Contents

Introduction

History makes no sense without prehistory, and prehistory makes no sense without biology.

—Edward O. Wilson, *The Social Conquest of Earth*

Humans are an exquisitely intelligent and capable species of ape. Not only are our complex brains a wonder of evolution, but our bodies are engineering marvels. Our physiology has been fine-tuned for efficient long-distance running; our hands are elegantly dextrous for manipulating and making; and our throats and mouths give us astonishing control over the sounds we make. We are virtuoso communicators, with myriad forms of language, able to convey everything from physical instructions to abstract concepts, and to coordinate ourselves in teams and communities. We learn from each other, from our parents and peers, so new generations don't have to start from scratch. Our culture is cumulative: we have amassed our capabilities over time. We have progressed from master crafters of stone tools to wielders of technologies such as supercomputers and spacecraft.

But we're also deeply flawed, both physically and mentally. In many ways, humans just don't work particularly well.

What do US presidents George W. Bush and Ronald Reagan have in common with actors Elizabeth Taylor and Halle Berry? They all almost choked to death on their food (a pretzel, peanut, chicken bone and fig, respectively).[1] In fact, choking is the third-leading cause of death at home today.[2] Compared to any other animal, we seem breathtakingly inept (literally) at the key survival skill of eating without accidentally killing ourselves. The reason for this relates to the changes to our throat that enabled us to form the complex sounds of speech and so become such expressive vocal communicators. During the evolution of our species, the larynx rose higher in the neck and changed its structure to allow more control over sound generation. In all mammals, the pipelines for breathing and eating share a short section of the same tube, with a small flap called the epiglottis serving as a trapdoor to close off the windpipe when swallowing. But the remodelling of the human throat significantly increased the chances of food getting stuck in the windpipe.[3] As Darwin noted: 'Every particle of food and drink which we swallow has to pass over the orifice of the trachea, with some risk of falling into the lungs.'[4]

This is only one of a number of basic design flaws in the architecture of the human body. We evolved to walk upright, but the posture puts huge strain on our knees, and back pain strikes most of us in our lifetimes. The wrist and ankle joints contain pointless vestigial bones that restrict movement and render us susceptible to twists and sprains.[5] We have a number of nerves that take ludicrously long and indirect routes through the body, as well as muscles that no longer serve any purpose (such as those used by other animals to twist their ears). The light-sensitive layer at the back of our eye – the retina – faces back-to-front, leaving us with blind spots in our vision. We're also riddled with defects in our biochemistry and DNA – data-corrupted genes that no longer work – which means, for instance, that we must eat a diet more varied than almost any other animal to obtain the nutrients we need to survive. And our brains, far from being perfectly rational thinking machines, are full of cognitive glitches and bugs. We're also prone to addictions that drive compulsive behaviour, sometimes along self-destructive paths.

Many of these apparent faults are the result of evolutionary compromise. When a particular gene or anatomical structure is needed to satisfy several conflicting demands at the same time, no one function can be perfectly optimised. Our throats must be suitable not only for breathing and eating, but also for articulating speech. Our brains need to make survival decisions in complex, unpredictable environments, but they need to do so with incomplete information and, crucially, very rapidly. It is clear that evolution strives not for the perfect, but merely the good-enough.

What's more, evolution is restricted, in finding solutions to new conditions and survival problems, to tinkering with what is already at its disposal. It never gets the chance to go back to the drawing board and redesign from scratch. We have emerged from our evolutionary history as a palimpsest of overlaying designs, with each new adaptation modifying, or being built on top of, what already existed. Our spine, for instance, is poorly conceived to support an upright posture with a large head on top, but we had to make do with the backbone handed down to us from our ancestors who walked on all fours.

To be human is to be the sum total of all our capabilities and constraints – both our flaws and our faculties make us who we are. And the story of human history has played out in the balance between them.

We migrated from our evolutionary cradle in Africa to become the most widely distributed terrestrial animal species on the planet. Around ten millennia ago, we learned to domesticate wild plants and animals to invent agriculture, and out of this grew increasingly complex social organisations: cities, civilisations, empires. And over this whole, staggering breadth of time, through growth and stagnation, progress and regression, cooperation and conflict, slavery and emancipation, trading and raiding, invasions and revolutions, plagues and wars – through all this tumult and fervour, there has been one constant: ourselves. In almost all key aspects of our physiology and psychology, we're basically the same as our ancestors living in Africa

100,000 years ago. Across cultures worldwide there's a wonderful diversity of beliefs, practices and customs, but while there are superficial differences in our appearances, and more significant genetic variations, to all intents and purposes we are built identically. The fundamental aspects of what it means to be human – the hardware of our bodies and the software of our minds – haven't changed.

In this book, I want to take a deep dive into human history and explore how our fundamental humanness has expressed itself in our cultures, societies and civilisations. How have different quirks of our genetics, biochemistry, anatomy, physiology and psychology manifested themselves, and what have been the consequences and ramifications – not just in terms of singular, momentous events but for the over-arching constants and long-term trends of world history?

As well as the idiosyncrasies of our humanity, we'll explore what we share in our body and behaviour with other animals. Much of our refined culture and society is no more than a thin veneer over our inherent animal nature. We are often no different from other beasts when it comes down to competing for resources and sex or trying to give our children the best chances in life. These primal drives have manifested themselves through history in everything from our family structures to the efforts of royal dynasties to control their bloodlines. We'll take in the latest research in anthropology and sociology, and also see how many aspects of our everyday lives are deeply rooted in our biology.

