When Charles Darwin launched his book *On the Origin of Species* on an unsuspecting Victorian audience in 1859, he triggered an intellectual shock wave that continues to send ripples around the world. One implication to which his book drew attention (though it was not one of Darwin’s own insights) was the fact that we humans are very much members of the animal kingdom. We are members of the order Primates, the group that contains all the monkey and ape species. In the past decade or so, we have gone one step further than any of Darwin’s contemporaries ever imagined in this respect. Genetic evidence has convincingly shown that, far from being a distant cousin of the monkeys and apes, we are very firmly embedded in the ape family as the sister species of the chimpanzees.

**Why do we need evolution?**

While Darwin’s theory of natural selection has been truly revolutionary in the history of science, it was not Darwin’s ideas on how species are formed that were to achieve such prominence in the long run. Looking back on the 150 years of intellectual history since *The Origin* was published, we can see a growing importance for his later books *The Descent of Man* (in which he explored sexual selection and reproductive behaviour) and *The Expression of the Emotions in Man and Animals* (in which he tackled the nascent field of psychology). Darwin’s ventures into the field of behaviour were much underrated—indeed, his theory of sexual selection, with its emphasis on the processes of mate choice, did not come to occupy the position of importance that it now does within evolutionary biology until more than a century after *The Descent of Man* was published. And in many ways, we are still absorbing the lessons of his work on emotions. But both books were extraordinarily prescient, in that Darwin put his finger on issues that have since come to be seen as fundamental to our understanding of human behaviour and the mind that underpins it.

The past three decades have witnessed an extraordinary explosion in our understanding of animal behaviour and its evolutionary components. This explosion has involved both the development of a very sophisticated body of theory, much of it underpinned by mathematical models and a volume of observational and experimental research on animal behaviour that would have excited the grand old man beyond measure. For it was Darwin’s genius to bring together a powerful combination of acute theoretical insight with empirical tests using data from a wide range of species. Known as the comparative method, this has remained the methodological cornerstone of the evolutionary approach to this day.

While the study of non-human animals progressed apace from the 1970s, the extension of these ideas to human behaviour and psychology had to wait for the better part of another two decades before its own explosive take-off. In part this reflected a nervousness on the part of biologists towards dabbling in things human, but also the distrust in which social scientists had held evolutionary and biological ideas since the early 1900s. However, from the late 1980s onwards, evolutionary ideas began to be applied in earnest to the study of human behaviour and the human mind. This field is so new that its findings are only available in the more specialized journals. This book is an attempt to draw together some of the more salient findings from this research in a form accessible to the general reader.
Before we begin, we need to make clear what an evolutionary approach to human behaviour does—and does not—entail. The value of the evolutionary approach is that it provides us with a sound theoretical framework which enables us to generate a set of precise hypotheses concerning behavioural responses and psychological mechanisms and subject them to rigorous tests using data from the real world.

We can ask questions about the history and development of a trait both over geological time (its **phylogenetic cause**) and within the lifetime of an individual (its **ontogenetic cause**), determine how a behaviour enhances survival and reproduction (its **functional or ultimate cause**) and identify the factors that trigger a particular behavioural response to occur (its **motivational or proximate cause**). Niko Tinbergen, who won the Nobel Prize in 1973 for his work on animal behaviour, pointed out that each of these questions, while appearing very different at face value, is really just a different way of asking the same question—why does an animal display a particular trait?—with the answer pitched at different levels of evolutionary explanation. Each of these four senses of ‘why’ is important, and each can be equally informative. But it is very important not to confuse these levels of explanation by providing, for example, a proximate level answer to a question that asks about the function of a behaviour. Partitioning the kinds of questions we can ask in this way is now known, in his honour, as **Tinbergen’s Four Whys**.

By formulating our questions carefully and making sure our answers are pitched at the appropriate level of explanation, we can identify whether behaviours are adaptations produced by the process of natural selection, whether they are by-products of selection for other traits, whether they were initially selected for other purposes but have been co-opted by evolution to serve a new role (sometimes known as ‘exaptations’) or whether they serve no evolutionary function at all. In other words, the aim of the evolutionary approach is to understand the advantages that traits confer on individual organisms, how these interact with other traits (for example, how having a large brain means that it takes longer for an animal to reach sexual maturity) and how a species’ evolutionary history constrains the range of adaptations that are possible.

**genetic determinism: the evolutionary red herring**

What an evolutionary approach does not involve, however, is any notion that all behaviour is genetically determined and that our biology is our destiny. This issue continues to exercise many people—mainly social scientists, but some biologists have also become surprisingly consumed by it. Much of the criticism leveled at evolutionary approaches to human behaviour seems to rest on the belief that an evolutionary explanation of behaviour necessarily implies that behaviour must be genetically determined. At face value, this may seem a reasonable conclusion to draw. After all, most discussions concerning the evolution of behaviour are explicitly couched in terms of ‘the gene for a behaviour’; moreover, the success of a given behaviour is explicitly measured in terms of its **fitness** (a term from population genetics that refers to the relative number of copies of a particular gene that an individual contributes to future generations).

Given this, it might indeed seem to follow that any discussion of evolution must mean genetic evolution. The logic of this argument would appear to be inescapable. But the fundamental question we have to ask is: does it have anything to do with the evolutionary study of behaviour? The short answer is no. There is a world of difference between claiming that we can provide an evolutionary explanation for behaviour and claiming that we are offering an explanation in terms of the genetic determination of behaviour. This is so for two reasons. First, no known species of organism (with the possible exception of single-celled creatures like viruses and bacteria) shows genetically determined behaviour in this way. Behaviour is simply too complex to be determined by single genes. More importantly, if a behaviour truly were genetically determined, it would
mean that the behaviour always developed in exactly the same way in each individual and that environmental influences exerted no influence whatsoever. This would result in behaviour that, by necessity, would be completely inflexible: the organism would always behave in the same way, irrespective of the circumstances. Genetic determinism on this scale is an excellent recipe for the rapid extinction of the species in question; it is not a particularly helpful foundation on which to base an effective interaction with a complex, constantly changing world.

Vertebrates evolved large brains precisely to allow them to adjust their behaviour to suit the circumstances in which they happened to find themselves on a moment-by-moment basis. The genes that code for the brain have been selected expressly to enable the organism to escape from a genetically driven existence. Ironically, given the fears of genetic determinism and the loss of ‘free will’, it is our genes that free us from these deterministic constraints.

An evolutionary approach to understanding behaviour is most definitely not about identifying a single causal link between genes and behaviour. This misunderstanding often arises because an evolutionary approach does require some genes in the system, so convention enjoins us to identify some arbitrary notional gene as the focus for our thinking. The genes in evolutionary explanations are no more than a device for keeping our thinking straight. This does mean that there are no specific genes involved, of course, but that is a question that has a purely empirical answer, which must be provided by developmental biologists, not by evolutionary psychologists.

Second, the evolutionary study of behaviour is not actually about the genes that determine behaviour, even in the weak sense that there must always be some genetic constraints on the capacity to behave at all. The point is that an evolutionary approach is concerned with a strategic analysis of behaviour: why does the individual behave in this way, in the sense of ‘what purpose does it serve for the individual?’. A strategic view makes no specific assumptions about what determines behaviour, it simply assumes that an individual’s choice of behavioral strategy is guided by evolutionary considerations (that is maximizing its contribution to the species’ gene pool in future generations).

**darwin, genes and behaviour**

The evolutionary approach to the study of behaviour raises four separate points that need to be clarified:

First, such explanations sound as though (and have certainly been interpreted as implying that) animals make explicitly conscious decisions about their genetic future. No organism can do that, not even humans. Rather, this kind of explanation makes no assumptions at all about how such decisions are made: it could be entirely genetically driven and unthinking, but it could equally be entirely learned and deliberate, or it could be anywhere in between. Which of these possibilities is correct is an interesting empirical question but the answer does not have any implications for whether animals are behaving strategically, or, indeed, whether evolutionary considerations have had a hand in their decisions.

Second, while organisms which behave in a way that increases the number of their descendents in future generations can be considered to have higher fitness, this does not mean that the actual goal of that behaviour is the maximization of fitness. The goal of an Ache hunter from Patagonia may be, on one occasion, to hunt and kill a tapir, or on another to marry off one of his children and dance at the wedding. The link to fitness can occur very far down the line and there is no reason to expect people, any more than other animals, to show behaviours that are overtly designed to increase their fitness (the number of descendents they leave), even though that is their eventual consequence. The achievement of a much more proximate goal can have fitness-enhancing effects, but there need be no direct link between the two. This extended link, via a se-
ries of intermediate proximate goals, between behaviour and its ultimate fitness consequences, allows us to explore organisms’ behavioural decisions by focusing on immediate short-term consequences such as maximizing energy intake (in the case of hunters) or maximizing the number of offspring sired (in the case of mating strategies), while assuming that successful solutions to these proximate problems will eventually carry through into higher fitness. In behavioural ecology, this is known as the phenotypic gambit.

Third, the assumption that organisms are designed to behave in such a way as to maximise their genetic fitness is a heuristic device rather than a presumption of fact: it provides us with very precise predictions, which can be subjected to clear empirical tests. In contrast, the criticism of genetic determinism is explicitly focused on the machinery that permits behaviour to occur—in effect, what enables the hardware to be produced. This is a how question and is clearly entirely different from asking why behaviour occurs.

Fourth, evolutionary explanations are statistical. Perhaps the commonest attempt to counter an evolutionary explanation is: ‘Well, my children don’t do that!’ A specific example, however, cannot negate a statistical rule. To disprove the claim, you need to show that on average children do not behave in this way. The statistical nature of evolutionary explanations is important—indeed crucial—because evolutionary change cannot happen if everyone behaves in the same way. Organisms have to constantly test their environment, whether this be physical or social, in order to determine whether they are behaving in an evolutionarily optimal fashion. Some individuals will inevitably get it wrong. But, now and again, this trial and error learning will yield a novel solution that is better than all the others. Gradually, this solution will spread through the population, as those who have it (or adopt it) reproduce more successfully. But even so, that solution will never be adopted by everyone in the population: individuals will continue to try out new ones, and some will continue to get it wrong.

In short, the dispute confuses two quite different kinds of question that one might ask of the world: why something occurs or how it occurs. The confusion probably arises because the word gene is used in both kinds of explanation. One focuses on genes as causes of behaviour (or the capacity to behave), the other focuses on genes as consequences of behaviour (that is to say, the effect that behaving in a particular way has on the genetic make-up of the next generation). Although evolutionary biologists keep these two meanings clearly separated in their minds, those who are less familiar with this approach often confuse them.

Although these two processes are necessarily linked, it does not follow that, in any particular case, the same set of genes is both cause and consequence. In large-brained organisms like mammals and birds, this evolutionary loop is often closed by the brain. Consider an organism that has a large brain, which enables it to adopt flexible behavioural strategies. This allows it to fine-tune its behaviour, in the light of current circumstances, so as to maximize the number of matings it achieves, thereby maximizing the number of offspring it contributes to the next generation. What is passed on from generation to generation and so makes both evolution and the behaviour possible, are the genes for a big brain. But the genes that code for the brain do not determine the behaviour (mating) that the brain gives rise to; rather, they merely determine the capacity to make flexible decisions that are well tuned to local circumstances.

Finally, it is worth remembering that when Darwin first formulated his theory of natural selection, he had no knowledge of genes at all. In fact, his new theory was much criticized for containing what many regarded as a very inadequate mechanism of inheritance. Darwin’s theory of evolution by natural selection was only rescued from the growing obscurity into which it fell after his death by the rediscovery of Mendel’s laws of inheritance.
Although Gregor Mendel, abbot of the monastery at Brno (in what is now the Czech Republic), was developing his laws of inheritance at the same time as Darwin was developing his grand theory, his ideas were not widely appreciated outside his home town (Darwin, who had a copy of Mendel’s paper, certainly failed to understand their significance). Remarkably, this key which unlocked Darwin’s grand theory remained overlooked in the dusty volumes of obscure libraries for more than half a century until it was rediscovered by geneticists in the early 1900s. The result was what is known today as the new synthesis—the amalgamation of Darwin’s theory of evolution by natural selection and Mendel’s laws of inheritance into a single unified theory.

In any case, Mendel didn’t know about genes either! For both Darwin and Mendel, inheritance was all about ‘fidelity of copying’ between parents and offspring. This has one very important implication: evolutionary processes do not have to depend on genes. Anything that causes a correlation between parents and offspring has the capacity to be a Darwinian process. The things that an organism learns in its lifetime and passes on to its offspring can also undergo a process of natural selection. It is entirely possible and equally evolutionary, for non-genetic inheritance to take place and for such non-genetic resources to be selected over time. Cultural processes can therefore have very important evolutionary effects and this is especially true of our own evolution. In other words, understanding human behaviour from an evolutionary perspective may not require the involvement of any genes at all.

