similar patterns (which they seem to be), then the greater the number of the neurons that compose a network, the more capacity the network should have to process information—as long as the larger network remains viable and affordable. If a larger brain were a scaled-up version of a smaller brain, built with more neurons that multiply the fundamental loops, like a computer assembled with one, four, or twelve cores, then the more processing units that form a brain, the larger its processing power should be.

Over the past fifteen years, my laboratory has been collecting data systematically on the numbers of neurons that compose the brains of different species, humans included, and can offer new insight that I like to think Darwin would have found illuminating. In quantitative terms, it turns out that the human brain, the seat of the human mind, is made in the image of other primate brains in every way we have checked—except that there's more of it.<sup>17</sup> Larger primate brains have more neurons of about the same average size as smaller primate brains, and humans are no different in this regard (Figure 2.1). Larger primate cerebral cortices have more neurons than smaller primate cortices, and the human cortex, with its 16 billion neurons on average, has as many neurons as could be expected in a generic primate cortex of about 1.2 kilograms. We also have just as many cortical neurons as could be expected for any mammal with our number of neurons in the cerebellum, one of those structures that forms loops with the cortex. Our cerebral cortex is exactly as folded as could be expected of a generic mammalian cortex with its surface area and thickness,<sup>18</sup> and uses the amount of energy—20 percent of all energy consumed by the body—that could be expected for its number of neurons.<sup>19</sup>

Even the size of the human brain is just as expected for the size of our body. Sure, the human fossil record demonstrates that the earliest members of our lineage had brains that were roughly the size of the brain of

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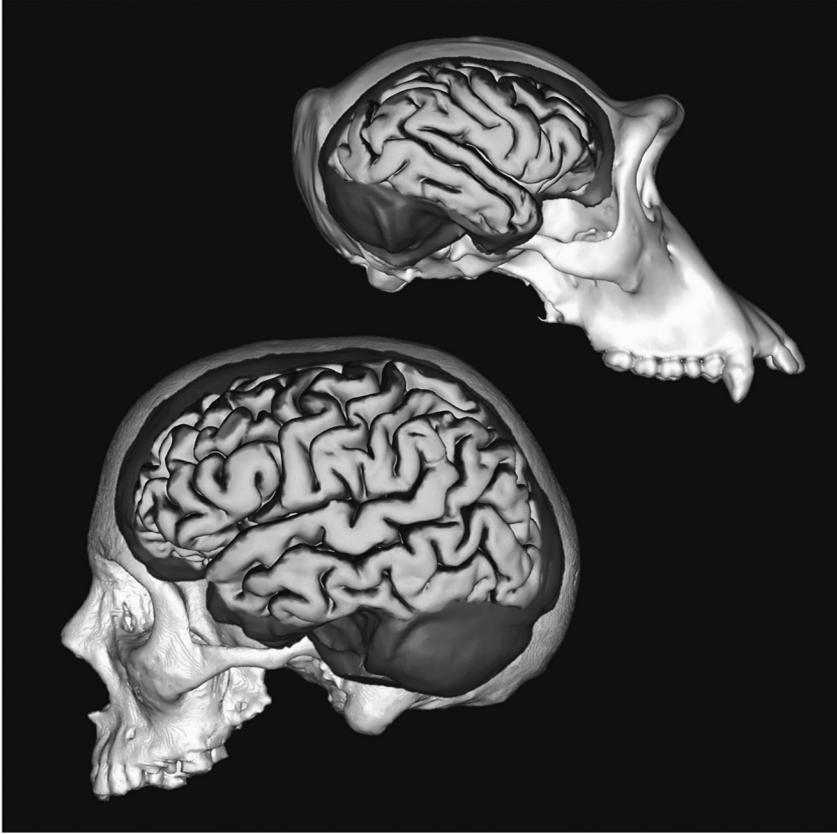


FIGURE 2.1. Brain size and shape in *Homo sapiens* and our closest ape relative, the chimpanzee. (Image courtesy of Aida Gómez-Robles and Jose Manuel de la Cuétara)

a modern chimpanzee; over the past 2 million years, the largest brain of any *Homo* species tripled in volume. Paleoanthropologists have observed that body size also increases over this time, and it is possible that brain increase is just a by-product of body-size increase. Even enlarged over its evolution, the human brain amounts to about 2 percent of body mass, as in most other primates. Here, it is great apes—gorillas and orangutans—that are the exception. Because larger animals tend to come with larger brains, the fact that gorillas and orangutans can be up to three times the size of a modern human but have brains that amount to only one-third the mass of ours was taken as evidence for decades

that the outlier—the special one—was the *human* brain, which is about seven times as large as it should be for our body size. Changing the reference changes the conclusion, however. Compared to most other primates, our brain is just as large as it should be, making the brains of great apes smaller than would be expected, given the trend of primate brains being 1 to 2 percent of body mass. Gorillas and orangutans have retained relatively small brains despite their larger body size. We found that there is good reason for that: these great apes are at the limit of the food-gathering capacity of primates in the wild,<sup>20</sup> given that all of us primates spend eight to nine hours per night lying down and still have other business than eating to tend to during the day, and larger brains would require more energy input in the form of food. So, yes, humans and great apes are dramatically different in the proportion between brain size and body size. But it's not humans who deviate from the primate norm; it is the great apes who were apparently forced to stick to not-very-large brains, retained despite, or exactly because, of their larger body size.

