Hidden Depths

The Origins of Human Connection

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Hidden Depths: the origins of human connection

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Foreword

When I first started the research for this volume, I set out to reveal the largely unexplored area of archaeological evidence for how some of our closest human emotional connections emerged. The idea for the book came out of the recognition that, all too often, evidence for what we see as *the better part of our natures* is sidelined or forgotten. Narratives of our human origins tend to either predominantly focus on discussions of violence or aggression, or be framed within ideas of humans as purely rational beings with little emotional motivations of any kind.

Journeys rarely go the way we envisage. Over the nine chapters, we do uncover a remarkable record of care for the vulnerable, collaboration, and inclusion. We learn about the collaborative group effort of early humans, the compassionate motivations of Neanderthals, and new levels of intercommunity tolerance. An evolutionary framework makes sense of why our uniquely human emotional connections, sensitivities and caring motivations may have paid off in our evolutionary past. Furthermore, a more interesting and complex picture than that framed as a simple ladder of progression towards ourselves is presented, with different hominin species exploring different evolutionary trajectories, not just of physical form but also of emotional disposition.

However, another and perhaps even more important story also unfolded as the volume was written. This was a story not of virtue but of vulnerability, and one in which we become more the unwitting passengers of evolutionary processes than its heroes. Alongside evidence for care, inclusion and tolerance came an unexpected and rather more precious insight. As our sensitivity to how others feel and our willingness to respond to those who need our help emerged, so too did our own emotional vulnerabilities. Our tendencies to act for the common good are driven by sensitivities around how others may see us. Our willingness to care for our loved ones is underlain by often painful empathy with their suffering. Our motivations to develop friendships and companionship and a sense of belonging to extended communities are motivated by our acute sensitivity to loneliness. All of these vulnerabilities make us who we are and structure how we feel, motivating us to make connections and to give and receive help. Moreover, it is these vulnerabilities that, in turn, also made human groups and communities resilient in the face of adversity. We often deride emotional vulnerability in modern societies. However, when we look in depth at our distant past, it is clear that the more socially sensitive and attuned to others' feelings we became, the more our species benefited from greater collaboration and connection.

I have been surprised by how little attention human emotional connections and, in particular, emotional vulnerabilities have received in our evolutionary story. Indeed, the role that our emotional lives played in our prehistoric past is rarely discussed. Some speculate that this may be because emotions can appear to be rather too woolly and not scientific enough as an area of study. I suspect, however, that it is our own discomfort with the vulnerability that our emotions present that may have played a more significant role. A narrative of our past as one of invincibility, innate success and independence seems far more enticing than one that takes into account our social emotions and, with them, interdependence and vulnerabilities. We prefer to see ourselves as distinct from other animals because of our superior intelligence, our complex language or our toolmaking abilities, even though underneath these exterior qualities lie a complex human emotional world and a level of sensitivity that are far more remarkable.

Things may be changing. Global developments in recent years have highlighted existential threats, such as climate change, inequality and the COVID-19 pandemic. These threats prompt both an increasing sense of being united by our shared futures, and a questioning of who we are as a species. The pressing issues of climate change cast a new light on humans as part of a wider natural world that we cannot always control, and as being vulnerable to changes within it. The COVID-19 pandemic has prompted us to view both our interdependence and our emotional vulnerability in a new light. We have all felt differently about ourselves and other people around us. We have been moved to tears by deprivation or suffering – the pain and grief of illness, families who are hungry, people who are scared, those who lose loved ones or are lonely. We have also grown to appreciate much more fully the depth of our capacities to care for each other and the power of human emotional connection. We have been inspired by the sheer numbers of people working so hard or even risking their lives to make sure that people they have never met were safe and well. We have missed simple human contact and, from small acts of kindness to inspiring acts of altruism, have grown to respect our common humanity ever more. It will be hard to forget the power of human compassion or how vulnerable we are, as humans, to loneliness, a lack of connection or even for many the intense grief at the loss of loved ones. In the face of a changing climate, we are reminded of the roles that our biology and physiology play in our lives, and how intimately we are connected to our existence as animals, and part of nature.

Amidst all of this, our need to know why we feel the way we do, and how we preserve the best of our experience, has never been more pressing.

Introduction

> Only from the heart can you touch the sky.
>
> Mawlana Jalal-al-Din Rumi

Aims

We readily accept that it is our emotional connections to the people whom we love and care about that make us human. We sacrifice for our loved ones, feel joy and pain in equal measure with our friends, and even reach out to connect to the lives and wellbeing of people we have never met. However, we rarely think about where these feelings come from. Our stories of human evolutionary success are so focused on intelligence, individual resilience or strategic collaboration that you might even imagine that our ancestors had no significant emotional connections at all.

The aim of this volume is an ambitious one. We hope to begin to better understand the distant evolutionary origins of our peculiarly human social feelings and how they drive our emotional connections to those around us. We hope to untangle why we respond so readily to others in need, why kindness is so important, and why our rather peculiar emotional vulnerabilities and sensitivities emerged. In doing so, we also hope to better understand our own feelings and uncover why the evolutionary background to our human emotional connections is important today.

We will, of course, build on existing research. Most obviously, we will build on decades of research into understanding why human minds are unique.

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These include approaches to the evolution of human intelligence in general, and to specific types of 'intelligence' (Overmann and Coolidge 2019; Overmann and Wynn 2019; Wynn and Coolidge 2016), including social intelligence (Dunbar 2003; Dunbar 2018). We will consider what we can learn from the emotional motivations of minds very different from our own, such as those of *our nearest living relatives*, chimpanzees, and those *of our closest friends*, dogs and their wolf ancestors. We will also build on a history of research into our emotions that began as far back as Darwin himself (Darwin 1872).

We will also expand existing research. Within archaeology, for example, aside from debates over evolutionary changes in emotional attitudes to death (Pettitt 2010; Pettitt 2018; Pettitt and Anderson 2019) or to childcare (Hrdy and Burkart 2020; Langley 2020), there has been only a limited body of research into how the archaeological record provides insight into the evolution of our modern social emotions or our close human emotional connections to others. Palaeolithic archaeology, in general, has tended to shy away from emotions, with discussions of how our minds evolved tending to focus on subjects such as thinking skills, the basis for art, or the origins of language (Coward 2016; Stade and Gamble 2019), or been limited to a cultural rather than evolutionary viewpoint (Lyons and Supernant 2020; Tarlow 2012). Evolutionary archaeology of those most human emotional capacities that affect our social lives is relatively novel. Furthermore, we hope to develop a wider interdisciplinary perspective on human origins, drawing on material evidence for real people and behaviours in the distant past.

We will bring something new. We are already aware that our human capacity for social collaboration was important in our distant evolutionary past. However, there is much more to discover about why our human emotional connections are such an important part of our evolutionary story. We need to delve into the specifics of archaeological and fossil evidence, as well as evolutionary understanding, to uncover what happened in our distant origins to make us capable of the emotional connections that bind us together today. Over the 7 to 8 million years of an evolutionary past that separates us from other apes, there have been many different ecological changes, selective pressures, evolutionary branches and offshoots, and many different societies and cultures with different types of social lives. It may be too much to expect to fully understand all we might wish to about the prehistoric past of our social emotions. However, we can at least hope to cast a far greater insight into the peoples and societies in the distant past that helps to explain why we feel the way that we do and, perhaps beyond this, we can hope to gain a fuller appreciation of why our emotions and emotional vulnerabilities are significant for the future.

We will also attempt to move away from traditional approaches to human evolutionary narratives (see Athreya et al. 2019; Porr and Matthews 2019). Specifically, we here move away from an idea of a ladder of progress (Athreya et al. 2019) and from the notion of humans as exceptional (Anderson 2019). We also seek to move beyond ideas of different variations of human as superior or inferior to each other, and from a focus on intelligence as some prime mover or defining feature of humanity (Anderson 2019). In doing so, we hope to piece together a new narrative of our origins that plays a more positive role in our modern worlds.

There are many avenues that have not been followed. There are voices, including those of indigenous populations, that have yet to be heard in our narratives of human origins (see Sterling 2015). Moreover, through the unfortunate ease of access to archaeological material and interpretations, we continue to rely most heavily on European material in discussions of the most recent periods of human evolution. There are new narratives around gender or sexuality in the past that remain to yet be told. Where we hope to progress in particular, however, is around a greater emphasis on narratives of physical and cognitive diversity, and in tackling the issue of different but equally valid ways of being human in both the past and the present (Wright, Spikins, and Pearson 2020).

Further, here we move away from concepts of a linear evolutionary progression to a more superior human form and, instead, move towards interpretations of evolutionary history in which there is no necessary single shared direction of movement, and in which a model of different evolutionary pathways connects more clearly with adaptations occurring in other social animals. This is a narrative in which the significance of our shared biology and how it connects us to nature is more clearly emphasised.

Challenges

Our emotional connections to people, and even other animals or things around us, are a challenge to research and understand, even more so in the distant past. They are, after all, some of the most inspiring, troubling and problematic elements of our uniquely human experience. The effects of our emotional connections are often intangible. Yet, we are so sensitive to how others feel that simply being with people who care about us makes us feel relaxed, safe and happy (Armstrong et al. 2021; Marsh 2019), and their care makes us healthier and more resilient to stress (Gilbert 2021). The feelings of those around us affect us so profoundly that emotions and motivations can cascade across our social networks (Fowler and Christakis 2010). Moreover, we are even affected emotionally by the wider economic and cultural systems in which we live (Becker, Hartwich, and Haslam 2021). As such, just as our emotional connections can elevate us, they can also bring us down or debilitate us. Whilst most of us discover our greatest joy and happiness in our relationships with others, our human emotional connections also mean that we can be disabled by grief and find it almost impossible to live without loved ones. We all too often find ourselves uniquely connected to another's suffering, crushed both emotionally and physically by cruelty or the wrong type of social connection, or debilitated by isolation or loneliness (Bzdok and Dunbar 2020; Gilbert 2021; Spreng et al. 2020). This emotional sensitivity seems hard to explain within a functional evolutionary framework, and is rarely acknowledged in broader society. Yet, far from a fault, it is also an essential part of human experience. Just living life as a human being, with the breadth of our emotional experience and all our emotional sensitivities and vulnerabilities, prompts us to question why we feel the way that we do, how far back these feelings go, and why they might even have been important for our survival.

We face a number of hurdles in building up a picture of the key developments in the complexity of human emotional connections. Firstly, we need to draw on the often-scanty material record left behind by our many different human relatives, a record that is not without constraints and issues. Secondly, we will need to navigate a challenging area of research lying between commonly accepted disciplines and, lastly and perhaps most importantly, to overcome our own assumptions and biases.

In bringing the material record to bear on the question of how our social emotions evolved, we will be disappointed if we expect some prehistoric Pompeii, or an obvious link between how people behaved and their emotional motivations. The further back we go in time, the less archaeological evidence is preserved, and the more difficult it becomes to interpret. Like fishing in ever deeper waters, further from the surface there is less to find and, what's more, we often come across unusual things that we do not really expect. The archaeological record of the Palaeolithic, for example, only starts with the earliest stone tools around 3.5 million years ago, and most of our archaeological record is made up of these highly durable stone tools, with the fortunate addition of some fossilised animal or, occasionally, human bones. Evidence for things like art or mortuary practices, or even the full range of the types of resources that people were hunting, gathering and eating, are extremely rare, and are often surprising in form. Some of the earliest mortuary practices, for example, seem to involve depositing bodies in particular places, including caves. Quite why remains something of an enigma (Pettitt 2010). We can only look with a certain amount of jealousy at the often-predictable results, large sample sizes and statistical confidence seen in many other areas of science, such as modern psychological studies.

More than this, what we do find may not be easy to interpret. The archaeological record gives us, at best, an indication of how people *behaved* in the past. How they *felt* is something that we have to infer, and rarely is this ever with any confidence when we are dealing with single cases. What people do is influenced by far more than simply their emotional capacities. Rather than expecting to find evidence that tells us with any certainty how any single individual might have felt, we must look instead for changing patterns of behaviours and what that can tell us about how emotional capacities were evolving and emerging, much as we might take the same approach to other areas of cognitive evolution (Wynn and Coolidge 2016). As we shall see in Chapter 2, the archaeological record for recovery from illness and injury, demonstrating probable care from others, is a good example. We cannot possibly be sure that someone was not cared for through some calculating motivations on the part of someone else who might possibly have wanted them to survive some injury for their own selfish reasons. However, when we see a pattern of many cases of care consistently appearing across long periods of time we can begin to reasonably infer the importance of evolved emotional tendencies to respond to others distress. We have to build an understanding by focusing on the patterns that tell us about how emotional capacities may have changed, and leave what any one person in the past actually felt to speculation. Of course, we cannot help but imagine how any individual might have felt suffering some severe injury and being cared for by those around them in the most difficult of circumstances but, when it comes to making inferences about how emotional capacities evolved, we will be limited to considering the patterns of broad scale change.

There are other, perhaps even more important constraints on what evidence is available, and these, ironically, result from our evolved tendencies themselves. Because we have evolved to pay the greatest attention to the types of things which might present a danger to us – violence or conflict, for example – these elements of our distant past also attract the far greatest attention (Soroka, Fournier, and Nir 2019). Tilley commented, for example, that the main publications about a brain injury in the Saint-Césaire Neanderthal focus almost exclusively on how this injury may have been the product of interpersonal violence, with almost no reference to the weeks or months of survival from injury, which strongly suggests care from others (Tilley 2015). Most of us have an image of Neanderthals as being brutish, competitive and violent, even though, as we shall see in Chapter 8, the evidence for interpersonal violence is quite scanty (with very few relatively clear cases) compared to that for lengthy and extensive interpersonal care (Spikins et al. 2019). All too often, it is those scant examples of violence that attract the most attention, both academic and public. The often-overlooked archaeological evidence for caring, supportive or sensitive behaviours will take a certain amount of *uncovering*.

A natural negativity bias may have made sense in a far-distant evolutionary world, where being particularly alert to the dangers posed by any possible predator or dangerous situation was critical to survival. However, basing our understanding of who we are on our intuition about what the past ought to have been like is a risky business. Because of this bias, the behaviours of the small numbers of others who are callous or cruel most attract our attention and give us the impression of an innate aggressiveness to human nature despite most of us being remarkably altruistic (Marsh 2019). A mythical violent or selfish past can be part of the assumptions we make when we create societies that bring out our worst selves and do not cater for either the better, more caring and more tolerant part or natures, or our sensitivities.

The archaeological evidence is only half of the story. Without an understanding of the biological basis of how hormones influence our emotional motivations, and the cognitive or social psychology of behaviours set within an evolutionary context, none of what we might find makes sense. We will also have to draw on insights from many different disciplines if we are to understand the process through which our evolved emotional capacities emerged. We need to understand what happens in the mind of an early human as they perceive and respond to others' suffering, how hormones and their evolutionary history influence what we do, what the evidence from fossil hominins means for the nature of changes, and the ways in which ecological circumstances drive species along different evolutionary branches. This type of interdisciplinary research is always challenging. As academics, we tend to be encouraged to stay within our disciplinary boundaries and become ever more specialised in a single area. The patterns and processes occurring in the past, from which our evolved emotional capacities emerged, did not happen in one neatly defined realm, however. From the biology of hormonal responses, to cognition, to ecological changes, social relationships and even cultures, we will have to have some grasp of all of these things to make sense of the evidence.

Perhaps the most significant challenge, however, comes from within – that of overcoming our own assumptions of and preferences for what the trajectory of our evolutionary past should look like. It is all too easy to write a pleasing narrative around the evolutionary past we want to believe in, whilst the actual history behind our emotional capacities may be far more useful to us.

Most obviously, we much prefer a success story. We almost always hear of human origins through a narrative of gradual progression towards a final form, ourselves, who we see as a kind of pinnacle of evolutionary success (Scott 2010). Indeed, the idea that evolution made us perfect, and that as a species we triumphed over adversity to become uniquely successful, is so hard baked into our culture that it can be hard to see past it. Surely, we reason, we *must* be better than any human species that came before us.

Not only in physical form, intelligence and technological capacity but also in emotional capacities. The ultimate success story. More advanced than any other on the planet.

Rather than a simple progression, there is abundant evidence for a much more complex story that speaks to us less of 'success' and more of a sequence of adaptations and changes, some more random than others. Recent years have demonstrated that human evolution is far more complex than we often assume, for example. We now know that there are many more species of human, existing in a complex relationship with each other, rather than any single evolutionary lineage (Galway-Witham, Cole, and Stringer 2019). More than this, evolutionary processes themselves are much more chaotic and undirected than we often assume. Different species simply adapted by responding to constraints and opportunities in ways that brought both advantages and disadvantages, but not intrinsically 'better' or perfect forms. Rather than any step being better, there were always compromises to be made. Human brain expansion facilitated great cognitive advancements, for example, but at the cost of high energy expenditures and risks in childbirth. Bipedalism may have freed up hands and brought certain energetic advantages, but imposed stresses on the spine. The same possibilities, constraints, advantages and disadvantages are true of how social emotions emerge. Shame or guilt may motivate more moral behaviour, for example, but can also come at a price. Shame, in particular, can have lasting negative effects on wellbeing (Longe et al. 2010). Moreover, certain changes or adaptations are often part and parcel of other developments, 'hangers on' in genetic terms, or simply made little difference. A simple story of evolution as a 'better' form winning out over others, or anything being 'perfectly evolved', is more myth than reality. Only by understanding the complexity of branches and compromises can we move away from our perhaps rather colonially inspired narratives of superiority and inferiority, and of anatomically modern humans (henceforth 'modern humans'), our own species, as naturally somehow exceptional. Even using the term 'modern human' for our own species is problematic, as it seems to imply a certain superiority. We may now be the only such surviving species but others to which this term could equally apply were our contemporaries for tens of thousands of years. There is, however, no better option that everyone understands.

The often chaotic and non-directional nature of evolutionary processes is perhaps even more significant to bear in mind when considering our emotions than any other human capacity. In the field of emotions, chance factors and the vagaries of circumstances play an important role in how capacities evolve and, moreover, compromises are rife. As we shall see, our evolved emotional capacities make us social, in the sense of being highly sensitive to each other's feelings, and highly responsive to culture, but also vulnerable, desperate for recognition, debilitated by grief, and made ill with loneliness. Our acute social sensitivity can be an advantage to collaboration, but also a vulnerability where we grasp at attention or follow a herd going in perhaps the wrong direction.

To find a more nuanced and more interesting explanation for the role our emotional connections played in making us who we are, we may need to let go of the comfort and satisfaction that come with believing we are some kind of pinnacle of a process of increasing perfection. This may not be a neat story. Nonetheless, that our shared human capacities for remarkable generosity, sharing, tolerance and altruism came about through imperfect responses, compromises and changes in direction, may make them even more remarkable.

Structure

We address different types of human emotional connection across the three parts of the volume. In the first two parts, we focus particularly on two suites of emotional capacities: in Part 1, those particularly focused on our emotional connections *within groups*, particularly our generosity and compassion for close kin and group members and increasing importance of trust and social reputation; and, in Part 2, those emotional connections driven through tolerance, sensitivity and connection to *people outside of our local or family circle*. These two distinct areas naturally lead to a focus on two key transitional periods in human origins. The first key transition, explored in Part 1, around the time of the origins of the genus after 2 million years ago, coincides with new types of collaboration based on sharing and caring behaviours within groups. This may be the time period when typically human generosity and compassion emerged, with implications for the significance of trust, and for broader areas of social relationships and cognition. More in-depth emotional connections emerging at this time will have brought with them increased pain at others' suffering, and concern for group wellbeing. The second key transition, explored in Part 2, is that of the emergence of our own species after 300,000 years ago, coinciding with evidence for regional connections between groups, based on new types of tolerance and the maintenance of friendships across large regions. This may be the time period when typically human needs for connection and belonging emerged, alongside capacities to form large-scale social networks, as well as sensitivities and vulnerabilities to emotional stresses and loneliness. In each of these two parts, we start with the evolutionary basis for key traits, move to archaeological evidence, and then consider the implication for our current interpretations and wider significance. In Part 3, we explore differing branches of emotional dispositions, the emotional lives of our close cousins, the Neanderthals, and how the differences between us may be explained by alternative, though different but equal, evolved emotional trajectories. Lastly, we consider why a reappraisal of the significance of our most human emotional capacities may be important for our understanding of human origins and beyond.