**disentangling the web**

In this book we will rely heavily on a strategic perspective. At each step, we will ask how humans behave in some particular respect. We will then go on to ask what cognitive and physiological mechanisms underpin this behaviour. Where we can, we will ask about the developmental processes involved, in an attempt to address the question of how genetic inheritance and learning interact to bring such behaviour about (however, what we can do in this respect is presently severely limited by our almost total ignorance of the processes involved). And, finally, in a few cases, we will ask questions about the evolutionary history of a particular phenomenon (although the number of cases where we really can say anything useful about this is even fewer). For the moment, our concern will mainly be to raise questions about the processes involved and point to possible ways ahead.

Evolutionary psychology has often been seen as an alternative to more conventional approaches in psychology, the equivalent of developmental psychology, cognitive psychology or social psychology. That, however, is to misunderstand what the evolutionary approach is all about. In biology, the evolutionary approach provides a unifying framework that allows different subdisciplines (behaviour, ecology, physiology, genetics, anatomy, biochemistry, etc.) to talk to each other. In effect, *Tinbergen’s Four Whys* spell out how the various subdisciplines are related and allow them to interact without confusing the issues or getting into pointless disputes. In our view, evolutionary psychology supplies the same service for psychology, creating a theoretical framework for unifying the various subdisciplines. To all intents and purposes, functional questions about why individuals behave the way they do (known in biology as behavioural ecology) are really just social psychology with an evolutionary backbone. Cognitive and developmental psychology, in turn, map neatly on to the mechanism and ontogenetic senses of *why*?

Only evolutionary history (phylogeny) is missing from conventional psychology. Despite Darwin’s interest in the evolution of the mind, psychologists have tended not to ask questions about the evolutionary past, instead, they have taken the present as the focus of their interests. But there is a good reason why psychology should be interested in evolutionary history. Comparative psychology has always stood as a reminder to psychologists that we share our evolu-
tionary past with other animals and in particular with the primates. Understanding just how and why we differ from non-human animals is a psychologically interesting question and knowing when those differences emerged may provide us with important insights into human nature.

In this book, we will not have much to say about the behaviour and psychology of non-human animals, even though comparative psychology is an important branch of evolutionary psychology. This is simply because it would require a much longer book to bring it all together. Animal research will, none the less, constantly be hovering in the wings, not least because almost all theories of behavioural ecology were developed through studying animals. The functional side of human evolutionary psychology thus builds on a vast mass of research: in applying these ideas to humans, we ask to what extent the same general principles underpin human behavioural decisions.

By the same token, we will have little to say about many of the more conventional aspects of cognitive psychology such as memory, perception, thinking and so on. These largely focus on questions about mechanisms, the fundamental building blocks of how we interface with the world. They are there and they surely have an evolutionary origin, but, consistent with our focus on strategic functional questions about behavioural decisions, our main concern will be with what has become known as social cognition, a higher-order layer of cognitive mechanisms specifically involved in the social decision-making that lies at the heart of human behaviour.

One last source of confusion needs to be clarified. Those who apply an evolutionary approach to human behaviour have, for the past decade or so, been locked in a trenchant and, at times, rather unseemly dispute about how such studies should be done, On the one side, those with a background in biology (and specifically, behavioural ecology) have stressed the importance of asking whether behaviour is adaptive in the conventional functional sense used by biologists (that is, that a particular behaviour has the consequence of enabling the organism to maximize its fitness). They have emphasized both individual differences in behaviour and the analysis of their functional consequences.

In contrast, those with a background in psychology have tended to focus on the universals of behaviour that are true of the species as a whole. As a result, they have concentrated on the cognitive mechanisms that produce behaviour—the design of the human mind, as it were. Because they view the neuro-cognitive hardware rather than behaviour as being the product of selection, they have insisted that the behavioural ecology approach is, in the case of humans, rather fruitless: they argue that there has been little change in the human gene pool in the last 10,000 years, since the invention of agriculture, and hence that much of our behaviour will inevitably be mal-adaptive because we are stuck with a Stone Age mindset in a modern industrial environment. The human mind, they argue, evolved to deal with conditions in the Environment of Evolutionary Adaptedness (or EEA), the historical time and place in which our ancestors evolved their particular characteristics. Hence we can only understand the mind as an adaptation if we see it against the background of the prehistoric environment in which it evolved.

We see little or no benefit in polarizing an artificial distinction. The fact is that the human mind, like the minds of all species with brains of a decent size, evolved to cope with environmental variability. The terrestrial environment has never been stable at any time in the Earth’s long history and any species that sought to evolve rigid cognitive mechanisms would be signing its own extinction warrant. Most vertebrate species are designed to be smart precisely so that they can adjust their behaviour to the constraints of current circumstances, whatever they happen to be. This is not, of course, to deny that some aspects of the human mind maybe much less
flexible than others. Rather, it is to say that we should not be prescriptive about what these might be until we have shown that they actually exist.

Instead of getting involved in an argument that is ultimately pointless and distracting, we prefer to bring both perspectives together as best we can. Cognition is an essential element in any account of the functional aspects of human behaviour. While it remains true that the structures of the human mind evolved in a particular environment, the EEA is an elusive concept since our minds, like our bodies, are the product of a long evolutionary history and it is probably not possible to identify a single point at which any one feature came to be.

In the chapters that follow, we will present evidence to show that many aspects of modern human behaviour are functionally adapted to evolutionary goals and that behavioural plasticity and flexible decision-making are key to achieving these goals. At the same time, we will also find aspects of human behaviour that seem to be resolutely intransigent in the face of changing environments. As a result, we will need to develop an integrated approach that draws together a whole range of disciplines to understand the complex explanatory web which underpins the way humans behave.

**summary**

An evolutionary approach provides us with a powerful framework for studying human behaviour and the mind. This is not because it offers us a different method to conventional psychological approaches but because it allows us to integrate them under a single unifying theory: Darwin’s theory of evolution by natural selection. In doing so, it is important to remember that an evolutionary approach does not necessarily imply that either behaviour or the mind that underpins the behaviour is in any way genetically determined. Learning is itself a Darwinian process and provides one of several possible alternative mechanisms of inheritance in addition to conventional genetic processes. Appreciating this enables us to widen the scope of things we study to include culture and the mechanisms of cultural inheritance.
chapter two

what evolution did for us

When Darwin first developed his theory, people assumed that animals behaved in ways that were good for the species as a whole. For example, female lionesses which suckled young cubs belonging to other females in their pride were assumed to be doing so in order to make sure that there were plenty of lions in the next generation and so the species wouldn’t become extinct. However, the most important thing to note about the theory of natural selection is that it is concerned with *individual* survival and not with the survival of the species. Although individual reproduction inevitably has the effect of perpetuating species, this in itself is not the purpose of reproduction (or evolution).

Individuals are selected to behave in their own reproductive interests and the fate of the species as a whole is irrelevant to individuals’ reproductive decisions. This must obviously be the case if natural selection is to operate in the way Darwin envisaged: since the whole process is based on the notion of inter-individual competition, any organism that behaves so as to benefit the species or group at some cost to its own reproductive interests is likely to leave fewer descendants than less noble-spirited individuals who just look after themselves.

darwin and natural selection

So how did Darwin envisage natural selection as operating? While his views on the importance of natural selection in the evolutionary process changed over the course of his lifetime and evolutionary biologists today continue to argue over the relative importance of selection as a means of evolutionary change, there is no doubt whatsoever that, with this idea, Darwin changed forever the way we think about the natural world.

The theory of natural selection is deceptively simple and is based on three premises and their logical conclusion:

*Premise 1*: All individuals of a particular species show variation in their behavioural, morphological and/or physiological traits (their *phenotype*). This is usually known as the *Principle of Variation*.

*Premise 2*: A part of this variation between individuals is *heritable* that is, some of that variation will be passed on from one generation to the next (or to put it even more simply, offspring will tend to resemble their parents more than they do other individuals in the population)—the *Principle of Inheritance*.

*Premise 3*: Whenever there is competition among individuals for scarce resources such as food, mates and somewhere to live, some of these variations will allow their bearers to compete more effectively than others. This competition occurs because organisms have a capacity to greatly increase in numbers and produce far more offspring than can ever give rise to breeding individuals (just think of frogspawn, for example)—the *Principle of Adaptation*.

*Consequence*: As a result of being more effective competitors, some individuals will leave more offspring than others, because the particular traits they possess give them some sort of edge: they are more successful at finding food, or mating, or avoiding predators. The offspring of such individuals will inherit these successful traits from their parents and ‘natural selection’ can be said to have taken place. Through this process, organisms become adapted to their environment. The success with which a trait is propagated in future generations relative to other variants of that trait, is called its *fitness*. Fitness is a measure of relative reproductive success (that is, rela-
tive to alternative variants of the same trait); strictly speaking, it is a property of traits. This is sometimes known as the Principle of Evolution.

By specifying a mechanism by which evolutionary change could be effected, it then became possible to formulate testable hypotheses aimed at explaining the anatomy and behaviour of organisms. If a trait was an adaptation, then it should show evidence of being well adapted to the purpose it was supposed to serve; and if it continued to confer a selective advantage on the organism that possessed it, then it should also help to increase the survival and reproductive success of those organisms relative to those that did not possess it (or which possessed inferior versions of it).

A second important consequence of Darwin’s position was that it made ‘group selection’ (evolution for the benefit of the species) an extremely unlikely (though not entirely impossible) explanation for the evolution of anything. Despite this, group selection remained firmly ensconced in the public imagination. Indeed, even biologists often failed to appreciate this point and it was not until the 1960s that the concept of group selection was finally laid to rest. Evolutionary biologists have remained extremely cautious of mentioning group selection ever since.

the ‘selfish gene’ as shorthand

Sometimes, however, even the individual is too gross a level to understand the workings of evolution. This is because, although natural selection acts on the survival and reproductive success of individuals, what actually changes over time is the frequency of genes in the population’s gene pool. Individuals are really transient beings: no matter how long their lifespan, they all die in the end. Genes are the entities that persist and provide continuity over time.

In his famous book *The Selfish Gene*, Richard Dawkins argued that there are some aspects of evolutionary biology which we can understand much better if we adopt a gene’s-eye view of the world and recognise that the evolutionary process consists of genes which help to promote the survival and reproductive success of the bodies in which they find themselves, rather than vice versa. To get this idea across more clearly, Dawkins made a distinction between ‘replicators’ and ‘vehicles’. Replicators are the entities (genes) that reproduce themselves and persist through time, whilst ‘vehicles’ are the entities (bodies) that the replicators construct to contain themselves and which increase the replicators’ ability to reproduce and leave as many descendants as possible.

For supposedly advocating ‘genetic determinism’, Dawkins came in for a lot of misguided abuse, mostly from people who didn’t take the trouble to find out what he really meant (see Malik [2000] for a review). It is vital to appreciate that when Dawkins talks about genes in this way, he is not suggesting that individual genes are consciously striving for their own ends; it is simply a shorthand way of speaking about evolutionary processes. What it really means is that, all else being equal, animals whose genes lead to the development of traits that increase an individual’s ability to survive and reproduce are more likely to be represented in the gene pool in succeeding generations than are individuals who had a different array of genes that resulted in traits that weren’t so successful in that particular environment. That is such a mouthful that no sensible biologist would want to repeat it every time he or she wanted to discuss the evolution of something. Dawkins provided us with a convenient contraction that needs only two words. However, it is important that, when we use his phrase, we bear in mind that it stands for that over-long sentence, and nothing more.

The significant point is not that a particular gene causes a particular behaviour, but that genetic differences between individuals (whatever these may be) are linked to behavioural differ-
ences that, in turn, result in certain individuals being more reproductively successful than others. That, as we noted in Chapter 1, is how genetic fitness is defined. Natural selection is always about relative differences between individuals, not absolute ones.

We also need to remember that evolution is always something of a compromise: at any one time, there are numerous selection pressures acting on the individual, in many different ways, with the result that a given adaptation may not always be the perfect solution to the problem in question. The classic example is that adaptations designed to enhance reproductive capacity are inevitably compromised by those geared toward enhancing survival. For example, a male could have enormously high fitness if he did nothing but mate all day but his mating activities are likely to be curtailed prematurely if he doesn’t spend some time feeding. Generally speaking, most organisms are jacks-of-all-trades and masters of none. In this sense, individual organisms, and not genes alone, are the units of selection, since the process of natural selection acts on the organism as a whole and not on genes in isolation.

It is also important to remember that other evolutionary processes can shape traits. Some traits may be historical accidents, produced by a sudden reduction in population size, such that only a very few individuals leave descendants from which the population can build up again. These **founder effects** can result in traits being fixed in populations despite the fact that they confer no real benefit on their holders—and may, in some cases, be detrimental. In a similar way, developmental constraints may result in traits that have not been directly selected for, but which have ‘come along for the ride’ as a consequence of selection for other traits.

