DARWIN'S UNFINISHED SYMPHONY

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HOW CULTURE MADE THE HUMAN MIND

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This book is dedicated to Henry Plotkin,
who started me off on this journey.

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FOREWORD

This book is the product of a collective endeavor. Although I am the sole author, I set out to portray the efforts of a team of researchers—the members of my research laboratory and other collaborators—who, over a period of 30 years, have shared the scientific challenge of trying to understand the evolution of culture. I hope to provide a compelling scientific account for the evolutionary origins of the human mind, our intelligence, language, and culture; and for our species' extraordinary technological and artistic achievements. More than that, however, this book sets out to capture something of the scientific process—to lay bare, in an honest way, our struggles, false starts, moments of insight and inspiration, and our triumphs and failures in a scientific journey of discovery. I present our story; that is, I introduce the members of the Laland lab, past and present, and depict our efforts to understand the tremendously exciting puzzle that comprises the evolutionary origins of human culture. I am no novelist and, although this book is written in a style designed to be accessible, it inevitably cannot possess the pace, thrills, or drama of fiction. I hope, nonetheless, that a little something of a detective story comes across, and that the reader experiences a modicum of excitement as they read how our experimental and theoretical findings provided the clues that fueled our investigation.

My first note of thanks must, of course, go to the researchers whose work is described in these pages. I have been privileged to work with some extraordinarily gifted individuals, and have constantly benefitted from the hard work, good ideas, clever experimentation, and ingenious theoretical work of countless undergraduates, Master's students, PhD students and postdoctoral researchers, as well as numerous collaborators both in my own and other institutions. These include Nicola Atton, Patrick Bateson, Neeltje Boogert, Robert Boyd, Culum Brown, Gillian Brown, Hannah Capon, Laura Chouinard-Thuly, Nicky Clayton, Becky Coe, Isabelle Coolen, Alice Cowie, Daniel Cownden, Lucy Crooks, Catharine Cross, Lewis Dean, Magnus Enquist, Kimmo

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Many people too have helped with the writing of the book. I would like to thank those who read the entire manuscript, one or more chapters, and/or provided helpful feedback or insights: Rob Boyd, Charlotte Brand, Alexis Breen, Gillian Brown, Nicky Clayton, Michael Corr, Daniel Cownden, Rachel Dale, Lewis Dean, Nathan Emery, Tecumseh Fitch, Ellen Garland, Tim Hubbard, Hilton Japyassú, Nicholas Jones, Murillo Pagnotta, Simon Kirby, Claire Laland, Sheina Lew-Levy, Elena Miu, Keelin Murray, Ana Navarrete, John Odling-Smee, James Ounsley, Luke Rendell, Peter Richerson, Christopher Ritter, Christian Rutz, Joseph Stubbersfield, Wataru Toyokawa, Camille Troisi, Stuart Watson, Andrew Whalen, and two anonymous external referees. Through their help, this book has been greatly improved, becoming both more scientifically accurate and more accessible to the general reader. Katherine Meacham also merits a special note of thanks for administrative support in numerous guises, from formatting, to editing notes, to compiling references, all of which were always conducted with extraordinary efficiency and attention to detail.

The idea of my writing this book was first devised as a graduate student at University College London, nearly thirty years ago. I was inspired on reading John Bonner's wonderful monograph *The Evolution of Culture in Animals* (1980, Princeton University Press). I loved the grand sweep and vision of Bonner's book, and was enraptured by the sheer scale of the question it addressed. However, an equally inspirational conversation with University of McMaster psychologist Jeff

Galef, doyenne of the field of animal social learning, helped me to set Bonner's contribution within the broader framework of the field that had Galef led so impressively for decades. With Jeff's help, I was able to recognize that, for all its merits, Bonner's book did not provide a thorough explanatory account of how human culture could have evolved from the social learning and tradition observed in other animals. That conversation with Jeff also brought home how a great deal of scientific work would be required before the mysteries underlying the evolution of culture could be unraveled. Bonner's visionary conception and Galef's demand for explanatory rigor combined to hatch the idea in my mind that perhaps one day I might rise to this particular challenge.

I would also like to thank Alison Kalett at Princeton University Press for commissioning this book, and pushing me to write it at least ten years before I felt I was ready, and also Betsy Blumenthal, Jenny Wolkowicki and Sheila Dean for help with the production. I am grateful to all at PUP for support, encouragement, and patience throughout a writing process that proved extremely protracted.

Much of this book was written while I was on sabbatical, based in Nicky Clayton's laboratory in the Department of Experimental Psychology, at the University of Cambridge in the United Kingdom. I am indebted to Nicky and the members of her Comparative Cognition Laboratory for making me feel at home and providing an environment, both tranquil and stimulating, that was conducive to productive writing. The final chapters of the book particularly benefitted from these exchanges. I am also very grateful to Gillian Brown, Sean Earnshaw, Julia Kunz, Ros Odling-Smee, Susan Perry, Irena Schulz, Caroline Schuppli, and Carel van Schaik for kindly providing images.

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Finally, and most of all, I would like to thank my thesis advisor, Henry Plotkin, to whom I owe so much. Henry taught me the ropes of the academic business with unfailing patience, generosity, and enthusiasm. He trained me in how to design experiments, how to think critically, how to balance theory and empirical work, and where attention to detail is important. Our regular, Friday morning discussions were a highlight of my PhD years, and I consider myself hugely privileged to have shared so much of his time.

KEVIN LALAND
March 2016
St Andrews, United Kingdom

PART I

FOUNDATIONS OF CULTURE

CHAPTER 1

DARWIN'S UNFINISHED SYMPHONY

> It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and so dependent upon each other in so complex a manner, have all been produced by laws acting around us. . . . Thus from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows.
>
> —**CHARLES DARWIN, *ON THE ORIGIN OF SPECIES***

As he looked out on the English countryside from his study at Down House, Charles Darwin could reflect with satisfaction that he had gained a compelling understanding of the processes through which the complex fabric of the natural world had come into existence. In the final, perhaps the most famous, and certainly the most evocative, passage of *The Origin of Species*, Darwin contemplated an entangled bank, replete with plants, birds, insects, and worms, all functioning with intricate coherence. The tremendous legacy of Darwin is that so much of that interwoven majesty can now be explained through the process of evolution by natural selection.

I look out of my window and see the skyline of St Andrews, a small town in southeastern Scotland. I see bushes, trees, and birds too, but the view is dominated by stone buildings, roofs, chimneys, and a church steeple. I see telegraph poles and electricity pylons. I look south, and in the distance is a school, and just to the west, a hospital fed by roads dotted with busy commuters. I wonder, can evolutionary biology explain the existence of chimneys, cars, and electricity in as convincing a fashion as it does the natural world? Can it describe the origin of prayer books and church choirs, as it does the origin of species? Is there an evolutionary explanation for the computer on which I type, for the satellites in the sky, or for the scientific concept of gravity?

At first sight, such questions may not appear particularly troubling. Clearly human beings have evolved, and we happen to be unusually intelligent primates that are good at science and technology. Darwin claimed, "the most exalted higher animals" had emerged "from the war of nature,"[1] and our own species is surely as high and exalted as species come. Isn't it apparent that our intelligence, our culture, and our language are what has allowed us to dominate and transform the planet so dramatically?

With a little more thought, however, this type of explanation unravels with disturbing rapidity, in the process generating a barrage of even more challenging questions. If intelligence, language, or the ability to construct elaborate artifacts evolved in humans because they enhance the ability to survive and reproduce, then why didn't other species acquire these capabilities? Why haven't other apes, our closest relatives, who are genetically similar to us, built rockets and space stations and put themselves on the moon? Animals have traditions for eating specific foods, or singing the local song, which researchers call "animal cultures," but these possess no laws, morals, or institutions, and are not imbued with symbolism, like human culture. Nor do animal tool-using traditions constantly ratchet up in complexity and diversity over time as our technology does. There seems a world of difference between a male chaffinch's song and Giacomo Puccini's arias, between fishing for ants by chimpanzees and *haute cuisine* restaurants, or between the ability of animals to count to three and Isaac Newton's derivation of calculus. A gap, an ostensibly unbridgeable gap, exists between the cognitive capabilities and achievements of humanity and those of other animals.

