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Introduction

DIFFERENT BRAINS

Different brains are everywhere around us. And they fascinate us.

Which parent of a young child has not wondered what happens inside that little head? And been delighted when the child suddenly produced a new behavior—a fascination with numbers, understanding how to twist jigsaw pieces to fit, or simply standing up—like a light went on?

Which dog owner has not pondered how much the animal truly understands? How similar the dog's thought processes are to our own?

We wonder about the brains of other people constantly. Their thought processes, whether they perceive the world exactly the way we do, what they know, think, and feel.

And then there are the truly alien brains. The tiny ants that are able to produce complicated colonies, some even using other animals as slaves. The octopus with its distributed processing centers in its eight limbs.

How do all these brains relate to our own?

This book aims to answer these questions. As any biological system, the brain is a product of evolution. Through descent with modification from a common ancestor each brain in the world today both shares some aspects with all others and is truly unique. By comparing brains and understanding what different circumstances occurred during their evolution, we can start to understand both our own brain and its relationship to other brains.

Science is currently going through a revolution in our understanding of the brain. In these pages I hope to share some of the new insights we have recently gained and—probably—shatter a few myths along the way. But before we do this, let's make sure we are all familiar with the main ingredients: evolution, comparative biology, and modern neuroscience.

Thinking about brain evolution

January 1871. Charles Darwin is sitting in his study in Down House, the manor in the Kent countryside where his family moved to get away from busy London life. He has just finished correcting the proofs of his new book, *The Descent of Man*. In this work, he explores whether the rules for evolution by natural selection apply to humans as much as to any other living being. It is a book he never intended to write. Although Darwin was a prolific writer, he was very cautious of revealing too much of his theories before he felt they were absolutely ready. When he first published his theory on natural selection, it was under pressure. A letter he received in 1858 tipped the balance. The explorer Alfred Russell Wallace had reached similar conclusions to Darwin and asked Darwin to forward his letter outlining his theory for publication. The fact that somebody was about to scoop him pushed Darwin to publish his ideas on natural selection. He always suspected his theory would be explosive. To keep it a bit under control, he refrained from mentioning what his theory meant for humans—that they were not the pinnacle of God's creation, but simply another life form among many.

The central problem that Darwin tried to address in his work was whether species are stable or can change over time. The Bible of course states that all species have been created in their present form, but the idea of gradual change—evolution—was already present in Victorian scientific thinking. During his voyage around the world on the HMS *Beagle*, Darwin noticed fossils of extinct animals that very much looked like the present-day animals living in similar locations. The present-day animals seemed to have evolved from the fossil ones. The problem was how did they change and why? Some people had proposed that changes occurring during life are passed on to the next generation; some favored a more directed evolution with solutions to problems appearing spontaneously in some individuals. Darwin agreed that variation was key. But he did not agree that variation could be acquired and passed on, or that variation had a goal in mind. The crucial element he added was selection. If there is random variation in the population, and some variations make you more likely to survive, then that means that some of the variations are simply more likely to spread. Darwin's crucial insight was thus not that evolution happens, but that adaptation occurs by natural selection among existing variants. This explains why a certain trait is present. At some point along the evolutionary path, a trait helped its owner survive or, more accurately, have more surviving offspring. No creation by God, no selection of acquired characteristics, no prospective insight of evolution. This was the theory he published in his seminal work, *On the Origin of Species* in 1859. Anticipating that his theory would stir up trouble, he decided to hardly mention humanity in his book.

Since the publication of his theory in 1859, things had changed. Sure, there had been uproar and fierce discussion, most famously at a debate at Oxford's Natural History Museum where the bishop Wilberforce is believed to have asked the Darwinists if they descended from apes on their mother's or father's side. But there had also been acceptance. In the beginning of his new book, Darwin explained how young researchers were increasingly accepting of his theory. The time was now right for him to systematically investigate how applicable his ideas were to humans.

It is worth thinking a bit about what Darwin's idea means. It means that to understand any aspect of life—be it an organism, an organ, or a behavior—we need to understand its ancestral history and the drivers and constraints of change. To start with the ancestral history, this implies that related animals are likely to be similar—their bodies and organs did not appear spontaneously from nowhere. This is why animals have rudimentary organs, like the muscles some of us have to move our ears. They are leftovers from something that our ancestors had. It means there are constraints. Selection can only work on the natural variation that occurs in the population, so changes are likely to be gradual. We also have to work within the context of an already functioning organism. We do not just grow an extra arm, because that would not be compatible with the existing body plan. Most importantly, it means that for a trait to have made it into the population, it should have given our ancestors some benefit, some advantage over those who did not have it. The advantages themselves are shaped by the environment of that ancestor. They have to work in those circumstances, without foresight. Importantly, adaptations at one moment in time can seriously constrain an animal in the future. An extreme example of that is the extinction of the dodo. Being a trusting non-flying big bird can be fine if you live on an isolated island, but works a lot less well when large human predators arrive—the dodo ended up being an easy dinner for hungry sailors. Natural selection for trusting dopiness worked well at some point in time, but less well at another point. So, to really understand why something is the way it is in biology, we need to take into account its adaptive benefits at the time that it appeared, not just its current function.