Space does not permit a full review of all these alternative evolutionary mechanisms, but suffice it to say that, when attempting an evolutionary analysis, we must be very careful to exclude all other possible explanations for a trait before accepting that something is an adaptation. Equally, we must not be quick to dismiss something as an adaptation merely because its evolutionary function is not obvious. Doing so almost always reflects a lack of knowledge on our part. Prematurely concluding that a phenomenon has no adaptive function is as heinous a sin as prematurely concluding that it does.

**altruism and the gene’s-eye view**

A gene-centred perspective on behaviour has been viewed as somewhat reductionist, as attempting to reduce something as complex as behaviour to something that is much simpler, like genes. However, when we take a ‘gene’s eye view’ this is not to imply that behaviour is genetically determined. As we explained in Chapter 1, all behaviour is the result of an interaction between genes and environment and, in the next chapter, we go into this in more detail in order to emphasize that gene—environment interactions are the key to understanding how behaviour develops in an organism.

A gene’s eye view has been of great theoretical value, since it has given us a way to understand certain facets of animal behaviour that were otherwise puzzling, since they seemed to require a ‘good for the species’ argument that didn’t quite square with Darwin’s theory of natural selection. Consider the female lions we mentioned at the beginning of this chapter: if behaviour must always be to the advantage of the individual rather than the species, why should a lioness suckle other mothers’ cubs and help promote their genes at the expense of her own? Such behaviour, where one animal provides a benefit to another, at a cost to itself, is termed **altruism** (which means ‘being unselfish’) and was one of the puzzles that taxed Darwin himself when he was developing his theory of natural selection.

Sadly for Darwin, this problem wasn’t solved until 1964, when a young graduate student, W.D. (Bill) Hamilton, pointed out that altruistic behaviour could evolve if the individuals that
benefited from the behaviour were related to the altruist. This is because close relatives share some of their genes in common: two siblings share roughly 50 per cent of their genes, while two cousins share 12.5 per cent, which they inherit from a common ancestor (parent or grandparent, respectively). If a female lion possesses a suite of genes that cause her to help raise her sister’s cubs, there is a good chance that the genes in question will be passed on, even if that female has no offspring of her own. This is because her sister has a 50 per cent chance of having inherited an identical copy of those genes, which she then passes on to her offspring. As far as evolution is concerned, it doesn’t much matter whose body the genes are in, as long as they get passed on.

So, the reason that lionesses in a pride feed one another’s cubs is because they are all sisters. Far from behaving unselfishly, female lions are actually helping themselves—or more exactly, their genes—by helping other animals. This kind of process, where animals help promote the survival and reproductive success of their relatives, is known as *kin selection*.

However, altruistic behaviour can also occur between animals that are not related to each other, and so kin selection cannot explain all cases of altruism. An alternative explanation for cooperation under these conditions comes from Robert Trivers, an American evolutionary biologist. He argued that it would be an advantage for animals to help non-relatives if they could be sure that the favour would be repaid at a later date. In this way, the benefits balance out. Obviously, this only works if animals interact with the same individual on a number of occasions (so that the benefits are swapped fairly) and also if they are able to recognize one other.

This process is known as *reciprocal altruism* and, compared to kin selection, occurs much more rarely. This is because, when benefits are exchanged in this way, there is a delay between one animal giving the benefit and the other returning it, which makes it rather easy for the second animal to cheat and take the benefit without repaying it. If reciprocation is not reliable, then it is not in the first animal’s genetic interest to cooperate at all and the exchange of benefits can never get off the ground. Behaviour systems based on reciprocal altruism are therefore much harder to get going than those based on kin selection.

A third evolutionary explanation for altruism, or cooperation, is known as *mutualism*. In this case, two or more animals cooperate to achieve a goal that benefits both of them at the same time. Co-operative hunting is an example of this: two animals that co-operate may be able to kill a much larger prey than either would be able to on its own. Co-operating lions, for example, are able to bring down zebra or buffalo, whereas lions hunting on their own usually have to make do with antelope, which weigh only a fraction of a zebra or buffalo.

**is the gene’s-eye view too narrow?**

The mechanisms of kin selection, reciprocal altruism and mutualism form the basis of most evolutionary explanations of altruism and it has become something of a heresy to suggest that altruism can evolve as a result of selection at any level higher than the individual. However, for many years, the evolutionary biologist David Sloan Wilson has argued against this position. Along with the philosopher Eliot Sober, Wilson has pointed out that, whilst group selection is indeed unlikely to occur, it is by no means impossible for selection to take place *at the level of the group*.

One striking example of this is that, within our bodies, our genes do not aggressively compete with each other for chromosome space, but co-operate in their collective replication and transmission. Similarly, we have many cell types living in harmony: individual cells do not behave entirely ‘selfishly’, reproducing at the expense of others, because to do so would be to put the vehicle that carries them at risk. (Cells proliferating out of control in this way are what we generally refer to as cancer, with obvious detrimental consequences for the body/vehicle.) Instead, the
body’s cells are prudent, reigning in reproduction and co-operating for the good of the whole organism.

At the cellular level, selection is at the level of the group (that is, the assemblage of cells that make up an individual) since this enables a functional vehicle to be formed, which can pass on genes to future generations more effectively than can a collection of selfish individual cells. Sober and Wilson argue that, under certain conditions, it is possible for animal groups to function as the vehicles of selection, where the animals that make up those groups evolve traits that help increase the survival of the group at the expense of other groups or individuals.

One of the most crucial conditions to be met is that there must both be competition between individuals in different groups and competition between individuals in the same group. In both cases, we have competition between individuals, as required by the theory of natural selection, but the difference lies in the level at which that competition occurs. Within groups, individuals are the vehicles and they are in direct, selfish, competition with each other. However, between groups, individuals in one group are joined together in the face of competition with individuals in another group. Sober and Wilson argue that, in this case, it is appropriate to consider the group as the vehicle of selection since, under these conditions, certain altruistic traits will be selected in individuals which increase the competitive ability (and hence the fitness) of the group as a whole, even though such traits may reduce the fitness of some individuals in that group, relative to others. That is, although selfish individuals will, on average, have more offspring than altruistic ones, the groups with greater proportions of altruists will produce more offspring in total than those with a greater proportion of selfish individuals (due to the benefits provided by the altruists) and so the total number of altruists will remain stable in the population as a whole.

For this to be true, it is crucially important that groups are in competition with each other and not isolated, each living on its own ecological island. If there were no compensating advantage to the group as a whole, then altruistic individuals would be ruthlessly exploited by selfish individuals and natural selection would soon eliminate all the altruists, who would have no way of bringing pressure to bear on those who tried to exploit their generosity, since the selfish exploiters wouldn’t care much whether or not the group existed. Groups also need to periodically split and re-form into new combinations, or at least show fragmentation and movement of individuals between groups, in order to prevent non-altruists from eventually coming to dominate a particular group.

Sober and Wilson refer to this as multi-level selection theory (MST) and call their specific mechanism of selection trait group selection, since a group can be defined as the set of individuals sharing a particular trait, as well as a set of individuals forming a cohesive group, as we would usually think of it. As an example of this kind of effect, Sober and Wilson describe how chicken-breeding programs in America, designed to increase the egg productivity of hens, have frequently produced strains of hyper-aggressive chickens that have a lower productivity than their progenitors. This is because, in today’s intensive poultry industry, competing aggressively for food and space may be an important factor in influencing whether a hen is a good egg layer. However, breeding selectively from these individuals may produce a population that is so aggressive that the resulting stress inhibits their laying. But, if the most social females are selected and placed into new groups, it is possible to increase egg-productivity by 160 per cent—a figure far in excess of that produced by standard individual-based breeding programmes. This is because, as well as selecting for egg-laying abilities, the breeders are selecting for traits that allow females to function well in groups. Thus, instead of aggressive chickens that are poor layers, selection at the group level produces chickens that lay more eggs per day, have lower mortality and
show so little aggression that they do not need to have their beaks trimmed to prevent them pecking other hens.

By no means all biologists accept Sober and Wilson’s argument, since many insist that the precise conditions required for it to work would be very unlikely to occur in the real world. This, of course, is an empirical issue and we cannot at present say whether or not this is the case. Other criticisms, however, are less valid, since they assume that Sober and Wilson are arguing for the kind of ‘good for the species’ group selection that biologists have shown to be biologically implausible. It should be obvious that MST differs from this kind of group selection, since conventional individual selection is an integral part of the Sober-Wilson theory. Traits that evolve at the group level do so because, ultimately, they bring fitness advantages to the individuals which make up those groups. Selection for individual traits at the group level is taking place and this then enables some groups to do better than others. Identifying strongly with one’s own group and showing a willingness to aid another individual on that basis alone is a trait that is selected for in individuals, but it can only operate at the group level. If nothing else, without the presence of groups, it wouldn’t be possible to discriminate against non-members, or to behave differently towards them; the selection pressure to do so simply wouldn’t exist.

Wilson argues that MST may be particularly relevant to humans, precisely because we are so intensely social. Individuals that got along better with their peers would have tended to leave more descendants—whether because their stress levels were lower, their mortality was reduced since they suffered less aggression from others or because sociable individuals and their offspring were more likely to receive assistance from others than were more irascible members of the group. If our skills at dealing with others were selected in just this kind of group context, it may account for our abilities to co-operate with people we have never met before (or that we never meet at all in today’s Internet age). Taking multi-level selection seriously would therefore seem to be essential when trying to provide an evolutionary explanation for many of our most striking social traits, and we shall return to it again throughout this book.

Interestingly, altruism is one of the few areas that has been given equal attention by evolutionary biologists and social psychologists. Psychologists have been interested in identifying the factors that cause individuals to act co-operatively and help one another altruistically. The in-group effect we described above, whereby people show a strong tendency to identify with and help others whom they perceive as belonging to the same group, is an extremely robust phenomenon, and has been studied by social psychologists for more than half a century. It can be produced even when groups are designated on the basis of quite arbitrary criteria (being allocated one geometric shape versus another or on the basis of preferences for paintings by Picasso over those by Matisse).

These psychological traits are the kinds of things that might be selected for at the level of the group and could help give one group a competitive advantage over another by increasing the cohesiveness of the group and making individual members more willing to defend and protect their group mates. Such traits can also help increase group harmony overall, so that the stresses and tensions of group living are reduced, which in turn can increase the relative reproductive success of a cohesive group over a fragmented one.

**niche construction theory**

One last evolutionary theory that we need to mention before we start reviewing human psychology and behaviour in earnest is Niche Construction Theory (NCT). Like multi-level selection, NCT is particularly pertinent to issues of human evolution, both anatomical and psychological. John Odling-Smee, who has been working on the ideas behind this theory for many
years, coined the phrase ‘niche construction’ to get across the central point that animals do not passively occupy ecological niches but actively modify them.

Active modification of an ecological niche by an organism changes the selection pressures that act on the organism itself: in effect, individual organisms may become the engineers of their own evolution. Spider’s webs, for example, modify the selective environments of the spiders that spin them, creating new opportunities for selection to act. Other forms of niche construction modify the selective environment of the constructing organism’s descendants. For example, there are many insects that provide their eggs with food. They may lay their eggs on a leaf, or even, in the case of parasitoids, in the body of another organism. In such cases, the modified niche is an example of what Odling-Smee and his colleagues, Kevin Laland and Marcus Feldman, call ‘ecological inheritance’. Ecological inheritance can have a profound effect on the evolutionary process since it represents a second form of inheritance that differs from standard genetic inheritance. Inheritance of land, chattels, money and status play an especially important role in human societies and may thus represent a particularly dramatic example of this process.

In other words, ancestral organisms can also transmit phenotypically modified habitats to their descendants, as well as their genes. If these ecologically inherited niches remain stable over time (that is, the process of ecological inheritance persists across generations) then they will result in new selection pressures being applied to organisms and new forms of adaptation arising, which may then lead to further modification of the niche by the organism. This, in turn, implies that environments can evolve as well as organisms.

Niche construction, then, is essentially a feedback process, and it is this feedback which gives it its evolutionary significance. Theoretical analyses using population genetic models have shown that traits whose fitness is affected by niche construction (so-called recipient traits) co-evolve with the niche-constructing traits themselves. In our own history, for example, the evolution of stone tools (a niche constructing trait) expanded the range of foods that early humans were able to eat (to include meat and bone marrow), thus selecting for changes in our digestive morphology and relieving a constraint on the evolution of brain size. Tool use, dietary changes and brain size continued to co-evolve and feed back on each other in evolutionarily significant ways.