A new narrative may reveal not only the significance of previously disregarded elements of past human lives, but also new perspectives on ourselves.

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Part 1

Compassion, Generosity and Trust

In this part of the volume, Part 1, we consider how and why our remarkably strong emotional bonds and tendencies to altruism within close-knit families and groups emerged. We begin in Chapter 1 with the evolutionary basis for our human capacities for empathy, compassion and generosity, before continuing in Chapter 2 to consider the archaeological evidence for caring behaviours for vulnerable group members. In Chapter 3, we consider the significance of increasing pressures to be trustworthy and to develop a positive social reputation, as well as the role of reputation in fostering human cognitive diversity. We particularly focus our attention on key changes taking place early in our evolutionary history with the emergence of the genus *Homo* after 2 million years ago.

Why do we have such strong attachments to our loved ones? What makes us so willing to help out the vulnerable? And how important has our capacity for compassion been to our evolutionary history?

CHAPTER 1

The Evolutionary Basis for Human Empathy, Compassion and Generosity

Abstract

How did we come to care so much for our loved ones, and to respond so readily to those in need?

If we look around at the types of empathy and emotional connections in other animals, we can gain some insight into the basic building blocks of our empathy, compassion and generosity. Studies of helping behaviour in other species can provide us with some important insights, for example. If we go back to basic roots as mammals we can see that this evolutionary history has formed the basis for our capacities for empathy, stemming from a need to respond to vulnerable young. However, human empathy, compassion and generosity is certainly more complex. This is where studies of our nearest living relatives, chimpanzees, provide insights into more complex capacities to share and to respond to others distress, as well as a certain social astuteness that is likely to have characterised the emotional capacities of our common ancestor living about 7 to 8 million years ago.

(Abstract continued on next page)

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(Abstract continued from previous page)

What happened after our split with other primates? How our emotional capacities evolved after our lineage split with other apes is a challenging question. Here animal comparisons reveal a certain paradox. Some far more distantly related animals demonstrate a more human-like altruism and compassion than those that are most closely related to us, such as demonstrating a certain willingness to collaboratively care for offspring, or to care for vulnerable injured adults, for example. Understanding what prompted these kinds of changes in human ancestors who came after our split with the ancestors of chimpanzees demands considering how different species find the best ways of adapting to the ecological and social environments, and how this affects their emotional reactions to each other.

Explaining the depth and breadth of our emotional connections to others remains a challenge. Building up our understanding of how and why human emotional motivations towards generosity and compassion emerged over the last few million years also depends on archaeological evidence of when helping and compassionate behaviours emerged, and why they became important, which is the focus of Chapter 2.

Figure 1.1: Family of Common Marmosets. Common marmosets – both male and female caring for the two small infants. Francesco Veronesi, CC BY-SA 2.0 via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Family_of_Common_Marmoset_-_REGUA_-_Brazil_MG_9480_(12930855765).jpg.

Introduction

Sometimes animals surprise us by doing something that seems uncannily human-like.

Marmosets (South American monkeys of the family Callitrichidae) are tiny, weighing only around 300–400g, and though they are primates they look entirely unlike humans, perhaps even a little more like squirrels. However, like humans they form pair bonds, and collaborate in childcare (Figure 1.1). Moreover, experimental research has shown that, given a chance to help others to reach a food treat, even if they know they do not get one themselves, marmosets will commonly put a lever to get food for others (Burkart et al. 2007). They will even resist the temptation to eat food whilst they wait for others to arrive to share.

Such a strength of emotional connection, seen through apparent acts of compassion or generosity, seems to resonate with our own feelings towards those we care about. However, seeing this kind of altruism outside of our own species can raise more questions than answers. Willing generosity to others in their group, and a response to their distress or needs, occurs in many species unrelated to humans, whilst those nearest to us are not necessarily the most altruistic. Whilst our nearest relatives, chimpanzees (members of the genus *Pan*, including common chimpanzees, *Pan troglodytes*, and bonobos, *Pan paniscus*), are without doubt the most socially intelligent of other animal species, they are not the most like humans in terms of generosity and compassion. Tiny marmosets are far more likely to be generous to others. Moreover, entirely unrelated mammals such as lions or wolves seem most similar to ourselves in their tendencies to take risks on others' behalves, care for each other or share food.

What can we learn from other animals about the biology of human generosity and compassion? What types of selection pressures may have led to the emergence of our own capacities to be compassionate or generous?

To begin to address this question, we first look at *what happens in our brains when we feel empathy, compassion and a willingness to help others*. Simply possessing a capacity for empathy and altruistic motivation does not, of course, provide any guarantee that we will apply those in practice. There are many reasons why any particular person, in any particular time or place, may feel a sense of empathy or compassion or may or may not reach out to help others.

Our experience through childhood can provide important insight into how our altruistic motivations develop, with potential significance for understanding of our own evolutionary history. The constructive helping that we see in the collaborative childcare demonstrated by marmosets is relatively complex compared to simpler emotional reactions to others' distress.

Understanding the situations in which emotional motivations to help others may have been advantageous helps to situate human evolutionary change within a wider evolutionary context. Comparisons with other primates and with more distantly related but highly collaborative species such as social carnivores provide further insights into the selective pressures acting on human emotional motivations towards others.

How do we respond to another's distress? The neurobiology of compassion

Empathy

We rarely pause to think about what actually happens in our minds when we reach out to console someone or respond to another's distress. In fact, if we try to search inwards to understand exactly what sort of processes or feelings are involved, it becomes almost impossible to gain any kind of clarity. A whole series of feelings, thoughts, assumptions and levels of emotional awareness are involved in enabling us simply to reach out and touch someone who seems distressed, but they happen so quickly and intuitively that we are rarely aware of them.

At the root of our emotional connection to others is empathy. We feel empathy for example when we sense a friend is upset or in trouble and might, for example, say that we *feel for them*. Empathy tends to be associated with our response to distressing feelings (as when, for example, we say we 'feel another's pain' or when we sense someone is afraid). However, we can also feel empathy for pleasurable and positive feelings, as is the case with *empathetic joy*. In a fundamental way, our capacity to empathise with others' feelings links people emotionally.

Whilst we often think of human empathy as elevating us above other animals, our *empathy* or ability to understand and share another's feelings is shared with many other social animals. The origins of our *capacity to connect to others' feelings* may even be ancient. Many people speculate that *some level of sensing how others feel* may even date as far back as 300 million years ago, with the first examples of animals who nurtured living young. Fossils of lizard-like creatures found in Canada, for example, appear to show an adult protectively curled around its young (Maddin, Mann, and Hebert 2019), behaviours that would eventually be seen in birds and mammals. It was amongst the ancestors of modern mammals, hamster-like cynodonts living around 250 million years ago, however, that a more pronounced infant dependence and maternal willingness to respond to the vulnerability and distress of their infant formed the basis of mammalian empathy (Brethel-Haurwitz et al. 2017; Marsh 2019). The brain structures and hormonal responses that allow us to sense others' feelings are common across all mammals (Feldman 2017).

The evolutionary reasons why mammals of all species feel empathy, particularly for their young, are well understood. Mammals are warm-blooded and typically give birth to live young, who are born vulnerable and immature and depending on their mothers for care (Marsh 2019; Snowdon 2011). This dependency means that, from rats to dolphins to horses, mammals *need* to be highly sensitive to the feelings and needs of their infants to pass on their own genes. Moreover, infants themselves develop a strong sense of attachment to caregivers, which influences their emotional relationships later in life (discussed in Part 3). Quite simply, those mothers who were best at detecting distress in their offspring were more likely to respond to their needs, perhaps a little quicker to provide them with food or warmth, for example, and were therefore more successful as parents, better able to raise healthy young. Infants who were better at eliciting support were themselves more likely to survive.

Although there are many complex social and cultural processes that influence how we react to other people around us, there are still signs of the biological basis of our empathetic and caring responses. As infants we intuitively begin to willingly act altruistically from as young as one and a half to two years of age, regardless of culture (Tomasello 2014; Warneken and Tomasello 2007). We are highly tuned to others' emotions, and our capacities to identify fearful faces at only seven months old are related to later altruistic tendencies from 14 months onwards (Grossmann, Missana, and Krol 2018). As adults, common human acts of altruism towards strangers such as giving to charity or donating blood have an intuitive emotional basis rather than being calculated responses (Marsh 2019). Moreover, those of us with a greater density of oxytocin receptors, and so more responsive to the action of this important bonding hormone, are more likely to carry out extraordinary acts of altruism, such as donating a kidney to a stranger (Brethel-Haurwitz et al. 2017).

What seems a relatively straightforward maternal response to distress in young has formed the neurological and hormonal basis from which our empathy in a whole range of other situations has evolved (Decety et al. 2012). Of course, some mammals only respond empathetically to their own infants and not to other infants or other individuals. However, social mammals who depend on collaboration to survive, such as social carnivores, show a similar empathetic response to closely related adults in their group who are injured or who need food. Collaborative mammals respond not only to their own young but to the young of other parents, collaborating in infant care (Decety et al. 2016; De Waal and Preston 2017; Frank and Linsenmair 2017; Kokko, Johnstone, and Wright 2002). Much of the complex collaboration in highly social mammals depends on being able to sense how others feel and respond by helping them appropriately (Decety et al. 2016).

The neurobiology of human empathy links our responses to this shared mammalian heritage. The same brain areas that are responsible for attending to vulnerable infants and are common to mammals as a whole have been co-opted in human empathy (Decety 2015; Decety et al. 2012; Panksepp and Panksepp 2013). There are many things that mark humans as distinctive. For humans, however, our empathetic responses can be triggered in a far wider range of situations than in any other animal, from our response to seeing photographs of our babies to our response to accounts of people in need. Nonetheless, our mind responds with the same brain regions (conserved neural circuits connecting brainstem, basal ganglia, insula and orbitofrontal cortex) and with a similar system of hormones as that in other animals (Decety 2015; Decety et al. 2012; Tousignant, Eugène, and Jackson 2017). Neuropeptides such as oxytocin and dopamine play particularly important roles (Madden and Clutton-Brock 2011). Oxytocin regulates lactation and maternal infant bonding in mammals as a whole, as well as some social behaviours in adults, such as teaching in meerkats and food sharing with non-kin in chimpanzees (Madden and Clutton-Brock 2011; Wittig et al. 2014). However, in humans this same hormone also plays a role in generosity, trust and altruism between non-related humans (Barraza and Zak 2009; Baumgartner et al. 2008; Kosfeld et al. 2005; Zak, Stanton, and Ahmadi 2007). Higher levels of oxytocin, in turn, have a positive effect on health (Gouin et al. 2010). Whilst oxytocin is a good example, other hormones are, of course, also important. Vasopressin plays an important role in caring behaviours, and dopamine drives reward-seeking behaviour that can be important in fostering repeated helping behaviours (Marsh 2019), as discussed in more detail in Chapter 6.

We would, of course, be wrong to see human empathy as *simply* about inherited neurobiology and hormonal responses. We know that our emotional responses to people around us, and our decisions to respond to others' distress or to act in generous ways, are far more complex than our biology. We are influenced by our moral judgements about others (Decety et al. 2012), our strength of trust or emotional commitment to them (explored in Chapter 3), and even wider social and cultural norms and assumptions (Becker, Hartwich, and Haslam 2021), as well as our conscious choices and decision-making. Nonetheless, our biology, and our involved capacities deriving from our distant evolutionary past, still play an important and often overlooked role in how we feel about other people and, in turn, how we behave. Moreover, the relationship between biology and culture is a complex one. As discussed in Part 2, our sensitivity to social and cultural context itself has a biological element, with this sensitivity an important way in which our minds can be primed for survival in caring or competitive contexts.

From empathy to constructive help

Empathy alone does not necessarily motivate any specific behaviour. Rather, it is only through a sequence of often complex feelings and thoughts that we can empathetically respond to others' needs. Through empathy we identify how others feel and, in some cases, our motivations to help them translate into compassion (Gilbert 2015; Goetz, Keltner, and Simon-Thomas 2010), whilst deciding *what* to do may involve many higher-level processes (Decety et al. 2012; Marsh 2019).

A lot goes on in our minds when we sense someone else's fear, distress or needs and respond to them. From feeling an empathetic response to constructively helping someone involves several levels of neurological processing (see Figure 1.2 and, for a fuller explanation, Decety et al. 2016). We identify someone's emotional distress according to factors such as our own

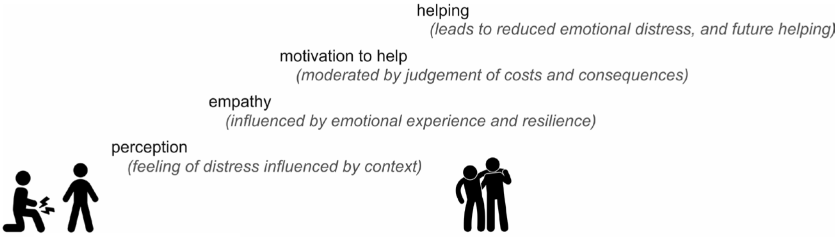

Figure 1.2: Illustration of emotional and cognitive responses leading from empathy to helping behaviour. Penny Spikins, CC BY-NC 4.0.

experience, our interpretation of their gestures or expressions, and our social context. This can then lead to a change in our own emotional state, often under the influence of a hormonal response such as that directed by oxytocin release, towards a motivation to help. This can then lead to the action of helping, depending on our cognitive appraisal of the circumstance and whether helping is constructive. Helping behaviours can lead to a reduction in our emotional stress (we feel better), a hormonal response (or 'warm glow'), or a sense of reward or achievement (under the control of dopamine), which leads to a reinforcement of helping.

Whilst we all share common inherited capacities to empathise and respond to others' needs, these several levels of response are also differently affected by our immediate context, past experience and individual differences. These include inherited differences (such as in oxytocin receptor densities; Marsh 2019), our immediate intimate social environment and the extent to which this has fostered a sense of security and trust (discussed further in Part 2), and the attitudes of our surrounding culture and our individual beliefs. While most of us respond intuitively as infants when people need help, our different cultures guide how we behave as adults and whether or not we squash our intuitive empathetic responses (Rajhans et al. 2016). Most of us help out someone when we 'warm to them', when we feel we can, and when we feel that their distress is genuine and undeserved, but none of us responds to the distress of vulnerability all of the time.

There are times in everyone's lives when we fail to be compassionate to others around us. This is not just because stress, anxiety or depression can hamper our abilities to connect emotionally to others. Though we cannot remember it, we have all experienced a time as infants before we developed our capacity to respond compassionately to others. Whilst our journey from infancy to adulthood cannot be taken as a model for our evolutionary journey as humans from a distant mammalian past, it does give us some insight into potential stages in our abilities to connect to others' feelings and respond to them.

Growing into our empathy: progressively complex responses through childhood development

If we could only remember our infancy better than we do, how we felt when we were babies and infants might give us a fascinating insight into different stages in human emotional connections to others and capacities to reach out and help.

As babies, we all start life at the simplest level of empathy – capable simply of emotional sharing, but nothing more complex. *Emotional sharing* or emotional contagion is the simplest element of empathy. Emotional sharing is driven by a sense of another's emotions through an association with a representation built on our own experience – the perception–action mechanism or PAM (De Waal and Preston 2017). As human babies, we show emotional contagion when we respond to hearing the cries of other babies by crying ourselves and illustrate a basic element of empathetic capacity in doing so. However, whilst this capacity illustrates a certain sensitivity to the feelings of others, simply sharing others' feelings is neither true empathy nor of constructive help. For example, when a peer is distressed monkeys display emotional contagion by screaming in turn in excitement (de Waal 2008). Whilst this emotional sharing is the basis of our emotional connection to those around us, it is not necessarily *actively* helping the individual in distress. In fact, in the case of the screaming monkeys, behaviours prompted simply by emotional contagion may actually make the distress worse – screaming alongside an individual in distress is not necessarily helpful and monkeys may even react by jumping on the distressed individual. A room of crying babies demonstrates a certain *sensitivity*, but, as many of us may have experienced, generally makes everyone, from the adults to the babies themselves, feel worse.

Thankfully, we quickly progress during infancy to more sophisticated levels of emotional connection. Differing levels of empathetic response are often thought of in terms of increasingly complex 'shells' – from the simplest *emotional contagion* to *empathic concern* and *consolation* and an integration with higher-level cognitive functions leading to more complex *perspective-taking and targeted helping* (Figure 1.3; for a discussion of differing levels of empathy, see De Waal and Preston 2017).

Empathetic concern and consolation are somewhat more cognitively complex and involve an ability to withstand both our own emotional reaction (our *emotional* or *affective empathy*) and that of others without being overwhelmed and to respond appropriately. By the time we are one year old, we are able to respond with empathetic concern and show some attempts at

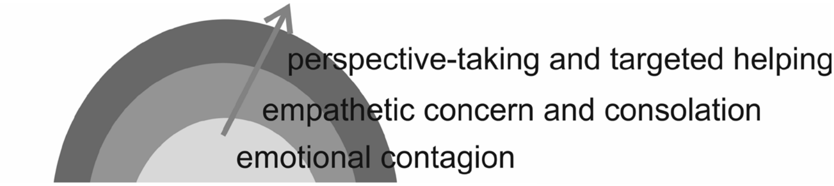

Figure 1.3: Levels (or shells) of empathetic abilities we experience from our earliest infancy to later childhood, and share with some other social animals. Penny Spikins, CC BY-NC 4.0.

consolation. Apparently cute attempts by one-year-olds to provide some emotional support through touch or sympathy illustrate quite a complex advance in their emotional skills.

Consolation may seem a relatively simple form of compassionate behaviour towards others; however, even this ability tends to be restricted to highly social mammals. Elephants, for example, respond to those who are in distress with physical contact and vocalisation (Plotnik and de Waal 2014). Wolves (*Canis lupus*) appear to ‘feel for’ the losers in a conflict, even if they were ‘bystanders’ and not involved, and console them through behaviours such as body contact, play or social licking (Palagi and Cordoni 2009). Patterns of consolation are widely recorded in apes, who ‘hug’ the losers of conflicts (Romero, Castellanos, and de Waal 2010). Bonobos (pygmy chimpanzees), in particular, seem notably attuned to others’ distress and willing to respond with gestures of comfort (Clay and de Waal 2013); see Chapter 7. These types of sensitivity to others’ feelings and capacity to ‘reach out’, physically calm distress and diffuse social tensions, with consolation in primates being shown to reduce anxiety (as seen in scratching) and heart rate (Aureli, Preston, and de Waal 1999; De Waal and Preston 2017; Fraser, Stahl, and Aureli 2008). Highly social animals that depend on each other’s help to survive tend to show greatest tendencies to respond to others in the group, and to be the most affiliative and affectionate to each other (Snowdon 2011). Pair-bonded marmosets are often found sitting with their tails twined together, and frequently turn to each other for affection and a sense of security. Though we tend to think of social carnivores like wolves, lions (*Panthera leo*) or hyenas (members of the family Hyaenidae) as fierce (and they certainly may be so towards us), they are highly affiliative and affectionate amongst themselves even as adults. That they feel a pleasurable sense of contentment at this affection towards each other, and also crave closeness and strong affection of bonds, keeps them together as a cohesive group. This same reassurance of emotionally sensitive touch is equally important to us (Suvilehto et al. 2019). Though we like to feel that, as humans, we are exceptional, much of the biology of our consolation behaviours connects us to other social animals.