In the early versions of *The Origin of Species,* Darwin did not really talk about brains. That changed in this new book. In building his argument for continuity between humans and other animals, he referenced work describing how similar the human brain looks to that of the orangutan. He then described many aspects of the brain's output—behavior and mental abilities—that he believed are similar between humans and nonhuman animals. He conceded that humans are particularly good at some things, like using tools, but argued these were mostly differences in degree rather than in kind. He also argued that such human abilities vary in the population, meaning there is variation that can be the target of selection. The brain, he argued, is subject to the rules of evolution by natural selection, just like any organ. Charting brain evolution was not Darwin's goal, however. He gave us all the ingredients to find out about brain evolution, but we still have to bake the cake.

Comparing brains

Autumn 1891, the island of Java in the then Dutch Indies. Eugene Dubois is directing his team of mostly convicts digging in the ground of a riverbank. Dubois had left a cushy position as lecturer at the University of Amsterdam, took on a position as army physician, and dragged his wife and newborn daughter out to the colonies, all to pursue his dream—to find the missing link between humans and great apes. He agreed with Charles Darwin that humans evolved from a common ancestor we share with the living apes—chimpanzees, bonobos, gorillas, and orangutans. He disagreed with Darwin on where this ancestor had lived. Where Darwin suggested Africa, Dubois bet on the tropics of Asia. His efforts would be rewarded. His men found a tooth and a skull cap, the top bone of the head. It had a heavy bow ridge. It was not an ape, but it was not quite human either, while the tooth looked more like that of an ape. A year later, Dubois's men found a femur, also known as a thighbone, about 15 meters from where the skull was found. Its shape suggested its owner had walked upright, just as modern humans do. From the skullcap of the head, it was possible to estimate the size of the brain that was housed in this head. It turns out it was about 900 grams, smaller than the 1.3 kilograms of modern humans, but much bigger than the 400 grams of the chimpanzee. Dubois was convinced he had found his missing link and termed the creature *Pithecanthropus erectus*, the upright ape-man. Today, the species is called *Homo erectus*. It lived between two million and 100,000 years ago and was the longest-living species of human ever to walk the earth.

If we want to know something about the bodies of our ancestors, one way is to go out and look for fossils, as Dubois did. Fossils are any preserved remains, impression, or trace of a once-living organism from a past geological age. They can be stone imprints of microbes, mosquitos preserved in amber, or DNA remnants, among others. But in most cases, what people associate with fossils are the petrified bones of animals. Unfortunately, soft tissue such as brains generally does not fossilize.

This leaves paleontologists with only very indirect measures of brains gone by. If a skull is found at a fossil site, it is possible to use it as a mold to create an endocast to get a rough estimate of the size and shape of the brain. We can then compare the size of the brain to the size of the body. Larger animals tend to have bigger brains, but if an animal has a particularly large brain for its body size, we say it is encephalized. This might mean that the animal has invested in brain size as an evolutionary adaptation. The study of the relationship between brain size and body size is part of the scientific field of allometry. Perhaps unsurprisingly, Dubois was one of the pioneers of this particular field. Upon his return from the tropics, he took up a position at the Teylers Museum for art, natural history, and science in the city of Haarlem in the Netherlands. At the time, the museum housed one of the most spectacular collections of animal skeletons in the world. The variety of fossil skulls allowed him to study encephalization of the brains of different mammals.

But the approach of using the skull to reconstruct the size of a brain assumes the entire space in the skull was previously filled by the brain, which is not always true. In many early mammals, the brain was kept in place by cartilage, another tissue that does not fossilize. Endocasts also only tell us about the outside shape of the brain, nothing about its cells and its internal organization. Some big brains contain folds, only some of which might leave an imprint on the skull that would in turn be visible in the endocast. If we know a bit about how different parts of the brain relate to such landmarks, it can help us reconstruct some of the brain, but it will always be an approximation. In all, fossils will always provide us with only limited information about their owners' brains.