Niche construction means that adaptation is no longer a one way process, whereby organisms respond exclusively to environmentally imposed problems but becomes two way, with populations of organisms setting problems for themselves, as well as solving problems set by the environment.

This has important implications for how we view evolution, since it enables experiences that an animal undergoes during its life to have an effect on the evolutionary process. When organisms niche construct, they become more than just ‘vehicles for genes’ because they are now able to modify the sources of natural selection that are present in the environment and so have some responsibility for selecting their own genes. Moreover, there is no need for niche-constructing activities to be genetically specified. Learning, and other forms of experience, may lead to animal niche construction; in humans, it may also depend on culture.

It should now be clear why niche construction is so relevant to an explanation of human evolutionary ecology and behaviour. We show a more diverse and sophisticated form of culture than any other species on the planet, and we have been constructing our own niche for hundreds of millennia—since, at the very least, the time we first invented tools, around two million years ago. The philosopher Matteo Mameli has argued that other humans may also have played a powerful niche constructing role during the course of human evolution, shaping our psychology and in par-
ticular our mind reading abilities—our ability to attribute thoughts, feelings, beliefs and desires to others—so that today, human psychological development is utterly dependent on the presence of other human minds for its normal expression: we are ‘mind shapers’, as well as mind readers (we will deal with this idea in more detail in Chapter 5).

However, as the philosopher Kim Sterelny points out, the fact that we have been constructing our niche for so long does raise some problems for understanding the evolution of human cognition, because it means that humans have, to some extent, freed themselves from the constraints imposed by the environment. Thus, while we might attempt to reconstruct the ecology of a species from a knowledge of habitat, weather conditions, predator densities and the like, this may be much more difficult when trying to understand patterns of human evolution, because much of our evolutionary history has been spent constructing our own niche, rather than being shaped by independent features of the natural environment. The selective environment of humans may therefore have been very changeable, even during periods when the physical environment remained entirely stable. For example, once hominids invented a means of carrying water with them, they were freed from the selection pressures imposed by increasing aridity in the physical environment. If this happened on a small local scale, it would leave few traces in the fossil record and make it difficult to determine the exact evolutionary course that humans had taken at this point.

Sterelny therefore suggests that we need to use a diversity of methods to probe the evolution of human cognition, including experimentation, modelling and computation, comparative studies of other species, archaeology and task analysis (where the cognitive demands of particular tasks are identified). It is also important to understand the adaptiveness of current behaviour, since this helps to reveal how our niche-constructing abilities influence the behavioural strategies that people follow, the cues people use to guide these strategies and the plasticity that people can display in the face of environmental constraints. Combining behavioural studies of humans with experimental psychology, along with the historical sciences of palaeoanthropology and archaeology, allows us to constrain the degrees of freedom we have in constructing a plausible scenario and moves us from ‘Just-so’ story-telling to hypothesis formation and testing. This is by no means an easy task and we are still very far from having achieved it. Conversely, the fact that the situation is more complex than we might originally have imagined does not, of itself, make the task impossible.

**the human revolution**

This brings us to one final issue — the history of human evolution. This is important to our discussion for two reasons. One is that, building on Tinbergen’s *Four Whys*, understanding the historical origins of our behaviour and psychology may help us appreciate their functional (or adaptive) significance. The other is that a particular view of human evolutionary history has come to occupy a more prominent position in evolutionary psychology than it really deserves.

Our lineage, the hominid (or in some terminologies, hominin) lineage, is a member of the African Great Ape clade (or family). Indeed, we share a more recent common ancestor with the chimpanzees than either of us shares with the other two Great Apes, (the gorilla and orang-utan). According to the genetic evidence, the human and chimpanzee lineages separated some time around 5-7 million years ago (MYA). Since there is little fossil material from that period and what little there is is controversial, we are not able to say very much about this period of our history other than that we come from a fairly typical Great Ape line. The earliest known members of the hominid lineage for which there is plentiful fossil evidence (the australopiths of the genera *Australopithecus* and *Paranthropus*) are in many ways (but especially in terms of brain size)
fairly standard apes. They differed from our Great Ape cousins only in that they walked bipedally, whereas apes normally walk quadrupedally (on four legs).

The big change came around 2.5 MYA, with the emergence of the genus *Homo*, to which modern humans belong. This was marked by an expansion in brain volume (from about 400 cm$^3$ to about 650 cm$^3$—still a long way short of the 1350 cm$^3$ typical of modern humans), a rapid increase in stature, some significant changes in the anatomy of the legs and hips (allowing more fluent bipedal striding) and, perhaps most significant of all, increasingly sophisticated stone tools. Although the later australopiths had probably begun to develop stone tools, these tended to be relatively crude hammers. With the appearance of *Homo ergaster* (around 2 MYA), stone tool manufacture underwent a dramatic shift, into what is known as the Acheulian industry, which is associated with the production of large, carefully made, symmetrical, tear-shaped hand axes.

The *Homo ergaster* period is accompanied by a number of important ecological changes in lifestyle. These included the occupation of more open (as opposed to wooded) savannah habitats further away from standing water, a larger ranging area and a more nomadic way of life. These changes resulted in the same species occupying virtually the whole of sub-Saharan Africa (except, probably, the densely forested areas in west and central Africa) and, for the first time in hominid lineage history, escaping the confines of Africa to colonize southern Europe and Asia as far east as China. The Asian branch of this lineage is usually known as *Homo erectus*, although the anatomical differences between the two species are somewhat arguable.

Two points are important about this phase of our history. One is that we were not alone. Through much of the period during which *H. ergaster/erectus* was present in Africa, there were other hominids alongside it. There may have been as many as five species of australopiths and *Homo* alive at the same time, often occupying the same habitats. The tree of human evolution is more like a bush than the traditional view of single straight stem leading from ape-like ancestors to modern humans. The second point is that the *ergaster/erectus* phase is remarkable for its stability over a very long period of time. For the better part of one and a half million years, there was surprisingly little change in either the anatomy of the species or the kinds of tools it made.

The origins of modern humans lie in a transition that occurred around half a million years ago. Although *Homo erectus* may have survived in parts of Asia until as recently as 60,000 years ago, it was replaced, in Africa, by one or more species of archaic humans (generically referred to as *Homo heidelbergensis*). These species are characterized by a significant enlargement in brain size (to about 1200 cm$^3$), somewhat more sophisticated stone tools and a relatively rapid dispersal through Africa and into Europe (but not Asia). In Europe, they eventually gave rise to the Neanderthals (*Homo neanderthalensis*), who so successfully occupied the Ice Age habitats of Europe until around 28,000 years ago. But in Africa, the archaic humans gave rise to a new, more lightly-built, larger-brained species: anatomically modern humans (*Homo sapiens*), the species to which we belong.

Anatomically modern humans turn out to have an unexpectedly recent origin. Analysis of the DNA of modern humans from around the world suggests that all humans alive today shared a last common ancestor as recently as 200,000 years ago (and possibly as recently as 100,000 years ago). (We won’t discuss the evidence for this in any detail here, you can read about it in any modern palaeoanthropology textbook.) We also now know that anatomically modern humans and Neanderthals belonged to different species. This has been confirmed by comparison of DNA extracted from the fossil bones of Neanderthals and Cro-Magnon peoples (the earliest representatives of anatomically modern humans in Europe). While Cro-Magnon DNA is indistinguishable from that of modern humans, that of Neanderthals differs significantly from both.
The appearance of modern humans in Africa is characterized by the simultaneous appearance of a more sophisticated tool technology about 100,000 years ago, including finely made arrow and spear points, blades with razor-sharp edges (known as microliths) and multi-barbed harpoons. These new weapons seem to mark a shift from hunting styles that use thrusting weapons (heavy spears — characteristic of archaic humans, including Neanderthals) to one using projectile weapons (javelin-like spears and bows and arrows). By the time modern humans arrived in Europe (around 40,000 years ago, some time before the Neanderthals became extinct), this technology had blossomed into fully-fledged art—buttons, beads, needles, Venus figurines, cave paintings and deliberate burials complete with grave goods (the latter from about 20,000 years ago).

The important lesson that has been learned during the last thirty or so years is that human evolution has been far from straightforward. Indeed, at times it hung on a demographic knife-edge. The appearance of anatomically modern humans, for example, seems to be associated with a genetic bottleneck: all living humans are descended from around five thousand breeding females who lived 150,000—200,000 years ago in Africa. They need not all have lived in the same place at the same time; nor need they have been the only breeding females then alive. This means that the total human breeding population (the ‘effective population size’ as it is called) was once very small indeed. Of all the humans living at that time in Africa, only a very small number (relatively speaking) formed the pool of individuals from which we all descend.

The occurrence of genetic bottlenecks often spells the end for a species, as unlucky accidents with respect to who manages to breed and who doesn’t can mean that, for example, congenital diseases are passed on to all members of the population. More generally, the reduction in genetic variability in the population means that it will be unable to respond adaptively to environmental change, because individuals with the right kind of genetic make-up are missing. Demographic bottlenecks of this kind imply that the species’ survival hung by a thread. They are also commonly associated with rapid evolutionary change.

**origins of the modern mind**

The appearance of Acheulian hand axes seems to mark a significant improvement in cognitive abilities, in particular the ability to imagine the shape of the future axe inside the cobble of raw stone. But even so, the cognitive skills of which *Homo erectus* was capable were evidently not in the same league as those achieved later by archaic humans (including the Neanderthals) or, in particular, anatomically modern humans. These shifts in technological competence imply marked changes in cognition, involving greater foresight, much finer motor control and hand-eye coordination and clear evidence of intention.

One particular feature of Acheulian hand axes stands out. *H. erectus* churned out exactly the same kind of tool for millennia after millennia; those produced at the end of the period were indistinguishable from those produced more than a million years earlier. We only have to contrast this with the speed at which mobile phone technology has changed in the last ten years to see how extraordinary this stability was.

This uniformity suggests that, despite an increase in brain size, *H. ergaster* and *H. erectus* were psychologically very different from modern humans. One suggestion is that they lacked the ability truly to imitate each other. ‘True’ imitation requires both the ability to understand the intention behind an act and the ability to repeat exactly the behaviours used to produce it. Copying someone’s behaviour without really understanding the goal behind it, as, for example, when very young children copy their father shaving, is termed ‘mimicry’ and is not as cognitively demanding.
True imitation means that, if you notice that the particular technique someone is using is better than yours, you can adopt his or her technique and so improve the quality of your own work. If you then modify the technique and further improve it, others will imitate your technique and take advantage of your innovation; as a result, tool form will gradually change over time. Without true imitation, tool form is destined to remain static.

It has therefore been suggested that, while *Homo ergaster/erectus* individuals would have observed other toolmakers to gain an idea of what a finished tool should look like, when it came to making their own tools, they did it in their own way, with actions that only approximated those of the skilled toolmaker. The result was an idiosyncratic method of tool production, even though the finished product looked the same. Without precise copying, any improvements in tool design would be lost after one generation, since no other individual would be able to replicate precisely the technique used to produce it. If true imitation had been possible then, whenever an improvement occurred, it would have been passed between individuals (most likely from older to younger generations) as each person copied precisely the sequence of actions used by the toolmaker.

One important implication of all this is that there is no one period in the past 5-7 million years which one can point to as a formative phase of human evolution. Our defining traits were acquired piecemeal, over a very long period of time. Bipedalism evolved very early on (perhaps 6-7 MYA); our striding walk and its associated anatomical changes came much later (around 2.5 MYA) but long before the surge in brain evolution that led very rapidly to the massive brains of modern humans (around 0.5 MYA). Meanwhile, although stone tools have a long history (perhaps dating back to 2.5 MYA), there is a series of very distinctive shifts in tool style and quality over time, culminating in the dramatic sea change of the Upper Palaeolithic Revolution, some time after 100,000 years ago, that suggests a succession of small but important cognitive developments. The human mind also evolved piecemeal.

This mosaic, characteristic to human evolution, is important, because there has been a strong tendency for evolutionary psychologists to relate aspects of the modern human mind back to the environmental conditions in which it evolved (the so-called Environment of Evolutionary Adaptedness, or EEA). While it maybe possible to identify the particular circumstances under which individual components evolved, the palaeontological evidence suggests that there is no generic period when everything characteristic of modern humans evolved as a suite of related and co-evolved traits. We are too much of a hotchpotch. Rather, our traits evolved over an extended period of our evolutionary history, some probably very early on, others very recently indeed.