This book explores the origins of the entangled bank of human culture, and the animal roots of the human mind. It presents an account of the most challenging and mysterious aspect of the human story, an explanation for how evolutionary processes resulted in a species so entirely different from all others. It relates how our ancestors made the journey from apes scavenging a living on ants, tubers, and nuts, to modern humans able compose symphonies, recite poetry, perform ballet, and design particle accelerators. Yet Rachmaninoff's piano concertos did not evolve by the laws of natural selection, and space stations didn't emerge through the "famine and death" of the Darwinian struggle. The men and women who design and build computers and iPhones have no more children than those in other professions.

So, what laws account for the relentless progress and diversification of technology, or the changing fashions of the arts? Explanations based on cultural evolution,[2] whereby competition between cultural traits generates changes in behavior and technology,[3] can only begin to be considered satisfactory with clarification of how minds capable of generating complex culture evolved in the first place. Yet, as later chapters in this book reveal, our species' most cherished intellectual faculties were themselves fashioned in a whirlpool of coevolutionary feedbacks in which culture played a vital role. Indeed, my central argument is that no single prime mover is responsible for the evolution of the human mind. Instead, I highlight the significance of accelerating cycles of evolutionary feedback, whereby an interwoven complex of cultural processes to reinforce each other in an irresistible runaway dynamic that engineered the mind's breathtaking computational power.

Comprehending the distinguishing features of humanity through comparison with similar characteristics in other animals is another central theme in this book, and a distinctive feature of my research group's approach to investigating human cognition and culture. Such comparisons not only help to put our species' achievements in perspective, but help us to reconstruct the evolutionary pathways to humanity's spectacular achievements. We not only seek a scientific explanation for the origins of technology, science, language, and the arts, but endeavor to trace the roots of these phenomena right back to the realm of animal behavior.

Consider, for illustration, the school that I see from my window. How could it have come into existence? To most people the answer to this question is trivial; that is, workers from a building company contracted by the Fife Council built it. Yet to an evolutionary biologist the construction represents an enormous challenge. The immediate mechanical explanation is not the problem; rather, the dilemma is to understand how humans are even capable of such undertakings. With a little training, the same people could build a shopping mall, bridge, canal, or dock, but no bird ever built anything other than a nest or bower, and no termite worker deviated from constructing a mound.

When one starts to reflect, the scale of cooperation necessary to build a school is astounding. Imagine all of the workers who had to coordinate their actions in the right place at the right time to ensure that foundations are safely laid, windows and doors are put in place, piping and electricity wires are suitably positioned, and woodwork is painted. Imagine the companies with whom the contractor had to engineer transactions, buy the building materials, arrange for delivery, purchase or loan the tools, subcontract jobs, and organize finances. Think of the businesses that had to make the tools, nuts, bolts, screws, washers, paint, and windowpanes. Imagine the people who designed the tools; smelted the iron; logged the trees; and made the paper, ink, and plastic. So it goes on, endlessly, in a voracious multidimensional expansion. All of those interactions, that endless web of exchanges, transactions, and cooperative endeavors—the vast majority carried out by unrelated individuals on the basis of promises of future remuneration—had to function for the school to be built. Not only did these cooperative transactions work, but they repeatedly operate with seamless efficiency day in and day out, as new schools, hospitals, shopping malls, and leisure centers are put together all across the country and around the world. Such procedures are so commonplace that we now entirely take it for granted that the school will be built, and even complain if completion is a little late.

I earn my living in part by studying animals, and I am captivated with the complexity of their social behavior. Chimpanzees, dolphins, elephants, crows, and countless other animals, exhibit rich and sophisticated cognition that reveals an often impressive level of intelligence that through the process of natural selection has become suited to the worlds they each inhabit. Yet if we ever wanted a lesson in what an achievement of creativity, cooperation, and communication the construction of a building is, we only have to give a group of animals the materials, tools, and equipment to build such a structure, and then see what happens. I would imagine the chimpanzees might grasp pipes or stones to throw or wave about in dominance displays. The dolphins might plausibly play with materials that floated. Corvids or parrots would perhaps pick out some novel items with which to decorate their nests. I do not wish to disparage the abilities of other animals, whose achievements are striking in their own domains. Yet science has accrued a strong understanding of the evolution of animal behavior, while the origins of human cognition and the complexities of our society, technology, and culture remain poorly understood. For most of us in the industrialized world, every aspect of our lives is utterly reliant on thousands of cooperative interactions with millions of individuals from hundreds of countries, the vast majority of whom we never see, don't know, and indeed never knew existed. Just how exceptional such intricate coordination is remains hard to appreciate; nothing remotely like it is found in any of the other 5–40 million species on the planet.[4]

The inner workings of the school and the activities of children and staff are just as astonishing to an evolutionary biologist like myself. There is no compelling evidence that other apes will go out of their way to teach their friends or relatives anything at all, let alone build elaborate institutions that dispense vast amounts of knowledge, skills, and values to hordes of children with factory-like efficiency. Teaching, by which I mean actively setting out to educate another individual, is rare in nature.[5] Nonhuman animals assist one another in alternative ways, such as provisioning with food or collaborating in an alliance, but they mostly aid their offspring or close relatives, who share their genes and hence also possess their tendency to help.[6] Yet in our species, dedicated teachers devote vast amounts of time and effort with children entirely unrelated to them, helping them to acquire knowledge, in spite of the fact that this does not inherently increase a teacher's evolutionary fitness. Pointing out that teachers are paid, which might be regarded as a form of trade (i.e., goods for work), only trivializes this mystery. The pound coin or dollar bill have no intrinsic value, the money in our bank account has a largely virtual existence, and the banking system is an unfathomably complex institution. Explaining how money or financial markets came into existence is no easier than explaining why schoolteachers will coach unrelated pupils.

As I gaze at the school, I imagine the children sitting at their desks, all dressed in the same uniform, and all (or, at least, many) sitting calmly and listening to their teacher's instruction. But why do they listen? Why bother absorb facts about events in antiquity, or labor to compute the angle of an abstract shape? Other animals only learn what is of immediate use to them. Capuchin monkeys don't instruct juveniles in how their ancestors cracked nuts hundreds of years ago, and no songbird educates the young about what is sung in the wood across the road.

Just as curious to a biologist is the fact that the pupils all dress the same. Some of these children will come from less fortunate backgrounds. Their parents cannot easily afford to spend money on special clothes for school. When they finish their education many of these young people will exchange school attire for another uniform (probably equally uncomfortable), perhaps comprising a suit, or the white and blue attire of doctors and nurses in the hospital down the road. Even the students at my university, replete with liberal, radical, and freethinking values often dress the same, in jeans, T-shirts, sweatshirts, and sneakers. Where did these proclivities come from? Other animals don't have fashions or norms.

Darwin provided a compelling explanation for the protracted history of the biological world, but only hinted about origins of the cultural realm. When discussing evolution of the "intellectual faculties," he confessed: "Undoubtedly it would have been very interesting to have traced the development of each separate faculty from the state in which it exists in the lower animals to that in which it exists in man; but neither my ability nor knowledge permit the attempt."[7] With the benefit of hindsight, we should not be surprised if Darwin struggled to understand the origins of humanity's intellectual achievements; it is a monumental challenge. A satisfactory explanation demands insight into the evolutionary origins of some of our most striking attributes—our intelligence, language, cooperation, teaching, and morality—yet most of these features are not just distinctive, they are unique to our species. That makes it harder to glean clues to the distant history of our minds through comparison with other species.