Ancestral humans and ancestral gorillas and orangutans seemingly went different ways in how their evolutionary paths were impacted by the trade-off imposed by a strict limit to how much energy is available through diet to power their brains and bodies. Great apes enjoyed the benefits of investing in larger and larger bodies, while paying the price of not affording a proportionately increased number of neurons; *Homo* stuck to the lean body shape of smaller primates, making more energy available to feed increasing numbers of neurons, especially once simple stone tools and eventually sophisticated cooking technologies were invented. One is not a better path than the other; both were successful in making it to now. Once *Homo* species cooked their food, they overcame the energetic constraints that otherwise apply to larger apes, and the possibility of a larger primate brain opened up to them in a trend that continued until the largest *Homo* brains had nearly tripled in size.

And so, here we are, the primate species with the largest brain and therefore the most cortical neurons among primates. Being a primate, in this case, turns out to be a very important distinction, for the non-primate way of putting brains together involves neurons that quickly become larger as they become more numerous.<sup>21</sup> As a consequence, a

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primate brain or cortex has more neurons than its non-primate counterpart, and the larger the brain, the larger the difference in favor of the primate species. A gorilla's cerebral cortex is somewhat smaller than a giraffe's but has five times as many neurons. The human cortex has three times as many neurons as an elephant's cortex, even though the human cortex is only half as large. But at about twice the size of a gorilla's cortex, the human cortex also has about twice as many neurons. Humans indeed are more similar to other primate species than any primate is to other mammalian species. We do have a brain made in the image of other primate brains. I like to think that Mr. Darwin would have appreciated that news.

To the best of our current knowledge, the most consequential distinction between human brains and other brains is that we have the largest number of neurons in any cerebral cortex, even including those of the largest whales. That is not because humans stand out from other mammals in how their cortex is built but simply thanks to the double distinction of being the species with the largest brain that is also built the primate way. Just as Darwin expected, there is a gradation in brain size and number of cortical neurons across mammalian species; it follows a relationship that can be described mathematically by a simple power law, and humans fall right along the line.

With more neurons in the cerebral cortex, including its prefrontal associative areas<sup>22</sup> and the hippocampus, it is only to be expected that a result will be an improvement in those cognitive capabilities that depend on representing the past and learning to make predictions from it, forecasting different scenarios, and choosing one according to the best criteria at hand. One of these capabilities is the very working definition of intelligence, according to physicist Alex Wissner-Gross: the ability to choose the course of action that leaves most possibilities open.<sup>23</sup> A new species with more neurons in the hippocampus and connected cortical areas, including the prefrontal cortex, should gain a boost in its decision-making capabilities and thus intelligence, as so defined. Curiosity, which stems from identifying patterns and breaches in them, investigating the sources, finding the problem caused by the changed pattern, and then solving it, should also grow with the number of cortical neurons

(although it is doubtful that the same logic applies at the much smaller scale of individual differences *within* a species, where environmental factors and opportunities are known to have huge effects, as examined later, in Chapter 5 of this book). The same logic applies to all other mental faculties that benefit from the complexity and flexibility that cortical processing brings to the table, faculties also long underrated in other animals. If there is a gradation in numbers of cortical neurons across species, there should also be a gradation in the cognitive capabilities they underlie. If one defines intelligence more broadly as behavioral flexibility, as I do, then it is only to be expected that the more the cortical neurons across species, the greater its capability for flexible and complex, and therefore intelligent, behavior.

Indeed, ever since Darwin, nonhuman primates, then non-primate mammals, and more recently birds have been awarded higher cognitive status than even Darwin himself might have suspected. He did consider that similar emotions were expressed across species, and we now know that the circuits underlying anger, fear, joy, and pleasure are very much the same. But shared across humans and other mammals are also maternal care, deceit, self-recognition, planning for the future, playing, learning by imitation, using and making tools, cooperating in problem solving, having a sense of beauty, and even appreciating the taste of food touched by fire. All mammals that have been examined have REM sleep, when cortical representations are reactivated from the inside and humans are known to dream. So it is only reasonable to expect that other mammals also dream, as the twitching and whimpering of sleeping pet dogs appears to confirm. And if they dream, then all that is required for imagination—an ability to conjure images in the absence of their stimulation through the senses—is there. Considered together with the finding that the self-representation network is also there in other animals, it is only to be expected that other mammals also have gradations of self-consciousness. We humans just happen to have loads of it, courtesy of 16 billion cortical neurons organized in loops within the giant loop that is our nervous system.