A reassuring touch is helpful but what about actual practical help? More complex cognitive appraisal (more complex thinking processes) is needed to move from empathy to more constructive compassionate action that goes beyond reassurance. This involves *empathetic targeted helping*. Empathetic targeted helping may be something we do every day in the smallest of ways when we open a door for someone, help them with something heavy, or the slightest of everyday actions. However, quite complex emotional and cognitive abilities underlie these behaviours. Typically, from around one to two years old we will start to be willing and able to help constructively (Vaish, Carpenter, and Tomasello 2009). In order to actively assist someone, we often need to place ourselves mentally 'in their shoes' (*cognitive empathy* or *perspective-taking*) and formulate an appraisal of what might help. We might, for example, notice that something is out of someone's reach and get it for them.

Targeted helping is somewhat rarer than consolation in the animal kingdom but is not unique to humans. Highly social animals will often respond to explicit pleas for help, such as responding to begging for food. Active response to distress has been recorded in several highly social mammals such as dolphins, wolves, elephants (members of the family Elephantidae) and rats (members of the genus *Rattus*) (Pérez-Manrique and Gomila 2017). Provisioning of ill or injured adults has also been recorded in a range of animals including mongoose (*Helogale parvula*) (Rasa 1983) and otters (*Pteronura brasiliensis*) (Davenport 2010). Social carnivores have even been known to provision ill or injured individuals with food for some considerable time, with a case of a wounded lioness being provisioned by others for nine months (Hart 2011; Schaller 2009). Behaviours that help are often more instinctive than explicitly thought through – tending wounds, for example, is a common extension of grooming behaviour that improves healing (Hart 2011). Provisioning of food to ill and injured peers or attending to their wounds may be an extension of the type of care typically given to vulnerable infants but nonetheless may significantly improve their chance of survival.

Sometimes a response to distress appears to involve a more clearly explicit appraisal of the situation and of what might help. Chimpanzees, for example, will sometimes spontaneously help someone who needs something out of reach (Melis and Tomasello 2013; Warneken et al. 2007). There are reports of chimpanzees occasionally providing food for others without simply acquiescing to a demand (Boesch 1992; Pérez-Manrique and Gomila 2017). In one case, an adolescent male helped a mother to carry her infant for a period of two days when illness forced her to drop behind the group (Pruetz 2011). Dolphins (members of the family Delphinidae) will support another injured dolphin at the surface so that it can breathe, for example, and elephants will lift another elephant who has fallen or cannot stand (Douglas-Hamilton et al. 2006; Pérez-Manrique and Gomila 2017). They may understand the distressed animal's need and desire to be supported or lifted, and how they themselves can make that happen, although, of course, it is always difficult to be sure whether surrounding animals are acting in intuitive ways as if their peer were a vulnerable infant or if they truly understand the situation. Evidence for a level of appraisal of the situation nonetheless exists in some instances. Rats who have been taught how to use a lever to get a food reward will choose to free a familiar rat in distress over the opportunity to press for chocolate (Bartal, Decety, and Mason 2011). In effect, the rats are making choices about different outcomes, taking into account their emotional responses to the distress of a cage-mate as well as their cognitive appraisal of how to help. When we respond to someone who needs help, it might feel like a simple act, but even simply helping involves a sophisticated emotional attunement and motivation to help, as well as cognitive appraisal of what would be helpful.

Few of us have any idea when we first reached out to help someone else who was in distress or needed help, or when we helped others without any cues. We tend to pay particular attention when infants first start to speak, or when they show some kind of complex spatial intelligence. However, the point at which we first understand that someone else needs our help and we reach out to help them is an often-overlooked but possibly far more significant turning point in our development. That we share this turning point with other animals makes it no less remarkable.

Most of the occasions when we connect emotionally to people around us, comfort someone close to us, or share our joys or sadnesses, leave no trace. For some helping behaviours there is at least some possibility, nonetheless, of surviving material evidence from the past, such as the remains of people who might never have recovered from their illnesses or injuries without some help from others, explored in Chapter 2. We also find material evidence for how people treat those who have died, or *mortuary practices*. A more complex relationship, however, exists between empathy and responses to death.

How does empathy for the living relate to how we treat people after death? The emotional meaning of responses to death in other animals is something that is often hotly debated. When does empathy end? Many mammals, such as dolphins, sea otters and elephants, as well as other apes, continue to express nurturing behaviour even to dead individuals (Gonçalves and Biro 2018; Reggente et al. 2016). This type of behaviour is most common with deceased infants. There are well-known examples of chimpanzees at Boussou, Guinea, carrying the mummified remains of their dead infants for several weeks (Biro et al. 2010; Fashing and Nguyen 2011; Fashing et al. 2011). It is also recorded with dead adults. Apes can show distress at the death of an adult group member, particularly in the cases of traumatic death, spending time with or handling the body (Anderson, Gillies, and Lock 2010), behaviour also seen in species such as elephants (Bearzi et al. 2018; Douglas-Hamilton et al. 2006) and free-ranging dingoes (Appleby, Smith, and Jones 2013). Of course, in strict evolutionary terms, given all the costs involved in raising an infant and that there may be conditions or illnesses from which infants will recover with continued care but from which they may lose consciousness or appear to be inanimate, it may only make sense *not to give up too soon*.

Whilst continuing to show some signs of nurturance after death is not compassionate helping as such, it may be influenced at least in part by generalised empathetic responses to an individual who appears to be vulnerable and in need of support. Attitudes to death in other animals are nonetheless extraordinarily difficult to interpret. We cannot, after all, 'get inside their heads' to understand what they are thinking and feeling. The reactions of animals to dead members of the group illustrate some of the difficulties we have in interpreting what apparently similar behaviours expressed by animals to ourselves actually mean, or indeed what any mortuary practices in the very distant evolutionary past might have meant. It seems certainly reasonable to conclude that many animals, not only other apes and other primates but also elephants or dolphins, show a level of emotional connection to others, and are distressed by the death, and that this may reflect a sense of loss (Reggente et al. 2016). This is not the only explanation, however. Their responses may also be related to the psychological incongruity of something that is usually alive and yet is inanimate (unmoving) (Gonçalves and Biro 2018). We remain uncertain to what extent non-human animals understand what 'death' means. It is clear that the death of a close peer feels disturbing, but exactly what goes on in the minds of animals who are clearly upset is a question that remains largely unresolved. Likewise, though closely related human species to our own, such as Neanderthals, must have experienced a very similar sense of loss to our own, when far more distantly related humans deposit a body of their dead kin somewhere particular they clearly feel some sense of loss, but what that death means to is something of a complex mystery.

Disentangling evolutionary mechanisms

Why did we evolve to care *so* much? Disentangling the evolutionary basis for complex caring behaviours can be challenging.

We can be reasonably confident about some of the key processes that drive general tendencies towards altruism in humans as well as other animals (described below), even though the relative importance of different processes may not be entirely clear. However, when it comes to specific behaviours, such as reactions to the death of peers or care and provisioning of ill or injured adult group members, the selection pressures mechanisms that lead to this behaviour can be difficult to understand or disentangle. Some behaviours are strongly influenced by learning and culture. For example, chimpanzees from a particular region of Guinea have been recorded carrying around the corpses of their dead infants for some time after death, although this is only very rarely observed in other regions, suggesting that the behaviour is not just about genetic inheritance (Biro et al. 2010; Lonsdorf et al. 2020). Their distress seems to be translated into this particular behaviour because they have observed it and learnt this as the usual response, and other behaviours in chimpanzees, such as particular types of grooming or uses of tools, are similarly subject to cultural differences (Vaidyanathan 2011; Whiten et al. 1999). In other cases, it is difficult to know whether any particular behaviour has been subject to specific selection pressures for precisely that behaviour, or is part of far more general tendencies. Continued nurturance of infants, even when they appear to be inanimate, may be a behaviour that is specifically selected for. Mothers who behave in this way over long timescales have the potential to be more reproductively successful because of the cases of apparently unresponsive infants who eventually recovered. However, this behaviour might equally simply be a side effect of far more general responses to vulnerable infants, rather than specifically selected for in its own right. In the same way, care and provisioning of ill and injured group members may just be a side effect of general tendencies to help out vulnerable individuals, rather than being specifically selected for, even if this behaviour does have a notable impact on future survival, perhaps of family members, and we can construct a plausible explanation for its emergence (as discussed in Chapter 2). Our plausible evolutionary explanations do not necessarily prove that the selection pressures that we might imagine were the critical ones influencing any particular behaviour. Plausible arguments, or 'just-so' stories, without any evidence, are not necessarily correct just because they appear to *make sense*.

Far from being, as we often imagine, a process that leads to increasingly perfect forms, evolutionary selection pressures often create apparently strange traits or behaviours that are difficult to explain. Particularly famous amongst these is the case of the peacock's tail, created through male competition to attract females who themselves judge the quality of a potential mate on the basis of their resplendent but highly impractical tailfeathers. Male peacocks (members of the family Phasianidae), despite being rather beautiful, are very far from being well adapted to practical survival. Before he understood processes of sexual selection, Darwin found explaining the exotic and impractical plumage of the male peacock a notable challenge (Richards 2017). Whilst we understand a great deal, there are still many processes that remain an area of debate.

Why be kind? The evolutionary advantages of compassionate helping behaviours

The reasons why any animals, and we as humans, might develop extensive and in-depth emotional responses to help others have been the subject of much research in biology.

It is not difficult to explain why selective pressures encourage a maternal response to infants' needs. However, we might wonder why the cost of effort on behalf of an adult could ever be an advantage, how empathy beyond that for vulnerable young might have evolved, and why this tendency is more pronounced in some species (particularly our own) than in others.

The *proximate* (or immediate) cause of helping behaviours lies, as we have seen, in the particular neurological, hormonal and cognitive capacities that govern responses to others' distress. However, the *ultimate* (or longer-term evolutionary) cause of such behaviours lies in how selective pressures affect the ways in which the emotional and cognitive capacities of different species evolve. In certain ecological and social contexts, responding to others' needs may be beneficial in an evolutionary sense, and thus these contexts exert selective pressures on existing capacities.

In different contexts, emotional motivations to help others can benefit those with such capacities in several different ways (see Table 1.1).

In many cases, helping directly improves reproductive success such as when the recipient is a close relative and, in this case, helping (or *kin-based altruism*) makes evolutionary sense as a way of safeguarding one's genes. This is the case not only in care of the young but for many social mammals who parent collaboratively or share proceeds from collaborative hunting. The benefits of helping each other in the context of a dependence on *working together and sharing food* to survive places evolutionary pressures on emotional motivations and cognitive abilities to respond altruistically to other group members. Some social carnivores, such as grey wolves, not only parent and hunt collaboratively but provide for, and even defend, sick or ill group members as they would offspring (i.e. by regurgitating food; Barber-Meyer et al. 2016), as well as taking risks to defend other adult pack members (Cassidy and McIntyre 2016; Jouventin, Christen, and Dobson 2016). These kinds of behaviours (and so the proximate cognitive-emotional basis underlying them) tend to 'pay off' in the long term.

Collaborative or *mutualistic altruism* can also benefit individuals who are not closely related. In such cases, the 'costs' of helping are often rewarded in different ways such as with food that might otherwise have been impossible to access alone. Common chimpanzees who collaborate to hunt monkeys may not be closely related (though sometimes will be); however, their efforts in collaborating 'pay off' in their share of the proceeds.

One more complex way in which helping can pay off is when favours are specifically remembered and returned at a later date, effectively following the tactic to 'help someone who has helped you before' or *reciprocal altruism*. Returning favours (or 'direct reciprocity') makes it possible to translate limited help in the present into help in the future, when it might be desperately needed, and to develop mutually beneficial collaboration even where the individual benefiting does not carry your genes. Reciprocity is even more cognitively complex than simply helping any individual in need, as the individuals themselves and the favours they rendered need to be remembered. However, direct reciprocity avoids 'wasting' help that might not be returned and allows pairs of individuals who are not kin to get help from each other when in need (and be prepared to provide it). This type of 'tit-for-tat' reciprocity is recorded in highly social animals who can be altruistic to close peers, including coyotes (*Canis latrans*) (Romero and Aureli 2008), rats (Dolivo, Rutte, and Taborsky 2016) and vampire bats (member of the subfamily Desmodontinae) (Carter and Wilkinson 2015), and is particularly common in primates, as in 'tit-for-tat' grooming, for example. Favours can be remembered for several months in chimpanzees (Schino and Aureli 2010), for whom such helping, whilst limited to 'low-cost' effort, includes not only sharing food or helping instrumentally (to achieve a goal) but also in taking risks to help out others in conflicts (Engelmann, Herrmann, and Tomasello 2015). Favours need not be explicitly remembered as discrete events but rather as a pervasive influence reflecting how each partner feels about (and feels sympathy towards and wishes to help) the other. Remembering of favours, and helping in return, uses different brain circuitry and hormonal responses from caring-based altruism (Marsh 2019). As we shall see in Chapter 3, remembering favours and making judgements about the propensity of others to act in our interests is an early basis for relationships based on trust and emotional commitments to another's wellbeing.

Whilst kin-based helping, mutualistic helping and reciprocal helping are explained through evident benefits, not all helping in social animals has any direct or indirect 'pay off' in such terms. Highly social animals are sometimes emotionally motivated to help non-kin who may never help them in return.

Type of helping behaviour	**Basis of behaviour**	**Example**
Kin-based altruism	'Help your relatives'	Shared parenting in wolves
Mutualistic altruism	'Help with a task which benefits everyone'	Hunting in chimpanzees
Reciprocal altruism	'Help someone who has helped you before'	Chimpanzee returning a favour of food, grooming or defence
Generalised reciprocal altruism	'Help someone if someone has helped you'	Domestic dogs who work together

Table 1.1: Different types of helping behaviour according to evolutionary drivers.

Generalised reciprocal altruism, helping others if you yourself have been helped, was thought to be restricted to humans, but has, however, been recorded in species such as rats (Dolivo, Rutte, and Taborsky 2016), vampire bats (Carter and Wilkinson 2015) and marmosets (Burkart et al. 2007). Working dogs (*Canis familiaris* or *Canis lupus familiaris*) also tend to help each other when they themselves have been helped and without expecting any direct reward (Gfrerer and Taborsky 2017). It may be that sometimes a more generalised tendency to help others in one's group pays off by helping the survival of the whole group in contrast to others (*group selection*) or in less direct ways (Taborsky, Frommen, and Riehl 2016). In vampire bats, a willingness to donate blood to unrelated individuals who would otherwise starve if they were unsuccessful at finding food increases the likelihood of survival of the group in general (Carter and Wilkinson 2015). Equally, a tendency to help vulnerable group members in need may, by necessity, be so cognitively general as to be expressed in many different situations. Many different mammals adopt infants of other species, responding as if they were their own, and adult male chimpanzees have been recorded 'adopting' unrelated orphan infants, for example, with no clear benefit to themselves (Boesch et al. 2010).

At various points in our evolutionary history, any or all of the mechanisms described above will probably have had important selection pressures on human emotional motivations towards altruism. There may also be selection pressures and processes unique to humans. Sexual or mate selection can influence the evolution of emotional capacities, for example. Generosity seems to confer advantages in finding a mate, with more generous people generally rated as physically more attractive (Zhang et al. 2014), as well as tending to have more children (Eriksson et al. 2018). There has even been speculation that selection for partner altruism became so important in our evolutionary past as to reach 'runaway' levels (where the trait is so extreme as to endanger survival; Nesse 2009). Our tendencies to heroism may, like the peacock's tail, be a price to pay for attracting a mate. As we shall see in Chapter 3, there also seem to be social benefits to being someone that others trust and having a 'good' reputation that make a tendency to compassion and generosity worthwhile in a more general social context. There may also be other complex processes at work. The evolution of human altruism may have depended on the 'policing' of cheats, for example, who might otherwise exploit naïve altruists (Egas and Riedl 2008; Fehr and Gächter 2002). Moreover, there are good arguments that culture itself plays a key role in how our emotional capacities have evolved. Humans become independent of the physiological limits of their bodies on where they survive, such as by tools or clothing or fire, by around a million years ago (Mondanaro et al. 2020) and the importance of how we learn and how we fit in has also had an important influence on how we involved (Heyes 2020). We might never entirely disentangle the relative influences of these different mechanisms, but we can at least hope to gain important insights into how these factors played a role in how we feel today and potential stages in the evolution of our caring emotions.

Animal comparisons: stages in the evolution of human empathy, compassion and generosity

Studies of animal behaviour do not just reveal interesting examples of empathy, responses to distress or helping. They can provide important insights into how human emotional motivations may have emerged.

Studies of our nearest living relatives, chimpanzees and bonobos, have been a particular focus of attention. This is not surprising as the behaviours of these apes can potentially give us important insights into the emotional capacities that our shared common ancestor, living around 7 to 8 million years ago, may have been likely to have possessed. This common ancestor is often seen as the 'starting point' of our human evolutionary journey.

Whereas most studies of cognition focus particularly on chimpanzees, understanding the evolution of our emotions demands considering more distantly related animals. There are ways in which distantly related but highly interdependent animals show emotional capacities and behaviours that are more similar to humans than those of other apes, suggesting that human evolution has been more complex than any straight line we might draw between chimpanzees and ourselves.

Comparing non-human apes and humans: emotional capacities and helping behaviours of human ancestors 7 to 8 million years ago

It might seem rather odd to compare ourselves to other apes. However, such comparisons help us to understand the most significant transformations that have taken place in our own evolutionary past.

There is a certain inescapable human-like quality to some of the social relationships we see in our nearest relatives. Apes in general, and chimpanzees and bonobos in particular, are highly social animals, spending a lot of time resting and grooming each other (Figure 1.4). Grooming releases positive opiates, reaffirms alliances and helps negotiate their roles in a complex dominance hierarchy, with touch showing similar effects in humans (Suvilehto et al. 2019). Further, being part of a large and complex social group is associated with high degrees of social intelligence – you need to be socially savvy to work out how to get along (Dunbar 2003). Many of the behaviours we see in chimpanzees and bonobos that demonstrate their capacity for empathy are familiar to us – such as contagious yawning, sensitivity to others' emotions, sympathetic concern, consolation behaviours and active helping (Clay, Palagi, and de Waal 2018). Moreover, chimpanzees and bonobos are highly socially astute and intelligent, and show a remarkable cunning, demonstrating behaviours that have even been compared to those seen in human politics (de Waal 1998).

We can be reasonably confident, therefore, that a certain social astuteness, with a sensitivity to others' feelings and capacity to respond to distress, was already present in the last common ancestor between ourselves and other apes. Of course, chimpanzees and bonobos followed their own evolutionary pathway since the split between their lineage and our shared ancestor living around 7 to 8 million years ago, and many features of their thinking and

Figure 1.4: Chimpanzees grooming. Like humans, chimpanzees are intensely social creatures. Grooming releases positive opiate based hormones and is the main means by which chimpanzees and bonobos affirm and negotiate social bonds. Chi King, CC BY 3.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:500px_photo_(188689963).jpeg.

social relationships must have been 'derived', that is, developed, during this period of separation. Moreover, chimpanzees and bonobos followed distinct evolutionary pathways from around 2 to 3 million years ago and developed distinctive features after the split (discussed in Chapter 7). On a broad level, their shared capacities to read others' emotions and motivations, to respond to distress, and to navigate complex social worlds nonetheless give us some important insights into how our distant ancestor may have been able to think and feel.