At the heart of this challenge lies the undeniable fact that we humans are an amazingly successful species. Our range is unprecedented; we have colonized virtually every terrestrial habitat on Earth, from steaming rainforests to frozen tundra, in numbers that far exceed what would be typical for another mammal of our size.[8] We exhibit behavioral diversity that is unparalleled in the animal kingdom,[9] but (unlike most other animals) this variation is not explained by underlying genetic diversity, which is in fact atypically low.[10] We have resolved countless ecological, social, and technological challenges, from splitting the atom, to irrigating the deserts, to sequencing genomes. Humanity so dominates the planet that, through a combination of habitat destruction and competition, we are driving countless other species to extinction. With rare exceptions, the species comparably prosperous to humans are solely our domesticates, such as cattle or dogs; our commensals, such as mice, rats, and house flies; and our parasites, such as lice, ticks, and worms, which thrive at our expense. When one considers that the life history, social life, sexual behavior, and foraging patterns of humans have also diverged sharply from those of other apes,[11] there are grounds for claiming that human evolution exhibits unusual and striking features that go beyond our self-obsession and demand explanation.[12]

As the pages of this book demonstrate, our species' extraordinary accomplishments can be attributed to our uniquely potent capability for culture. By "culture" I mean the extensive accumulation of shared, learned knowledge, and iterative improvements in technology over time.[13] Humanity's success is sometimes accredited to our cleverness,[14] but culture is actually what makes us smart.[15] Intelligence is not irrelevant of course, but what singles out our species is an ability to pool our insights and knowledge, and build on each other's solutions. New technology has little to do with a lone inventor figuring out a problem on their own; virtually all innovation is a reworking or refinement of existing technology.[16] The simplest artifacts provide the test cases with which to evaluate this claim, because clearly no single person could invent, say, a space station.

Consider the example of the paper clip. You might be forgiven for assuming that what is, in essence, just a bent piece of wire was devised in its current form by a single imaginative individual. Yet that could not be further from the truth.[17] Paper was originally developed in first-century China, but only by the Middle Ages was sufficient paper produced and used in Europe to create the demand for a means to bind sheets of paper together temporarily. The initial solution was to use pins as fasteners, but these rusted and left unsightly holes, such that the pinned corners of documents sometimes became ragged. By the middle of the nineteenth century, bulky spring devices (resembling those on clipboards today) and small metal clasps were in use, and in the decades that followed a great variety of fasteners came into existence, with fierce competition governing their use. The first patent for a bent wire paper clip was awarded in 1867.[18] However, the mass production of cheap paper fasteners had to wait for the invention of a wire with the appropriate malleability, and a machine capable of bending it, both of which were developed in the late nineteenth century. Even then, the earliest paper clips were suboptimal in form—for instance, these included a rectangular-shaped wire with one overlapping side, rather than the circular "loop within a loop" design dominant today. A variety of shapes were experimented with for several decades of the twentieth century before manufacturers finally converged on the now standard paper clip design, known as the "Gem." What appears at first sight to be the simplest of artifacts was in fact fashioned through centuries of reworking and refinement.[19] Even today, in spite of the Gem's success, novel paper clip designs continue to emerge, with a wide range of cheaper plastic forms manufactured over the last few decades.

The history of the paper clip is broadly representative of how technology changes and complexifies, and such transformations occur in other areas too. Humanity's rich and diverse culture is manifest in extraordinarily complex knowledge, artifacts, and institutions. These multifaceted, composite aspects of culture are rarely produced in a single step, but are generated by repeated, incremental refinements of existing forms in a process known as "cumulative culture."[20] Our language, cooperativeness, and ultrasociality, just like our intelligence, are frequently lauded as setting us apart from other animals. But, as we shall see, these features are themselves more likely products of our exceptional cultural capabilities.[21]

I have dedicated my scientific career to investigating the evolutionary origins of human culture. In my research laboratory we do this both through experimental investigations of animal behavior, and through the use of mathematical evolutionary models that allow us to answer questions not amenable to experimentation. We are part of a wider community of researchers who have established that many animals, including mammals, birds, fishes, and even insects, acquire knowledge and skills from others of their species.[22] Through copying,[23] animals learn what to eat, where to find it, how to process it, what a predator looks like, how to escape that predator, and more. There are thousands of reports of novel behaviors spreading through natural populations in this way, in animals ranging from fruit flies and bumblebees, to rhesus macaques and killer whales. These behavioral diffusions occur too rapidly to be attributed to the spread of favorable genes through natural selection, and are unquestionably underpinned by learning. The behavioral repertoires of some species vary between and within regions, in a manner that is not easily explained by ecological or genetic variation, and is often described as "cultural."[24] Some animals appear to have an unusually broad cultural repertoire, with multiple and diverse traditions, and distinctive behavioral profiles in each community.[25] Rich repertoires are observed in some whales and birds,[26] but outside of humans, animal traditions reach their zenith in the primates, where various socially transmitted behavior patterns, including tool use and social conventions, have been recorded for several species, notably chimpanzees, orangutans, and capuchin monkeys.[27] Experimental studies of other apes in captivity provide strong evidence for imitation,[28] tool use, and other aspects of complex cognition;[29] at least these are complex relative to other animals. Yet, in spite of this, the traditions of even apes or dolphins just don't seem to ratchet up in complexity like human technology does, and the very notion of cumulative culture in animals remains controversial.[30] Perhaps the most credible candidate was proposed by the Swiss primatologist Christophe Boesch, who has argued that the use of hammerstones to crack open nuts by chimpanzees has been refined and improved over time.[31] Some chimpanzees have begun to deploy a second stone as an anvil on which to place the nuts that they smash, and a couple of individuals have even been seen to insert another stabilizing stone to wedge the anvil securely. While Boesch's claim is plausible, and would meet some definitions of cumulative culture if confirmed, it remains uncorroborated. Even the most complex variant of nut cracking could plausibly have been invented by a single individual, which means this tool use need not imply any building on the shoulders of chimpanzee predecessors.[32] The same issue arises for all chimpanzee behaviors that have excited claims of cumulative culture;[33] there is no direct evidence that any of the more elaborate variants have developed from simpler ones. Circumstantial evidence for cumulative culture in other species is equally contentious—notably in New Caledonian crows,[34] a bird renowned for manufacturing complex foraging tools from twigs and leaves.[35] Novel learned behavior frequently spreads through animal populations, but is rarely, if ever, refined to generate a superior solution.

In striking contrast, the invention, refinement, and propagation of innovations by humans is extremely well documented.[36] The most obvious illustration comes from the archaeological record;[37] this can be traced back 3.4 million years to the use of flake tools by a group of African hominins known as australopithecines, who may have been early human ancestors.[38] The technology, known as Oldowan because it was first discovered at the Olduvai Gorge in Tanzania, consisted of basic stone flakes struck off a core with a hammerstone that were used to carve up carcasses and extract meat and bone marrow.[39] By 1.8 million years ago, a new stone tool technology arose, known as Acheulian, and associated with other hominins, *Homo erectus* and *H. ergaster*. Acheulian technology consisted of hand axes that were more systematically designed and particularly well suited to the butchery of large animals.[40] Acheulian technologies, together with the appearance of hominins outside Africa and evidence for systematic hunting and the use of fire, leave no doubt that by at least this juncture in our history, our ancestors benefitted from cumulative cultural knowledge.[41] By around 300,000 years ago, hominins were combining wooden spears with flint flakes,[42] building dwellings with fire hearths,[43] and producing fire-hardened spears for big game hunting.[44] By 200,000 years ago, Neanderthals and early *Homo sapiens* were manufacturing an entire tool kit from the same stone.[45] African sites dated to 65–90 thousand years ago provide evidence of abstract art, blade tools, barbed bone harpoon points,[46] and composite tools, such as hafting implements and awls used to sew clothing.[47] Between 35 and 45 thousand years ago, perhaps earlier,[48] a plethora of new tools appear, comprising blades, chisels, scrapers, points, knives, drills, borers, throwing sticks, and needles.[49] This period also introduced tools made from antler, ivory, and bone; raw materials transported over long distances; construction of elaborate shelters; creation of art and ornaments; and ritualized burials.[50] Technological complexity escalated further with the advent of agriculture, which was swiftly followed by the wheel, the plow, irrigation systems, domesticated animals, city-states, and countless other innovations.[51] With the industrial revolution, the pace of change accelerated again.[52] Human culture continues relentlessly to grow in intricacy and diversity, culminating in the mind-boggling technological complexity of today's innovation society.

Whether or not chimpanzees, orangutans, or New Caledonian crows have managed some crude advancements over their basic tool-using habits, the scale of difference when compared with the monumental advances of humanity is breathtaking. In some limited respects, animal traditions resemble aspects of human culture and cognition,[53] yet the fact remains that humans alone have devised vaccines, written novels, danced in *Swan Lake*, and composed moonlight sonatas, while the most culturally accomplished nonhuman animals remain in the rain forest cracking nuts and fishing for ants and honey.