Many of the requirements and restrictions of our bodies are obvious. We can survive within only a certain range of temperatures, and the efficiency with which our lungs can extract oxygen from the air limits how high we can live. (The highest permanent settlement today is the town of La Rinconada, at 5,100 metres of altitude in the Peruvian Andes.) Our need for a constant intake of water and nutrients to survive also determines the environments in which we can permanently settle. Our inability to drink seawater has historically limited oceanic voyages that relied on supplies of fresh water. Our life cycle, with the long period of development before reaching sexual maturity, governs how quickly we can reproduce and grow populations. Our bodies are vulnerable to being invaded by microscopic organisms and other parasites, which can have fatal consequences. The force our muscles can exert limits the achievements of our labour and has driven us both to harness beasts of burden such as the ox, camel and horse and to develop technology. And our need to sleep dictates the activity cycles of society.[6]

But features of our body have influenced human cultural development – the customs, behaviour and skills that we learn from each other – in more subtle ways as well.

All spoken languages use intricate sequences of sounds created by our upper respiratory tract: air is exhaled from the lungs, and the vibrations of the vocal cords are modified by our throat, mouth, tongue and lips. This sophisticated capability for vocalisation is considered one of the defining characteristics of our species.

Speech is composed of a series of open sounds or vowels – such as ah, ee, oo – interspersed with a greater diversity of consonants: collectively, these are the phonemes of language. Consonant phonemes can be created in a large variety of ways: the plosive release of air for a ‘p’ or ‘t’; the fricative restriction of airflow within the mouth for ‘f’ or ‘s’; the steady airflow around the sides of the tongue for ‘l’; the nasal resonance of ‘n’. All the world’s languages are composed of a total inventory of around 90 different sounds, although most don’t use more than about half of them;[7] English, for example, is composed of around 44 discrete phonemes.[8] By far the most common consonant sound in human speech is ‘m’, which seems to be the simplest to form. It’s used in 95 per cent of the 450 languages studied in detail by the UCLA Phonological Segment Inventory Database (UPSID) – from Abipon to Zuni (and including !Xu).[9] This widespread phoneme is produced by bringing both lips together and sending air through the nose, and it is similar to the lip-smack behaviour of chimpanzees and other primates.[10] It's the phoneme that begins one of the first words ever spoken by over 5 billion of us: a linguistic variant of 'mama'. Thus all languages around the world are dominated by the sounds we find easiest to produce – by the anatomical limits of being human.

Some features of our bodies have profoundly influenced not only what we're physically capable of but how we think about the world. The fact that we have five fingers on each hand (and five toes on each foot) – that we are *pentadactyl* – is an evolutionary happenstance that became fixed in our fish-like ancestors around 350 million years ago. (It is shared by all other four-limbed vertebrates, from crocodiles to birds to dolphins.) But it has come to have profound implications for our conception of numbers and numerical calculation. We have ten digits to count on, and so most ancient cultures around the world adopted a base-ten numerical system.* We think in round numbers of tens or hundreds or thousands – rather than in multiples of, say, six, 36 and 216, as we might if we were tridactyl. By the fifth century AD, the Indo-Arabic numeral system had devised the place-value notation which then developed into modern decimal numbers and the metric system for measurements. Our entire conception of mathematics is ultimately founded on the number of digits that sprout off our forelimbs.

Other aspects of the world we created are inextricably linked to our anatomical traits too. The beat of the second is roughly equivalent to our resting heart rate; the inch was traditionally the thickness of a thumb; and the mile was defined as a thousand Roman paces and thus the composite of our base-ten counting system and the length of the leg.

As we'll see, it's not just our physical features that have left indelible marks on our world. Our evolved psychological

* There were exceptions, however. The ancient Sumerians, for example, used a combination of base-ten and base-sixty (which is useful as lots of numbers divide into it), which is the reason why we still split an hour of time into sixty minutes and then sixty seconds, and why there are 360 degrees in a circle.

mechanisms and predispositions have influenced human culture in very particular ways. Many of these are so deeply ingrained in everyday life that we tend to overlook their biological roots. For example, we have a strong tendency towards herd behaviour – fitting in with those in our community by copying their decisions. In evolutionary terms this has served us well. In the natural world full of dangers, it is probably safer to follow everyone else, even if you're not convinced it's the best course of action, rather than risk going it alone. Often, even if we feel we're right, we are loath to stand out from the pack. Such herd behaviour is a way of crowd-sourcing information – others may know something we don't – and can serve as a quick judgement tool, allowing us to economise on the time and cognitive effort in deciding everything for ourselves from scratch. For example, walking through an unfamiliar city looking for a good place for dinner, we're naturally drawn to the busy restaurant rather than the empty one next door.

This herding bias has caused the surges of fads and fashions throughout history. It influences the adoption of other cultural norms, religious views or political preferences as well. But the same psychological bias also destabilises markets and financial systems. The dot-com boom of the late 1990s, for instance, was driven by investors piling in to back internet companies even though many of the start-ups were not financially sound. Investors followed one another, assuming that others had a more reliable assessment or simply not wanting to be left behind in the frenzy, only for the bubble to burst and stock markets to fall sharply after early 2000. Such speculative bubbles have recurred through history since 'tulip mania' in the early-seventeenth-century Netherlands, and the same herding behaviour is behind modern boom and bust cycles such as in cryptocurrency markets.