**Summary**

Evolution does not work for the good of the species, but for the good of individuals. An understanding of the workings of natural selection can often be enhanced by taking a ‘gene’s eye view— but when doing so, we must always bear in mind that selection acts on the organism as a whole. Taking a ‘gene’s eye’ perspective has helped solve many of the puzzles of evolution but when dealing with our own evolution there are other evolutionary mechanisms that we need to consider. In particular, multi-level selection and niche construction are essential for understanding patterns of human evolution, due to our species’ sociality and intelligence. The human line began with a family of upright apes and branched out into an array of specialized and well-adapted hominid species. The modern human suite of physical and behavioural characteristics has been put together slowly over evolutionary time and some of these characteristics were shared with our sister species. For most of our evolution we have not been the only hominid species around and our current domination of the planet is really a lucky accident.
Humans, like all monkeys and apes, are intensely social. It is this sociality that has given primates their evolutionary edge, making them both one of the longest-surviving lineages of mammal (their origins go back to the age of the dinosaurs) and one of the most widespread. Sociality is the consequence of an attempt to cope, in a collaborative fashion, with the challenges of survival and successful reproduction. In most cases, these advantages derive from savings of scale but in the case of monkeys and apes, it is based on a genuine attempt to solve these problems communally. However, by living together, animals inevitably incur costs. The social systems we observe are the outcome of an attempt to balance the costs and benefits of sociality, to trade off one against the other.

In Chapter 4, we saw how human sociality shapes us as children and endows us with the ability both to understand others as individuals as well as to gain an understanding of our culture. In this chapter, we explore in more detail the nature and origins of human societies and consider what is perhaps the fundamental problem that they all face: the free-rider.

primate societies

Human societies are complex. This is self-evident from our everyday experiences. Large-scale societies of the kind that characterize the modern world are, however, a relatively recent phenomenon. Towns of even a few thousand individuals appeared only with the neolithic societies of the Near East, around 7000 years ago; cities of more than a million individuals probably date back no more than a few hundred years. For most of human evolution, we lived in small-scale hunter-gatherer societies, characterized by very small, relatively unstable groups, often dispersed across a very large area. It was only with the emergence of agriculture, around 10,000 years ago, that permanent settlements of any size became possible.

Primate social systems, including those of humans, are implicit social contracts where, in effect, members agree to forgo their immediate self-interests, in order to gain greater benefits, in the long run, by solving some ecological problem more effectively. For most primates, this ecological problem will usually be predation risk. By banding together, individuals reduce their exposure to the risk of being caught by a predator, either because they benefit from a ‘many eyes’ advantage (the time needed to monitor the surroundings for predators can be shared, thus reducing the cost to each individual) or because the presence of many individuals is an effective deterrent to most predators. There is evidence to suggest that, as primate species have colonized more terrestrial and/or more open habitats (where the risk of predation is higher), they have evolved larger groups. In some cases, however, the predators in question may be competitor primate species or even individuals of the same species (for example, males who may commit infanticide).

Group living, however, necessarily incurs costs for its members, simply by virtue of the fact that they are forced into close proximity. These costs typically come in two forms. Direct costs arise as a result of conflict over resources: individuals involved in conflicts waste time and may incur injury. A particularly important form of injury, in this context, is the effect that conflict may have on the endocrine and immune systems: even very modest levels of stress, from casual harassment, can depress the immune system and, in the case of female primates, disrupt the menstrual cycle to such an extent that functional infertility results. Indirect costs arise when one individual takes the resources (food, water, refuge sites) that another could have used, thus obliging
the latter to search further afield. One of the most obvious indirect effects in primates is the need for larger groups to travel further each day, often around much larger territories.

During the course of hominid evolution, our ancestors extended their ecological niche and occupied more open habitats. In doing so, they became semi-nomadic on a very large scale: southern Asia, as far east as China, had been colonized by 60,000 years ago, a mere 10,000 years after leaving Africa. The need to cope with increased predation risk almost certainly forced them to live in larger, more co-operative social groups. However, a fully nomadic lifestyle (one that allowed our ancestors to colonize new continents from their African homeland very quickly) probably depended on the ability to share widely dispersed key resources (those that will always be there, however bad the famine or drought). This would have necessitated large-scale exchange networks that covered an area of sufficient size to guarantee that, no matter how bad the drought, there would always be at least one resource depot large enough to accommodate everyone.

Humans share, with their Great Ape cousins, the fact that they live in fission-fusion social systems. These are social groups that are normally dispersed over a wide area, such that only a few members are in physical contact at any one moment. This is particularly clear in modern hunter-gatherer societies: in these, the members of the community are usually dispersed among a number of campsites. Each camp is a temporary home for 25-50 individuals (5-10 nuclear families); individual families may choose to leave and join other camps at anytime. However, not every family in the region can join any camp that happens to be convenient. Although casual passers-by may be given shelter, camps normally consist of families (or individuals) from a specific community of 100-200 people, who collectively share rights of access to the resources that their territory has to offer.

The hunter-gatherer community is a virtual group. Although the entire community may gather in one place from time to time—for example, to celebrate coming-of-age rituals or to arrange marriages—this is very much the exception rather than the rule; such events only happen once every year or so. The sense of community that people have comes from knowing who is related to whom (biologically or socially), knowing their individual life histories and knowing that they form part of a specific network of relationships. Even more importantly, perhaps, those relationships are invariably expressed in terms of privileges and mutual obligations.

**the social brain**

Primates in general, not just humans, have unusually large brains for their body size and this is mainly a consequence of the fact that they have an unusually large neocortex. The neocortex is the thin outer layer of the brain (it is just a few cells deep) within which most of the processes we recognize as conscious thought take place: it evolved in mammals but large neocortices are a primate speciality. Primates have larger brains than other mammals because they have much larger neocortices. The neocortex typically accounts for between 10—40 per cent of total brain volume in other mammals but begins at around 50 per cent in prosimians (the most ‘primitive’ and mammal-like of the primates) and rises to around 80 per cent in modern humans.

It is now widely recognized that primates’ large brains are significantly associated with the distinctive social skills that primates display, an explanation known as the social brain hypothesis. The social brain hypothesis suggests that the demands of living in permanent social groups selected for a kind of intelligence that was particularly adept at tracking the relationships that exist between oneself and all the other members of the group and, more importantly perhaps, keeping track of the relationships that the other animals in the group have with each other.

The main evidence to support this hypothesis comes from a series of studies by Robin Dunbar and his co-workers, which showed that relative neocortex volume correlates with various measures of social complexity across the primates. These indices of social complexity include such
things as the size of the social group (see Figure 1), the size of grooming cliques (or coalitions), the amount of social play, the use of tactical deception (giving false information to mislead rivals) and, in males, the use of more subtle social strategies to undermine the power-based dominance of higher ranking males in the competition for matings. Importantly, for present purposes, they also showed that neocortex volume correlates with the length of the developmental period between weaning and puberty (the period of socialization), suggesting that animals which typically live in larger, more complex, social groups need an extended juvenile period in order to learn and assimilate everything they need to know to manage their social world.

These relationships seem to be specific to the neocortex, and not, by and large, to other sub-cortical regions of the brain. Indeed, they seem to be specific to the more forward (frontal) parts of the neocortex, such as the frontal lobe (the part of the brain associated with what psychologists refer to as ‘executive’ functions: those processes we associate most closely with rational thinking and behavioural control). However, as we noted in Chapter 4, some smaller components, elsewhere in the brain, do also correlate with social group size in primates: these include the size of the parvocellular visual pathway (but not the visual areas as a whole) and one element (but not all) of the amygdala (a part of the ancient limbic system that is concerned with handling emotional cues).

The more rearward (dorsal) regions of the neocortex, such as the visual areas, are largely unrelated to indices of social complexity—despite the fact that the primary visual cortex (usually referred to as area V1) is often the largest single area in the primate brain. This is significant, because, across the primates (including humans), the more frontal regions of the neocortex (the non-V1 regions) have enlarged at a disproportionate rate. In effect, the brain has evolved (and develops in the foetus) from back to front, from the visual areas at the back of the head to the frontal lobe over the eyes. The result is that larger-brained species like Great Apes and especially humans have non-V1 areas and, in particular, frontal lobes that, both absolutely and relatively to the volume of non-cortical brain, are much larger than those of smaller brained species. The significance of this will become clear later.

Humans fit this primate relationship between group size and neocortex size surprisingly well. The typical size of hunter-gatherer communities (around 150 individuals) is exactly the size predicted by the relationship between group size and neocortex volume in primates (and, specifically, the relationship for apes). In traditional horticultural societies, villages typically consist of
around 150 people. More importantly, recent studies suggest that this size of social grouping may even be characteristic of post-industrial societies. A study of Christmas card distribution lists, for example, revealed that the number of friends and acquaintances a person has is of about this order too (a mean of 154 individuals for a sample of 42 respondents).

**a very social mind**

When you plot group size against neocortex volume, one striking feature is the fact that monkeys and apes lie on separate lines (Figure 1). That is, the slopes for the two sets of primates lie parallel, with apes having much smaller groups for a given neocortex size. This is interesting for two reasons. First, the division does not follow simple taxonomic lines: the New and Old World monkeys lie on the same line, despite the fact that the Old World monkeys belong taxonomically with the apes. This suggests that something peculiar happened during the evolutionary history of the apes, quite soon after their ancestors parted company with the ancestors of the Old World monkeys (around 25 MYA). Second, it suggests that apes have to use more computing power to maintain a group of a given size than monkeys do. In other words apes (and, hence, humans) must be doing something more complicated than monkeys to maintain the cohesion of their social groups, and this must have something to do with the complexity of their relationships rather than just with their number.

The one thing that characterizes ape (and human) societies, above all else, is that they have dispersed (or fission-fusion) social systems. In effect, apes have to work with a mental world that includes virtual individuals as well as individuals who are physically present, whereas monkeys only have to work with the latter. A plausible explanation is that factoring both present and absent individuals into one’s social calculations may be especially taxing cognitively and hence require much more computing power (that is, a larger neocortex).

These cognitive constraints on group size exist as a consequence of our evolutionary heritage. They reflect the demands that natural selection made on our species’ sociality during the long hunter-gatherer phase of our existence. This phase was characterized by a form of multi-layered fission-fusion society in which relationships with members of the wider community had to be factored into the relationships with those with whom one happened to be sharing a campsite. This kind of dispersed society may have been critical in allowing our ancestors to adopt a nomadic existence within very large territories. It allowed them to balance the immediate demands of reducing predation risk (by forming temporary hunting camps) whilst at the same time ensuring access to limiting resources on a longer time-scale (through a network of trading relationships).

Our ability to achieve this balance partly stems from the fact that we consider our relationships with others to be real and enduring entities, even in the absence of the people concerned. We think of people even when we don’t see them and incorporate them into our lives even when they live on the other side of the world. This, in turn, is linked to our ability to engage in both shared and collective intentionality; our representational abilities (and our language abilities: see Chapter 8) allow us to conceive of mental entities that have no real world manifestation and we understand that people are motivated by beliefs and desires that can be more powerful than and as real as any solid real world object. Given this, it is a small step to view a relationship as a ‘solid bond’, something that holds people together across space and time, so that constant interaction is not necessary.

**circles of intimacy**

Neither in modern post-industrial nor in traditional hunter-gatherer societies do we interact with every other member of our community. There is considerable ethnographic evidence (from both traditional and modern societies) to suggest that the groupings of about 150 individuals that
seem to be so characteristic a feature of human social networks are actually structured into a series of hierarchically inclusive subgroupings.

It is as if each of us sits in the centre of a series of expanding circles of acquaintance, with each circle corresponding to a very characteristic number of individuals (see Figure 2). These natural groupings seem to cluster at about 5 (the support clique, from whom we would seek emotional or other support in moments of crisis); 12-15 (the sympathy group, with whom we have particularly close relationships); 35 (equivalent in size, interestingly enough, to the typical size of hunter-gatherer overnight camps); 150 (equivalent to hunter-gatherer clans); 500 (recognized in the ethnographic literature as a megaband) and 1500 (equivalent to the tribe, normally defined as the group of people that speak the same language or dialect). (Note that, at each level, the circle includes all those individuals who belong to lower levels.)

The evidence discussed in the previous section suggests that there may be an important distinction between those individuals who belong within the 150 circle and those who lie in the larger groupings beyond. This distinction seems to relate to our knowledge of these individuals as individuals. The figure of approximately 150 seems to correspond to the number of people whose relationship to you is explicit and personal, with a history of past interactions and some level of intimacy. These are the people with whom you like to try and maintain contact, in whose life histories you have more than a passing interest. They are the people who, you feel, would be willing to help you with a favour—mainly because there was a sense of obligation between you, either because of some level of intimacy or because of an obligation of kinship or fellowship in an organization or community.

Those who lie outside the circle of 150 we know only as *categories* of individuals: we can label them as belonging to a particular class (say, ‘policemen’ or ‘librarians’) and that label provides us with guidelines on how to interact with them. We can recognize many of them as individuals, but we know little about them as people. Our relationship with these individuals lacks the personal warmth that characterizes our relationships with the inner group.