Of course, we are also vastly different from any chimpanzee or bonobo. In many ways, comparing ourselves to non-human apes can seem rather bizarre when we possess so many emotional and social traits that seem to mark a vast gulf between ourselves and our nearest living relatives. Love, poetry, imagination, complex beliefs and ideologies, and abilities to understand abstract concepts or communicate in complex ways and understand philosophical debates are but some of the many apparently fundamental distinctions that divide us.

The marked differences between ourselves and other apes in emotional capacities and behaviours are important, however, and perhaps more interesting than the similarities. If we can take them apart into some of the key constituents, they tell us about the important transitions that must have taken place after our lineage split from other apes. In fact, whilst many of the ‘golden barriers’ supposedly separating humans from other apes have broken down over the past decades, it is in the realm of emotional sensitivity, empathy and altruism that we perhaps see the most marked distinctions. If we can begin to understand what transformations have taken place, and why changes in emotional capacities might have been important, our understanding of what was significant about our human evolutionary past may also change.

It seems obvious, but human motivations to help others are more in-depth and more extensive. At an intimate level, we routinely respond to the needs not only of our own infants but also our partners and families and friends. Moreover, whilst chimpanzees’ infants are cared for almost solely by their mothers, fathers often play a significant role in parenting in human societies, with grandparents and wider kin, and even friends, also playing an important part. Beyond this intimate scale, we respond to the needs and feelings of friends, wider social groups and even distant strangers. Chimpanzees are predominantly self-focused, only rarely reaching out to console others, or to share food. Whilst humans have been characterised as hypercollaborators (Tomasello 2014), the rigid hierarchies of chimpanzees are based on competition, with only rare collaboration. Our emotional sensitivities to others’ feelings and our level of emotional connection are also far greater. We can identify others’ feelings from even the slightest of facial expressions, indicating emotions from joy and fear to bewilderment and surprise. On the other hand, chimpanzees, in particular, are far less aware of how others feel. They are less sensitive to faces and instead pay more attention to body postures (Clay, Palagi, and de Waal 2018). For chimpanzees, being powerful is more important than being sensitive. Moreover, we respond empathetically to a far greater range of situations and vulnerabilities. We respond to not only vulnerable young but also vulnerable adults we know, vulnerable adults we do not know, entirely different species (discussed in Chapter 6) and even apparently vulnerable objects that seem to need our help and nurturance (discussed in Chapter 7).

We are also far more socially astute. We identify others' motivations with remarkable accuracy from the slightest of facial expressions, and are finely tuned to others' distress (Grossmann, Missana, and Krol 2018; Marsh 2019). This astuteness combines with empathy and an understanding of others' minds to produce many apparently uniquely human feelings, such as gratitude or awe, guilt, pride or shame. Gratitude, for example, plays a key role in inspiring generous behaviour, which cascades along networks of social interactions and, moreover, makes people more emotionally resilient. Gratitude seems to be a uniquely human emotion, depending on sufficient cognitive empathy to accurately interpret whether someone has selflessly acted on our behalf. It is only late in childhood (around 11 years old) that we start to feel and express gratitude (Emmons and McCullough 2004). Gratitude is influenced by our biology (vanOyen Witvliet et al. 2018) but also profoundly affected by our sense of attachment to our caregivers (discussed in Part 2), as well our culture, experience and deliberate choices (Mendonça et al. 2018). Other complex human emotions, such as awe, are equally dependent on both emotional and cognitive capacities.

Psychological experiments have illustrated that important differences between ourselves and other apes emerge in early human childhood. Of course, we do not all develop at the same rate, and differences in our heritable sensitivities to others' distress make up the very variability on which evolutionary changes work (Marsh 2019). Nonetheless, general developmental changes are common to most of us. At only seven months old we will show attention to fearful faces, with altruistic tendencies emerging by around 14 months (Grossmann, Missana, and Krol 2018). By only two years old, we will already show strong motivations towards altruism and a willingness to help others, and, moreover, more sophisticated helping behaviour than any adult ape (Tomasello 2014; Warneken and Tomasello 2007); see Table 1.2.

How these marked differences in helping behaviours emerge through our infancy and childhood gives us some particularly useful insights into the complex relationship between social thinking skills, and emotional motivations and the potential stages through which our ancestors may have passed en route to being human.

As humans, we have exceptional capacities for anticipating others' needs. Even as young infants, we are more willing to help others and far better able to anticipate the needs and goals of someone whom we wish to help. Indeed, the most obvious difference in helping that we might notice between human infants and non-human apes is that infants can give unsolicited help (without explicit cues or demands). Unsolicited help (i.e. help in response to a need but without a cue being provided) is extremely rare in apes. Apes will typically help someone reaching for an object (Warneken 2016; Warneken 2018) and chimpanzees can even, in some situations, understand another's goal and adapt their helping towards it (such as selecting the appropriate tool an individual needs for a task to give to them; Yamamoto, Humle, and Tanaka 2012). However, even chimpanzees tend to only specifically act on *a cue that help is needed* (Warneken 2016). Chimpanzees will, for example, (sometimes) respond to another's hunger or desire for food when they *overtly beg*, such as by reaching out towards the food, but not foresee that an individual may need food or give them food because they are aware that they do not have any. Human infants will, in contrast, infer what help is needed *unsolicited*. If someone loses something to a bully, yet remains stoic and shows no sign of distress, for example, we will want to comfort them from around 18–24 months of age, appreciating that the situation is one in which we ourselves will be likely to be upset (Vaish, Carpenter, and Tomasello 2009). By two years old, we will tend to give something to someone who is 'empty-handed' without any cue or request (Warneken 2018). Unsolicited helping of this kind demands affective empathy (an emotional response to another's situation) as well as a sophisticated level of perspective-taking. Debates exist over the extent to which non-human apes, and chimpanzees in particular, possess *theory of mind* (the ability to understand what another individual is thinking) (Call and Tomasello 2008). However, whether non-human apes possess a true theory of mind or not, it is clear that at one and a half to two years old we show a more sophisticated mental model than any adult ape of what others think and believe, and use this when helping others.

A further significant difference is that, even as young infants, we can direct our help *towards long-term goals, rather than immediate desires*, something not seen in any other animal. If adults wanting a cup of water ask for a cup that an infant knows will leak, then three-year-olds will pass the adult *not* the cup they ask for but one without a hole in order that they can drink

Helping behaviour	**Primate species**	**Example**	**Human development**	**Example**
Consolation	Apes, monkeys and some highly social mammals	Adult chimpanzees hugging the loser of a fight	Infants in their first year	Touching or hugging someone in distress
Targeted/ situational helping	Apes, some monkeys and some highly social mammals	Adult chimpanzees passing someone an object that is out of reach	Infants from one to two years old	Passing an object that has been dropped
Unsolicited helping	Rare – bonobos in an experimental setting	Helping another individual gain food without an explicit clue	Infants from two years old	Giving a toy to someone who is 'empty-handed'
Helping towards long-term needs or goals	Rare – potentially seen rarely in some types of collaborative hunting	Hunting in Taï chimpanzees, where certain individuals assume particular roles	Infants from three years old	Passing a cup without a leak to drink water, even when asked for a leaky cup
Morally discriminate helping	Not recorded – (though apes preferentially help allies according to remembered favours)	—	Infants from two to three years old	Helping a 'nice' adult in preference to a 'mean' one

Table 1.2: Stages in empathetically motivated helping seen in apes and human infants.

effectively from it (Martin and Olson 2013). Making a distinction between what is requested and what is actually needed is cognitively complex, but particularly significant in terms of *being able to act in the best interest of others*. In this case, infants have identified the ultimate long-term goal and what will achieve that goal, they have also been motivated to help and, moreover, they have overridden a direct request, putting the best interests of another above pleasing them. Even as infants, we show sophisticated abilities to *coordinate different actions towards an end goal*, such as when one individual performs one task and another does something else, both contributing to the shared goal (Warneken 2018). To do this we use both a mental representation of the end goal and one of how different activities contribute to it, combined with our notable emotional motivations to help.

Both *unsolicited helping* and *helping towards long-term goals* might appear simple but they require both affective concern for others, and complex cognitive abilities, and both types of helping influence the type of collaboration which can take place. Without unsolicited helping, someone who is ill or injured and may not be able to make an explicit request for help is likely to perish, for example. Likewise, helping towards an end goal through different activities opens up possibilities for new types of collaboration.

It might seem a little bizarre to compare human infants with fully adult chimpanzees. However, the distinctions that we see between helping behaviours in fully developed adult chimpanzees and those of young human infants give us some important insights into potential stages in the human evolutionary past. Our own development of children does not, of course, in any way replicate the way in which we have evolved, but it does give us some insights into the possible sequence of changes in emotional and cognitive capacities that might have taken place in the past and how they may have influenced social relationships and communities.

Actively helping others depends on both social understanding and emotional motivations (or social cognition and affective cognition).

Cognitive empathy

It is our social thinking skills or cognitive empathy (broadly speaking, 'theory of mind' abilities; Dunbar 2003) that has attracted the most research attention. Though our understanding of others' thoughts and that of others' feelings inform each other, they are distinct, and are related to different brain functions (Eres et al. 2015; Stietz et al. 2019; Watanabe et al. 2014). Cognitive empathy helps us to understand others' beliefs about us (for example, our

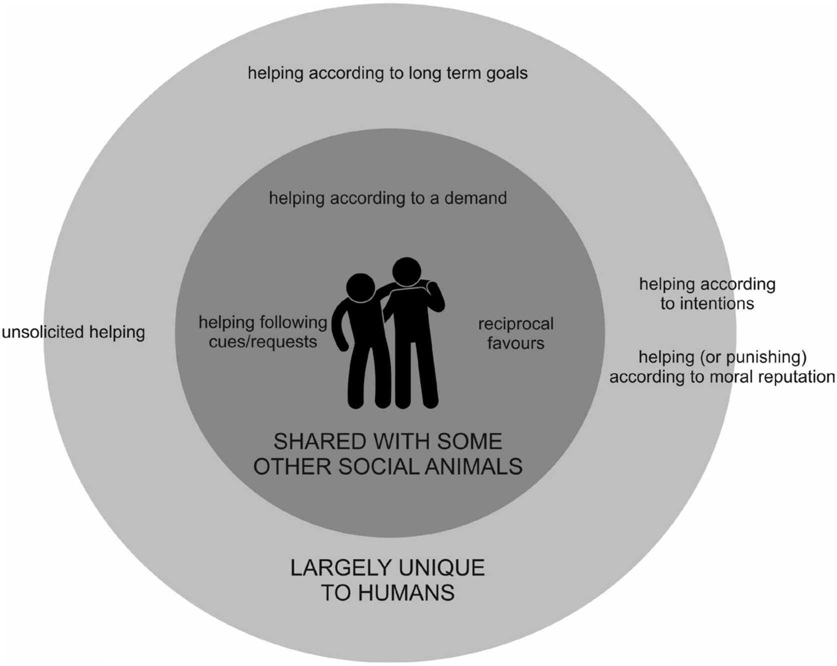

Figure 1.5: Increasingly complex cognitive empathy seen in humans compared to some other social animals. Penny Spikins, CC BY-NC 4.0.

reputation in their eyes), whilst affective empathy helps us to emotionally relate to how they feel.

In simple terms, comparisons between other apes and human infants illustrate that, in our development, we increasingly outsmart other apes in terms of our abilities to help using our cognitive empathy, that is, by taking others' perspectives and using our complex executive functions to better understand others' needs, as well as how we can help. Certain key stages seem to be evident (see Table 1.2 and Figure 1.5).

Affective empathy

The evolution of our emotional cognition through affective empathy (or emotional empathetic response) has received far less research attention than our social thinking skills. This is perhaps, at least in part, because emotional motivations are often seen as 'woolly' and difficult to research.

Moreover, it is hard to ignore the possibility that we also feel rather more ambiguous about whether our emotional capacities are 'something to be proud of' or something more of a weakness (as discussed in the introduction to this book).

There is a more complex issue, however. A further complexity is the lack of a clear link towards our nearest relatives. Considering potential stages in the evolution of our emotional motivations to help others presents us with a rather difficult and surprising paradox. Chimpanzees are remarkably self-focused and it is other far more distantly related animals who show a much more human-like ability and tendency to connect to others' feelings, respond to others' needs and to help when required. This seems counterintuitive. Chimpanzees and bonobos are the animals that are most closely related to us. Yet other, much more distantly related species behave in more human-like ways where altruism towards members of the group are concerned. These include species such as distantly related primates (as discussed in the introduction to this chapter) and even more distantly related animals such as social carnivores. Capacities that link more to wolves, hyenas or squirrel-like monkeys seem not to be so elevated as are more analytically social thinking skills.

This paradox tends to receive little attention (it is inconvenient, after all).

Rather than our nearest relatives, we find that some of the most distantly related primate species to ourselves, New World monkeys of the family Callitrichidae, are those who seem to connect most deeply to those around them and are the most affectionate and altruistic to their peers. As we have seen in the Introduction, these monkeys, including marmosets and tamarins, are tiny, and remind us more of squirrels than chimpanzees. However, they are pair-bonded, and collaborate to raise offspring, with infants cared for not only by parents but also by other helpers (Rapaport 2011). As a result of this close interdependence, they respond much more widely to others' needs and show a much greater affective empathy than do most other primates. Marmosets and tamarins, for example, show not only a concern for fairness (Yasue et al. 2018) and capacities to share but also loyalty to their mate and great investments in efforts in shared care of offspring. Certain brain areas in males are active when recognising their mate (Bales et al. 2007), associated with pleasurable hormonal responses due to the release of the hormones oxytocin and dopamine, as we also see in humans (Abraham and Feldman 2018; Feldman 2017). Many argue that, in their willingness to be generous and in the sharing of care, they are a better analogy for early humans than are much more closely related chimpanzees (Burkart and Finkenwirth 2015; Erb and Porter 2017).

Pair bonding has arisen in many very distantly related species, and there may be different selection pressures and ecological and social situations which make mutual investments in offspring worthwhile. Amongst New World monkeys, the wide distribution of females, and threats to the survival of offspring looked after by only one parent, may have been particular factors in selection pressures on males, in particular to be much more emotionally invested in their mate and offspring. Cooperative breeding increases in harsher environments (Smaldino et al. 2013). Human pair bonds and, moreover, collaborative infant care may have been a response to ecological demands of challenging environments, though responses to particular social structures may also have been important (Rooker and Gavrilets 2016). Pair bonding and collaborative parenting are likely to have played a significant role in changes in emotional dispositions in humans, as well as allowing increasingly vulnerable young with a larger brain size to be raised successfully (Burkart, Hrdy, and van Schaik 2009; Hrdy 2011).

Collaborative defence also plays a role in increasing emotional investments in others' wellbeing and willingness to take risks on behalf of the whole group in some, more distantly related, mammals. Meerkats, for example, collaborate to raise offspring and defend their group, and to teach valuable skills to the next generation (Rilling 2011). Many argue that collaborative defence evolved after the split with other apes, as early humans moved into more open environments with many predators (Hart and Sussman 2011).

However, even more distantly related animals seem even more similar to humans in terms of their motivations to help others in their group, to share what they have and to respond to their needs.

Though we are apes, there is good reason, in terms of our emotional motivations, to see similarities between ourselves and more distantly related mammals – social carnivores such as wolves and lions (Thompson 1975).

Social carnivores help others within their group much more extensively than do apes – as we have seen above, highly social mammals collaborate to look after their offspring, hunt together, share food and even in some cases provision those who are sick or injured. Social carnivores are highly interdependent, depending on each other for their basic food necessities, and sharing infant care, as well as showing each other frequent gestures of warmth and affiliation. From modern hunter-gatherers to people in modern industrialised societies, like social carnivores (and unlike apes), we look after others' offspring, depend on shared food and care for the ill and injured.

Wolves and hyenas may have a bad reputation for being fierce and aggressive, but their willingness to be generous and emotional motivations towards altruism within their own group are remarkable (Jouventin, Christen, and Dobson 2016). Groups of hyenas may operate in ways that share similarities with highly collaborative early humans. Spotted hyenas collaborate between kin and non-kin to hunt and to defend their group from competitors or predators, for example (Smith et al. 2012). Despite their far greater separation from humans in phylogenetic terms, they can potentially contribute to our understanding of the evolution of human generosity and compassion (Schaller and Lowther 1969; Smith et al. 2012).

Wolves are also a particularly good example of highly intelligent mammals who have strong emotional connections to others in their living group and help each other in remarkably costly ways (Smith et al. 2012). As social carnivores, wolves hunt together, risk their own lives to defend others, willingly share food, care for each other's offspring and can also care for the sick and injured, regurgitating food as they would for pups. Thus, empathetically motivated helping within any group of wolves is far more costly than that seen within groups of chimpanzees. Like humans, wolves also thrive on frequent gestures of care and affiliation between each other (Figure 1.6). They have evolved to be highly sensitive and responsive to each other's emotions, displaying their own facial and body expressions (Bekoff 2002), and some traits of a theory of mind (Horowitz 2011). Like other apes, and humans, they also display yawn contagion, a response related to empathising (Romero et al. 2014). They also have large brains, low levels of sexual dimorphism and a sophisticated social cognition that exceeds that of their near relatives who do not need to collaborate to survive (Borrego and Gaines 2016). As we shall

Figure 1.6: Wolf photographed at Polar Zoo, Norway. Wolves show remarkable generosity to others in their pack – taking risks on others' behalves, sharing food, and displaying strong, affectionate and often playful affiliative emotions to each other. Johannes Jansson/norden.org, CC BY 2.5 DK, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File: Varg _fotograferad_pa_Polar_Zoo_Norge_(15).jpg.

see in Chapter 7, it may be no surprise that the animals that we choose to share our lives with are descendants of wolves, rather than closer primate relatives. Social carnivores are far happier to share our social rules, form close attachments with us, and see us as part of their close-knit social group.

Perhaps surprisingly, wolves are not even the most social of canids and their relatives. African painted wolves (*Lycaon pictus*) are even more strongly collaborative and interdependent. They are even more hyper-carnivorous, and so more dependent on collaborative hunting, than wolves, and routinely support and provision their ill or injured pack members. African painted wolves often attract less interest or attention than other canids because they have less expressive facial expressions, yet they are no less expressive of their feelings or attentive to those of others. It is simply that, on their particular evolutionary branch, emotional communication occurs more through vocalisations, body postures and ear positions (Creel and Creel

2002). Their level of interdependence can bring disadvantages, with African wild dogs being threatened with extinction since their highly collaborative care for young means that they depend on more than a single breeding pair to successfully bring up offspring. This issue of different types of communication, and the effects of high levels of interdependence on vulnerability to extinction, is also relevant within our own evolutionary past, particularly in contrast with Neanderthals (Chapter 8).