This book is the third in a trilogy of titles – each of which can be read separately – in which I wanted to explore the grand scale of history and the making of our modern world from a different angle. The first was *The Knowledge: How to Rebuild*

Our World from Scratch, which used the conceit of a manual on how to reboot civilisation as quickly as possible after some kind of apocalypse. It used the notion of the loss of everything that we take for granted today to peer behind the scenes of the modern world, explore how it all works and reveal how different discoveries and inventions enabled humanity's progress. The second book, *Origins: How the Earth Shaped Human History*, zoomed out and explored how features of the planet we live on – from plate tectonics to climate belts, from mineral resources to atmospheric circulation – have profoundly influenced the human story. *Origins* took us from the emergence of our species in the giant crack of the East African rift valley, through millennia of rising and falling civilisations and empires, right into the modern world, showing how the distinct fingerprint of the natural world can be discerned even in politics today.

What I want to do in this book is extend this line of inquiry and put the focus on us – to tell the human story from the perspective of biology and the essence of what it means to be human. I am a biologist by training, and so for me this represents something of a return to my home turf. I'm hoping to reveal the profound and often surprising ways in which intrinsic aspects of our anatomy, genetics, biochemistry and psychology have left their mark on human history.

We'll explore how romantic love and the human family developed as a consequence of our quirky evolution, and how marriage came to be exploited as a political tool by ruling dynasties. Why were European royal families particularly prone to unreliable reproduction, and how did other dynasties solve the problem – in the process creating sterile soldiers akin to those of ant colonies?

We'll take a detailed look at how our vulnerability to infectious diseases has played a multitude of pivotal roles in the history of the world. How did endemic diseases lead to the political union of England and Scotland or help double the size of the United States overnight? Epidemics helped the spread of a once-obscure religion and ushered in the decline of feudalism but also drove the transatlantic African slave trade to the Americas.

Fundamental features of human populations such as growth rate and the balance of males and females can have far-reaching consequences, and we'll explore the effects of such demographic forces. We'll also discover ways to alter our state of consciousness, and how by affecting our minds psychoactive substances came to change the world. We'll explore how alcohol became an intoxicating social lubricant, the stimulating impact of tea and coffee, the invigorating moreishness of tobacco, and how the poppy was wielded as a tool of imperial subjugation.

Errors in our genetic code have far-reaching ramifications. We'll see how a rare mutation that arose in Queen Victoria had disastrous consequences for the ruling dynasties across Europe a century later and also had a hand in the Russian Revolution. Another defunct gene, shared by all of humanity, played a defining role during the Age of Sail and inadvertently led to the emergence of the world's most notorious criminal organisation.

Finally, we'll explore the wide-ranging consequences of bugs in our mental software. Which particular cognitive bias gripped Columbus, was a powerful factor that led to the invasion of Iraq half a millennium later, and today lurks behind the problem of political polarisation? Which other mental glitches resulted in the disastrous Charge of the Light Brigade in the Crimean War and today haunt international trade negotiations and territorial disputes such as that between Israel and Palestine?

But we'll start by examining our evolution and see why, long before we cultivated wild plant species and tamed wild animals to create agriculture and civilisation, we first had to domesticate ourselves. How did humans develop to coexist harmoniously in larger and larger populations and cooperate successfully on shared ventures?

Chapter 1

Software for Civilisation

There is nothing to which nature seems so much to have inclined us, as to society.

—Michel de Montaigne, 'Of Friendship'

There are many advantages for animals to living in groups. It makes finding mates much easier; it allows for successful hunting in packs; and it offers safety in numbers and protection from predators. But compared to herds of wildebeest or schools of fish, there is a great deal more complexity in human societies. We have an incredible propensity to cooperate. The key to human success has been not just our adept tool use, made possible by the dexterity of our hands, but our willingness to offer a helping hand to one another, even if we're unrelated or unlikely ever to meet again. As Nichola Raihani puts it in her excellent book *The Social Instinct*, 'Cooperation is our species' superpower, the reason that humans managed not just to survive but to thrive in almost every habitat on Earth.' We teach one another skills and exchange information that we would never have worked out for ourselves in one lifetime. This process of cultural learning enables the spread of new capabilities not only throughout populations but cumulatively over generations.

In this chapter, we'll look at two major developments in human evolution that were key prerequisites for our ability to create complex, largely peaceable societies and work together in the huge enterprises that we call civilisations:* the reduction in reactive aggression and the development of the social software in our brains that enables unparalleled levels of cooperation.[1]

TAMING OURSELVES

It is simplistic to think of aggressive behaviour in terms of a single sliding scale from docile to violent. There are two forms of human aggression which are quite distinct from each other. Reactive aggression is a hot-headed response, an impulsive lashing out against an immediate threat. On the other hand, proactive aggression is driven less by impulse and emotion: it is calculated, premeditated action towards a specific goal. Throughout our development as a species, the expression of these two forms of aggression shifted in different directions – we evolved to be very moderate with the first, but highly proficient at the second. If we view aggression as a dualistic phenomenon, we can see that there is no contradiction in saying humans can be both brutal and benign.[2]

Our closest living relatives, chimpanzees and bonobos, live in mixed groups of males and females. These groups are fluid in their size and composition, splitting into smaller groups to forage different areas during the day, before reconvening to sleep at night. Over longer timescales, individuals move between different groups dispersed across the landscape; related chimpanzee males, for example, stick together but mate with females from neighbouring communities once they are old enough to breed.