Tempting though it may be to view "culture" as the faculty that sets humans apart from the rest of nature, the human cultural capability obviously must itself have evolved. Herein lies a major challenge facing the sciences and humanities; namely, to work out how the extraordinary and unique human capacity for culture evolved from ancient roots in animal behavior and cognition. Understanding the rise of culture has proven a remarkably stubborn puzzle,[54] largely because many other evolutionary conundrums must be addressed in the process. We must first understand why animals copy each other at all, and we must isolate the rules that guide their use of social information. We then need to identify the critical conditions that favored cumulative culture, and the cognitive prerequisites for its expression. The circumstances leading to the evolution of the abilities to innovate, teach, cooperate, and conform must all be established. Also critical is knowing how and why humans invented language, and how that led to complex forms of cooperation. Finally, and crucially, we need to comprehend how all of these processes and capabilities fed back on each other to shape our bodies and minds. Only then can researchers begin to understand how human beings uniquely came to possess the remarkable suite of cognitive skills that has allowed our species to flourish. These are the issues with which my research group has wrestled for many years, and our studies and those of others in our field, are beginning to provide answers.

Some readers might be surprised by the suggestion that understanding the evolution of the human mind and culture has proven a major challenge. After all, Darwin wrote at great length about human evolution, and that was 150 years ago; unquestionably, extensive progress has been made in the intervening period.[55] In fact, in *The Origin of Species* Darwin did not mention human evolution at all, except to say in the final pages that "light will be thrown on the origin of man and his history."[56] Darwin took a long time, well over a decade, to elaborate on this enigmatic statement, but he eventually brought forth two huge books on the topic: *The Descent of Man and Selection in Relation to Sex* (1871) and *The Expression of the Emotions in Man and Animals* (1872). Strikingly, in these books, Darwin says rather little about human anatomy, but instead concentrates on the question of the evolution of "the mental powers of Man." This focus is highly significant. To Victorian readers, as to us, there seemed to be a far greater divide between the mental abilities of human beings and other animals than between their bodies. Darwin recognized that understanding the evolution of cognition was the greater challenge if he was to convince his readers that humans had evolved. The origin of mind was the key terrain over which the battle regarding human evolution was to be fought.

The account given in *The Descent of Man* is typical of Darwinian reasoning. Darwin maintained that there was variation in mental capacity and that being intellectually gifted was advantageous in the struggle to survive and reproduce:

> To avoid enemies, or to attack them with success, to capture wild animals, and to invent and fashion weapons, requires the aid of the higher mental faculties, namely, observation, reason, invention, or imagination.[57]

Darwin attempted to counter the widespread belief, brought to prominence through the writings of French philosopher René Descartes, that animals were merely machines driven by instinct, while humanity alone was capable of reason and advanced mental processing.[58] Instead, Darwin sought to demonstrate both that animals possessed more elevated cognition than hitherto conceived and that human beings possessed instinctive tendencies. Through extensive use of examples, such as rats learning to avoid traps and apes using tools, Darwin documented how many animals exhibit signs of intelligence, and how even simple animals are capable of learning and memory. Much of his analysis reads a little anthropomorphically today; he claimed that the songs of birds demonstrate an appreciation of beauty, that their behavior near a nest revealed some concept of personal property, and even that his dog showed the rudiments of spirituality. Yet the data Darwin presented were a serious challenge to the established, stark, Cartesian human-versus-animal mental divide.

Darwin also documented the evidence that human beings possess behavioral characteristics in common with other animals, cataloguing an amazing array of shared facial expressions.[59] For instance, he noted that monkeys, like human beings, have "an instinctive dread of serpents" and will respond to snakes with the same screams and the same fearful faces as many of us do. Through these efforts, Darwin established a scientific tradition that perpetuates to this day and that seeks to demonstrate that the differences in mental ability between human beings and other animals were not as great as formerly believed.

What is of relevance here is that Darwin's approach to explaining the evolution of the human mind is, in essence, identical to his strategy for accounting for the evolution of the human body. He sought to shrink the apparently chasmic gap between the intellectual abilities of human beings and other animals by showing that for any given character, humans are sufficiently animallike, or animals sufficiently humanlike, that it is possible a chain of intermediary forms could have been forged by natural selection. The data he presented did not demonstrate such chains; nor were they intended to. Darwin merely set out to illustrate that the construction of such a case for continuity of mind was, in principle, highly plausible.

Darwin's stance contrasted decidedly with that of his contemporary Alfred Wallace, who had struck upon the idea of evolution by natural selection around the same time. Wallace concluded that the complex language, intellect, and the music, art, and morals of human beings could not be explained solely by natural selection and must have resulted from the intervention of a divine creator.[60] History has perhaps judged Wallace harshly, with the fact that he despaired of a scientific explanation for the origins of mind leading some to interpret his position as indicative of some weakness of character, in comparison to Darwin's courageous stance.[61] Any such conclusion would be unjust. Wallace's evaluation of the evidence was primarily an honest reflection of the state of knowledge at the time. The explanations that Darwin offered to account for the evolution of mind were, as he conceded, "imperfect and fragmentary."[62] Darwin's position was based on the firm belief that in the future science would provide more concrete evidence to bridge the mental divide; a stance now being vindicated.

Comprehending the evolution of the human mind is Darwin's unfinished symphony. Unlike the unfinished compositions of Beethoven or Schubert, which had to be assembled into popular masterpieces using solely those fragmentary sketches left by the original composers, Darwin's intellectual descendants have taken up the challenge of completing his work. In the intervening decades great progress has been made, and rudimentary answers to the conundrum of the evolution of our mental abilities have started to emerge. However, it is only in the last few years that a truly compelling account has begun to crystallize. Darwin thought that competition, for food or mates, drove the evolution of intelligence and, in its broad thrust, this assertion is supported.[63] However, what was not recognized until recently was the central role played by culture in the origins of mind.

Darwin and his intellectual descendants have unearthed findings that have substantially shrunk the recognized differences between human and animal cognition relative to the strict dichotomy that was accepted in the Victorian era. We now know that humans share many cognitive skills with their nearest primate relatives.[64] A long list of strong claims of human uniqueness—humans are the only species to use tools, to teach, to imitate, to use signals to communicate meanings, to possess memories of past events and anticipate the future—have been eroded by science as careful research into animal cognition has revealed unanticipated richness and complexity in the animal kingdom.[65] Yet the distinctiveness of human mental ability relative to that of other animals remains striking, and the research field of comparative cognition has matured to the point where we can now be confident that this gap is unlikely to be eroded away completely.[66] A hundred years of intensive research has established beyond reasonable doubt what most human beings have intuited all along; the gap is real. In a number of key dimensions, particularly the social realm, human cognition vastly outstrips that of even the cleverest nonhuman primates.

I suspect that in the past, many animal behaviorists have been loath to admit this for fear that it would reinforce the position of those who denied human evolution altogether. A "good evolutionist" emphasized continuity in the intellectual attainments of humans and other primates. Dwelling on our mental superiority was portrayed as anthropocentric, and was often tainted with a suspicion that those who would set humans apart from the rest of nature must have some personal agenda. Humans might be unique, but then, it was argued, so are all species. At the same time the media has been rife with "talking" apes and Machiavellian monkeys, giving the impression that other primates were as cunning and manipulative as the most devious and sinister humans, with untapped potential for sophisticated communication, and possessing rich intellectual and even moral lives.[67] Political and conservationist agendas fed into this doctrine, leading to the assertion that other apes were so similar to us that they merit special protection or human rights, and it has even been suggested they actually are people.[68] Reinforcing this perspective is a long-standing and highly successful genre of popular science books that challenged readers to contemplate their animal selves. We have been vividly portrayed as "naked apes" adapted to a small-group forest existence, and then thrust suddenly into a modern world with which we are ill equipped to cope.[69] We (at least, the males among us) have been designated "man the hunter," shaped by natural selection for a life of brutal aggression.[70] Other tomes depict us as so laden with baggage from our animal heritage that we will be driven to destruction.[71] The authors of such books were often authoritative scientists, who explicitly drew on knowledge of animal behavior and evolutionary biology to justify their assertions.