No one would suggest that we are *just like wild canids such as wolves*; however, these highly social and interdependent species may give us a far better insight than our closest relatives into how human generosity, compassion and empathy evolved. It goes without saying that humans show additional extended capacities in responding altruistically in more extensive ways to non-kin and strangers, to other animals, and even to inanimate objects (Figure 1.7). However, highly collaborative species and those that parent

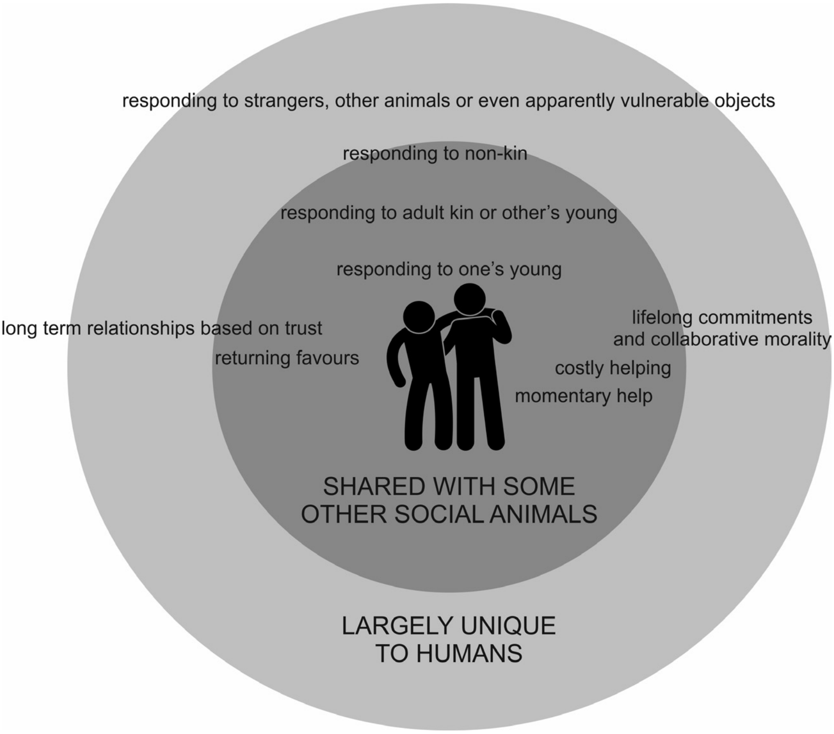

Figure 1.7: Increasingly extensive affective empathy seen in humans compared to some other social animals. Penny Spikins, CC BY-NC 4.0.

collaboratively and appear bonded tend to give us a better indication of intermediate stages in the evolution of human social emotions.

Evolutionary pressures on emotional motivations

How could distantly related social mammals be more similar to us in terms of emotional motivations than those that are far more closely related?

One answer may lie in a combination of the influence of ecology on selection pressures acting on social behaviours and the speed with which tendencies to particular hormonal responses can change in evolutionary time.

The relationship between hormones and behaviours is complex, and caring behaviour, for example, is influenced not only by inherited genetics but also by factors that influence the expression of particular genes (epigenetics), personality, experience and culture (see Figure 1.8; for a more detailed discussion, see Marsh 2019). However, subtle evolutionary changes in hormone systems can have far-reaching effects on emotional motivations and behaviour (discussed in more detail in Chapter 7). Moreover, there are

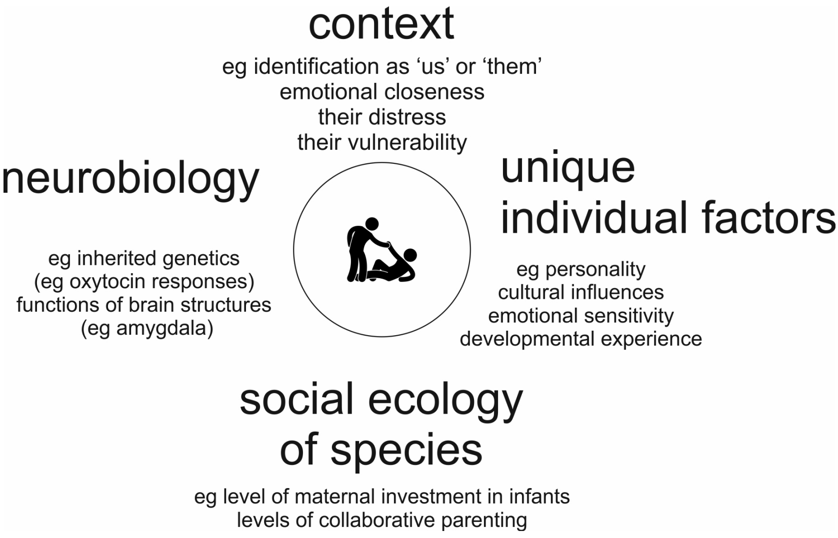

Figure 1.8: Some of the factors associated with variations in caring motivations and behaviours. Penny Spikins, CC BY-NC 4.0.

common patterns across species in factors influencing care, and how these influence neuroendocrine function.

Heritable changes that influence the production of particular hormones have a key role to play in directing different types of social behaviours. Evolutionary changes in bonding hormones such as between different species have far-reaching effects on emotional responses and caring behaviours (Carter et al. 2008).

Changes in genes that affect oxytocin production or uptake is one example. As we have seen, mammals all share a nurturing response to our young that is mediated by oxytocin. This means that mammalian mothers feel a similar sense of warmth when nurturing their young, as we do. Their empathetic responses to their infant's needs are rewarded by oxytocin release (Decety et al. 2012). Oxytocin is also key to pair bonding across a range of social mammals. It mediates the feel-good response many men feel on seeing their partner's face (Scheele et al. 2013), and pair bonding in a wide range of species such as marmosets (Smith et al. 2010) and prairie voles (Carter et al. 2008). Oxytocin also has an important role to play in collaboration beyond maternal/paternal and pair bonds. Oxytocin is implicated in peaceful group associations within mammals in general (Romero, Onishi, and Hasegawa 2016) and is part of hormonal systems, also including hormones such as testosterone (discussed in Chapter 6), which promote collaboration in primates and humans (Trumble, Jaeggi, and Gurven 2015). Sharing food, including with non-kin, is mediated by oxytocin in wild chimpanzees, for example (Wittig et al. 2014).

Artificially changing levels of oxytocin has particularly interesting effects on social behaviour. In dogs, elevated levels of oxytocin increase social play (Romero et al. 2015), for example, and, in meerkats, elevated levels of oxytocin increased social teaching behaviours (Madden and Clutton-Brock 2011). Many social behaviours in mammals, beyond nurturance such as play (Romero et al. 2015) and social learning (Madden and Clutton-Brock 2011), are also influenced by oxytocin-mediated social bonds. In humans, oxytocin also plays an important role across many different human social bonds, from close romantic relationships to family bonds (Ten Velden, Daughters, and De Dreu 2017). Artificially increasing oxytocin increases interpersonal trust

(Baumgartner et al. 2008; Kosfeld et al. 2005), generosity (Zak, Stanton, and Ahmadi 2007) and gratitude (Algoe and Way 2014), and oxytocin is also implicated in empathy for strangers (Barraza and Zak 2009). Mutual gazing increases oxytocin levels between humans and dogs (Nagasawa et al. 2015). Even quite subtle changes in these hormones have far-reaching effects on emotional responses and social behaviours, including caring behaviours.

The effects of evolutionary changes in hormonal responses can be complex. There is, for example, a darker side to the group altruism brought by oxytocin, once dubbed the 'cuddle hormone'. Elevated levels of oxytocin can also enhance motivations towards defending an in-group against out-groups that appear threatening (De Dreu et al. 2011). For this reason, oxytocin has been seen as a hormone that makes people more sensitive to social clues, rather than more prosocial per se. It is associated with stimulating motivations to 'tend and defend' one's loved ones, even where the defence may involve aggression (Ne'eman et al. 2016). In many ways, oxytocin is more about *emotional commitments*, and support of particular loved ones, rather than being friendlier or simply more altruistic. There is some evidence that, for females, oxytocin can promote more of a 'tend and befriend' response than 'tend and defend', promoting motivations to reach out to develop stronger relationships and so strengthening, rather than disrupting, networks of relationships (Taylor et al. 2000). Whether these responses are cultural or genetic remains to be resolved but, evidently, feelings of warmth towards certain others, stimulated by oxytocin, can affect *how we actually behave* in differing ways. As we shall see in Chapter 6, the impact of changes in testosterone are equally complex.

Subtle changes in inherited genetics that influence hormones like oxytocin (such as oxytocin receptor densities in the brain) can have quick and far-reaching effects on emotional responses and social behaviours. Many speculate, for example, that hormonal changes in oxytocin and in vasopressin are likely to have been key to changes in the role of fathers in infant development in human evolution (Abraham and Feldman 2018; Feldman 2017) and other changes in these hormones, later in human evolution, may have been important in changes in intergroup tolerance (discussed in Part 2).

We can be confident that changes in hormonal responses to particular situations played a key role in changes in human emotional responses.

However, in the absence of directly identifying genetic signatures related to particular hormones (discussed for later human evolution in Chapter 7), precisely which hormones, and how they may have changed, remains an area of debate. Recent research suggests a related opioid β-endorphin may be important in maintaining long-term relationships through feelings of trust, calmness and relaxation in the presence of long-term mates, kin and allies, for example (Pearce et al. 2017). Crosstalk or an intimate relationship between oxytocin and dopamine in striatum, combining motivation and vigour with reward-seeking social focus, may also be important (Feldman 2017: 80). Whilst oxytocin provides the soothing and tranquillity necessary for bond formation via its effects on the hypothalamic–pituitary–adrenal (HPA) axis, dopamine provides a sense of anticipated reward and pleasure, and influences drives to reconnect and act to maintain long-term bonds, potentially important in early human origins (DeLouize et al. 2017). Changes in other hormone systems are also implicated in increasing collaboration. Pair-bonded mammals, for example, typically show a reduction in testosterone, as efforts in competition for mates become less worthwhile (Trumble, Jaeggi, and Gurven 2015). However, much as oxytocin plays several roles, testosterone can play a role in in-group collaboration 'against' out-groups or in defence. The precise nature of hormonal changes promoting greater collaboration in different species is likely to have been subtly different.

Ecological changes putting selective pressures on increased collaboration, whether this be due to a need to defend against predators, to collaborate to exploit resources (such as collaborative hunting in social carnivores) or to collaborate in childcare, can exert selection pressures on hormonal responses and, in turn, influence changes in typical emotional responses to vulnerable infants or other group members.

Social carnivores illustrate this effect. They need to work together in order to survive. This is because social carnivores typically have to hunt collaboratively to be able to tackle prey that would be impossible for individuals alone, collaborate to defend themselves from predators that might otherwise overcome any individual in isolation, share food and share the care of vulnerable young to give their offspring the best chance of survival. All of these behaviours involve extended caring responses beyond maternal infant bonds and group affiliations. As a result, selection pressures have acted on existing mammalian empathy and other traits present in the ancestors of

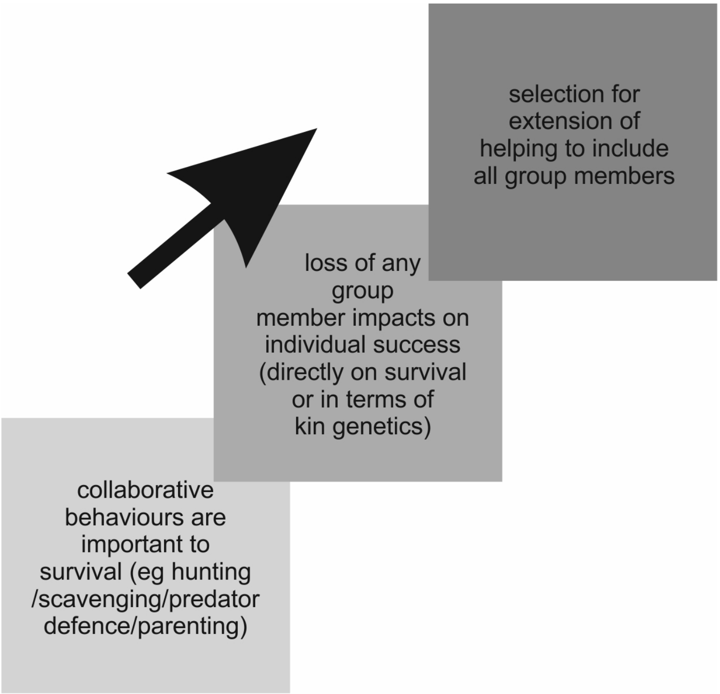

Figure 1.9: Selection pressures acting in highly collaborative social mammals, and particularly social carnivores, towards the extension of empathy to all group members. Penny Spikins, CC BY-NC 4.0.

social carnivores to create neurological and hormonal responses, not only to one's own young but also to other adults in the group, and other offspring (Decety et al. 2016). Emotional motivations to help others in the group 'pay off' because, over the long term, such efforts improve evolutionary success. This is most obviously the case where group members are predominantly kin who carry shared genes; however, altruism towards group members can pay off even in groups including or made up of non-kin where each individual is important to group survival (and helping them improves one's own survival chances) (Frank and Linsenmair 2017); see Figure 1.9.

Selection pressures act most particularly on neuroendocrine responses, which may change relatively rapidly, often responding far more quickly than changes in hard skeletal morphology or more complex areas of cognition. Where sharing behaviours, caring or generosity pays off, therefore, we expect brain and communal responses to favour individuals more prone to be generous or compassionate to other group members. For this reason, in ecological situations in which individuals are highly dependent on other members of the group for their own survival, responding to others' needs and being prepared to give generously and to share start to feel pleasurable. This mechanism is likely to have been as significant for early humans as for any other social collaborative animal. As Allen explains, 'generosity produced pleasurable feelings in certain humans – and thus made those humans more likely to be generous again – they thereby became the ones who are more likely to survive' (Allen 2018: 11).

Implications for the evolution of human empathy, compassion and generosity

Pulling the above together, we can see that comparisons both with our nearest living relatives, chimpanzees and bonobos, and with more distantly related species that share human emotional motivations towards vulnerable infants and group members, suggest that certain key distinctive transformations in human empathy, compassion and generosity, and the strength of our emotional connections, took place during the last 7 to 8 million years of human evolution.

In very simple terms, we can imagine these changes as additional 'shells' of particularly human cognitive empathy and affective empathy (Figure 1.10). These particularly human capacities are not widely seen in our nearest relatives, so are likely to have emerged after our split with other apes around 7 to 8 million years ago. These are, however, likely to have been influenced by contexts we share with other highly social animals, which place pressures on

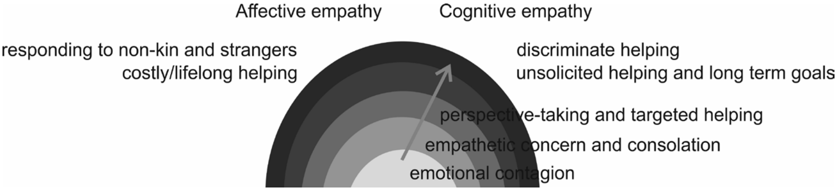

Figure 1.10: Additional levels of uniquely human developments in affective and cognitive empathy building on capacities shared with some social animals. Penny Spikins, CC BY-NC 4.0.

collaboration, as well as probably uniquely human selection pressures operating through culture, complex cognition or reputation (discussed in Chapters 2 and 3). Ecological changes, or movements into new ecological niches in which survival is based on group interdependence (e.g. for defence against predators or when hunting dangerous animals), would have placed selective evolutionary pressures on emotional responses to others' needs, for example.

Of course, this characterisation is bound to be an oversimplification. Moreover, no one would pretend that we can summarise the complexities of what makes being human distinctive, such as the depths of how we feel about each other or our love or emotional connection, in such simple terms. Nonetheless, an abstract model such as this may help us to understand some of the potentially key stages to how our particularly human emotional connections and caring motivations evolved.

Relatively subtle changes affective or cognitive empathy can have far-reaching effects on social relationships and communities. Caring behaviours directed towards others' infants or vulnerable adults have a significant impact on both infant survival and recovery from illness and injury, for example. Abilities to think through helping towards long-term goals or without particular requests also have significant impacts on the complexity of resource-seeking behaviours and sharing. Furthermore, concerns over fairness and justice, and willingness to punish antisocial behaviour, provide the basis for a transformation from competitive hierarchies in which the strongest survive to egalitarian collaborative social systems based on interdependence and give and take.

There is, nonetheless, a catch to any simplification such as this. It is always tempting to see evolutionary changes and adaptations, particularly those in humans, as a progression towards something better. However, we should be wary of seeing ourselves as some pinnacle of progress (as discussed in the introduction to this volume). We are simply just another unique species, no matter how remarkable our caring responses and emotional connections to others may be. We have to remember, firstly, that adaptations are always compromises. There is a cost to complex cognitive processing in terms of the costs of brain enlargement of the energetics of brain development, and to emotional responses to care for others in terms of the individual energetics of such care, as well as the emotional costs of responding to others' distress. As we discussed in the Introduction, our tendencies to care deeply about our loved ones make us vulnerable, even as they make our close group stronger. Our affective and cognitive empathy comes at a price. Secondly, there will be options and branches even in our own evolution, and different options of emotional responses that were neither better nor worse (discussed in Chapters 8 and 9), many of which have failed to leave traces visible today through often chance processes, rather than any simple line to ourselves. If we want to get away from the idea that there was some predetermined process that elevated humans, we have to better understand these compromises and options.

Many questions remain.

It is difficult to explain the in-depth and extensive nature of human altruism. Why might we, unlike other animals, be motivated to help strangers and to respond to the distress of other species and even nurture inanimate possessions? Moreover, we cannot help but wonder when key transformations took place and what happened. How far back can we trace distinctively human motivations to connect emotionally to others and respond to their needs? How significant were these motivations in our evolutionary history? And what types of selection pressures were particularly important in driving the evolution of our unique emotional capacities?

Only by turning to the material record to provide clues to how human behaviour has changed over the last few million years, in Chapter 2, can we begin to better understand why and how our most human emotions emerged.

Conclusions

Our gut feelings and emotional reactions play a key role when we react with compassion or generosity to others' needs, from giving blood to everyday acts of kindness. We rarely consider this biological basis to our emotional connections, perhaps preferring to see ourselves as purely rational beings, yet it is genuine emotional connections that form the basis for our strongest bonds. This biological basis has emerged because of the complex selection pressures acting on our ancestors, from long-distant early forms of social mammals to more recent ape ancestors. Because of this, our nearest living relatives, chimpanzees and bonobos, share many emotional and social characteristics with humans, and give us important clues as to the emotional capacities of our last shared ancestor. However, neurobiological changes can occur quickly in an evolutionary context, and subtle changes can have far-reaching effects. Other social mammals who are more dependent on each other for survival, and who share food, share infant care or collaborate to defend themselves from predators or find food, can sometimes be more human-like in their willingness to help each other. Some of the most significant changes in human social relationships and societies over the last few million years may derive from subtle but important changes in emotional motivations (affective empathy) and social thinking abilities (cognitive empathy), some of which we see in other animals and some of which are unique to humans.

Perhaps surprisingly, it is distantly related primates such as the marmosets, discussed at the start of this chapter, or even social carnivores such as hyenas or wolves who can give us important insights into the evolution of our close emotional relationships to those around us. Whilst we may identify changes in affective and cognitive empathy since our separation from other apes, we would be wrong to conclude that such changes brought a certain superiority over other species. Many of the changes taking place bring us closer to other animals such as these rather than further away. Our social lives within highly collaborative groups, the willingness to defend our kin, share care for our offspring and look after the vulnerable, make us more similar to many social carnivores, for example (explored further in Part 2).

By considering the material record for human behaviours (in Chapter 2), we might begin to understand why and how these important transformations took place in human emotional motivations after the split with other apes.

Key points

- There is a significant biological basis to the building blocks of our emotional connections in human empathy, compassion and generosity.

- Individual social behaviours are influenced not only by our biological responses but by other factors including our cognitive appraisal of particular situations, personal experience and beliefs, social relationships and culture as well as by specific circumstances.

- Selection pressures towards altruistic motivations lead to several different forms, including kin-based altruism, mutualistic altruism, reciprocal altruism and generalised reciprocal altruism. All of these, as well as uniquely human selection pressures, such as pressures to develop a positive social reputation or specific mate selection pressures, are likely to have been influential in our evolutionary past.

- Comparisons with our nearest living relatives, chimpanzees and bonobos, can provide insights into the emotional and social capacities of our last shared ancestor around 7 to 8 million years ago. They also provide insights into key changes in affective and cognitive empathy that have taken place during human evolution.