This periodic division and reassembly of groups is known as fission-fusion social organisation. In such mixed groups of chimpanzees, outbreaks of aggression and violence are commonplace.

* For the purposes of clarity, what I mean by civilisation here is a complex social organisation, characterised by the centralised political and administrative state, a high degree of role specialisation, a stratified social structure, a distinctive cultural output and dense populations living in urban settlements.

Males harass females, and there is frequent antagonism and vicious competition between males over reproductive access to the females. Male in-fighting establishes a hierarchy, and the alpha male must use violence, or the threat of it, to maintain his position at the top. Male chimpanzees also form gangs to patrol the boundaries or their territory or invade that of neighbouring groups. They attack, and sometimes kill, males from other groups to expand their sphere and gain access to more resources or females. Bonobos are generally less violent than chimpanzees, but they also exhibit aggression both to other members of their group and to outsiders.[3]

While aggression is a way of life for chimpanzees, human evolution took a very different trajectory. The rates of physical aggression among other primates – even the more peaceful bonobos – are more than a hundred times higher than among humans.[4] Indeed, acts of reactive anger are remarkably rare within traditional hunter-gatherer societies today. These groups are also notably egalitarian, with no despotic alpha male or strong dominance hierarchy.

The key development in human evolution appears to have been the emergence of coalitions of males to keep in check or remove any would-be tyrant. There were two key drivers of this transition in our social structure: language and weapons. The ability to communicate effectively enabled individuals to conspire and plan a coordinated move against a tyrannical top dog, while reassuring one another of their shared intent and commitment. In short, language opens up the ability to plot the disposal of a despot. And when launching such an attack, the use of projectile weapons, such as a rock or spear, permitted a decisive move without any one individual exposing themselves to great physical risk.[5] Such coalitions tend to attack only when they have overwhelming numbers and are assured of victory. The same calculated mathematics of relative strength has been at the forefront of every general's mind throughout human history.[6] The first such planned killing of a despot would have happened hundreds of thousands of years before the assassination of the Roman dictator Julius Caesar in 44 BC.

The effectiveness with which individuals could join forces to safely challenge and dethrone aggressive despots levelled the playing field. An individual's influence within society became decoupled from their personal physical might, and instead came to rest on the strength of their social network and the reputation they had gained based on their generosity or supportiveness. Power shifted, from a dominant alpha male who acquired and then maintained his authoritarian position through brute force and the threat of violence against any challengers, to the wider group in a more equitable distribution. A new kind of political system had arisen and transformed the fabric of early human communities: strict hierarchy gave way to a more egalitarian structure. This reduction in reactive aggression and increased placidity of humans laid the foundations for the development of complex cooperation and cultural learning.[7]

This ability for coordinated alliances to keep violent despots in check with planned proactive aggression[8] created the selection pressure to reduce hot-headed reactive aggression. Unlike a chimpanzee in the prime of his strength, it no longer paid for humans to lash out at rivals in an attempt to rise to the top. Indeed, gaining a reputation for being violent only risked a coalition of opponents later rising against you. Collective punishment of reactive aggression resulted in its evolutionary suppression. We domesticated ourselves.*

* We can see a similar process in the domestication of wild animals. Compare any domesticated creature to its wild relatives – a dog to a wolf, a pig to a boar – and you notice, alongside an increased tolerance of humans, a marked reduction in reactionary aggression – the result of generations of selective breeding picking the traits for peaceful cohabitation.[9] The animals we domesticated exhibit more docile, placid behaviour compared to their wild relatives; they also tend to have a smaller amygdala, the part of the brain involved in the fear response and aggression.[10] (Domesticated animals also tend to exhibit a common cluster of physical traits including smaller muzzles and teeth, floppy ears and changes in pigmentation. On the whole, these were not targeted directly by selective breeding but are by-products of selection for less reactive aggressive behaviour.[11]) Interestingly, many of the genes that have been favoured in the domestication process of wild animals have also

As this shift in human social structure progressed, other, milder sanctions could be used to maintain balance within the group, without needing to resort to proactive violence. Anyone getting too big for their boots became the target of public ridicule, shaming or ostracism – we still find these patterns and rituals at work in hunter-gatherer societies today. But the threat of being attacked by a coalition of those who a dictator would attempt to dominate remained the ultimate deterrent. While the ability for a community to remove a despot does not guarantee an equitable and fair society, it is a prerequisite and goes a long way to levelling out a dominance hierarchy.

So, while hot-headed, reactive aggression was suppressed in the human evolutionary lineage, calculated, proactive aggression remained.[13] Surprise attacks from one settlement or village against another were motivated by the desire to remove competitors or acquire resources or mates. The more recent extension of such behaviour, emerging with the development of city states and civilisations, is all-out warfare. Indeed, war is the ultimate expression of proactive aggression, ordered by rulers, planned by strategists and commanded in the fray of battle by generals.