In my view, too much has been made of superficial similarities between the behavior of humans and other animals, whether by inflating the intellectual credentials of other animals or by exaggerating humanity's bestial nature. Humans may be closely related to chimpanzees, but we are not chimpanzees, and nor are chimpanzees people. Any agenda to "prove" human evolution by demonstrating continuity of our mental abilities with those of other living animals is no longer required; it has become anachronistic. We now know for certain what Darwin could only suspect: several extinct hominin species existed over the intervening five to seven million years since humans and chimpanzees shared a common ancestor. Archaeological remains leave little doubt that these hominins possessed intellectual abilities intermediate to that of humans and chimpanzees.[72] The gap between apes and humans is real, but this is not a problem for Darwinism, because our extinct ancestors bridge the cognitive divide.

Nonetheless, demonstrating the authenticity of the mental ability gap between humans and other living primates is a necessary platform for this book. That is because, ostensibly, we humans live in complex societies organized around linguistically coded rules, morals, norms, and social institutions, with a massive reliance on technology, while our closest primate relatives do not. Were these differences illusory, either because human cognition is dominated by bestial tendencies that can be explained in the same manner as that of other animals, or because other animals possess hidden powers of reasoning and social complexity, the problem of explaining the origins of mind would melt away in the manner that evolutionists have anticipated, and perhaps hoped, for a century. However, the differences, as we shall see, are not illusory, and the challenge does not melt away.

Consider the genetic evidence. Perhaps the most misunderstood statistic in science is that humans and chimpanzees are 98.5% similar genetically. To many people, this statistic implies that chimpanzees are 98.5% human, or that 98.5% of chimpanzee genes work in the same way as ours, or that the differences between humans and chimpanzees are attributable to the 1.5% of genetic differences. All such inferences are wildly inaccurate. The 98.5% figure relates to similarity in the DNA sequence level across the entire genomes. Human and chimpanzee genomes comprise a long series of DNA base pairs, with tens of thousands, even millions, of base pairs in each protein-coding gene. Humans have something in the region of 20,000 protein-coding genes, although these make up only a small portion of our genome. The 1.5% represents about 35 million nucleotide differences between the two species. Most of these do not affect the gene's function at all, but some have big effects. Even a single change can affect how a gene operates, which means that a human and chimpanzee gene could be virtually identical and yet function differently. Many of the affected genes code for transcription factors (proteins that bind to DNA sequences and thereby regulate the transcription of other genes), thereby allowing the small sequence differences between the species to be amplified.[73]

Further genetic differences between humans and chimpanzees result from insertions and deletions of genetic material,[74] differences in the promoters and enhancers that switch genes on and off,[75] and between-species variation in the number of copies of each gene. Copy number variation has arisen through both gene loss and the duplication of genes (typically in the hominin lineage); the latter can be adaptive in cases where more gene product is required.[76] One study found that 6.4% of all human genes do not have a matching copy number in chimpanzees.[77] In addition, genes can be read in a variety of different ways to produce multiple diverse products, as different regions of the gene (exons) are spliced together. This "alternative splicing" is not a rare phenomenon. More than 90% of human genes exhibit alternative splicing, and 6–8% of genes shared by humans and chimpanzees show pronounced differences in how they are spliced.[78]

More important than differences between genes, however, are between-species differences in how the genes are used. Genes might be thought of as children's building bricks—broadly similar blocks that are assembled in different species in dissimilar ways. Human and chimpanzee genes could be exactly identical and still work differently because they can be turned on and off to different degrees, in different places, or at different times. Allan Wilson and Mary-Claire King, the pioneering Berkeley scientists who first drew attention to the striking genetic similarity between humans and chimpanzees, speculated that the differences between the two species have less to do with genetic sequence differences and much more to do with when and how those genes are switched on and off.[79] The intervening years have confirmed this supposition.[80] The Encyclopedia of DNA Elements (ENCODE), a massive research project launched by the US National Human Genome Research Institute in 2003 to identify all functional elements in the human genome, recently found around eight million binding sites, and variation in these largely regulatory elements is thought to be responsible for many species differences.[81]

An instructive comparison here is between the English and German languages. In terms of their written symbolic form (i.e., the letters used), these two Indo-European languages are identical, although only German speakers make use of the umlaut, recognizable as two dots over a vowel, which changes its pronunciation.[82] Yet it would clearly be ridiculous to claim that all differences between the two languages are attributable to the umlaut, or that to master German, an English speaker merely has to master the rules of umlaut usage. The differences between the two languages relate far more to how the letters are used, to how they are combined into words and sentences, than to differences in the phonological elements. So it is with genes. Among the key empirical insights to emerge recently from the field of evolutionary developmental biology (or "evo-devo") is the finding that evolution typically proceeds through changes in the gene regulatory machinery—through "teaching old genes new tricks."[83] Such changes include the timing of protein production, the region of the body in which the gene is expressed, the amount of protein produced, and the form of the gene product. The differences between human and chimpanzees relate far more to how *all* our genes are switched on and off than they do to the small differences in the sequences.

Among the sample of genes that do differ between humans and chimpanzees, a disproportionately high number are expressed in the brain and nervous system.[84] Genes expressed in the brain have been subject to strong positive selection in the hominin lineage, with over 90% of such genes upregulating their activity relative to chimpanzees.[85] Such differences are likely to have a big impact on brain function. Unlike many other tissues, gene expression patterns in the brains of chimpanzees have been found to be far more similar to those of macaques than to humans.[86] In terms of their anatomy and physiology, chimpanzee brains resemble those of monkeys far more than those of humans.[87] Human brains are more than three times the size of chimpanzee brains and have been structurally reorganized in comparison; for instance, the former have proportionally larger neocortices and more direct connections from the neocortex to other brain regions.[88]

What this means is that humans and chimpanzees are not so biologically similar that we should assume they ought to be behaviorally or cognitively alike. Chimpanzees might be our closest relatives, but this is only because all other members of our genus—*Homo habilis*, *Homo erectus*, *Homo neanderthalensis*, and more[89]—as well as all the *Australopithecines*, and all other hominins (*Paranthropus*, *Ardipithecus*, *Sahelanthropus*, *Kenyanthropus*) are extinct. Had they endured, chimpanzees would surely have a lower status in the minds of humans, and less might have been expected of them.

Let us put aside any preconceived notions and consider what exactly *is* special about the mental capabilities of humans. Careful experimental analyses of the cognitive capabilities of humans and other animals over the last hundred years have allowed researchers to characterize the truly unique aspects of our cognition. This is no trivial matter, because history is littered with claims along the lines of "humans uniquely do X, or possess Y" that have subsequently fallen by the wayside when established in another species. Comparisons of humans with other apes have also isolated features that the former share with other animals. Indeed, examining shared traits has proven as insightful as investigating human uniqueness, because such comparisons help us to reconstruct the past; this allows inferences to be made about the attributes of species ancestral to humans so that the evolutionary history of traits seen in modern humans can be understood. Nonetheless, some striking differences remain.

Consider, for example, research into human cooperation, which in recent years has been subject to intense investigation through the use of economic games. One is called the "ultimatum game," where two players must decide how to split a sum of money. The first player proposes how to divide the sum between them, and the second can either accept or reject this proposal. If the second player accepts, the money is split according to the proposal, but if the second player rejects, neither player receives anything. The most interesting feature of the ultimatum game is that it is never really rational for the second player to reject, since any offer is better than nothing. Hence, we might expect the first player to offer the absolute minimum and then keep the bulk of the sum. However, that is not what humans typically do. Humans frequently make far more generous offers (the most common offer is 50%, a "fair" division), and are much more prone to reject offers (those less than 20% are typically rejected) than would be expected if behaving entirely rationally. Moreover, the magnitude of offers and rates of rejection vary from one society to the next in a manner consistent with a society's cultural norms. For instance, particularly generous offers may be observed in a culture of extensive gift giving.[90] Humans seem predisposed to cooperate, and expect the same of others. Our behavior is often motivated by a sense of fairness and consideration of others' perspectives, and frequently adheres to the conventions of society. We even feel a compulsion to be fair to absolute strangers, irrespective of whether they are likely to be seen again. These conclusions are echoed in literally thousands of experimental findings, set across a very wide range of contexts and spanning broad scales of interaction.[91]

What happens when chimpanzees are asked to partake in such games? Psychologists Keith Jensen, Josep Call, and Michael Tomasello presented a simplified version of the ultimatum game to chimpanzees. The clever experimental setup allowed the "proposer" chimpanzee to choose between two options, one that shared a food reward equally with another chimpanzee, and another that gave the proposer a greater proportion. They found that chimpanzees tended to select the option that maximized their own returns with little regard to whether or not this was fair to others.[92] Compared to humans, the chimpanzees might appear to have behaved in a selfish manner, but their behavior, rather than ours, is the rational response. Studies like these, and there are many, support the argument that hominins may have been subject to selection promoting both consideration of others and sensitivity to local norms of fairness.[93] This is not to suggest that other apes never cooperate; chimpanzees, much like most other primates, cooperate in restricted domains.[94] However, extensive experimental data has established that other apes do not cooperate as extensively as humans do.