Even within the network of 150 it is possible to see noticeable differences in the intimacy of relationships. In the study of Christmas card distribution lists mentioned earlier, respondents...
were asked to specify, on a 0-10 scale, how intimate they felt their relationship was with each member of the households to whom they were sending cards. When recipients were ranked in order of intimacy, the total set of recipients tended to cluster rather strikingly at just the kinds of groupings identified above. Significantly, these feelings of intimacy seemed to correlate very tightly with frequency of contact. The sympathy group, of 12-15, for example, seemed to correspond to everyone who was, on average, contacted at least once a month. Interestingly, kinship seemed to have special status in the context of these groupings: kin were significantly over-represented (relative to their availability in the population) within the circle bounded by the sympathy group of 12-15. More detailed study of the size and composition of these various groupings suggests that they may represent real cognitive constraints on the numbers of individuals we can hold in a given degree of intimacy or emotional relationship.

In effect, each circle of intimacy consists of a fixed number of boxes into which we can slot the individuals we meet. Once all boxes in a given circle have been filled, we cannot easily add new individuals. If someone new and exciting comes into town and we want to add them to our social circle at a particular level of intimacy, someone else will have to drop out of that level to make room. Face-to-face contact seems to be crucial in maintaining the quality of the relationship at any given level; failure to maintain contact with someone will have the result of weakening the tie. Old school or college friends, with whom you once spent a great deal of time, gradually become more distant as one grows older. With time, each individual slides inexorably across the circles of intimacy towards the outer edges of mere acquaintance. When you meet up, you can enjoy a few moments of reminiscence but, in all but a very small number of cases (typically those in which the original relationship was one of great intimacy or intensity), a real renewal of the relationship is possible only by starting again from scratch. Your knowledge of them is too out of date, and you no longer have enough in common with them to create a bond of the appropriate intensity. Time, it seems, is another constraint on the number of individuals we can fit into a given social circle.

However, it is clear that the ultimate limit is created by cognitive factors, which influence our ability to maintain coherent and intimate relationships with many individuals. People vary considerably in the size of their social circles at any given level. Social networks, for example, can vary in size from 100-300, even though they have a strong peak at around 150 and similar variance can be seen in the sizes of the more intimate inner circles. In part, these differences reflect a sex difference in sociability: on average, women have larger social networks at any given level than men, even though there is almost complete overlap in the two distributions. In part, it also reflects within-sex differences in personality: there is, for example, a negative relationship between sympathy group size and score on the neuroticism scale of the commonly used MPI personality test: those who score more highly on the neuroticism scale have fewer close friends.

Both these effects owe their origin to differences in social competence and social skills. Evidence for this comes from a study in which individuals were asked to list all the people they contacted at least once a month (one operational definition of the sympathy group) and then tested on advanced theory of mind tasks (the core form of social cognition, which we discussed in Chapter 4). For the test, subjects were presented with a short story detailing a particular social event and asked to identify who was thinking what in the story—with questions that ranged up to nine levels of embedded intentionality. For a sample of 60 subjects, there was a very significant correlation between sympathy group size and achievable level of intentionality (that is, the highest level at which subjects could correctly answer questions about the mind state of the characters in the story). This suggests that social skills and social cognition competency maybe directly
related—a conclusion that is supported by experimental evidence which suggests that higher order intentionality capacities are lost when individuals are suffering from psychotic conditions such as paranoid schizophrenia or bipolar disorder (manic depression).

**trust and reciprocity**

The evidence discussed in the previous two sections suggests that our social networks of around 150 people depend on intimate personal knowledge of the individuals included in these circles. That knowledge seems to have important implications for the nature of the relationships involved. It creates a sense of trust and obligation that smooths the process of interaction—and, in particular, reciprocation and co-operation. The importance of trust and obligation at this level of social organization is emphasized by a number of relevant observations.

The Hutterites, a fundamentalist Christian group, who came from Europe to settle in Dakota and southern Canada during the middle of the nineteenth century, continue, even now, to live a strictly communal life in which the farmland is owned communally and the farm work shared equally. However, they invariably split communities once their size exceeds about 150 individuals because, they say, it is not possible to manage a community that is larger than this by peer pressure alone: you need a police force. Since police forces are anathema to the very concept of their way of life, they prefer to avoid the problem by ensuring that community size is always below the critical limit.

A second example is provided by ‘small world’ experiments, in which subjects are given a large number of named individuals in different parts of the world and asked to identify someone they know who could be persuaded to take letters to them (passing the letters through the hands of intermediaries if necessary). The results suggest that subjects exhaust their lists of approachable first contacts somewhere between 125-150 individuals. Since this task explicitly asked subjects to request a favour (taking a letter and, if necessary, asking someone else to pass it on in turn), it essentially measures the number of individuals that subjects feel they could ask a favour of without fear of being rejected out of hand or feeling too embarrassed about making such a request. This suggests that a sense of obligation (a willingness to say ‘yes’ without demanding an immediate quid pro quo in exchange—a definition, perhaps, of true friendship) may be a crucial aspect of the relationships we have with those who are part of our 150 social network.

This kind of evidence suggests that what makes human societies possible is the fact that the members implicitly agree to honour their social obligations. We agree not to steal each other’s property, to repay debts—if necessary with interest and not to steal each other’s spouses. If we didn’t abide by these rules (most of the time, anyway), social life in groups would not be possible. Each family would be forced to space out sufficiently far to avoid risk of conflict or exploitation—indeed, even family life might be impossible, because families themselves are essentially social contracts between couples (and children?).

Trust becomes important in this context, because we do not have the time to check everyone else’s reliability and honesty. We simply have to assume that those we meet will abide by the rules. This does not, of course, mean that we are at the mercy of everyone else in society. Much will depend on the dynamic social environment we happen to be part of. History tells us that social life is subject to dramatic mood swings: periods of calm and stability alternate with periods of civil war and chaos. During stable periods, trust and reciprocity grow and we may be willing to act generously towards strangers. But during more troubled times, trust breaks down and we may draw in our social horns to focus our goodwill on the core members of our social networks—those whom we know we can trust and on whom we ourselves depend. In climates of suspicion, everyone is looking over their shoulders to check on who is following them. In effect,
we are dealing with a predator-risky environment, although in this case the predators are other members of our own species (perhaps even our own community), rather than the more conventional carnivorous kind.

**deacon’s paradox and the free-rider**

The importance of trust emerges in one particular social context, which we call Deacon’s Paradox. In his book *The Symbolic Species*, Terrance Deacon pointed out that human societies have a peculiarity that exposes them to seriously disruptive forces: that is, humans form pair-bonds, yet have a sexual division of labour. This division means that men and women are often physically separated for long periods of time whilst they are engaged in their different foraging activities. Men and women must agree to honour the integrity of each other’s pair-bonds, otherwise the entire fabric of society would collapse.

Yet, as we know from everyday life, other people’s relationships aren’t quite as sacrosanct as they really ought to be: affairs and illicit liaisons do occur. However, they don’t occur with as much frequency as they would if mating were a complete free-for-all, especially given that neither men nor women are around all the time to guard their mates and prevent them forming liaisons with rivals. Moreover, as we suggested in Chapter 5, women may have explicit evolutionary interests in shopping around for ‘good genes’ even when they are in stable, pair-bonded, relationships, just as much as men may have interests in any siring they might be able to achieve on the side.

Deacon argued that the capacity to form symbolic contracts, such as formal marriage pacts, has been crucial in the evolution of human sociality. These contracts amount to a formal public declaration of commitment that other members of society recognize — and are willing to police. Up to a point, the fact that in traditional societies men and women tend to spend their time apart from their spouses, in single-sex groups where their activities can be monitored, helps to police the system. But neither sex is always under the watchful eye of the other members of society who have a stake in their sexual honesty.

Deacon’s Paradox highlights a more general problem, with which any social system founded on an implicit social contract has to contend, namely the destabilizing effect that free-riders inevitably have. Free-riders are those who take the benefits of the social contract but do not pay all the costs. In any social contract, there will always be a temptation to take advantage of the generosity of others. The benefit to the free-rider is often considerable, because they are able to steal a march on everyone else. Consider the classic case, where members of the community exploit a common resource, such as a forest or common grazing land. This resource will last forever if every member of the community uses it sparingly and does not take more than their fair share of the renewable portion of the resource (the proportion that can be replaced by natural growth). However, there is always a temptation to take slightly more — to graze one extra cow on the common or to cut down an extra tree. By doing so, they (and their family) benefit, by having a little extra to see them through the winter. But everyone else pays the cost for their selfishness because there will be less for them to use — the resource will be used unsustainably and eventually will not be available to future generations.

The members of society which the free-rider exploits are forced to behave altruistically: they contribute to the fitness of the free-rider at the expense of their own fitness. These costs may be small in the short term, especially if they are shared between all the other members of the society. But they necessarily add up in the long term. And if the pressures are great enough, the effect of many individuals behaving as free-riders will be such as to impose a very significant burden on the rest of the community. At that point, the implicit agreements that bind the society together will fall apart. Suspicion and a reluctance to engage in reciprocal deals, will increase,
making the natural flow of interactions and relationships less fluid. Willingness to co-operate on trust will decrease and gradually the virtual bonds that hold the social system together will dissolve. Freeriding will eventually be held in check by our personal experience of an individual freerider’s behaviour: once bitten, we will be reluctant to trust that particular person again. But once we reach that point, the element of trust that helps to hold society together has been lost.

Computer simulations have shown that the free-rider problem becomes increasingly intrusive under two general conditions: when social groups are large and dispersed and when the costs of co-operation are low (that is, when individuals are willing to co-operate without being too inquisitive about whom they are sharing their resources with). Under these two conditions, free-riders will find it relatively easy to locate naïve individuals who are unaware of their behaviour. Both are, as we noted above, features that are particularly characteristic of human social systems.

As with all primate groups, the tensions created through living cheek-by-jowl have to be held in check, lest they overwhelm the benefits and drive the members of the group apart. Primate social groups are held in balance because monkeys and apes can bring to bear sophisticated social cognitive skills that allow them to manage the disruptive forces that act within their societies. These skills are, presumably, underpinned by the computing power of primates’ unusually large brains. We explore these processes in more detail in Chapter 11.

**summary**

Humans are embedded in networks of social relationships that form a series of expanding circles around each individual. Our ability to keep track of the constantly changing world of our social relationships depends on the advanced social cognitive capacities that we share with our monkey and ape cousins. The ‘social brain hypothesis’ refers to the fact that primates have unusually large brains compared to other animals and that these enhanced cognitive capacities are related to the fact that they have a more complex social life. At the core of this lie the concepts of trust and obligation, which enable individuals to co-operate in groups to solve the problems of survival and successful reproduction in more efficient ways. However, any such system is inevitably plagued by free-riders (those who take the benefits of co-operating, but fail to pay all the costs) and mechanisms are needed to keep them under control, in order to avoid the delicate balance of relationships in co-operative social systems from being destroyed.
Humans are characterized by two features that seem to differentiate them very clearly from all other animals: language and culture. In one sense, drawing a distinction between these two is something of a false division. Culture, in the human sense, depends on language: in the absence of language, human culture would not exist, because language is necessary for the exchange of things cultural. Conversely, language is an integral part of culture: the language that we speak is one very important aspect of our culture. However, it is convenient to differentiate between them in order to consider their evolutionary aspects, because language entails anatomical adaptations for speech that are quite separate from anything to do with culture as such. First, however, we consider how and why human language and culture are unique.

**the uniqueness of human being**

Over the last century, social scientists have made a great deal of the claim that language and culture are the defining features of humanity. They are, after all, what set us apart from brute beasts. Equally, ethologists have, over the years, been at pains to claim that neither language nor culture are unique to humans. This debate has played such a central role in discussions of what makes humans unique that we need to spend a little time evaluating the claims made by each side. We deal with language first because, historically, it was the first to be explored in any detail.

Language is a system of communication in which arbitrary signs or signals stand for concepts. Conventionally, human language uses an auditory medium, so that language and speech are intimately related. However, as the deaf community demonstrates, human sign languages are as fully functional as are conventional spoken languages. The defining features of language are: the arbitrariness of their signal-meaning relationships (where the sounds or signs used to stand for concepts bear no iconic relationship to the concept itself—the male and female signs used to label public toilets, for example, bear a deliberate iconic relationship to the concept they refer to in a way that the words *male and female* do not); the role of grammar in facilitating the coding of complex information; the fact that the sounds are graded rather than discrete (sounds vary into each other rather than being completely different in the way that, for example, a scream and a sigh are categorically different) and the fact that the sounds produced are not, in themselves, emotionally charged (in the way that a scream, for example, most certainly is). This is not to say that emotional overtones cannot be added to human speech sounds but that the nature of the sound itself is not directly caused by the utterer’s emotional state: the same sound (or word) can be uttered in any number of different emotional states but still mean the same thing (that is, refer to the same concept or idea).