In normal life, lethal violence is socially prohibited; in war, on the other hand, the very objective is to kill a decisive number of the enemy. But humans generally have a deep-rooted aversion to discharging violence upon one another – a biologically encoded peacefulness borne of our evolution within egalitarian social organisations. While leaders may try to rouse their men with proclamations about the honour and glory to be had on the battlefield – fighting for God, king or fatherland – many soldiers throughout history, many of them farmers mustered from their fields, have found the thought of killing another person utterly abhorrent. The social traits and inclinations that enabled humanity to live harmoniously in complex societies and develop civilisation

---

been positively selected in the human lineage since our evolutionary split from the Neanderthal lineage over 500,000 years ago, reflecting common genetic changes relating to brain function and behaviour.[12]

must be overcome to prepare us for war. In order to induce troops to kill, military training is often directed towards increasing aggression, and propaganda aims to dehumanise the enemy.[14]

CIVILISATION AND THE RE-EMERGENCE OF THE DESPOT

This largely egalitarian social structure is believed to have held sway for the great majority of our history as anatomically modern *Homo sapiens*. But the desire for personal power and dominance never disappeared. Indeed, the conditions created by the introduction of agriculture and the arrival of the earliest civilisations led to the re-emergence of despotic supreme rulers.

In a hunter-gatherer society, the fresh meat from a successful kill, or foraged perishable plant products such as fruit, must be consumed immediately before they go off, so it makes sense to share them among the group. In any case, the group is constantly on the move and does not have the capacity to accumulate a stockpile of resources.

With the development of agriculture, humans began to live in permanent settlements alongside their fields or pastures. Farmers were no longer limited to the possessions they could personally carry. What's more, the glut of food produced at harvest time, and the need to store the surplus in granaries, created commodities that could be hoarded. Thus was born the concept of wealth. Agricultural surplus enabled denser and denser concentrations of humanity, the emergence of cities and greater levels of social organisation, leading to more complex states and the development of civilisation.

While there is evidence that some hunter-gatherer populations were not perfectly egalitarian and did exhibit degrees of sedentism, social stratification and specialisation of roles within the community,[15] it is clear that these characteristics all became much more widespread and pronounced with the advent of agriculture.

Individuals who assumed a position of leadership, perhaps through their skill in rallying peers to work together in successful shared enterprises like constructing and maintaining irrigation systems, were able to exercise authority over such vital infrastructure and accumulate resources for themselves. Those exerting control over the distribution of valuable caches of food and other assets could withhold resources to exercise leverage or use them to buy allegiance to quash leadership challenges or uprisings. And through the transmission of material riches and social rank from one generation to the next by familial inheritance (something we'll come back to in the next chapter), initially small differences in resource wealth – and the influence and stature it affords – came to be amplified. Rulers were able to consolidate their position; privilege and power became increasingly concentrated in elite classes and the social structure ever more stratified. In an agricultural world dependent on established infrastructure and city life, people were less able to simply move away and had little choice but to put up with increasingly autocratic rulers.[16]

This disparity of power was only exacerbated by the innovation of the first metalworking processes and the production of bronze weapons, armour and shields. In the ancestral condition, the general availability of potential weapons – any heavy stone or pointed branch could be wielded against an enemy – fostered egalitarianism. But when superior weapons and armour are difficult to manufacture, or the raw materials rare and expensive, the effect is to bolster the dominance of the despot. Only the top dog controlling the wealth can afford to buy the loyalty of fit, strong men and equip them with cutting-edge arms technology. It becomes a great deal harder for an ad hoc coalition of individuals to remove a tyrant. Indeed, a state is often defined as a coherent polity that is able to operate a monopoly on violence within its boundaries – with the sovereign ruler controlling where and when that violence is directed.[17]

COOPERATION AND ALTRUISM

We have not only modified our patterns of aggression to live peaceably together in large groups, but become prodigiously cooperative and uniquely altruistic. It's important to distinguish between the two: altruism delivers a benefit to the recipient at the expense of the donor; whereas cooperation benefits both parties. Cooperation is widespread in the animal kingdom. Hyenas working in packs to bring down an antelope far larger than themselves collectively achieve a goal that no one individual could on their own. But the sheer extent of cooperation exhibited by humans overshadows anything like that of any other species on the planet. Civilisation is itself the ultimate expression of cooperation – of large groups of people contributing to the same shared venture.

Much of the assistance that humans give one another is altruistic. This means that one individual helps another at a cost to themselves – in terms of food, energy, time or other valuable resources – seemingly with no immediate personal benefit. At first consideration, such acts appear to be difficult to explain within the context of evolution. If every individual in a population is in competition with others to survive and reproduce, what can be gained by helping another, especially at a cost to oneself?

Natural selection is often thought about in terms of an individual's ability to survive in a particular environment, compete against members of their own species as well as others and succeed in finding food and mates. Those with advantageous traits prevail and reproduce, so in the next generation more individuals carry the particular genes that produce those traits, and over time a species adapts to become better suited to its environment. The real success of an individual isn't just the number of progeny they are able to produce but the number of progeny that themselves survive to go on to reproduce. It's taking the long view: fitness is about maximising the number of *grandchildren* you have.[18]

But there's another key insight here. Selection favours not only traits that advantage your own direct descent – your number of grandchildren – but also those that contribute to the reproductive success of relatives. A particular gene propagates not only if a given individual who carries it gains an advantage, but also if related individuals – who are likely to be carrying copies of the gene – survive and reproduce. This is the concept of inclusive fitness.