Many prominent primatologists believe that cooperation is at least partly constrained in other primates by a lack of understanding of the perspective of other individuals with whom they are required to cooperate.[95] Research into this topic was initiated in a classic study by comparative psychologists David Premack and Guy Woodruff, who asked, "Does the chimpanzee have a theory of mind?" They questioned whether chimpanzees, like adult humans, understand that other individuals may have false beliefs, intentions, and goals.[96] Their study triggered a spate of experimental investigations comparing the performance of chimpanzees and young children. In the main, the data led many researchers to answer Premack and Woodruff's question in the negative. More recent studies, however, suggest that chimpanzees may have some precursors of a theory of mind.[97] For instance, there is evidence that chimpanzees can infer a human experimenter's intentions; they react very differently when a person refrains from giving food because they are unwilling to do so compared with when they are unable to do so, or when doing something on purpose rather than by accident.[98] Other studies suggest that chimpanzees can understand the goals, perception, and knowledge of others to a limited degree. However, these conclusions remain contested,[99] and crucially, such studies provide no evidence that chimpanzees understand that others may possess false beliefs.[100] In contrast, children typically understand that others can have false beliefs by the age of four years, and possibly much earlier,[101] which implies that this capability evolved in the hominin lineage. Moreover, humans readily comprehend many orders of belief and understanding; for instance, you could *understand* that I could *claim* my wife *believes* that her daughter *thinks* her mother's hair looks best short, whereas in fact my daughter is only saying that to make her mother happy. Such beliefs about beliefs about beliefs are a natural and common aspect of human cognition, and our species can comprehend up to six orders. Other apes struggle with first-order intentionality.[102]

A reader unfamiliar with research in comparative psychology might reasonably wonder why the field should contrast the performance of chimpanzees of all ages with that of human children in laboratory tests of cognition.[103] Ostensibly, the fairer comparison would be of the two species at the same age. The general rationale for comparing chimpanzees to children (often at nursery school age) rather than to adult humans is that adults have been greatly enculturated by human society; the use of children thus represents an attempt to tease out the inherent differences between the two species prior to culture becoming too great a confounding factor. However, whether this argument holds water is contentious; after all, even four- or five-year-old children will have been hugely encultured. A more pragmatic rationale for the comparison may be closer to the truth; that is, with most cognitive tasks, there would be little point in comparing adult humans with adult chimpanzees, because the former would far outstrip the latter. Even human toddlers outperform the adults of other ape species in tests of mental ability. For instance, developmental psychologist Esther Herrmann and her colleagues gave a battery of cognitive tests to two-and-a-half-year-old children, as well as to chimpanzees and orangutans ranging from 3 to 21 years of age. These researchers found that, even at such a young age, the children already had comparable cognitive skills to adult chimpanzees and orangutans for dealing with the physical world (e.g., spatial memory, object rotation, tool use), and had far more sophisticated cognitive skills than both adult chimpanzees and orangutans for dealing with the social realm (e.g., social learning, producing communicative gestures, understanding intentions); they typically performed twice as well as (nonhuman) apes in the tasks.[104] While other experiments have established that chimpanzees do show impressive proficiency in social learning and social cognition,[105] those studies that directly compare species nonetheless consistently reveal strong differences between humans and other apes.[106] The hypothesis that social intelligence, in particular, blossomed among our hominin ancestors is now widely accepted.[107]

Communication is perhaps the most obvious respect in which there appears to be a major, qualitative difference between the mental abilities of humans and other primates. Animal communication comprises various classes of signals concerning survival (e.g., predator alarm calls), courtship and mating (such as the red sexual swellings of some monkeys), and other social signals (for instance, dominance displays).[108] Such signals each have very specific meanings, and typically relate to the animal's immediate circumstances. In contrast, language allows us to exchange ideas about matters distant in space and time (I could tell you about my upbringing in the English Midlands, or you could inform me of the new coffee shop in the next town). With rare exceptions, such as the honeybee waggle dance through which bees transmit abstract information about the location of nectar-rich flowers, animals do not communicate about phenomena that are not immediately present. Chimpanzees do not tell each other about the termite mound they found yesterday, and gorillas do not discuss the nettle patch on the other side of the forest. Some primate vocalizations do appear to symbolize objects in the world: famously, vervet monkeys, which range throughout southern Africa, are thought to possess three distinct calls that are labels for avian, mammalian, and snake predators,[109] and similar claims have been made for several other primates. However, primate vocalizations largely consist of single, unrelated signals that are rarely put together to transmit more complex messages, and any atypical composite messages are highly restricted. For instance, some monkeys simultaneously inform others of both the existence of a predator and of its location.[110] In contrast, human language is entirely open-ended, allowing humans to produce an infinite set of utterances and to create entirely new sentences through their mastery of symbols.

A romance exists around the notion that animals, such as chimpanzees or dolphins, might covertly harbor complex natural communication systems as yet unfathomed by humans. Many of us quite like the idea that "arrogant" scientists have prematurely assumed that other animals don't talk to each other when they failed to decode the cryptic complex of calls and whistles. Sadly, all the evidence suggests that this is just fantasy. Animal communication has been subject to intense scientific investigation for over a century, and few hints of any such complexity have arisen. To the contrary, it has proven remarkably difficult to provide compelling evidence that the signals of chimpanzees or dolphins possess a referential quality.[111] Chimpanzees are unquestionably smart in many respects, but their communication is not unambiguously richer, and may even be less language-like, than that of many other animals.[112] This means that communication systems cannot be arrayed on a continuum of similar forms, with human language at one end of the spectrum, closely aligned to some highly complex animal protolanguage, and passing through less and less sophisticated animal communication systems to end up with, say, simple olfactory messages at the other end. Rather, language appears qualitatively different. Even if the gulf between human language and the others were ignored, and animal communication systems were aligned on a continuum from simple to complex, current evidence implies that those species most closely related to humans are not the ones with the most complex natural communication systems.[113]

Perhaps apes are capable of more complex communication than they exhibit in their natural environments. A simple continuity argument might yet be resurrected if apes could be trained to talk, and several high-profile studies have pursued this dream.[114] Other apes, of course, are not anatomically suited to complex vocalization; their vocal control and physiology aren't capable of speech production. This much was established in the 1940s by American psychologists Keith and Cathy Hayes, who raised a young female chimpanzee called Viki from birth in their own home, endeavoring to treat her identically to their own children. Viki learned to produce just four words—"mama," "papa," "cup," and "up"—and by all accounts, the pronunciation was not compelling. If that sounds like a disappointment, it was at least more successful than the only previous attempt. This was made by Winthrop and Luella Kellogg, another husband and wife team of psychologists, who reared a female chimpanzee called Gua with their son Donald; Gua was seven months old when they started and Donald was close in age. The Kelloggs were forced to abandon the exercise after a couple of years, when Gua hadn't learned a single word, but Donald had started to imitate chimpanzee sounds! Real progress had to wait until the 1960s, when a third couple, Allen and Beatrice Gardner, tried again, but this time with the ingenious idea of teaching American Sign Language to Washoe, their young chimpanzee. Washoe is reported to have learned over 300 signed words, many through imitation, and to even to have passed on some of these to a younger chimpanzee called Loulis. Washoe also spontaneously combined signs; for instance, on seeing a swan, Washoe signed "water" and "bird," to much acclaim. The investigation generated considerable excitement and triggered a series of studies of "talking apes," including Nim Chimpsky, Koko the gorilla, and Kanzi the bonobo who were all taught signs or to use a symbolic lexicon.