- More distant relatives of social mammals who depend on collaboration for survival can provide us with analogies for human altruistic motivations towards vulnerable infants, vulnerable adults and mates. Our emotional connections are in some ways more similar to these far more distantly related social mammals than to our nearest relatives.

- Subtle but important changes in human emotional responses to vulnerable infants, adults and mates and in abilities to make long-term commitments and be concerned with fairness and justice are likely to have had far-reaching effects on the character of human social relationships in the evolutionary past.

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CHAPTER 2

Material Evidence: caring for adult vulnerabilities

Abstract

What can archaeological evidence contribute to our understanding of the origins of human empathy, compassion and generosity?

We have seen in Chapter 1 that our human capacity for compassion and our tendencies to help others have an important evolved biological basis. Here, we focus on what the preserved material evidence of early humans and their behaviours can contribute to our understanding of how our emotional motivations to help others emerged. We particularly consider often-overlooked archaeological evidence for care for adults made vulnerable by illness or injury. This evidence demonstrates a deep past to human emotional motivations to help those around them. Furthermore, changing emotional motivations are a response to wider context and selective pressures, similar to those also seen in some other social mammals. A critical appraisal of evidence for responses to illness and injury suggest that significant changes in helping behaviour and responses to vulnerability may

(Abstract continued on next page)

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(Abstract continued from previous page)

have taken place around 2 million to 1.5 million years ago – around the time of key ecological changes and a transition to a new hunting niche. Responses to vulnerability and motivations to help may have been a central element to cognitive-emotional changes that set humans on a track that is distinctive and much more interdependent than that of other apes. Considering the archaeological evidence for care allows us to add a time depth and an explanation for the model of changes in cognitive and affective empathy outlined in Chapter 1.

An understanding of the potential significance of care prompts further questions, such as around different evolutionary pathways in emotional motivations, the relationship between biology and culture in care for illness and injury, the extent of human dependence on such care, and its significance in terms of extended lifespans. Nonetheless, it is clear that an extension of human empathy, compassion and generosity from at least 2 million years ago played a much more significant role in our evolutionary origins than is usually accepted, prompting us to reconsider the driving factors leading to human evolutionary success.

Following on from the significance of interdependence, we consider the formation of relationships based on emotional commitments and trust, and the increasing importance of social reputation, in Chapter 3.

Figure 2.1: Left: Shanidar 1. Osama Shukir Muhammed Amin FRCP(Glasg), CC BY-SA 4.0, via Wikimedia Commons: https://en.wikipedia.org/wiki/Shanidar_Cave#/media/File:Shanidar_I_skull_and_skeleton,_c._60,000_to_45,00o_BCE._Iraq_Museum.jpg. Right: Reconstruction of a Neanderthal male. Neanderthal Museum, Mettmann, CC BY-SA 4.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Homo_sapiens_neanderthalensis-Mr._N.jpg.

Introduction

Our image of our distant past often tends to be rather a brutish one. Even if we no longer imagine thuggish cavemen wielding clubs and surrounded by dinosaurs, we certainly assume that our distant past was a battle for survival in which there was no time for ill health, and few people were in any way kind.

The archaeological evidence does not support this image. In fact, it paints a very different picture. Whilst the infectious diseases that plague large and settled communities were rare, people throughout the Palaeolithic period (from the time of the earliest recovered stone tools, over 3 million years ago, to the end of the last ice age around 10,000 years ago) frequently suffered general wear and tear on bones and muscles, as well as injuries sustained hunting and gathering resources. Most skeletal material from that period shows signs that people were commonly living with the effects of illness and injuries. However, recovery from even severe injuries or illness, or at least survival despite them, was common, suggesting willing care from others for adults who could not care for themselves. This different picture may help to reframe our ancestors as interdependent, and often vulnerable, people whose emotional connections to each other were key to their shared survival.

One famous skeleton, found in Shanidar cave in Iraq, illustrates particularly well the extent to which evidence for caring behaviours has changed our assumptions about the character of our ancestors. This particular skeleton, Shanidar 1, or 'Ned', has been the subject of much debate about the emotional dispositions of Neanderthals (*Homo sapiens neanderthalensis*) and the extent to which they were kind or callous (see Figure 2.1).

Ned had certainly had a very rough life. He lived around 45,000–70,000 years ago and survived a remarkable level of injury and impairment. His bones were excavated between 1957 and 1961, and demonstrated many different injuries. Probably, as a young adult, he had suffered a blow to the left side of his face, resulting in blindness or only partial sight in one eye. He also had a hearing impairment; a withered right arm, the lower part of which had been lost after a fracture, and possible paralysis; deformities in his foot and leg, leading to a painful limp; and advanced degenerative joint disease (Crubézy and Trinkaus 1992: 411–12; Kent 2017; Trinkaus 1983; Trinkaus and Villotte 2017; Trinkaus and Zimmerman 1982: 61–62). How he suffered his eye-watering range of injuries is not entirely clear, though there has been speculation that he may have been injured in a rock fall.

What was remarkable about this individual was not his injuries themselves but the length of time over which he had survived despite them. He had been injured at least 10 to 15 years before his death, with the curvature of his right leg compensating for injuries to the left (Trinkaus and Zimmerman 1982: 67–68). Yet Ned lived until he was aged between 35 and 50, relatively old for a Neanderthal, despite his range of debilitating impairments. These restricted mobility, ability to perform manual tasks, and perception (Spikins et al. 2018). Solecki (1971), and later Trinkaus and Shipman (1993), argued that he could not have survived without daily provision of food and assistance. Trinkaus and Zimmerman even commented (1982: 75) that Neanderthals 'had achieved a level of societal development in which disabled individuals were well cared for by other members of the social group'. Aside from Ned himself, there are many other cases suggesting care against the odds. We now have a wealth of evidence for Neanderthal care, with more than 20 cases of probable care for illness or injury recorded (Spikins et al. 2019). In many, it is clear from the severity of illness or injury and evident lack of possibility of recovery that only genuine caring motivations rather than any calculated reasons explain the help the injured received (Spikins et al. 2018).

After his treatment in life, Ned was also carefully buried after death. He was one of many Neanderthals who were either buried or given a specific mortuary treatment (such as disposal in pits or clefts) at death (Pettitt 2013), the meaning of which remains a topic of much debate (Pomeroy et al. 2020).

Ned seems to provide almost incontrovertible evidence for the emotional motivations of Neanderthals, who seem to have cared deeply for their group members. His care must have been quite extensive, possibly requiring help beyond simple provision of food and water, and perhaps also including aid to keep up with the highly mobile lifestyle of his fellows. The combination of our image of Neanderthals as thuggish with our assumptions about a competitive and individualistic past constrained academic willingness to accept the evidence from Ned, and from other examples, of apparently extensive care, however. His extensive care seemed to contrast with every assumption about our human past as being individualistic and competitive. Davies and Underdown (2006: 148–49) commented that 'the extensive intragroup care needed to sustain such infirm members is surprising unless they provided some valuable service'. Such evidence, portraying Neanderthals in a very different light from traditional tendencies to see them as some kind of brutish 'other' (Madison 2020; Wragg Sykes 2020), has only recently been widely accepted. As we shall see in this chapter, its implications for our evolutionary origins have not yet been fully discussed.

Building on Chapter 1, in which we identified important transformations in human emotional connections, and in compassion and generosity, in the last few million years of human evolution, here we consider what the material record might contribute to our understanding of when and how these changes took place. Further, we consider the implications of these changes for our understanding of the role of care for the vulnerable in our human origins.

Archaeological evidence for the emergence of human compassion and generosity

The material record of past behaviour, and the chronology it provides about changes in human behaviours, emotions and motivations, rarely plays much of a role in discussions about how our emotional minds evolved. It is common to simply draw an imagined line between our nearest relatives, chimpanzees, and ourselves and imagine that the emotional and cognitive abilities of hominins must have lain somewhere along a path between the two. This can be misleading, giving a false impression of human evolution as a progressive advancement rather than a series of pathways and options (as we discussed in the introduction to the volume), and preventing us from appreciating some of the similarities in emotional connections that we share with often distantly related animals.

The archaeological record may provide important insights into the key changes taking place in compassion, generosity and helping behaviours in the 7 to 8 million years that separate our common ancestor from ourselves. The most useful source of evidence is, perhaps, the skeletal evidence of survival from illness and injury, like that demonstrated by Ned (described above), and what this implies about the changing nature of care individuals received from others. However, making sense of this record is not necessarily straightforward and demands critically appraising alternative explanations for recovery from illness and injury, developing an understanding not from any one single case but from the pattern of cases, and considering the ecological and social context and other evidence for responses to vulnerability.

Taking these provisos on board, we nonetheless see a more extensive care for others than we may have imagined. Moreover, this material record is important, as it gives us an opportunity to better understand changes that have taken place since our last common ancestor with other apes, and how these changes relate to distinctively human capacities for affective and cognitive empathy we considered in Chapter 1. At the simplest level, the material record suggests a progression through time from the earliest possible cases of care for the vulnerable, which represent early developments in cognitive and affective empathy, to both a greater frequency of care and a more complex relationship between intuitive responses, long-term planning and cultural traditions. Care for illness and injury may have been both more economically and more socially significant then we tend to imagine.

These developments are reviewed and discussed from the earliest stages of the earliest beginnings of care to evidence for care around the time of the emergence of 'humans' (early members of the genus *Homo*) to later periods of human evolution incorporating archaic and modern humans.

Before two million years ago: earliest beginnings?

Some of the earliest evidence for possible care for illness and injury come from pre-human contexts over 2 million years ago. Evidence from our hominin ancestors (members of 'tribe' Hominini, or extinct and modern species of humans and pre-human ancestors) suggests that, even as early as 3 to 4 million years ago, australopithecines were already becoming notably social in their orientation compared to their nearest relatives. Canine size, often an indication of the extent of male aggression, is much reduced in *Ardipithecus*, for example (Hare 2017). There is also some evidence, albeit contentious, that sexual dimorphism, another measure of male aggression, had also reduced (Plavcan 2012; Plavcan et al. 2005). An increasing need to collaborate to defend against predators may have been a key selection pressure, making it more advantageous to help others than to hinder them (discussed in Chapter 1).

The earliest potential example of helping behaviour for injured or diseased individuals comes from skeletal remains of two australopithecines found in South Africa. The first case is that of a probable *Australopithecus africanus* from Sterkfontein in South Africa (Stw 363), dated to around 2 to 2.5 million years ago (Pickering and Kramers 2010). Remains of the foot bones of this hominin show damage to the foot (compression fracture of the calcaneus, with the talus driven into the upper surface of the calcaneus), which is likely to have led to severely impaired mobility for at least six weeks after the break (Fisk and Macho 1992). The second case, an *Australopithecus sediba* boy (around 12 to 13 years old) from Malapa (MH1), dating to around 2 million years ago, showed evidence of a bony tumour of the spine (a primary osteogenic tumour, which affected the right lamina of the sixth thoracic vertebra). This tumour is likely to have limited movement of the shoulder and upper right part of the back, as well as causing chronic pain

Figure 2.2: *Australopithecus sediba*. Reconstruction of Australopithecus sediba. Copyright Neanderthal Museum, Holger Neumann.

and muscle spasm (Randolph-Quinney et al. 2016). Given the continued arboreal component of mobility in *Australopithecus sediba*, this is likely to have limited mobility. Both cases may suggest some element of at least food provision given continued survival with the conditions. Figure 2.2 shows a reconstruction of this hominin.

These earliest cases of potential evidence for helping the ill or injured individuals suggest a notable survival despite injury that would affect mobility for at least several weeks if not months. Clearly, severe injuries and illnesses that affect mobility make it difficult not only to move to find food but also to find water, and to defend oneself or escape from predators.

There are, however, debates over how to interpret such finds. The extent to which survival despite injury or impairment can *confidently* be interpreted as implying help from others rests on the *implications* of impairments for assistance from others or, conversely, whether these individuals could have survived independently (for a detailed discussion, see Tilley 2015b). In many ways, in making inferences about the likelihood that any individual would have been cared for, we are dealing with a balance of probabilities with different factors to take into account. The injuries themselves are implied from skeletal material, with a certain degree of uncertainty, and their implications for impairment can vary according to the individual, and within a context in which our understanding of the physiology and anatomy of past hominins is far less developed than it is for modern humans. Their interpretation demands a fuller consideration than it might get if we were dealing with modern peoples.

Doubts about implications?

An important part of the debate over how to interpret the significance of injuries in past hominins in terms of helping from others has been analogies with injuries in other primates. In cases of limb and spine injuries, such as those of the australopithecines described above, it has been argued that even serious injury may not necessarily imply care, since there are cases of modern primates who appear to have been able to survive severe injuries unaided (Dettwyler 1991). If the australopithecines were able to survive unaided, despite injuries that we would usually expect to demand care, then the potential evidence for helping behaviour would be cast into doubt.

Certainly, modern primate populations can often include individuals with limb impairments still managing to forage independently (Munn 2006). Turner et al. (2012) noted, for example, that female Japanese macaques with limb deformities at Awajishima Monkey Centre, Japan, were equally able to climb trees or groom others through compensating with posture or use of other limbs. Individual accounts, such as that of a one-armed gibbon still able to brachiate (swing between the trees) effectively (Sayer, Whitham, and Margulis 2007), also point to remarkable abilities to adapt to limb impairments.

The existence of primates surviving limb injuries may appear to suggest remarkable individual resilience without care. However, there are several reasons why such studies of non-human primates may not be relevant analogies for the impact of past hominin injury on survival.

Perhaps the first, and most obvious, is that non-human primates have a far greater resilience to limb (and back) injury than do our own bipedal ancestors, as their hands and feet can be co-opted to support mobility or manipulation, depending on which limb is damaged. The one-armed gibbon (above), who was able to brachiate effectively, did so by using their lower limb 'instead of' one arm. There are cases of chimpanzee populations, for example, where up to 20% of individuals have survived a serious injury and manage to cope with injured limbs (Munn 2006). However, these are unusual extremes. Moreover, their use of a hind limb to compensate for loss of use of a forelimb, or vice versa, plays a key role in their adaptations, a luxury not available to bipedal hominins.

The types and rates of injury in modern primates are not a good analogy for early hominins either. Particularly high rates of injury typically relate to unusually high rates of intra group violence in common chimpanzees, which are unknown in other primates, as well as being much higher than in modern hunter-gatherers (Wrangham, Wilson, and Muller 2006). Thirteen of 20 individuals from chimpanzee populations at Kanyawara and Ngogo showed healed trauma, for example. However, this is largely due to bites from intraspecific aggression (Carter et al. 2008). Anthropogenically induced injuries through traps and snares are also common in non-human primates (Stokes and Byrne 2006), as well as those caused by introduced diseases. In wild primates in general, injury rates of around 1% are more typical (Turner et al. 2012).

A further confounding factor is that many primate comparisons come from zoos or provisioned wild populations. Turner, for example, documented notable survival despite disability in a provisioned population of macaques (Turner et al. 2014). However, whilst these individuals may cope despite disabilities, impairments in populations who are *not* provisioned by humans are known to have a notable effect on their risk of mortality. Disabilities that slow foraging can reduce food intake at times of resource stress and affect time available for social grooming (Turner et al. 2014). Deformations affecting symmetry can alter the pace of injured animals. Furthermore, general deformations potentially increase mortality risk from climbing (Turner et al. 2012), added to which, predators will actively target injured individuals who are less able to escape.

Trinkaus and Villotte (2017) concluded that comparisons with the level of independence, despite injury of primates such as those in zoos and those who are provisioned by humans, underestimates the impact of injury and impairment on survival unaided in the wild. An image from modern primates of common, severe injury being survived without care in early hominis is not supportable. Focusing on adaptations to impairments in otherwise healthy individuals also overlooks the issue that perhaps the most significant effect of injury is in the risk of mortality during a period of incapacitation, rather than how individuals cope *after* healing has taken place. For hominins, being incapacitated for a notable period, under a threat of predation and unable to find food and water, would have been likely to be life-threatening without help. Even severe restrictions on mobility are likely to have brought considerable risk of mortality in a context of high predation and limited adaptability of forelimbs to improve mobility.

The nature of helping in australopithecines

Given the injuries, it is *probable* that some level of helping, at least with food resources and potentially protection from predation, seems likely in the case of Stw 363, who would have had difficulty walking for at least six weeks, and quite possibly also in the case of MH1.

There are a number of reasons why it may have begun to make sense for australopithecines to be motivated to help each other. Though there were various different species of australopithecines, they all were small (around 1.2 to 1.5 m high) and bipedal, making them rather defenceless, living in a more open habitat than their ancestral forest-dwelling relatives. Though bipedal, they still retained a capacity to hang from trees (as shown by their curved fingers). The earliest stone tools, dating to around 3.3 million years ago (Harmand et al. 2015), as well as cut-marked bones from a similar time period (McPherron et al. 2010), show that australopithecines probably used such tools to scavenge meat, sinews or marrow from animal carcasses. Exploiting carcasses would have put them in confrontation with dangerous predators, placing selective pressures on means to defend themselves as a group, and thus on collaboration, communication and prosociality (Bickerton and Szathmáry 2011).

The *cognitive complexity* of helping implied by either of the australopithecine cases need not necessarily have exceeded the complexity seen in other apes, however. Neither of the australopithecines was fully incapacitated and they were thus likely to be capable of reaching a water source unaided (even if more slowly). Most significantly, they were capable of requesting food. Food begged from others, or provisioning by kin, could have been enough

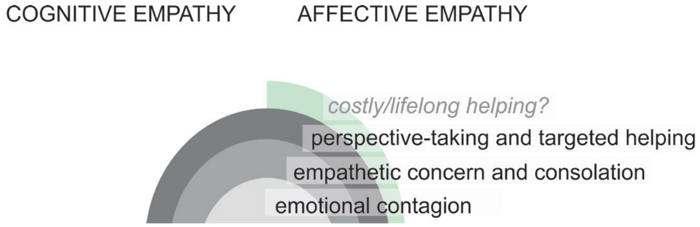

Figure 2.3: Possible implications of the material evidence for care for levels of cognitive and affective empathy shown in australopithecines. Penny Spikins, CC BY-NC 4.0.

to keep these hominins alive for some time. Nonetheless, willingness to undertake more costly helping behaviour than we have seen in non-human primates by around 2 million years ago may nonetheless be an indication of changes in affective empathy to include adult group members, and have been important in how empathy and social relationships developed in later hominins; see Figure 2.3.

After two million years ago: the emergence of 'humans'

Ecological contexts may have been playing a role in increasing interdependence and, with it, probable selection pressures on affective empathy (described in Chapter 1), around the time when the earliest 'humans' emerged.

As environments became increasingly variable and heterogenous, between about 3 million and 1.8 million years ago (Potts 2012; Potts 2013; Potts and Faith 2015), an opening up of new opportunities, as well as new constraints, seems to have led to a proliferation of different hominin forms. These included the earliest members of the genus *Homo* or 'human' species, with at least three species contemporaneous around 2 to 1.5 million years ago (Antón, Potts, and Aiello 2014), as well as other contemporary non-*Homo* species. It is difficult to know how the adaptations of any of these different species differ from each other. Nonetheless, many argue that a selection for flexibility and adaptability in response to highly variable environments seems to have been a significant factor in the emergence of a distinct early human cooperative adaptation (Antón, Potts, and Aiello 2014;

Domínguez-Rodrigo et al. 2014; Grove 2011). Environmental variability, resulting in year-to-year, monthly or even shorter-term changes in the types and quantities of resources available, places a particular challenge on survival. As shortfalls in resources become more frequent, increasing any individual's risk of mortality or of failing to reproduce, it makes more and more sense to share resources according to needs (Barkai et al. 2017; Domínguez-Rodrigo et al. 2014; Smith et al. 2012). Seen as one of the most significant periods of transformation in human evolution, biological changes include marked brain expansion, slower maturation and changes in body form that have been interpreted as a response to changes in ecological niche involving a greater dependence on meat eating (Balter et al. 2012; Foley 2016; Roach et al. 2018; Schroeder et al. 2014).