By this rationale, an individual can help copies of their own genes survive and spread by assisting their relatives, in proportion to how closely related they are. More specifically, an individual's genes will prosper if the cost incurred by the individual in helping a relative divided by the benefit received by that family member is less than their degree of genetic relatedness. This is known as Hamilton's rule, after evolutionary biologist W. D. Hamilton, who expressed it in a mathematical formula. But it's best understood with an example. You are 50 per cent genetically related to a full sibling – which is to say, there's a 50:50 chance that any randomly picked gene of yours is identical in your brother or sister through descent – and provided that any action you take to help gives them at least twice as much benefit as it costs you, then it will lead to an overall advantage for your shared genes. This key realisation led evolutionary biologist J.B.S. Haldane to quip once to friends in a London pub that he would jump into a river and risk his life to save two brothers, but not one, or to save eight cousins, but not seven.[19] By helping your family members, particularly if they are close relatives, you are indirectly serving your own genes. This evolutionary strategy of assisting the survival and reproduction of relatives, even at a cost to oneself, is known as kin selection.

Apparently altruistic behaviour directed towards relatives is still self-serving, therefore, in that it helps to propagate the genes that you share. In small, close-knit communities, with little coming and going of individuals from other groups, the people surrounding you are likely to be related and so it pays to be generally helpful towards other individuals in your own group.

Kin selection is everywhere in the animal world: many species have been shown to preferentially help their immediate family, or those in their group who are odds-on likely to be related and so share many genes. What's more, many animals, including humans, appear to possess an encoded appreciation of Hamilton's rule: they not only behave more altruistically to kin compared to non-kin, but are also more altruistic towards closer kin than more distant relatives.[20] Within human populations, kin selection expresses itself in everything from charging towards a predator to protect family, going hungry to feed siblings or helping to raise a sister's youngsters (or diving into a river to save a particularly unfortunate group of eight cousins).*

Kin selection provides a neat explanation for most of the altruism we find in nature. But it cannot account for acts of generosity towards non-relatives. How can a behaviour be evolutionarily advantageous if it comes at a cost to yourself, but you cannot count on the beneficiary sharing any of your genes? The fact that, compared to other animals, humans are freakishly kind to non-relatives demands another explanation.

RECIPROCAL ALTRUISM

The theory that is generally believed to explain how non-related individuals may benefit from helping each other is known as reciprocal altruism. The idea is that if one individual helps another, even if paying a cost in doing so, the favour is returned at a later time. In this way, cooperation can evolve as a series of mutually altruistic acts.[22]

* One form of kin selection has become known as nepotism, originally describing favouritism granted to relatives. The word itself derives from the Italian for 'nephew'. Catholic bishops and popes, in making influential appointments, would often favour their relatives, often nephews. As the next pope is elected by the cardinals, this enabled them, despite having taken vows of celibacy, to attempt to continue their own dynasty.[21]

Such reciprocal altruism isn't nearly as common among non-human animals as kin altruism, but there are examples in a few species that, like humans, have an ecological necessity for social interactions.[23] Evidence for reciprocal exchange can be found among other primates, including baboons and chimps, as well as among rats and mice, some birds and even fish.[24] One of the best-studied cases is that of vampire bats. These bats feed on the blood of large wild mammals, as well as of our domesticated livestock. But finding a meal can be difficult, and because of their high metabolism, these animals need to feed every day or two. Vampire bats live in large groups, and if one individual has successfully fed it will often regurgitate blood to share with a less fortunate colony-mate. A bat that altruistically shares blood one night is likely to have the favour returned another day when the tables have turned.[25]

There's a simple economic principle lying at the core of why reciprocal altruism works so well. Those who successfully gathered food often have acquired more than they need to survive. The surplus becomes less valuable, making only a marginal difference to their prospects. But for an individual that does not yet have enough to eat, that extra unit of food is still very valuable – it could mean the difference between life and death. So a benefactor can donate some of their surplus to someone in need at minimal cost to themselves but huge benefit to the recipient. In the case of the vampire bats, one feast on an animal supplies more than enough sustenance and so an individual who successfully foraged has food to bestow on another, less fortunate bat who may otherwise have starved to death. Later, when fortunes have shifted and the original recipient has a surplus, they can return the favour, again with the greatest possible utility being extracted. Thus reciprocal altruism is a form of asset exchange, and each donor can receive a profitable return on their investment.