Even more importantly, we also know by now that the intellectual benefits of having larger numbers of cortical neurons are not strictly

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limited to biology: they expand into a culture that transcends individual living experiences. Contrary to expectations that larger animals live longer as their metabolic rate decreases (which would supposedly slow down the rate at which damages accumulate), it turns out that maximal life span is extended together with the number of neurons in the cerebral cortex, regardless of body size or metabolic rate.<sup>24</sup> The greater the number of cortical neurons in a warm-blooded species, whether bird or mammal, the longer the maximal longevity of the species. This recent finding explains a number of contradictions in the former metabolic-rate-based framework, such as how a 300-gram cockatoo can live for as long as fifty years, but a lab rat of similar body mass will not make it past three years. It also accounts for why gorillas have a shorter maximal life span than our species, about half the length, even though, with bodies two to three times heavier than ours, their metabolism is slower.

Increased longevity comes along with lengthened childhood, too—another characteristic that used to be considered distinctive about the human species, a derived evolutionary feature. But, again, this may have been because the measuring stick was gorillas and orangutans. If they are larger than us, they should mature later than we do. But it is humans who mature later, at about thirteen years of age, versus eight in those great apes. However, when numbers of cortical neurons are used as the metric to predict age at sexual maturity and maximal longevity, then humans once again fall right along the line, as do great apes. Yet again, humans are not special animals; we are as slow to mature and to age as could be expected of any warm-blooded animal with our number of cortical neurons.

Why more cortical neurons are accompanied by longer lives is a completely new and open question. We first have to ask whether there is any causation involved; it could be that more cortical neurons are just a very good proxy for something else that really matters in extending life. It could also be that damages accumulate stochastically at the same rate across all warm-blooded animals, regardless of their specific metabolic rate (my favorite hypothesis at this point), and so having more neurons—the one type of cell in the body that does not replenish itself during our lifetimes—endows cortical networks with more resilience

to accumulating damages. With more cortical neurons still healthy enough to keep body and mind functioning as an integrated whole, life would keep going on much longer.

However it happens, though, the fact that those animals that have more cortical neurons also are slower to mature and live longer has enormous consequences. Without going down the rabbit hole of what comes first or what drives what, it seems fitting that longer-lived animals have more cortical neurons that allow them to deal with the increased amount of information that they will encounter over their extended lifetimes, starting with their longer, parent-sheltered childhood. Likewise, the increasing knowledge accumulated over a longer life gets to be passed down to a next generation that has both more neurons and more time to assimilate it. The story of human evolution thus gains a new dimension with the near tripling in brain size and therefore number of cortical neurons over the past 2 million years. It is a story of presumably increased cognitive capabilities, yes, but also of delayed maturation and increased longevity, and therefore of increasing overlap between generations and, with it, growing opportunities for cultural transfer, learning, and systematization of knowledge.<sup>25</sup> Biology changes, and culture benefits from it.

The implications of accepting the biological and evolutionary continuity between humans and all other mammals are manifold, starting with the fundamental realization that if the same principles that orchestrate behavior in other animals apply to us, with the difference that we have enough neurons to fully represent our own predicaments and use our past to interfere in our future, then there is no longer reason to believe that consciousness is exclusive to humans. Instead, it must differ in degree, not quality, across species, depending on how neuron-rich their cortical circuits are and thus how complex and intricate their representations of self and world can be. I have been asked where to draw the line: What animals have enough cortical neurons that they should be granted personhood and humanlike rights? How many is enough—1 billion? That would include monkeys and all cetaceans but leave out dogs. Or should it be 5 billion, which would separate only elephants, great apes, and the largest-brained cetaceans, besides humans,

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from the pack? In recognition of gradation, I prefer to argue that the only reasonable course of action is to be respectful toward all creatures, the neuron-rich and the neuron-poor. While it is fine to focus on what distinguishes humans from all other creatures, I prefer to emphasize how biology and neuroscience teach humans to be more humble toward the world, to encourage the appreciation that what has come to distinguish modern humans from all other animals is the culture and technology accumulated over hundreds of thousands of years, and faster and faster at each generation. Thanks to all the achievements those 16 billion cortical neurons in our brain have earned us, human biology is no longer enough to make us modern humans. It takes learning, systematizing the know-what and know-how in past and current generations, figuring out ways to pass it on, and then learning some more. But all the while, we never stop being primates—exactly as Darwin told us.

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