If fossils are so unreliable, what else can we use? The solution is to compare the brains of living species. Contrary to the

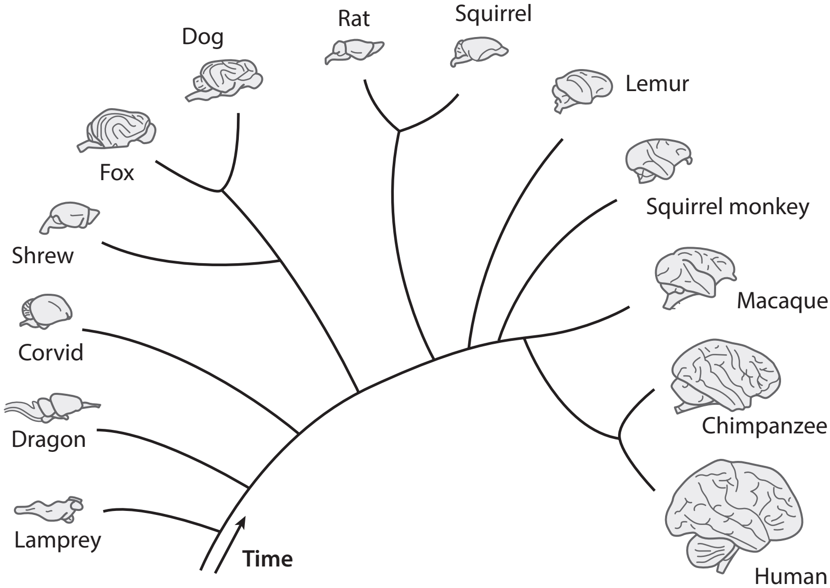

FIGURE 0.1. Evolutionary tree showing the vertebrate brains discussed in this book.

famous picture of human evolution where a chimpanzee slowly morphs into a modern human over evolutionary time, all currently living species are what we call crown species. This means that all animals are the current representative of a unique lineage of them and their ancestors back to their most recent ancestor with another living species. In other words, all currently living species are to some extent equally evolved and none are the ancestors of others. We have a common ancestor with chimpanzees and this ancestor was likely a great ape; chimpanzees are not our ancestors but our sister species. By systematically comparing similarities and differences between living species, it is possible to reconstruct their ancestral relationships. Traditionally this was done by looking at similarities and differences in the size and shape of different organs or similarities and differences in developmental patterns. Nowadays this is mostly done through comparison of genetic material. Animals whose genetic material is more similar are assumed to have diverged from a common ancestor more recently than animals whose genetic material differs more. Using this approach, we now have a pretty good idea of the evolutionary tree of living animals.

We can use this understanding of the evolutionary tree to investigate how the brain has changed. If we compare the brains of, say, a human and a chimpanzee, any feature that they share is thought to have been present in their common ancestor. If we find anything that is different, something changed in the lineage leading up to the human or in the lineage leading up to the chimpanzee. To find out which it is, we can look at an additional species. Gorillas had a common ancestor with humans and chimpanzees about nine million years ago. If we find something that is different between humans and chimpanzees, but is shared between gorillas and chimpanzees, we can infer it is due to a change in the line leading up to humans. If we then would also know how the environment of early humans differed from that of chimpanzees and gorillas, we can start figuring out what the role of the human feature was.

What about when very distinct animals share a particular feature? For instance, humans, elephants, and dolphins all have very big brains for their body sizes, but they are not very closely related. In fact, all of them have much more closely related animals with much smaller brains. This could be a case of convergent evolution, where a similar feature has evolved multiple times in unrelated species. Convergent evolution is really useful, because we can use it to link the brain to its environment. If the feature not only evolved multiple times, but it did so under similar circumstances, we have a much better idea what problem that part of the brain helped to solve.

Ultimately, we want to understand what changed in the relationship between an animal and its environment, its *ecology*. If an animal's environment changes and it needs new strategies to survive, variations that occur in the population might mean that some individuals start being more successful. Differences between individuals in bodies and brains—they often go together—will mean that selection can do its work. We should keep in mind, though, that we are looking at animals that are the results of long evolutionary histories, even since the time of their most recent shared ancestor with another species. Humans did not suddenly appear from a common ancestor with chimpanzees due to a single change in ecology. More likely, two populations of human-chimpanzee ancestors got separated, the circumstances for the two populations changed in different ways, and step by slow step, different adaptations got favored in the two populations. The species that survive today, we call "chimpanzee" and "human," but they are the surviving end results of many experiments to adapt to circumstances over time.

The comparative method gives us a way of studying brain evolution when fossils are not available. If we can analyze enough brains, find what's similar and what's different, and relate that to the animals' ancestral history and their current circumstances, we can get an idea of what was driving their evolution.