By engaging in this practice, both parties have extracted the maximum value from a surfeit they possessed at different times. For this reason, the behaviour is often also called delayed altruism. Competition is said to be a zero-sum game: for one individual to gain, another must lose. But cooperation is non-zero-sum: both sides can profit from the arrangement and often substantially so. This dynamic is utilised by both vampire bats and early humans sharing food and other resources or performing a service for one another. As Raihani points out, 'Reciprocity is so fundamental for driving cooperation that it has become enshrined into well-known proverbs. *Quid pro quo*. You scratch my back, I'll scratch yours. Do as you would be done by. One good deed deserves another. These maxims exist in other languages too. In Italian, *una mano lava l'altra* translates into the particularly lovely "one hand washes the other", a phrase that also exists in German (*ein Hand wäscht die andere*). In Spanish, *hoy por ti, mañana por mi means*, roughly, "today for you, tomorrow for me".'[26]

The problem with altruistically providing resources or services willy-nilly, helping others when you can't be certain that they will reciprocate in the future, is the risk of being played for a sucker. Cheaters can take advantage of your indiscriminate generosity, and you end up paying all the costs of helping but receive few benefits back. For the system to work, freeloaders must be held in check: those who don't reciprocate need to be punished by being refused help next time so as to incentivise mutually cooperative behaviour. If the recipient refuses to repay the kindness when fortune swings in their direction, the original altruist needs to remember and desist from helping them again in the future: once burned, twice shy. This tit-for-tat behavioural strategy is also found in some animals: ravens, for example, have been found to refuse to help other individuals who cheated in the past.[27]

FRIENDSHIP AND THE BANKER'S PARADOX

Keeping a mental ledger on which individuals did or did not reciprocate favours carries its own cognitive burden, however, and human evolution has devised a solution to this. After repeated rounds of reciprocation with the same individual we begin to relax our monitoring of the exchanges. In other words, we come to trust one another, and the relationship develops into a deeper bond: friendship. A friend serves as a trusted collaborator and ally in other social interactions, and we suspend the mental accountancy on keeping track of their behaviour and no longer explicitly expect or demand any particular favour to be repaid. The bond is its own assurance of reciprocity and an investment in the future.[28] We know that friendships sour, of course, but only after a long history of one partner taking more than they give back.

The bond of friendship is biologically mediated through oxytocin, the hormone that serves in all mammals to drive maternal care of their young, and in humans sustains the pair-bond between sexual partners long enough to successfully raise children together (which we'll come back to in Chapter 2). Friendship among humans is an extension of this close-knit relationship between parents and their offspring: we also forge a tight bond to those with whom we regularly reciprocate. It is this neurochemical bond that makes the pain of betrayal by a close friend so much more intense than the vexation of being cheated by a stranger.

In particular, the bond of friendship may solve a problem known as the banker's paradox. When you are facing financial ruin and most need a loan, the bank is unlikely to grant you one as you represent a terrible credit risk. On the other hand, when things are going well the bank is only too happy to offer you funds. This same dynamic would also have posed a deep problem for reciprocal altruism in the world of our ancestors. Individuals may be least likely to receive help when they most need it, because they are least able to reciprocate. Why would a non-relative come to your aid, with a greatly reduced chance of being paid back the favour? The evolution of friendship provides a solution to the quandary. The oxytocin-mediated bond between friends makes them irreplaceable to each other. So if a friend falls seriously ill, rather than callously abandoning them to find someone else with whom to engage in reciprocal altruism, you have an emotional stake in their well-being that compels you to help them pull through. A friend in need is a friend indeed. In this way, friendship may have developed in human evolution as a form of insurance against desperate times.[29]

There are a few known examples of reciprocal altruism in the animal world – such as among the vampire bats – but the practice is exceptionally common among humans. It accounts for a great deal of the generosity and cooperation seen in our interactions, especially within small, tight-knit societies where individuals have a high probability of encountering one another again so altruistic deeds can be repaid. But one extraordinary feature of human behaviour, compared to all other animals, is our propensity for helping each other even when there can be no expectation of regular interactions. This is the kindness of strangers. Humans often ungrudgingly offer assistance even to those they have never met before and can have no great expectation of ever encountering again. How can such one-off acts of kindness be explained? Kin selection and reciprocal altruism cannot account for this behaviour; there must have been other things at work in the development of our species.

One possible explanation is an evolutionary mismatch. The ancestral human condition was life in small bands with most individuals related to one another. Under these circumstances, kin selection and reciprocal altruism can comfortably explain generous acts between tribemates: you're either directly helping copies of your own genes or repeatedly interacting with the same individuals for a favour to be returned. But this simple evolutionary strategy would have no longer worked so well as humans began living in larger, more complex societies, particularly when ever-greater populations settled in urban environments, dominated by fleeting interactions with strangers with no familial connection. On my morning walk into work, I pass more strangers on the street than my hunter-gatherer ancestors probably encountered in a lifetime. Yet in general we continue to cooperate with those around us, even though there is no longer any genetic self-interest.

Our minds evolved to drive behaviour that was adaptive in our ancestral conditions, in small, kin-based communities on the African savannah, and this cognitive operating system has not had a software update as the social environment has rapidly transformed. Thus our altruistic dispositions are not calibrated to our evolutionarily novel world. This produces the apparently maladaptive behaviour of helping strangers when the favour will never be returned by them. [30]

But there's a better explanation for why humanity is so prolifically cooperative without an expectation of direct reciprocation – and it actively explains this apparently paradoxical behaviour rather than just seeing it as an evolutionary programming hangover.

INDIRECT RECIPROCITY

The notion of indirect reciprocity holds that rather than returning a favour to the same altruist, the benefactor pays it forward to others. A helps B, who then helps C, who then helps D and so on. The favour is transferred around the community, until sooner or later it returns to A. What goes around comes around. And there's an additional level: another individual who witnessed A's initial act of kindness towards B helps A themselves in order to build a relationship with somebody they know to be generous: Z helps A. The same two individuals don't need to encounter each other again, as is required for direct reciprocity, but benefit from the altruistic behaviour of the group as a whole. Helpful people are themselves more likely to receive help, whereas freeloaders who refuse to help others are punished or excluded.[31] Such indirect reciprocity is a uniquely sophisticated form of human cooperation,[32] and for the system to work, it needs two crucial functionalities not possessed by other animals.