The traditional view would be that animal communication fails on all these criteria. Their sounds are emotionally charged, have no syntactic (grammatical) structure and do not refer to specific concepts (that is, have meaning or semantics). These claims have, however, been challenged by ethologists. Many species of birds and animals are now known to have different calls for different kinds of predators (technically known as ‘reference’). Vervet monkeys, for example, have one kind of call for terrestrial predators like leopards, another for aerial predators like eagles and yet another for snakes. The animals respond to the call with the appropriate evasive action (running for trees, dropping down out of the canopy and standing to peer around into the grass, respectively) they do not need to see the calling animal. Similarly, marmosets are said to have a simple form of grammar that alters the meaning of a particular call.
However, while we can recognize that these claims are all true and that they demonstrate that the precursors of human language are well developed among non-human primates, we are, none the less, obliged to note that no non-human species (not even the honey-bee, with its much vaunted waggle-dance ‘language’) has a system of communication that is as complex as human language. Recent research has shown that while tamarins (close relatives of the marmoset) can understand simple place-type grammars, they do not understand more complex grammatical rules, which allow sounds that are far apart in the sequence of utterances to be related to each other (something that requires the kind of hierarchical processing of sounds that is required in parsing long grammatically structured sentences). Bees, for example, can tell each other about the locations of nectar sources but that is all: they cannot use their language system to comment on the weather, upbraid lazy drones or discuss where would be a good location for a new hive next summer. So far as we know, such topics of conversation are exclusive to the human species.

Whilst it is relatively easy to define what we mean by language, it has proved much more difficult to arrive at a wholly satisfactory definition of culture. The fact that human behaviour varies so much between different societies makes it seem obvious that it must be cultural in origin. This implies that it has been learned from other members of our immediate social group. This has, however, led to quite different approaches in the three disciplines that take an interest in culture (social anthropology, ethology and psychology).

Traditionally, social anthropologists have understood ‘culture’ to refer mainly to those aspects of human behaviour which are learned from other members of society. None the less, a famous survey carried out in the 1950s concluded that anthropologists have used the term to refer to more than 140 different kinds of phenomena and that it was all but impossible to identify any one of these as being ‘right’. In practice, most of these 140 different usages boil down to just three kinds of phenomena: rules of (usually social) behaviour (for example, rituals, forms of greeting, table manners, etc., including metaphysical and other beliefs about the way the world is); artefacts (things that are made, like tools or structures—what archaeologists usually refer to as material culture’) and literature, music and art (what we might refer to as ‘high culture’). Seen in these terms, it is clear that all three share a property, namely the fact that, in one way or another, they involve ideas in someone’s mind. I have a mental image of how you should behave in a particular situation (or why the world is as it is); I have a pattern in my mind when I construct a particular pot or tool; I intend to convey a particular story or meaning when I compose a play or paint a picture. For anthropologists, culture is about meaning and about how that meaning is envisaged.

Ethologists have tended to emphasize the phenomenon of culture—the behaviour itself. They note that, when behaviour patterns are learned from others, this can lead naturally to diverging patterns in neighbouring populations. When seeking evidence for culture, they thus tend to place most weight on differences between populations in their habits or styles of behaviour. They have therefore been content to refer to the way that bird or whale songs differ between neighbouring populations (or, within the same population, across generations) as examples of animal culture. When chimpanzee populations in different parts of Africa use different implements for breaking open the hard shells of palm nuts or different types of techniques for obtaining termites from their mounds, ethologists have been content to label these as cultural differences. The populations differ in their styles of behaviour in ways that are not obviously a simple consequence of their local environments. There is no reason why chimpanzees in one population should use grass stems to fish for termites but another population uses twigs.
Psychologists, in contrast, have focused on the mechanisms by which culture is learned. Psychologists point out that behavioural differences can arise through a number of learning processes, some of which we would not want to call cultural. An animal (or, indeed, a human) might have its attention drawn to some aspect of the natural world (say, a food item) by the behaviour of another member of its group. However, if it then figures out how to handle that feature for itself, by trial and error, the result may well be different behavioural traditions in two adjacent populations but we would not want to refer to this as cultural in any meaningful sense. Instead, psychologists insist that the term cultural be reserved for those cases where we can be absolutely sure that an individual is truly imitating what another does, understanding both the object of the act and the means used to achieve it, so that its doesn’t need to engage in any trial and error learning in order to work out what to do. When we see evidence for copying of this kind, they argue, then we really can be sure that we have a piece of cultural behaviour.

Anthropologists, ethologists and psychologists thus differ in the criteria they use to identify culture. The first emphasize the social meaning of behaviour, the second the phenomenological variation between populations, whilst the third give central place to the mechanisms of transmission (culture as a process of social imitation). We cannot sensibly say that one definition is more correct than another, because they focus on different questions. We have to decide which task we are engaged in and then use the appropriate definition.

For our purposes, we will understand culture to mean behaviours that are learned from other members of society, and we won’t worry too much about the details of the mechanisms involved. Our interest will perhaps be closer to that of the anthropologists: we will focus mainly on the rules of behaviour that underpin human sociality.

**how and why language evolved**

The conventional assumption has always been that language evolved to allow the exchange of information about the physical environment. Conventionally, this has been interpreted as having, for example, something to do with the organization of hunts, other plans for the future or the giving of instructions (for example, how to make a stone tool). The last decade has, however, seen the emergence of an entirely new suggestion—that language evolved for essentially social purposes. Among the possibilities that have been suggested are the co-ordination of social contracts (something that requires the understanding of symbolic relationships), pair-bonding (the Scheherezade Effect, whereby linguistic skills are an honest cue of mate quality and mates use language to keep each other entertained and ensure their continued commitment to the relationship) and social bonding (to facilitate the cohesion of large social groups: the gossip hypothesis).

However, whilst all three are plausible possible functions subserved by language, we need to ask whether all three were simultaneously present at the origins of language or if one was the primary function and the others arose afterwards. Whilst any of the three would have significant selective advantages, the gossip hypothesis has the added advantage that it would allow an additional problem to be solved, that is, how to bond large social groups. Thus, social contracts (and, in particular, agreements to respect others’ rights to particular mates or marriage partners) maybe important for the smooth functioning of society but it is not a problem that is particularly intrusive until you have large social groups, in which there are many rivals. In any case, respecting others’ mates or even keeping mates entertained is something that many other species of mammals and birds manage to do without benefit of language. However, once large social groups are in place, the large number of ever-present rivals greatly raises the stakes and social contracts and Scheherezade mechanisms may suddenly come into their own. In contrast, the gossip hypothesis
explicitly argues that language was a prerequisite for evolving large groups because it provided the essential mechanism needed to weld them into coherent, stable communities of individuals.

The essence of the gossip hypothesis stems from the observation that monkeys and apes use grooming to bond their social groups. Grooming stimulates the brain to release endorphins (the brain’s own painkillers), creating a light ‘high’. In some way that we do not really understand at present, the sense of warmth and contentment generated by the flood of endorphins makes monkeys and apes more trusting of, and committed to, the individuals with whom they engage in grooming. Physical contact of this same kind (stroking, rubbing, petting, massaging) has exactly the same effect on us—and we view those with whom we share these activities as special. Physical contact is a mode of communication and one that seems to be particularly capable of high emotional charge. We are able to read a great deal more about the intentions, desires and honesty of the person concerned from a touch than from anything that they might say. A touch is, literally, worth a thousand words.

The critical point in this context is that the time devoted to social grooming correlates with social group size in monkeys and apes. The bigger the group, the more grooming needs to be done by each individual, in order to achieve the same level of social integration. The reasons why this might be so need not detain us here. The important point is that there will inevitably be an upper limit on the amount of time that can be devoted to social grooming and this will ultimately set a limit on the size of group that can be bonded in this way. If a group exceeds this size, it will not be sufficiently cohesive, and will tend to fragment and break up.

This limit on grooming time appears to be about 20 per cent of total day time: the demands of foraging mean that it is not really practicable for animals to devote more than this to social interaction. This sets an upper limit on group size of about 70-80 individuals. But natural human groups average about 150 individuals and if the monkey and ape grooming rates applied to these, we would have to devote around 45 per cent of our time to social grooming. This would be difficult to sustain in the face of the competing demands of foraging. Data from a number of natural human populations suggest that in practice we devote only around 20 per cent of our day to social interaction (the same as the upper limit observed in monkeys)—we use the time we have more efficiently, and that efficiency comes from exploiting a novel medium of communication: language.

Language allows us to use our limited social time more efficiently in at least three, quite separate, ways. One is that it allows us to ‘groom’ several individuals at a time: at any one time, conversations typically consist of a single speaker with up to three listeners. (If more listeners join the group, the conversation will very quickly split into two separate sub-conversations—unless somebody very important is the focus of attention!) In contrast, grooming is very much a one-on-one activity for monkeys and apes: even humans are apt to become affronted if our ‘grooming’ partner tries to divide their attention between us and someone else. Second, it allows us to exchange information about other members of our network and so keep better tabs on its constantly changing state. For monkeys and apes, what they do not see, they can never know. Third, it allows us to comment on (and so police) the behaviour of others.

**when did language evolve?**

Irrespective of why language might have evolved, there remains the question of when it evolved. Unfortunately, only bones are preserved in the fossil record, not behaviour, making it difficult to determine just when phenomena like speech or language might have evolved. However, three sources of anatomical evidence provide hints. One is the diameter of the nerve that activates the tongue (or at least the hole through the base of the skull through which it passes). Because speech involves fine motor control of the tongue and lips, it is perhaps no surprise to find that this nerve is (relative to body size) much larger in humans than in other monkeys and
apes. Similarly, speech requires fine control of breathing and hence of the chest and rib case; again, humans exhibit a distinctive thickening of the vertebrae in the upper chest compared to monkeys and apes, because they have more nerves devoted to controlling breathing. Examination of fossil hominids suggests that both kinds of neural enlargement occurred around 500,000 years ago, with the first appearance of archaic humans (*Homo heidelbergensis*).

A third source of anatomical insight comes from examining the relationship between group size (as predicted by neocortex size using the primate relationship) and the grooming time required to bond social groups (again, using the standard relationship for primates). If we assume that there is a limit to grooming time above which it is simply not possible to go, we may be able to determine when this happened by plotting the predicted grooming time requirements for different hominid populations against their archaeological date. If we take a threshold at about 30 per cent of time spent grooming as the critical limit (allowing some slippage above the observed 20 per cent in monkeys and apes as individuals try to make time savings elsewhere in order to invest in their relationships), we find that this threshold would be breached at about 500,000 years ago, with the appearance of *H. heidelbergensis*. Thus, all three anatomical sources seem to point to about the same time.

More recently, analysis of a genetic difference between humans and apes for a gene that is thought to underpin the capacity for grammar has suggested that the two key mutations (at the FoxP2 gene locus) appeared around 200,000 years ago (roughly when anatomically modern humans, *Homo sapiens*, appeared). This raises the interesting possibility that the capacity for *speech* might have preceded the capacity for *grammar* by some considerable time. How could this be?

One possible reason stems from the observation that speech and language are two quite separate phenomena, as reflected in the fact that some human languages (for example sign languages) do not involve speech. A reasonable interpretation for the apparent temporal separation between the capacity to speak and the capacity for grammatical language is that language was preceded by a phase that used some form of non-linguistic articulated speech for social bonding. The obvious candidate is music—specifically, wordless singing. The possibility that language may have been preceded by a form of communal singing allows us to resolve several puzzles that are otherwise difficult to explain. One is the evolution of music itself and the fact that music clearly has very deep emotional valency for us. The second is that it provides a neat bridge between non-human primate vocalizations and human speech that does not require some kind of massive jump: we already find what amounts to wordless song in monkey and ape vocal exchanges. More importantly, perhaps, singing requires exactly the same kinds of vocal control as speech. Stepping up the intensity of song might provide an intermediate step, by putting one of the key prerequisites for language in place. Third, music provides a bridge to language, because it seems to involve the same endorphin charge as grooming (we experience the same sensations of warmth and lightheadedness after singing and especially after communal singing) but at the same time breaks through the grooming threshold: we can sing while we work, and we can sing with more than one individual at a time. Finally, music is clearly phylogenetically older than language: this much is clear from the fact that our musical sense is based in the right hemisphere of the brain (whereas language is based in the left) where it seems to exploit much older, more primitive, neural mechanisms.