Yet the vaulted claims that apes had produced language do not stand up to close scrutiny, a point on which virtually all linguists concur.[115] The animals had successfully learned the meanings of signs, and were able to produce simple two- or three-word combinations, but they showed no hint of having mastered grammatical structure or syntax. Human languages differ from animal communication systems in the use of grammatical and semantic categories, such as nouns, adjectives, and conjunctions, combined with verbs in present, past, and future tenses, in order to express exceedingly complex meanings. Washoe, Koko, and Kanzi may have comprehended the meaning of a large numbers of words and symbols (although none was able to learn as many different words as a typical three-year-old child) but more to the point, none of them acquired anything resembling the complex grammar of human language. Even enthusiastic devotees of the complexity of ape communication have acknowledged the contrast.[116] A world of difference separates a chimpanzee communication and a Shakespearean comedy.

Equally romantic is the notion that science has not yet gauged the full depth of the moral lives of animals, a premise that sells an awful lot of popular science books and flushes the coffers of Hollywood moviemakers. Television shows and storybooks are full of animals, from

Lassie, to Flipper, to Champion the Wonder Horse, who can grasp complex situations, often more effectively than humans, and who exhibit humanlike moral emotions such as sympathy or guilt. Once again, the scientific evidence is disappointingly dull; many popular books claim that animals understand the difference between right and wrong, but precious few scientific papers demonstrate this. Instead, claims of animal morality are heavily reliant on anecdotal reports, including stories of apes (but also dolphins, elephants, and monkeys) behaving as if they possess sympathy or compassion for another animal; for instance, these animals appear to console sick or dying individuals or "reconcile" after a fight.[117] However, such reports require careful interpretation.

Animals unquestionably lead rich emotional lives; strong scientific evidence demonstrates that many form attachments, experience distress, and respond to the emotional state of others.[118] Yet, that is not the same as possessing morals. Animals sometimes behave as if they can tell right from wrong, but there are usually alternative ways of interpreting such examples. The animals might be following simple rules without much reflection or care for others. For instance, grooming the victims of aggression might be beneficial if this provides a prime opportunity to forge new alliances. Primates may reconcile to obtain short-term objectives, such as access to desirable resources or to preserve valuable relationships damaged by conflict.[119] Rather than feeling guilt after being reprimanded, your dog may simply have learned that giving you "the eyes" will lead to more rapid forgiveness on your part. Instead of feeling sympathy for another individual that screams, an observing animal may respond emotionally out of fear for itself, a phenomenon known as emotional contagion.[120] Some writers have interpreted reconciliation after fights in monkeys as indicating that the protagonists feel "guilt" or "forgiveness," arguing on evolutionary grounds that it is parsimonious to assume that our close relatives experience the same emotions and cognition as ourselves.[121] However, this reasoning appears more questionable when we learn that fish behave in the same way.[122] Are we to assume that they also have a sense of forgiveness? Another concern is that for every anecdote suggesting particular animals possess moral tendencies, there are typically many more from the same species showing selfish and exploitative behavior.[123] The scientific literature is rife with reports of animals behaving indifferently to the distress of others, or taking advantage of the weak. Expressions of "moral" tendencies are, at best, rare events in other species.

Human beings are very much a part of the animal kingdom, and well over a century of careful research by scientists in several fields has established many continuities between our behavior and that of other animals. Yet despite this, important differences between the cognitive capabilities and achievements of humans and those of our closest animal relatives have been experimentally ratified. This divergence demands an evolutionary explanation. One-hundred-and-fifty years ago, Charles Darwin penned the first credible accounts of human evolution but inevitably, with fossil data scarce, the arguments brought to bear were designed more to illustrate the kinds of processes through which humans might have evolved, rather than to relate the actual story of our origin. In the intervening time, the unearthing of literally thousands of hominin fossils by paleontologists has allowed a detailed history of our evolutionary ancestry to be scripted.[124] Yet that history is largely written of teeth and bones, supplemented by clever inferences about diet and life history, together with stone tools and archaeological remains. Knowledge of the history of the human mind remains rare, speculative, and circumstantial.

Darwin recognized that a truly compelling account of human evolution would have to account for human mental abilities, including our culture, language, and morality, and in spite of extensive and productive scientific research for over a century, this remains a monumental challenge. The sheer magnitude of this task has not always been universally recognized. In the struggle to establish, and then to not undermine, the case for human evolution, the scientific community has perhaps been reticent to acknowledge that humans are cognitively very different from other apes. I confess that this is the mindset with which I began my scientific career. As data from comparative cognition experiments accumulated, however, and the striking differences between the mental abilities of humans and other apes began to crystallize, evolutionary biologists like myself have been forced to accept that something unusual must have happened in the hominin lineage to humanity. That supposition is reinforced by anatomical data, showing a near quadrupling in hominin brain size in the last three million years,[125] by genetic data showing massive upregulation of gene expression in the human brain,[126] and by archaeological data showing hyperexponential increases in the complexity and diversity of our technology and knowledge base.[127] Not all of the respects in which human beings excel are so flattering; we also exhibit unprecedented capabilities for war, crime, destruction, and habitat degradation. Yet these negative attributes also serve to highlight the distinctiveness of our evolutionary journey. How is it all to be understood?

This book sets out to explain the evolution of the extraordinary human capacity for culture, and in the process aims to provide answers to the conundrum of the human mind's emergence. An account is given of how the most singular and definitively human capabilities intermingled to forge a collective existence in our species. The explanation given for the origins of mind and culture cannot be the whole story—far from it, since indubitably many diverse and complex selection pressures must have acted on an organ as complex as the human brain and a cognitive capability that is so multidimensional. The story told is far from conjecture, however; it is supported all the way by scientific findings.

Yet this book is not just about the evolution of culture; it is a description of the scientific program of research dedicated to its unraveling. It synthesizes my work, and that of my students, assistants, and collaborators, who as a team have pursued this topic for over 25 years. It depicts how modern research proceeds, including how scientific questions are addressed, how serendipitous findings are capitalized on, how researchers can be led in new directions by data, and how different scientific methodologies (experiments, observations, statistical analyses, and mathematical models) are interwoven to construct a deeper understanding of a problem. I set out to depict, in an honest way, our struggles, false starts, and moments of insight and despair. In a very real sense, this book is a detective story, describing how one puzzle led to the next, how we followed the trail of clues, and how gradually our efforts were rewarded with a climax as rich and convoluted as in any whodunit mystery. The "answer" that gradually becomes clear as the book progresses, may perhaps be regarded as a new theory of the evolution of mind and intelligence.

Our story begins with the seemingly prosaic observation that countless animals, from tiny fruit flies to gigantic whales, learn life skills and acquire valuable knowledge by copying other individuals. Perhaps surprisingly, an understanding of why they should do so—that is, why copying should be so widespread in nature—had eluded science until quite recently. Indeed, the puzzle was sufficiently challenging that we were forced to organize a scientific competition to address it. The competition solved the conundrum by conclusively demonstrating that copying pays because other individuals prefilter behavior, thereby making adaptive solutions available for others to copy. Running the competition taught us a vital lesson: natural selection will relentlessly favor more and more efficient and accurate means of copying.

Once we understood why animals copy each other, we began to appreciate the clever manner in which they did so. Animal copying was far from mindlessly or universally applied; social learning is highly strategic. Animals follow clever rules, such as "copy only when learning through trial and error would be costly," or "copy the behavior of the majority," which have proven to be highly efficient methods of exploiting the available information. What is more, we began to find that we could predict patterns of copying behavior using evolutionary principles. Subsequently, our experimental and theoretical analyses started to reveal how selection for more efficient and accurate copying had seemingly led some primates to rely more on socially transmitted information. This process supported traditions and cultures comprising databanks of valuable knowledge that conferred on populations the adaptive plasticity to respond flexibly to challenges and create new opportunities for themselves. This heavy reliance on social learning had other, less obvious, consequences as well, including a transformation in how natural selection acted on the evolving primate brain, and its consequent impact on primate cognition. In certain primate lineages, social learning capabilities coevolved with enhanced innovativeness and complex tool use to promote survival. The same feedback mechanisms may have operated in other lineages too, including some birds and whales, but with constraints that did not apply in the primates. The result was a runaway process, in which different components of cognition fed back to reinforce and promote each other, leading to extraordinary growth in brain size in some primate lineages, and to the evolution of high intelligence.

One key insight was that, under stringent conditions identified by mathematical models, this runaway process favored teaching, which is defined here as costly behavior designed to enhance learning in others.