Firstly, not only must there be witnesses observing interactions, and whether either party acts generously or selfishly, but that valuable information on the behaviour of individuals must be shared in a common pool of information for the entire group. In other words, members of a community must gossip about one another. If an individual becomes known for unreliability, for selfishly accepting benefits and not helping others, members of the community will simply withhold aid the next time the swindler is in need. It's not quite true that 'cheats never prosper' – they can often get away with it in the short term, especially in larger, more anonymous communities – but they are caught out sooner or later and their reputation is stained. Gossip, therefore, is a key prerequisite for ensuring indirect reciprocity doesn't become overburdened by freeloaders, and its omnipresence in human cultures spans from the campfire to the water cooler. Indeed, gossip and chit-chat came to replace other relationship-forging activities in primates, such as grooming.

This prolific sharing of information throughout the community on each member's behaviour – like a social internet mediated by chit-chat – creates a reputational system for determining every individual's suitability for cooperation attempts. An individual who acts generously to others develops a good reputation; an unreliable freeloader gains a bad reputation, and others know to avoid them in future interactions. Natural selection favours an individual who acts kindly because others are inclined to help them later, and so evolution has crafted human psychology to makes us care deeply about our reputation, while gossip keeps us playing fair.

The first rule of life in a gossiping society is to be careful what you do – or, more importantly, to be careful about what others will think about what you do.[33] Human society thus became a crowd of minds simulating other minds – inferring the motivations and attitudes of others and how they are likely to perceive your actions so that you can better manage your reputation. Our conscience is an expression of this – it's our inner voice that warns us someone might be watching and makes us consider how they would likely perceive our action so that we can avoid social punishment.[34]

The second crucial facilitator of indirect reciprocity is the punishment of cheats. In the repeated one-on-one interactions of direct reciprocation we looked at earlier, an individual remembers if another person cheated them previously and so can refuse help next time. Chimpanzees are also known to take revenge for acts that personally disadvantaged them.[35] However, a behaviour unique to humans is a party who wasn't directly involved in an exploitative interaction punishing the cheat for no material gain to themselves – something that is known as third-party, or altruistic, punishment.[36]

Altruistic punishment behaviour in humans can be explored with simple economic games. The kind I'll discuss here involves a group of players contributing to a collaborative outcome that is advantageous to all – what is known as a public good. Such cooperative endeavours are ubiquitous in human societies, from hunting a large kill to digging and maintaining a channel system to irrigate farmers' fields to constructing a municipal building. The history of civilisation is the history of people contributing to public goods, and as civilisation has advanced, the number and complexity of public goods has increased accordingly.[37] Cities and states provide services such as decent roads, a clean water supply, emergency services, public education, healthcare, law and order and national defence. The outcome can be enjoyed by the entire community, but only those who participated bore the costs.

Public goods are vulnerable to being undermined by slackers who may get away with putting little to nothing towards the shared venture but still reap the rewards. The public good game is often set with each player having a pot of money, and in each round of the game they can choose how much to contribute to a communal pool. At the end of the round, players pocket what they had kept behind in their personal pot, and the shared pool is multiplied by some factor (between one and the number of players) and distributed evenly among everyone. The best possible outcome for the group as a whole is for all players to contribute their entire pot so that everyone maximises the multipliable funds and thus their individual returns. But a free-riding player can profitably cheat on the cooperative effort and pitch in nothing – keeping not only their own entire pot but also the dividend of everyone else's generosity.

What tends to happen is that most participants contribute about half of their personal pot to the shared pool – a reasonable, cautious approach. However, as the players realise that some of their number are putting very little into the shared pool, or even nothing at all, everyone's contributions decrease round on round towards zero.[38] The cooperative venture collapses under the self-serving actions of freeloaders.

But there's a simple modification to the rules of the game that can enforce cooperation and rescue the shared venture to everyone's benefit. The addition of a sanctioning system allows players to spend some of their own game money to reduce the income of those they felt had cheated – for example, they can pay £1 to reduce a cheat's take-home by £3. The inclusion of such altruistic punishment radically changes the dynamics of the game. Now the individual contributions towards the common good tend to rise – sometimes to over 70 per cent of each individual's pot – and remain at that level round on round. It seems that people are willing to incur a personal cost to punish cheaters, and this altruistic punishment is very effective at both deterring free-riders and encouraging greater cooperation among the group as a whole. And so in real life too, inveterate cheats whose selfish or antisocial actions sabotage the community risk punishments including the denial of benefits, social exclusion or ostracism – or may even become the target of proactive violence.

The key motivation driving altruistic punishment seems to be innate and emotional – players report feeling indignation or anger towards the free-riders and an impulsive desire to punish them.[39] Studies have found that the righteous punishment of cheats triggers the same surge of the neurochemical dopamine in the reward centres of the brain as crucial biological functions such as sating hunger or thirst, having sex or providing parental care. (We'll come back to the dopamine system in Chapter 6.) It