**darwin, genes and culture**

Evolutionary biologists became interested in the phenomenon of culture partly because it promised an opportunity to explore a mechanism of inheritance that was radically different from
that governing the inheritance of genetic traits, with which they were more familiar. Conventional biological traits are passed from one generation to the next by a particular mechanism—the molecule known as DNA, via sexual reproduction. However, the possibility that there might exist in the natural world other forms of inheritance, which gave rise to novel evolutionary processes, has always intrigued biologists. One that has excited considerable recent interest is the possibility that viruses might be able to convey genetic material from one individual to another and insert this new material into the genetic code of the recipient individual. Such a mechanism may be responsible for AIDS and it is now being harnessed to create a new medical technology. However, a second mechanism has been familiar to us for a very long time: learning.

On reflection, learning (and in particular social learning) is an obvious Darwinian process: it involves the selective retention and transmission of phenomena (usually rules or ideas). Indeed, the phenomena concerned may even arise in the first place as a novel accident, much like a genetic mutation. While genetic transmission and learning share many key similarities, they are, of course, very different. None the less, setting these important differences aside, they function in very much the same way to transmit information selectively down the generations.

The term "meme" was coined by Richard Dawkins to provide a term which we could use to describe units of culture in the same way we think of units of biological inheritance (genes). You should note that, in this sense, ‘gene’ does not refer to segments of DNA but rather to what geneticists refer to as Mendelian genes (after the founding father of modern genetics, the monk Gregor Mendel, whose contribution to modern evolutionary theory we discussed in Chapter 1). Mendelian genes are phenotypes, or bits of the body (eye colour, a finger, horns) and while they have an obvious relationship to the DNA that codes for them, they are not exactly identical to these chunks of DNA (see Box, opposite). Memes are the cultural equivalent of Mendelian genes, and represent phenomenological units of transmission.

The use of the term meme in this context—and, indeed, the whole idea of a Darwinian process of cultural evolution—has often been criticized by anthropologists (in particular) as being

MEMES, MENDELIAN GENES AND DNA

The mechanisms of inheritance were first worked out in detail from a series of very careful experiments on peas and other flowering plants, by the Austrian monk and amateur scientist, Gregor Mendel, in the 1850s. He showed that characters (or traits) like pea colour or texture were inherited across generations in a manner consistent with their being passed on by what he termed factors (later termed genes by early twentieth century biologists). A century later, Mendel’s factors came to be equated with DNA, the biological molecule found in every living cell that is responsible for the cell’s capacity to reproduce itself.

The strands of DNA found in the nucleus of every cell consist of a series of chemical instructions for making new bodies. However, Mendel’s factors are not exactly identical to the segments of DNA that modern biologists also refer to as genes. Mendelian genes are really the characters themselves (eye colour, five-fingeredness, etc.), which are transmitted between parents and offspring with some degree of consistency, whereas the genes on the strands of DNA are more like a recipe to create these characters. Most bits of the body are produced by several separate tiny segments of DNA which can be in different locations on the DNA strand (known as chromosomes), and sometimes even on different strands; equally, some DNA genes can influence several different characters. (That biologists use the term gene to refer to several different kinds of biological entity is sometimes confusing to non-biologists; biologists, however, always know from the context just which definition is being used.)

Memes are more like Mendelian genes, in that they are observable elements (rules of behaviour, ideas) that are passed on, more or less intact, from a cultural parent to a cultural offspring. Memes differ from genes in that the mode of transmission is by learning (rather than biological reproduction); in some ways, memes have more in common with viruses and other ways that infections are transmitted. This means that they can involve biologically unrelated individuals (teachers and pupils) and can reproduce themselves much more quickly (learning can be more or less instantaneous). Despite this, however, the same processes of selection are involved.
based on an inappropriate analogy with genes and conventional Darwinian evolutionary processes. Genes, so the argument runs, are bits (either of DNA or the body) that can be individually identified but culture cannot be split up into small components (such as individual behavioural rules or the designs on a ceramic pot). Culture is a unitary phenomenon that is passed on from one generation to the next as a monolithic whole. We become members of our community by absorbing its culture (its ideas, beliefs, rules of behaviour) lock, stock and barrel. This might seem a reasonable line of argument but unfortunately it does not really stand up to closer inspection. This is so for three, quite separate, reasons.

First, genes (or even traits, in the Mendelian sense) are not unitary phenomena that can be separated off from the rest of the organism’s biology. An arm is a Mendelian trait that is, no doubt, underpinned by some fairly explicit bits of DNA, but it does not make sense to view an arm in isolation from the body to which it is attached—or, indeed, the embryological environment in which it developed. The arm only has biological meaning when it is part of a body, just as a particular rule of behaviour or belief about a particular kind of supernatural being only has social meaning when it is part of the cultural set of a particular society. Geneticists and evolutionary biologists have no problems discussing arms, their evolutionary adaptations and history in isolation. But this does not mean that they are ignoring the rest of the body: the whole is implicit in the argument. In short, this criticism is based on a misunderstanding of what biologists mean when they use a Darwinian approach to analyse biological phenomena.

Second, the anthropologists’ view that culture is inherited as a monolithic unitary phenomenon (a view that owes its origins to Emil Durkheim, one of the founding fathers of modern sociology in the early 1900s) reflects a particular historical perspective. Anthropologists (and sociologists) have tended to focus on the here and now of social phenomena. As a result, they ask how the individual acquires the cultural beliefs that it has. The answer is, of course, from its parents, peers and teachers, over a comparatively short period of its early life. Children tend to acquire this information relatively uncritically, believing a thing to be the case or a particular way of doing things to be the right one because they have been told so. But this is a strictly developmental view and lacks an historical (or evolutionary) perspective. We should also ask how a particular culture came to be or why two societies that once had a common origin should end up believing very different things. And it is this second sense that is the focus of Darwinian explanations. How individuals learn their culture is a developmental issue, and a different sense of Tinbergen’s *Whys*. We can still legitimately ask how, when and why cultures change over longer time-scales.

Finally, archaeologists studying the historical development (evolution) of Indian basketware and pottery patterns in the historical American West have recently shown that the patterns and elements of basket and pot design tend to segregate through time in parcels. In other words, they are not entirely individual phenomena that can be added or subtracted at will but neither is basket design a monolithic phenomenon that is passed down through the generations. Successive generations adopt or abandon particular suites of characters because they are better in some functional sense or because they suddenly become fashionable. These character sets are transmitted through time as cohesive units but they can mix and match at will with any of the other sets of traits that define basket design as a whole. In other words, we can isolate components of a particular cultural phenomenon and analyse its behaviour as a simple Darwinian trait.

One final issue we need to consider is some of the real differences between genes and memes, which have important implications for how we analyse their behaviour from a Darwinian point of view. Genetic traits can—for the most part—only be passed from parent to offspring. Cultural
processes, however, exhibit more complex patterns of inheritance. In addition to conventional transmission from a parent to its biological offspring (known as vertical transmission), the inheritance of cultural traits can occur between peers (members of the same biological generation: horizontal transmission) as well as between biologically unrelated members of the parent and offspring generations (for example, teachers to pupils: oblique transmission). This complicates the dynamics of transmission enormously.

Because the mode of transmission is different, it is inevitable that the dynamics of memic transmission will be different. Learning is a naturally faster process of replication than biological reproduction, which has a fixed turnaround time, set by the reproductive cycle of the species concerned. The speed of transmission for a cultural process is limited only by how fast a naive individual can be found in the population and how long that individual takes to learn the new rule. There is no long delay created by gestation, lactation or the business of socialisation. However, just because learning can make cultural evolution rapid, this does not mean that cultural phenomena will always be extremely labile. Cultural inheritance can sometimes be surprisingly slow. One reason for this is that the heritability of cultural phenomena (that is, the correlation between the behaviour of parent and offspring) is surprisingly high, higher than for many biological phenomena. Children tend to adopt their parents’ religion, political views and leisure interests quite reliably but their body weight correlates only about 20 per cent with that of their parents (the rest of the variation in body weight being a result of environmental influences during development). In part, this is a consequence of the intensity of social learning in childhood that we discussed in Chapter 4.

intentionality, language and culture

Hitherto, there has been a tendency to see language as a broadcast activity, much on the analogy of a lighthouse beaming out a message, which is captured by a listener somewhere ‘out there’. But this is to miss a key aspect of language, namely that it’s a form of social communication in which the listener plays as big a part as the speaker. The listener has to make use of considerable mind-reading capacities in order to figure out just what it is that the speaker is trying (intends) to say. (Mind-reading is the capacity to understand the contents of another’s mind—to see the world from their point of view. We discussed mind-reading or Theory of Mind, ToM and its associated concept of intentionality in Chapter 4.) At minimum, the listener has to engage in second order intentionality (’I suppose that you are intending to mean ...’). If the conversation is about someone else, then third order may be required: ‘I suppose that you think that James intends...’.

Theory of Mind is important in language for another reason, to do with some peculiarities in the way we use language. Language can be an extremely precise tool for exchanging information but we often deliberately seem to go out of our way to obfuscate. We use metaphors constantly: hardly any word in any human language has only one meaning and most have several that are metaphorical. We speak of water running, of people being rocks (on which to lean in times of trouble), of pulling doors behind us (when we don’t mean pull in the literal sense of dragging across the road). ToM allows us to sort the metaphorical from the literal meanings, to know when someone is being ironic or sarcastic—and, perhaps most important of all, when they are joking. Joking is a phenomenon that is peculiar to humans and we need ToM to engage in it, as is amply demonstrated by the inability of those who lack it (for example, autistic individuals) to understand both jokes and metaphors.

According to the philosopher John Searle, ToM and language are linked to culture in a profound way. You will recall from Chapter 4 that, as children develop, they move from a shared to
a collective intentionality: their growing understanding of their own and other people’s minds allows them to understand and absorb the views and practices of their culture. Searle argues that a very large part of this collective intentionality is the creation, understanding of and adherence to institutional facts. Institutional facts are facts about the world that exist only because we all agree that they do: marriage, government and money are obvious examples. The particular piece of paper in your wallet or purse is worth five pounds because we all agree that it is: there is nothing inherently valuable about any piece of paper. Searle argues that language and ToM are crucial to the generation of institutional facts and therefore to culture as we know it, because an institutional fact is inherently symbolic and therefore utterly dependent on language. We need ToM to understand that facts of this kind are arrived at by collective agreement and that they exist in everyone’s mind in the same way (that is, we all possess the same belief).

These are skills that appear to be unique to humans. Although there is some evidence that chimpanzees (and perhaps other Great Apes) can just about manage the kinds of tasks associated with ToM, their performance is limited to that of children who are on the threshold of acquiring it, and is very inferior to that of even six year old human children, whose ToM capacities are securely developed. And so far as we know, Great Apes are the only animal species capable of giving humans any kind of run for their money in these terms. Monkeys and all other animal species, are limited to first order intentionality. To borrow a phrase coined by Robert Seyfarth and Dorothy Cheney, monkeys are good ethologists (they understand how to read and manipulate others’ behaviour) but they are poor psychologists (they don’t understand the mind behind the behaviour). Human competencies are not limited to second order intentionality. Normal adult humans are capable of handling problems that involve up to fifth order intentionality, with some exceptional individuals able to perform at higher levels.

There is some evidence to suggest that the levels to which different species can aspire are ultimately dependent on the volumes of core regions of the brain. The frontal lobes of the cerebral cortex may be especially important in this respect, for they are thought to play a critical role in allowing us to separate out reality from fiction as well as to consider alternative scenarios of how things might turn out in the future. If so, then, the relative volumes of these parts of the brain in different species may explain why humans can achieve such startlingly high levels of intentionality, whilst, other species cannot. Analysis of the relative volumes of different parts of the neocortex in primates suggest that it is only with the brain volume of the Great Apes that sufficient spare capacity becomes available to allow individuals to aspire to second order intentionality and this may explain why there is some evidence for ToM capacities in chimpanzees but not in smaller-brained monkeys. ToM and higher orders of intentionality may essentially be an emergent property of the computing power of brains of a certain size and hence of how much neocortical volume can be spared from basic perceptual processing, motor coordination, memory and other conventional cognitive processes.

**Summary**

Language and culture (the capacity to transmit ideas and rules of behaviour from one individual to another through social learning) are unique to humans. Although animals may exhibit both, to some degree, what they have is but a pale reflection of what we find in humans. We suggest that both phenomena are associated with the fact that humans live in large, dispersed social groups that are constantly threatened by free-riders. Aside from the benefits of transmitting knowledge about the world, language provides us with a mechanism for bonding large social groups through a form of ‘grooming at a distance’. Not only does language allow us to make declarations of social interest in the people we talk to but it also allows us to exchange informa-
tion about the state of our social networks, to update ourselves on what is happening and to ad-
monish those who fail to toe the social line. Shared culture, likewise, provides a way of identify-
ing individuals who belong to our social community, those with whom we share obligations and 
those on whom we can count for moral or economic support when we need it. Both depend on 
the advanced forms of mind-reading that only humans are capable of and thus probably have a 
relatively recent evolutionary origin.