The precise changes and pressures at these key points of transition in human evolution remain debated. Whether ecological changes were *the key prime mover* encouraging hominins to move into an increasingly meat-eating niche, or whether increasing reliance on hunting was in any case a progressive change already taking place within the *Pan*/hominin lineage, or whether it was a rather unique combination of pressures towards interdependence from predation alongside an existing ape social intelligence that led to new types of hominin collaboration, remains unclear. However, there is general agreement that hunting, risk-taking and sharing food underlies this transformation in early members of the genus *Homo*. Changes in emotional relationships, rather than simply cognitive capacities to plan or come to agreements, seem to lie at the heart of these transformations (Hrdy and Burkart 2020; Spikins 2015).

Although attention tends to focus on what are seen as our ancestors, within the earliest members of the genus *Homo* there were other alternative trajectories or other journeys along which alternative ancestors may have travelled. Alternative forms were also around during this period. The robust australopithecines seem, particularly, to have responded to ecological changes by specialising increasingly on the exploitation of plant food, in potentially less risky and more wooded environments (Cerling et al. 2011; Towle, Irish, and De Groote 2017). Their rough diets led robust australopithecines to develop a bony crest to support jaw muscle, huge strongly built jaws and large teeth to process tough vegetation. We can certainly imagine that relying for subsistence on plant materials is likely to have been much less demanding of social or emotional understanding than relying on meat (the exploitation of which would require working together whether confronting predators or hunting). The buttressing of robust australopithecine faces has even been suggested to be an adaptation to violent confrontations using fists (Carrier and Morgan 2015), though other explanations more rooted in supporting large jaws suggests that this maybe goes a little too far.

As far as early members of the genus *Homo*, or true 'humans', are concerned there is clear material evidence for greater interdependence. The earliest evidence for stone tool use comes from around 3.3 million years ago (Harmand et al. 2015), when stone tools seem to have been used for scavenging meat from bones left by higher-level predators. However, stone tool marks on large animal bones are found from around 2.6 million years ago (Domínguez-Rodrigo et al. 2005) and provide clearer evidence of being used in early access to carcasses. The butchering of small antelopes at Kanjera South in Kenya, around 2 million years ago, has been interpreted as evidence of active hunting (Plummer and Bishop 2016). This hunting of animals larger than the hominins themselves has been seen as good evidence for collaborative hunting and, in turn, the sharing of hunted meat (Domínguez-Rodrigo et al. 2014). By 1.3 million years ago, faunal assemblages at BK at Olduvai suggest active hunting of not only small and medium-sized prey but also large ungulates (Domínguez-Rodrigo et al. 2014). Early humans even hunted extremely dangerous giant gelada baboons at Olorgesailie by around half a million years ago (Isaac and Isaac 1977; Shipman et al. 1981). Thus, regular consumption of meat from large mammals has particularly been associated with the emergence of *Homo* (Balter et al. 2012; Pante et al. 2018). Physiological adaptations to increased meat eating were apparent from at least 1.5 million years ago, at least on the basis of the appearance of hyperostosis, indicating anaemia through lack of iron, in a child 1.5 million years old (Domínguez-Rodrigo et al. 2012). Longer periods of infant dependency point to increasingly collaborative childcare alongside other major changes such as brain expansion (Burkart et al. 2014; Hrdy and Burkart 2020).

Evidence for care of the ill and injured

Within this broader picture of sharing, not only of meat but of risks in hunting and time and effort in childcare, we also see emerging evidence for care for the ill and injured. The earliest potential evidence for extended care in early *Homo* occurs at around 1.8 million years ago. This evidence comes from the survival of a near toothless hominin from Dmanisi in Georgia (D3444/D3900) (Lordkipanidze et al. 2005). The individual had lost all but one tooth (the left canine) several years before death, identifiable through bone resorption. Soft animal foods, such as brain, may have been easier for this individual to eat, and it is thus plausible that others provisioned or even processed (chewed) their food for them. The excavators interpreted this specimen as evidence of care for those who were ill (Lordkipanidze et al. 2005). DeGusta (2002; 2003), however, argued that toothless hominins could have survived by finding their own foods, drawing on evidence for survival in similar cases seen in primates. Certainly, primates with quite severe tooth loss have been recorded surviving, such as a surviving toothless bonobo (Surbeck 2020) or a healthy baboon from Kibale National Park who was missing the premaxilla and most of the maxilla and nasal bones (Struhsaker et al. 2011). This individual, however, possessed third molars, which will have at least made cutting and chewing of food possible. No surviving primate is recorded with the extent of tooth loss seen in the Dmanisi specimen, nor for this lengthy a period (Thorpe 2016). Trinkaus and Villotte (2017) noted that, in several cases, including the Dmanisi individual, tooth loss is accompanied by severe inflammation and periodontal disease. Whilst managing to find sufficient soft food without help for several years despite being unable to chew *may have been possible*, on the basis of analogies with living primates, surviving a period of this type of *systemic illness* is a more reliable indicator of care from others. Individuals in this state will have felt extremely ill and would have been in pain. Toothlessness remains a difficult issue to interpret in terms of care (Gilmore and Weaver 2016); however, the Dmanisi evidence, with systemic infection, can be cautiously interpreted as likely evidence of care from others.

Two particularly convincing examples of care that clearly go beyond that recorded in non-human primates also emerge after 1.8 million years ago, however. Both are from East Africa – an adult female *Homo ergaster* (1808) from Koobi Fora, and a young male *Homo ergaster*/*Homo erectus* (WT1500) from Nariokotome.

The *Homo ergaster* female from Koobi Fora (Lake Turkana, Kenya) is by far the most famous. Dating to around 1.6 million years ago, this partial skeleton of a probable *Homo ergaster* was recovered in 1974. The most notable feature of her skeletal remains is a build-up (as much as 7mm in places) of coarse woven bone in the limb bones, with sub-spheral lacunae within this bone accumulation (Walker, Zimmerman, and Leakey 1982: 248). The cause of this pathology has been debated. The effect on the bones is, however, typical of hypervitaminosis. One possibility is that of an excessive consumption of carnivore livers (something experienced by Arctic explorers who resorted to eating their sled dogs) (Walker, Zimmerman, and Leakey 1982), another being an overconsumption of bee brood larvae (Skinner 1991). Hypervitaminosis would have caused this individual to have suffered from health implications including peeling skin, vomiting, diarrhoea, headache, convulsion, oedema, inflammation of the optic nerve, muscular stiffness, itchy rash, and inflammation of the nail beds, as well as periods of unconsciousness and severe pain for several weeks or, perhaps more likely, even months before her death (Skinner 1991; Walker, Zimmerman, and Leakey 1982). She will have been extremely vulnerable throughout this time.

What is clear is that 1808 was unable to find food for herself or defend herself from predators for a substantial period and, for at least some of the time while she was ill, was unlikely to have been able to give clear cues as to her needs. She would, however, have needed providing with food and water and to be protected from predation (Walker, Zimmerman, and Leakey 1982). In cognitive terms, her care is likely to have demanded instrumental helping (of providing a safe place to rest), proactive sharing (of food), as well as responses to unsolicited cues (such as for food and water despite any severe pain, lack of consciousness etc.). Help in this case would have been not only *unsolicited* but also *extensive and costly*, suggesting both more extensive affective empathy (emotional response) and more complex cognitive empathy (higher-level functioning) to infer what help would be needed to keep this individual alive than is seen in any non-human primate.

Care for a young male *Homo erectus*/*Homo ergaster* (WT 15000 or 'Nariokotome Boy'), dated to 1.6 million years ago from Nariokotome, would also have necessitated complex cognitive and affective empathy. This individual, who was around eight years old at death (Graves et al. 2010), had a herniated disc and suffered extensive remodelling of part of the spine (the articular processes of L4 and L5) several months before their death (Schiess et al. 2014). As a result, he would have suffered from disabling backache

Figure 2.4: *Turkana Boy* (detail). Reconstruction of Nariokotome (Turkana) Boy, typical of a *Homo erectus/Homo ergaster*. Copyright Neanderthal Museum, Holger Neuman.

and recurrent sciatica, which would have restricted walking, bending and other daily activities. It is difficult to see how he could have foraged successfully or kept up with a mobile group. Hausler et al. argued that this case also provides evidence for advanced social care and nursing at this time (Haeusler, Schiess, and Boeni 2013: 3). Figure 2.4 shows a reconstruction of this individual. An example of possible dental treatment in a further *Homo erectus* individual from Swartkrans in South Africa has also been seen as possible evidence for care from others (Ripamonti et al. 2020).

Extended provisioning of the ill and injured, and unsolicited help, would have been an important element in keeping small collaborative groups of *Homo erectus* viable in conditions with high injury risk, and may even have been a key factor making the colonisation of northern temperate zones possible (Spikins et al. 2019). Control of infectious diseases is unlikely to have been a key factor in the emergence of healthcare practices, given evidence that early hominins lived in small inward-focused social groups (discussed in Chapter 4) and the prevalence of injuries and degenerative rather than infectious diseases in the palaeopathological record. Nonetheless, at

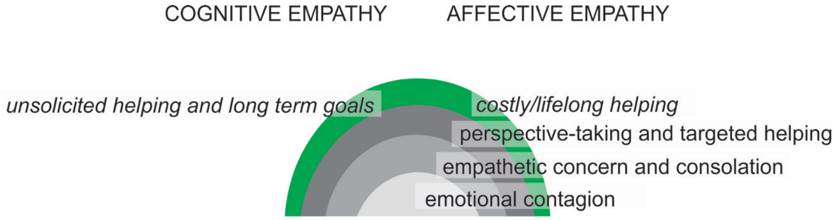

Figure 2.5: Possible implications of the material evidence for care for levels of cognitive and affective empathy shown in early members of the genus *Homo*. Penny Spikins, CC BY-NC 4.0.

a later date, as populations became larger and more connected, care may also have been important in managing infectious diseases (see Kessler 2020; Kessler et al. 2017).

Whether this care represents as complex a level of cognitive or affective empathy as we identified as characteristic of humans today remains a question. We can be confident that early members of the genus *Homo* had some abilities to provide unsolicited help (such as for the female *Homo ergaster*, who will have spent some time unconscious and unable to request help but yet need protection) and towards long-term goals (such as through providing water), and helping is costly, though not lifelong. However, there is as yet little evidence for helping of non-kin or strangers or discriminate helping (Figure 2.5). Of course, such more emotionally extensive and cognitive complex care may have existed at this time but not leave any material evidence.

The significance of even intuitively motivated care, much like that for vulnerable young, is nonetheless clear. We can see how important simple provisioning and protection becomes to survival through considering modern hunting and gathering societies. For modern hunter-gatherers, even with the benefits of a modern mind, reduced risks of predation seen in early humans and complex technologies including projectiles, care for illness and injury is still essential to maintaining survival. Sugiyama (2004) reported that, amongst the Shiwiar hunter-gatherers, for example, around 50% of adults had been incapacitated and unable to forage for at least a month, and would not have survived without provisioning and care from others.

Care as part of increasing interdependence

Social transformations around this time have typically been viewed from the perspective of biological changes in the body, or as an example of increased intelligence overall, or social and collaborative intelligence. However, changes in emotional dispositions may have played a key role in how humans affected a transformation from being individuals within a loose group to highly collaborative bands. Individuals who had begun a journey to being more interdependent could now work like a 'single predatory organism' (Whiten and Erdal 2012).

Increased meat consumption provides direct fuel for brain expansion, but changes in emotional dispositions leading to cooperative breeding may also be critical to being able to support ever larger brains by reducing the energetic costs to mothers of raising large-brained infants (Hrdy 2011). This involvement of fathers and others in childcare may have been key to allowing humans to break through a 'grey ceiling' of limits to social and cognitive intelligence that affect other species (Isler and van Schaik 2012).

Through sharing risk, foodstuffs and care via tendencies to mutual generosity, humans will have reduced the risks of individual failure as well as being able to hunt larger game (see Figure 2.6). Moreover, modern foragers both hunt and gather, with the former giving higher returns but the latter being more reliable. Starchy foods, such as tubers, may have played an important complementary role, perhaps as fallback foods (Hardy et al. 2015; Marlowe and Berbesque 2009). A social carnivore-like level of collaboration also provides potential means of adapting to risk in other ways. Hyenas, for example, hunt food and collaborate to defend their group with non-relatives (Schaller and Lowther 1969; Smith et al. 2012), and group sizes can alter according to the season or ecological context. If early humans also lived in flexible groups, this could have been important to adapting to seasonal or longer-term ecological changes. This flexibility of community may have been particularly important as a means by which human communities adapted to ecological changes (Grove, Pearce, and Dunbar 2012).

The care for illness and injury described above is most probably the most archaeologically visible element of extensive emotional motivations to help

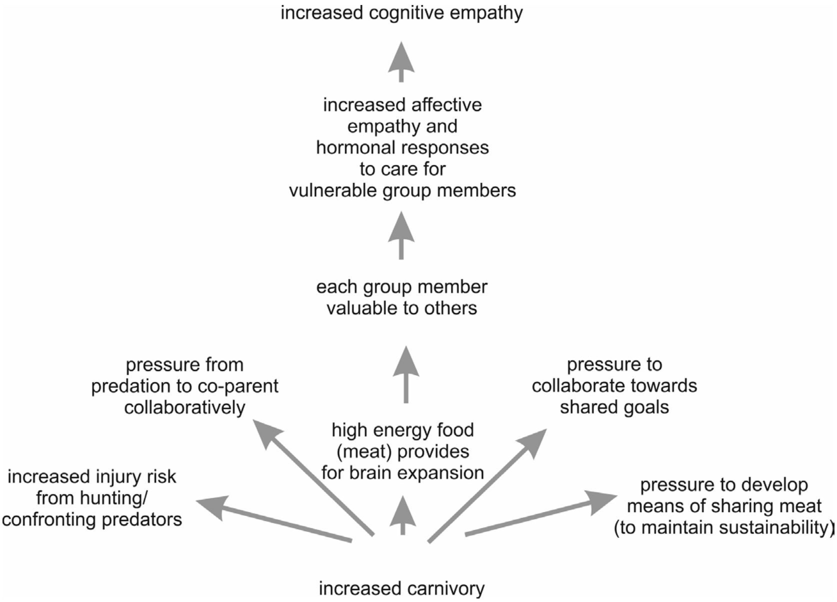

Figure 2.6: Selection pressures on affective and cognitive empathy driven by increased meat eating. Penny Spikins, CC BY-NC 4.0.

others within one's group (Hrdy and Burkart 2020; Spikins 2015). However, interdependence and increasingly strong emotional connections, supported by changes in particular brain regions as well as bonding hormones (discussed in Part 2), will have affected many different behaviours (including the sharing of food, shared care of offspring and collaborative defence and resource gathering; Feldman 2017), much like changes in the helping, sharing and affection that also developed in increasingly interdependent social carnivores.

Support for the primacy of emotional and social changes before other areas of cognition comes from one particularly notable alternative human adaptation. Studies of crania of *Homo naledi*, from the Rising Star Cave system in South Africa (Berger et al. 2015), demonstrate that this species had a complex forebrain, in common with other members of the genus *Homo*. Endocasts showed frontal parts of the brain associated with processing emotions and understanding social relationships such as the pars orbitalis, which involves Brodmann's area 47, associated with the recognition and production of social emotions, social inhibition, and emotional learning (Holloway et al. 2018: 5741). However, *Homo naledi* had a very small overall brain size, similar to that of the australopithecines. Their emotion processing capacities seem to be ancestral to *Homo* and may explain behaviours such as the deliberate deposition of their dead in the Di Naledi chamber. Emotion processing, rather than brain size, seems to be key, not only to complex social practices such as these but also to some degree of adaptive success, with *Homo naledi* surviving alongside other large-brained hominins until at least 300,000 years ago. The late existence of this small-brained but socially and emotionally complex human is interesting, not only in demonstrating different evolutionary pathways and different ways of being human but also when we consider what it may mean about possible constraints. Whilst *Homo naledi* remained successful despite larger-brained contemporaries, there are, as yet, no known hominins making a living with a large brain but underdeveloped social and emotional processing areas. This may add additional support to the significance of emotional connections, rather than analytical processing capacities, to what made us human. Care for illness and injury may have had other consequences, aside from forming the basis for complex areas of cognition, particularly in its influence on human cultural evolution and our dependence on the cultural transmission of ideas.

After half a million years ago: later periods of human evolution

By around half a million years ago, we see diverse species of humans occupying northern latitudes, including Europe, as well as Africa and Asia. These species were quite different in form. One broad type included humans who were very robust with prominent brow ridges, such as the northern-latitude and Asian group including Neanderthals, Denisovans or *Homo longi*. Another broad type was of much smaller- and small-brained humans, such as *Homo floresiensis* or *Homo naledi*. A third type of humans, appearing in Africa from 300,000 years ago, were more gracile, with reduced brow ridges. The latter, gracile type includes the ancestors of our own species. Despite their differences, interbreeding occurred between these different forms and all are generically termed archaic or pre-archaic *Homo* or Middle Pleistocene *Homo*, though, as we shall see in Part 2, some differences between these types may be significant in terms of tolerance and emotional sensitivity. It is in this period that we see the earliest evidence for long-term commitments from the group as a whole, suggesting a sense of collaborative investment in care, as well as uncalculated care for even the most severe of injuries and illnesses.

At Sima de los Huesos in northern Spain, at least three of the around 28 individuals of pre-archaic/Neanderthal populations deposited in a mortuary pit appear to have been supported through particular pathologies (Carbonell and Mosquera 2006). The best-known of these cases of extended care, that of an eight-year-old child with craniosynostosis, a torsioning of the crania, is perhaps not particularly surprising (Gracia et al. 2009). Maternal care for infants, even those who are ill or different, is recorded in apes, such as an infant chimpanzee with Down's syndrome in Mahale Mountains National Park, who was carefully looked after by their mother (Matsumoto et al. 2016). Moreover, craniosynostosis does not always have noticeable cognitive implications. However, the continued survival for several years of a different individual, an elderly man with a deformed pelvis who would only have been able to walk with the aid of a stick (Bonmatí et al. 2010; Bonmatí et al. 2011), does point towards support of the vulnerable, regardless of whether they could contribute in an economic sense. A further hominin with possible hearing impairment (Trinkaus and Villotte 2017) is at least suggestive of a certain level of accommodation for difference.

It is, however, in descendants of the Sima de los Huesos populations that we see the most widespread evidence for extended care (see Figure 2.7). Neanderthal populations, the occupants of Europe from around 300,000 to 30,000 years ago, who are discussed in more depth in Chapter 8, provide us with many notable examples of care for the ill and injured.

Life was most certainly challenging for these populations. Famines were not uncommon and, in the often cold and arid environments in which they lived, finding food seems to have demanded high levels of mobility, with resultant stress on their bones. Though it is difficult to interpret injury rates precisely, given the nature of the archaeological record, it seems from the skeletal material available to us that illnesses and injuries appear to have been frequent, with most Neanderthals suffering a severe injury of some kind before they reach adulthood (Berger and Trinkaus 1995; Pettitt 2000). Healthcare may have been part of the adaptations that allowed occupation in such difficult conditions, particularly given a heavy reliance on hunted

Figure 2.7: *Homo sapiens neanderthalensis*. Reconstruction of a Neanderthal. Copyright Neanderthal Museum, Holger Neumann.

meat and small group sizes, all of which will have made the survival of each person significant to the whole group (Spikins et al. 2018).