This high-fidelity information transmission allowed hominin culture to diversify and accumulate complexity. Experimental studies and other data suggested that selection for more efficient teaching may have been the critical factor that accounts for why our ancestors evolved language. In turn, the appearance of widespread teaching combined with language was key to the appearance to extensive large-scale human cooperation. As our investigation proceeded, further lines of evidence supported our account, and a picture of what had happened in our lineage began to emerge. Human genetic data, for instance, testified to an unprecedented interaction between cultural and genetic processes in human evolution, fueling a relentless acceleration in the computational power of our brains. The data suggested that the same autocatalytic process has continued right up to the present, with accelerating cultural change driving technological progress and diversification in the arts, leading directly to today's human population explosion and the resultant planetary-scale changes.

What surprised us most about our investigations, however, was that only when we finally felt that we were closing in on a reasonable understanding of the evolutionary origins of the human capability for culture, did it dawn on us that we had stumbled upon so much more. We had inadvertently assembled insights into the birth of intelligence, cooperation, and technology. We had a novel account of the origins of complex society, and a new theory of why humans, and humans alone, possess language. We could explain why our species practices 10,000 or so different religions,[128] and could account for a technological explosion that has generated tens of millions of patents.[129] We could also elucidate how humans can paint sunsets, play football, dance the jitterbug, and solve differential equations.

Something remarkable happened in the lineage leading to humanity. Such a dramatic and distinctive enhancement in mental ability cannot be observed in the ancestry of any other living animal. Humans are more than just souped-up apes; our history embraces a different kind of evolutionary dynamic. All species are unique, but we are uniquely unique. To account for the rise of our species, we must recognize what is genuinely special about us, and explain it using evolutionary principles. Doing so requires analysis of the evolution of culture, because it turns out that culture is far more than just another component, or an outgrowth, of human mental abilities. Human culture is not just a magnificent end product of the evolutionary process, an entity that, like the peacock's tail or the orchid's bloom, is a spectacular outcome of Darwinian laws. For humans, culture is a big part of the explanatory process too. The evolution of the truly extraordinary characteristics of our species—our intelligence, language, cooperation, and technology—have proven difficult to comprehend because, unlike most other evolved characters, they are not adaptive responses to extrinsic conditions. Rather, humans are creatures of their own making. The learned and socially transmitted activities of our ancestors, far more than climate, predators, or disease, created the conditions under which our intelligence evolved. Human minds are not just built *for* culture; they are built *by* culture. In order to understand the evolution of cognition, we must first comprehend the evolution of culture, because for our ancestors and perhaps our ancestors alone, culture transformed the evolutionary process.

CHAPTER 2

UBIQUITOUS COPYING

> It is impossible to catch many [animals] in the same place and in the same kind of trap, or to destroy them by the same kind of poison; yet it is improbable that all should have partaken of the poison, and impossible that all should have been caught in the trap. They must learn caution by seeing their brethren caught or poisoned.
>
> —DARWIN, *DESCENT OF MAN*

The brown rat does not, as its Latin name (*Rattus norvegicus*) misleadingly implies, originate in Norway, but rather in China, from which it has spread to all continents apart from Antarctica over the last few hundred years. It has been described as one of "the most successful nonhuman mammals on the planet."[1] Its range and versatility are remarkable; colonies of rats scavenge a living on human garbage in Alaska, subsist on beetles and ground-nesting birds in South Georgia, and flourish in almost all farms and cities in between.[2]

The rats' success in part reflects a long history of dependence on humanity, a relationship in which we have proven an unwelcoming and brutal partner. Yet, in spite of centuries of traps, poisons and fumigations, no pied piper has ever managed to eradicate this most perseverant of pests. The reason, as Darwin intuited, is that rats cunningly avoid all agents of extermination; and they do so through copying.

In Darwin's day, the presiding belief was that children and monkeys imitated, but that the behavior of most animals was controlled by instincts.[3] The adage "monkey see, monkey do" and the phrase "to ape" betray the widespread belief that primates, and perhaps primates alone, copy each other's behavior. As with so many scientific issues, Darwin was ahead of his time in recognizing that copying is ubiquitous in nature. Today, extensive and incontrovertible experimental evidence for social learning exists in a very wide variety of animals.[4]

Darwin suspected that a long history of trapping mammalian pests would select for their "sagacity, caution and cunning,"[5] and certainly rats possess these qualities. Decades of control attempts failed in part because rats react to any change in their habitat with extreme apprehension.[6] For several years I studied rat behavior. I observed how any novel food or new object is slowly and stealthily stalked, the body crouched so low that the belly is almost on the floor, with the rat ready to turn tail at the slightest provocation. If nothing bad happens the curious rat will eventually take some food, but feeding will be highly sporadic at first, with only very small amounts of any new food taken.

Up until the middle of last century, the poisons that humans used required rats to eat substantial amounts to be lethal, and the modest amounts of bait ingested frequently just left the rats ill; this would inadvertently train them to avoid the new food source. Despite the occasional initial success in reducing pest numbers, after a short period of trying a new poison, rates of bait acceptance would become increasingly poor, and colonies would rapidly return to their initial sizes.

In the 1950s, the advent of Warfarin, a slow acting poison, proved a successful innovation in the battle to control rats, because the pests felt unwell sufficiently long after consuming the food to not develop bait shyness. Warfarin-type poisons were used against rats and other rodents all over the world, but always with only partial success, eventually giving the population of survivors time to evolve a genetic resistance.

Frustration that rats should remain so stubbornly difficult to eradicate eventually became the impetus for detailed research into rat behavior in the middle of the last century. Fritz Steininger, a German applied ecologist who spent many years studying ways to improve methods of rodent control, was the first scientist to provide data that supported Darwin's belief that rats learn socially to avoid poisons.[7] Decades of observation and experiment led Steiniger to the view that inexperienced rats were dissuaded by experienced individuals from ingesting potential foods by individuals that had learned the bait was toxic. This was an important insight, although Steiniger's interpretation was not correct in the details. In fact, the information transmission mechanisms turn out to be multiple, diverse, and subtle. Decades later, a Canadian psychologist called Jeff Galef—the world's foremost authority on animal social learning—finally got to the bottom of this puzzle.

With a beautifully designed series of experiments conducted over more than 30 years, Galef and his students painstakingly revealed the multiplicity of means by which the feeding patterns of adult rats influence the food choices of other rats, particularly the young. Galef discovered that rats do not actively avoid consuming foods that make others sick, but do acquire strong preferences for eating foods that healthy rats have eaten. These mechanisms are so effective that they support colony-wide dietary traditions that efficiently exploit safe, palatable, and nutritious foods, while leaving toxic foods largely untouched.

Remarkably, the transmission mechanisms begin to operate even before birth. A rat fetus exposed to a flavor while still in its mother's womb will, after birth, exhibit a preference for food with that flavor. Feeding garlic to a pregnant rat enhances the postnatal preference of her young for the odor of garlic in food.[8] The flavors of eaten foods also find their way into the milk of lactating mothers, and suckling rat pups' exposure to such flavors is sufficient to culture a subsequent preference for the same food.[9] Later, when rat pups take their first solid meals, they eat exclusively at food sites where an adult is present,[10] primarily because they follow the adults to these sites and thereby learn cues associated with food.[11] Even when removed from the social group and presented with foods in isolation, youngsters will eat only those foods that they have seen adults eat.[12]

Rats do not even need to be physically present to shape the dietary decisions of the young. When leaving a feeding site, they deposit scent trails that direct young rats seeking food to locations where food was ingested.[13] Moreover, feeding adults deposit residual cues in the form of urine marks and feces, both in the vicinity of a food source and on foods they are eating.[14] As a graduate student at University College London, I investigated the role that these cues played in transmitting dietary preferences. I found that rats leave a rich concentration of marks and feces in the vicinity of food sites,[15] cues that effectively contain the message that "this food is safe to eat." If I disrupted the cues in any way, either by cleaning off the urine marks but leaving the feces, or by removing the feces but not the urine marks, or even by replacing the food with a different food, the "message" immediately lost its potency, and other rats no longer preferred that site. Rats seemed attuned to copy each other faithfully—unless they encountered anything suspicious, in which instance they would rapidly switch into a cautious mode.