Scanning brains

Summer 2016, a basement in Oxford. My colleague Sasha and I are sitting behind a series of computer screens, staring at images coming in. From behind a shielded door comes the sound of the MRI scanner. MRI scanners are standard in every hospital, used to look at the inside of people's bodies without the need to open them up or to expose them to potentially harmful X-rays. The technology has revolutionized medical assessments. The MRI scanner in our basement is smaller than the standard hospital issue. It is optimized to scan rodents. Mice, rats, and other small rodents are frequently used in medical research to test ideas before they are applied to humans. What is in the scanner today, though, is not a mouse or a rat. It is the brain of a macaque monkey. Sasha and I concentrate on the screens as the first image of the brain becomes visible. "Looks good," he says.

Comparing brains has always been a laborious endeavor. Brains are not a uniform whole. Different parts of the brain have different types of cells and group cells together in different ways, forming distinct regions. To really understand a brain, we need to map out the different brain regions. Before MRI, this meant lots of painstaking work. To map out brain regions, one had to get a brain and slice it into very thin slices. The slices were then treated with various chemical compounds that make different structures of the cells visible. Then one looked through a microscope to see how the cells are organized. When the pattern of organization changed, this would indicate that we had moved into a new brain area. This was done by hand, slice by slice, all through the brain. For a brain as large as the human, this could take years.

Taking years to study a single brain is not feasible in today's scientific funding landscape. Thankfully, biology is living through a time of technical revolutions, giving rise to a new generation of comparative scientists. In neuroscience, techniques like MRI allow us to scan whole brains in minutes. The information they provide is not quite at the level of the cells under the microscope, but it is getting closer all the time. The technical revolution is nowhere greater than in genetics. Whereas the deciphering of the first human genome took 13 years and $300 million, while I write it is now closer to 1 day and $1000. Probably when you read this, it will be less still. There are also high throughput methods that can determine where in the brain certain genes are expressed, allowing us to investigate how genes get switched on and off during development, including in the brain. In short, it is now possible to get lots of different types of information about brains in a relatively short period. It is the reason why I started contacting zoos to ask about their animal brains. Many neuroscientists are finding brains to study using the new approaches. Some acquire governmental permits to capture some animals, scan their brains, and release them again. Others focus on cadavers that are found in nature and studied by governmental agencies for pathogens. Others, including me, work with zoos. Many zoos have a research mission. They want to learn about the magnificent animals they care for. So, if after the animal dies we can learn even more about them by saving their brains, spines, or eyes, they contribute. Without them, a lot of my research would not have been possible. It is how I ended up on that summer day scanning a monkey brain in an Oxford basement.

Plan of the book

The work of the new comparative neuroscientists, and the generations of researchers whose shoulders they stand on, means that we learn more and more about the wonderful diversity of brains we can find in nature every day. It means we can finally study where our brain comes from. In this book, we will take up that challenge.

We will use the comparative method to travel through the animal kingdom. In each chapter, we will compare two or three animals that are representative of larger groups—reptiles and mammals, rodents and primates, foxes and dogs, chimpanzees and humans, rodents and birds—and see what circumstances they lived in and how their brains adapted accordingly. We cannot trace the entirety of brain evolution in a single book. Therefore, we will concentrate on comparisons that are ultimately relevant to understanding our own human brain. This is not because we humans are in any way the pinnacle of evolution or that we are more evolved than any of the other brains we discuss. It simply because, as humans, we tend to mostly be interested in ourselves.

Because the brain is involved in so many complex behaviors, it helps to focus a bit on a basic function. I will argue in the first chapter that a useful way to study the brain is to view it as a foraging device, an organ that produces the behaviors needed to help us find the nutrients we need to survive. Different animals, we will see, need to solve different problems in their foraging. Studying these problems helps us understand differences in the organization of their brains.

In the first chapter, we will look at some relatively simple brains: the sea squirt, the lamprey, and the bee. We will use these simple brains to see where brains come from and what they are for. The lamprey has a brain similar to that of an early vertebrate, and we will use it to introduce some of the major subdivisions of the brain. In the second chapter we will look at two major groups of animals, reptiles and mammals, represented by the Komodo dragon and the shrew. They show us how animal life adapted to life on the land and, in the case of mammals, to produce a very flexible part of the brain. In the third chapter we will look at the group of animals that we belong to: primates. Comparing them with the most populous group of mammals, the rodents, we will see how the primate brain specialized for a lifestyle dominated by vision and fine movement skills. Within primates, some groups adapted to life in an uncertain environment, as we shall see in the fourth chapter. One type of behavior that has evolved a number of times in different groups of animals is sociality, the ability to live together with conspecifics. We still take this topic up in the fifth chapter and then see how this sociality influenced human evolution in the sixth chapter. Finally, in the last chapter, we will look at some other interesting brain adaptations and what they tell us about general patterns of brain evolution.

Throughout this journey, we will encounter strange brains, big changes in the world's climate, happy accidents, and wonderful behaviors. Let's go.

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