Shanidar 1 was not alone in surviving severe injury and lasting impairment. An individual from La Chapelle-aux-Saints was also cared for despite a range of impairments and, perhaps most importantly, with no real hope of recovery (Bouyssonie, Bouyssonie, and Bardon 1908; Dawson and Trinkaus 1997; Trinkaus 1985), later being carefully buried (Dibble et al. 2015; Rendu et al. 2014; Rendu et al. 2016); see Figure 2.8. Tilley (2015a) described his pathologies in detail, including extensive tooth loss and severe, chronic periodontal disease; temporomandibular joint arthritis; severe osteoarthritis in lower cervical and upper thoracic vertebrae, and moderate to severe degeneration of lower thoracic vertebrae; osteoarthritis in both shoulder joints; a rib fracture in the mid-thoracic region; degeneration in the fifth proximal interphalangeal joint of the right foot; and severe degeneration and likely chronic osteomyelitis in the left hip (Tilley 2015b: 228). Most particularly, degenerative disease in the spine and shoulders would have affected his upper body movement, whilst his diseased left hip would have imposed

Figure 2.8: The La Chapelle-aux-Saints Neanderthal burial. Musée de La Chapelle-aux-Saints, Corrèze, France. 120/V. Mourre, CC BY-SA 3.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Reconstitution_sepulture_Chapelle-aux-Saints.jpg.

significant pain and restricted the use of his left leg to bear weight. Underlying infection, both localised and systemic, would also have taken a progressive toll on his health and strength over the last year of his life. We can only imagine how ill and vulnerable he must have felt.

Both La Chapelle-aux-Saints 1 and Shanidar 1 would have been unlikely to have survived lengthy and severe impairments without involvement from the whole group in their care. Moreover, given that improvements would evidently have been unlikely, such care must have been uncalculated. Even provisioning a single individual who was immobile, or with severely impaired mobility, for a short time would have been difficult. However, the extended provisioning and care in place (which in the case of La Chapelle-aux-Saints 1 can best be described as nursing) would also have demanded a sharing of responsibility. That care was uncalculated, irrespective of whether these individuals would recover or ever return the investment in them, is evident, changing many of our preconceptions of Neanderthals.

Other cases of serious injury, such as fractures of weight bearing bones, are also likely to imply a period of provisioning. La Ferrassie 1 (Tilley 2015a) and Tabun 1 (Abbott, Trinkaus, and Burr 1996) have recovered from severe breaks to their main leg bones, for example, and Shanidar 3 a break or sprain of the right foot leading to marked osteoarthritis (Trinkaus 1983). La Ferrassie 2, a young female adult buried in close proximity to La Ferrassie 1, displayed evidence of a proximal fracture of the right fibula that is completely healed, although with significant distortion (Heim 1976). Wynn and Coolidge (2011) argued that those with lower leg injuries ought to have been too much of a burden to sustain and may have been abandoned, and Berger and Trinkaus (1995: 138) commented that 'abandonment of older individuals who could no longer move with the social group is likely to have been common. This would have occurred especially in cases of severe lower limb injury'. The healed injuries in these individuals point in contrast, however, to care *despite* immobility. It is possible that human populations routinely adapted their mobility patterns around the need to leave the vulnerable or young to be cared for in particular locations. It has been argued that Wonderwerk cave in South Africa could be one such location. This cave was apparently used extensively for shelter, with evidence for the use of fire without any intensive use of stone tools (Chazan 2021).

Might immobile individuals, or those with restricted mobility, have been able to contribute to tasks suitable to their abilities? This would have been unlikely in cases of severe pain or systemic infection. However, in other cases we might expect some activities to be possible. We do not know whether Neanderthals felt only certain people could perform particular tasks. Some authors have argued for a lack of gender-based division of labour in Neanderthals (Balme and Bowdler 2006; Kuhn et al. 2006). However, recent evidence from dental microwear suggests that at three sites, l'Hortus (France), Spy (Belgium), and El Sidrón (Spain), females were chewing different materials, perhaps indicating preparation of hides (Estalrrich and Rosas 2015). Even so, cold, arid and high-latitude environments demand substantial time investments in making all the kinds of things that are needed to survive (Bleed 1986), and, whether this is the manufacture of clothing or tools, there will have been sedentary occupations providing possibilities for those with limited mobility to contribute. Moreover, groups of Neanderthals will have included within them children, many of them vulnerable and with reduced mobility themselves due to their age. Neanderthal children did not reach adulthood until approximately similar ages to modern hunter-gatherers (Ponce de León et al. 2016), and at least half of any group was likely to consist of children (Shea 2006). As well as sedentary contributions by making things (such as clothing or tools), opportunities to contribute to childcare are likely to have existed for those who could not travel far. Further, the lengthy period of dependency of Neanderthal children carried other implications for care provision. Rather than any radical change to mobility or provisioning, healthcare for those with reduced mobility may have tapped into existing adaptations to care for vulnerable young.

Even where individuals remained *mobile*, many conditions may have required some care or accommodation. Individuals with breaks to major bones in the arms will also have needed at the very least an accommodation of suitable tasks, for example. The serious arm injuries of Neanderthal 1 (Feldhofer) (Schultz 2006), Krapina 180 (Eddie 2013) and La Quina 5 are likely to have affected their ability to forage independently, for example. As discussed, unlike other primates, humans cannot use either arm or leg as alternative limbs (for weight bearing or manipulation). Other injuries such as the projectile point injury to the ninth rib of Shanidar 3, speculated to be a result of interaction with modern humans (Churchill et al. 2009), will also have affected health and mobility. Furthermore, head injuries can also require care depending on severity. St Cesaire 1 (Zollikofer et al. 2002) and Krapina 37 (Russell 1987) suffered severe head wounds that had afterwards healed, in the case of the St Cesaire Neanderthal over a period of several weeks.

Toothlessness, as previously discussed, remains a rather more difficult case. Primates with quite severe tooth loss can survive unaided for some time. Nonetheless, Trinkaus argues that it is likely to have had more significant impact, with severe inflammation, as seen in Aubesier 11 and Guattari 1 (Trinkaus and Villotte 2017). Other conditions also had a lifelong effect, like that of an archaic human woman from Salé in Morocco with congenital torticollis who reached adulthood, despite the condition, which is associated with reduction mobility of the neck as well as other debilitating symptoms (Hublin 2009).

The level of care given to those in need, even where there will evidently be no direct 'pay off' (as is the case with Shanidar 1 and La Chapelle 1) argues that care was in no way calculated but a genuine immediate response to vulnerability. These were likely to be societies with strong bonds based on empathy and high levels of trust, promoting the kind of social and emotional environments that foster a willingness to take risks and costs on others' behalves.

Care amongst Neanderthals also implies a sophisticated level of knowledge and planning. High rates of healing and low rates of infection (Trinkaus and Zimmerman 1982: 75) argue for planned care practices for the injured. Bitter-tasting plants with no nutritional value found in dental calculus provide evidence for possible medical consumption, for example (Hardy 2018; Hardy 2019; Hardy et al. 2012). Poplar in the dental calculus of a Neanderthal with a dental abscess from El Sidrón may have been used as a painkiller as it contains salicylic acid (which acts as a painkiller in aspirin) (Weyrich et al. 2017). Ochre may also have been used as an antiseptic (Velo 1984) and tar may also have been chewed for the same reason, as well as in maintaining the teeth (Aveling and Heron 1999). Toothpicks were also used, in the case of an individual from Cova Foradà in Spain to apparently attempt to treat periodontal disease (Lozano et al. 2013). Medicinal knowledge is likely to have been handed down over generations and culturally variable in different regions. Whilst particular practices of care tend to be culturally specific, a knowledgeable, organised and caring response is typical from archaic humans onwards. Though there is no direct evidence, we reasonably assume that birth assistance was widely practised – Neanderthal babies were born with a modern human pattern of head rotation at birth (Ponce de León et al. 2008), demanding assistance, and birth assistance has even been recorded in bonobos (Demuru, Ferrari, and Palagi 2018).

As we shall see in Part 2 of this volume, there are important differences between societies of archaic humans and the descendants of these populations who left Africa after 100,000 years ago – modern humans, anatomically and cognitively identical to ourselves. Care for the ill and injured, however, shows only subtle differences.

There continue to be examples of uncalculating care for those in need, regardless of any possible direct 'pay off', as well as care that must have been shared between many individuals. The Ohalo 2 individual, from the Upper Palaeolithic of south-west Asia dated to 23,000bp, for example suffered a thoracic injury causing ossification of the sternum and adjacent cartilage. He would have struggled to have breathed actively, making anything more than very short bursts of activity impossible. Care from the rest of his group would have been likely to have been needed to support him (Trinkaus 2018a). Like other key Upper Palaeolithic examples in Europe, such as Barma Grande 2, Brno 2, Cro-Magnon 1, Dolní Věstonice 15, Rochereil 3, Romito 2, and Sunghir 2 and 3 (Trinkaus 2018a), his level of survival despite injury or impairment provides good evidence for empathetically motivated care from the small hunting and gathering groups of which these individuals were a part.

Where we see subtle differences is around a certain unusual attention to disability and impairment. Individuals with impairments were apparently selected for particular burial in Upper Palaeolithic Europe (around 30,000 to 10,000 years ago), for example (Formicola 2007). Examples include the Romito child, with dwarfism, buried under a depiction of an aurochs (Mallegni and Fabbri 1995), two juveniles at Sunghir in Russia, one with severely bowed legs and another with severe facial abnormality (prognathism), interred with elaborate burial goods, including 16 mammoth ivory spears (Trinkaus and Buzhilova 2018), the central individual of an elaborate triple burial at Dolní Věstonice who had severe limb abnormalities (Trinkaus et al. 2001) and a woman from the same site with a facial deformation (buried under the scapula of a mammoth, and covered with red ochre). In the latter case, a figurine with the same facial deformation as the woman was also found from the same site, suggesting that her facial difference made her in some way special.

We can see various types of accommodations for illness or injury in modern hunting and gathering populations. Amongst the modern-day Baka, individuals with severe mobility impairments take on important social roles (Toda 2011). Whilst the differentiation of individuals with disabilities remains enigmatic, it best represents in general terms the significance of *reputation*, with the determination of disabled individuals to overcome adversity gaining them a certain respect.

To some extent, some forms of social differentiation may be apparent in archaic populations, even if less visibly so. We may see a different treatment of different people in Neanderthal populations in mortuary practices, where older males with injuries may be more likely to be buried after death, and in distinctive practices around children, such as the burial of a child with possible grave goods at Dederiyeh in Syria (see Spikins et al. 2014).

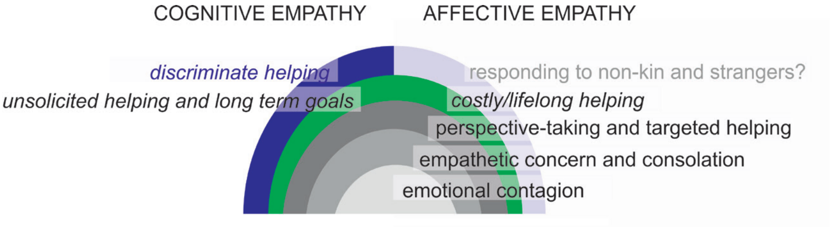

Figure 2.9: Possible implications of the material evidence for care for capacities in cognitive and affective empathy in archaic and modern humans. Penny Spikins, CC BY-NC 4.0.

It is clear that archaic and later humans were capable of complex planning around care, and had the emotional capacities which prompt us *to costly and lifelong acts of care* for those we love (see Figure 2.9). A *different treatment of different people* provides us with evidence of discriminate helping, one of the more complex features of cognitive empathy identified in Chapter 1. The question of an extended affective empathy, prompting an extension of helping to non-kin and strangers familiar to modern societies is, however, almost impossible to identify from survival from illness and injury and is a topic we turn to in Part 2.

It is not difficult to identify a broad pattern of changing responses to vulnerable, ill and injured individuals, from possible early examples, perhaps not dissimilar to those practices seen in other mammals and particular social carnivores, to more widespread, long-term and knowledgeable care later in human evolution. Interpretations of care, and of what behaviours mean in terms of the emotional motivations underlying such care, particularly if we try to focus on individual cases, are not without their issues, however. There have been a number of issues raised with interpretations of care that warrant discussion.

To what extent can archaeological evidence be used to infer key changes in emotional connections and capacities for compassion?

There are several key challenges to address in making inferences from skeletal records of recovery from illness and injury. Firstly, there are many biases affecting the archaeological record that may influence our interpretation. Secondly, there are a number of unknowns. Most particularly, it can be difficult to infer the extent to which any individual may have been able to survive alone or tolerate particular conditions, particularly when we are dealing with hominins who were anatomically and perhaps even physiologically different from ourselves. Lastly, evidence for helping, particularly in the complex societies of cognitively modern humans, is not always evidence of compassionate motivations – helping can be motivated by calculated intentions rather than genuine empathy or compassion.

The issue of bias is a pervasive one when dealing with archaeological evidence. Only certain types of materials are preserved, under particular conditions and in particular places. Human and animal bones can sometimes be preserved where the conditions are suitable for their preservation. Some of our best-preserved skeletal records come from particular contexts, most notably burial practices, which may not be a representative sample of the people at the time (Spikins et al. 2014; Spikins et al. 2018). Moreover, we can sometimes question the reliability of inferences from a small number of individuals spread out over large areas of time and space. Neither can modern biases be discounted: until recently, fragile infant bones were only rarely recovered on excavations, further biasing the record. Interpretations can never be entirely straightforward.

Inferring implications in terms of care is also difficult. We usually underestimate the prevalence of injuries and illnesses requiring treatment as even quite severe injuries and illnesses often leave no trace on the human bones. In fact, well over 90% treatments for illness or injury in wilderness locations, many of which would have contributed to saving lives, would leave no indications on skeletal evidence (Spikins et al. 2019); see Figure 2.10. Our evidence of illness and injury is thus only a tiny window onto the actual injuries, illnesses and impairments that people experienced in the past.

Whilst the restricted visibility of most pathologies requiring care means that our estimates of care are underestimated, other factors may elevate our impression of the care that was given to particular individuals. It is often difficult to infer exactly the nature of injury or illness. Few skeletal remains from the distant past are complete and most are missing many elements, which makes inferring the implications challenging. Alternative explanations for the pathologies seen in 1808 include yaws (*Treponema pertenue*) (Rothschild, Hershkovitz, and Rothschild 1995) and sickle cell anaemia (Jefferson

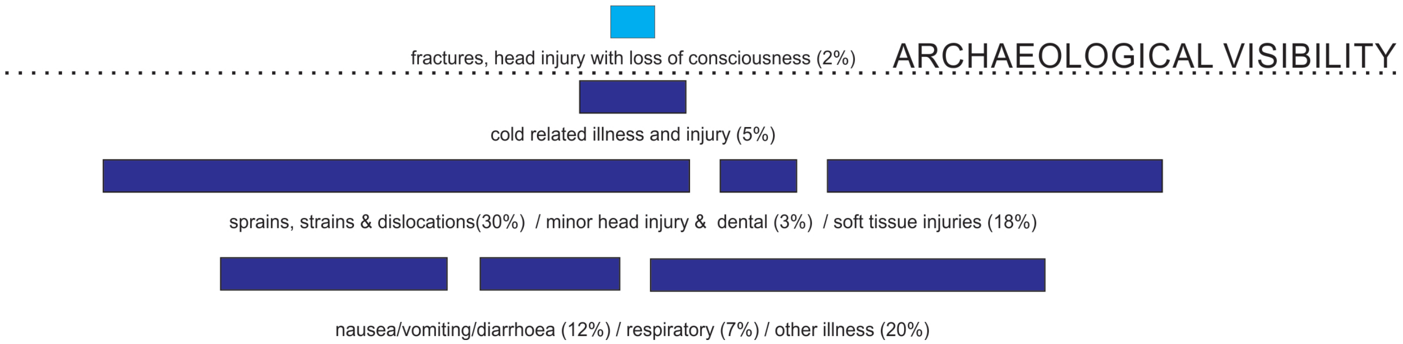

Figure 2.10: Medical treatment in wilderness locations. National Outdoor Leadership school's incidents requiring medical attention in wilderness activities in Wyoming, Alaska, Arizona, Washington, Idaho, Mexico, Chile and the Yukon Territory; 1051 individuals (average age 22 years) 1998–2003. Data from McIntosh et al. 2007. Penny Spikins, CC BY-NC 4.0.

2004), for example, though hypervitaminosis best fits the bone pathology (Dolan 2011). We also have to bear in mind that our modern analogies may not be as relevant for early hominins as we might hope, and individuals in the past may have been more independent than we might give them credit for (Degusta 2002; Dettwyler 1991). Cowgill (Cowgill et al. 2015), for example, noted that a young female buried at Sunghir during the Upper Palaeolithic showed extensive evidence for sustained mobility despite notable bowing of her legs, demonstrating that she kept up with the group despite this impairment. Self-care and self-medication may also be a factor. A *Homo erectus* from Swartkrans with probable intentional removal of an M3 molar that is likely to have been infected and shows subsequent bone regrowth around the side might conceivably have removed this tooth by themselves rather than needing help from others, for example (Ripamonti et al. 2020). These issues mean that the less severe cases of pathology are more debatable in terms of care from others.

Making inferences about emotional motivations from past behaviours, themselves inferred from material evidence, is also subject to a number of challenges.

It is clear that were all born with *a capacity* for compassion, generosity and a whole range of helping behaviours (as we have seen in Chapter 1), and that helping and provisioning of group members is unsurprising given its appearance in highly independent mammals such as many social carnivores, African painted wolves being a particular case.

A broad capacity for compassion is not, however, enough to infer that this must have been a motivation in the past in any particular instance. A particular challenge to interpretations of archaeological evidence for helping in the past is, however, the *possibility* of particularly human motivations of deception, adherence to norms, or concerns with status rather than genuine empathy (Figure 2.11). Other animals do not deceptively help individuals that they do not care about, nor do they help because of a social or cultural norm, so we reasonably assume that *their* helping reflects an immediate emotional response. Modern humans and by implication potentially earlier species besides are much more complex in their decision-making, however. At one extreme, a response to distress that is *always calculated* (rather than genuine) would be considered a disorder in humans; nonetheless, in large

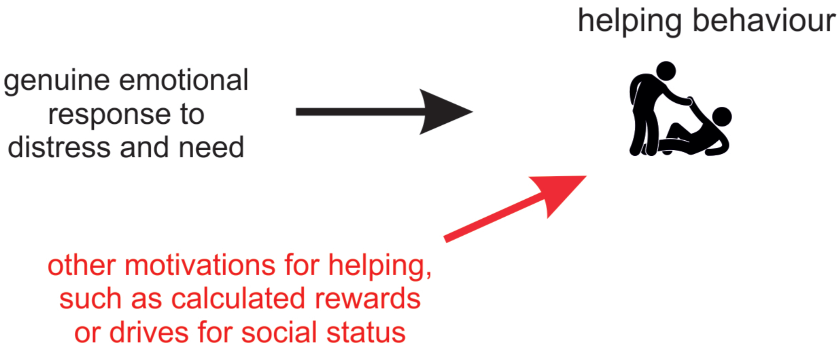

Figure 2.11: Alternative motivations for helping in response to others' needs or distress. Penny Spikins, CC BY-NC 4.0.

human societies where relationships of different kinds are formed with many different people, helping others on a day-to-day level can be motivated by all kinds of complex social factors. These can include motivations such as a desire to improve social standing, or for recognition, as well as calculated self-interest (Böckler, Tusche, and Singer 2016). Moreover, tendencies to compassion can be blocked by stress, depression or anxiety (Gilbert 2005).

In fairness, our experience in modern industrialised societies is not necessarily a good analogy for the past, as small-scale hunting and gathering societies operate far more intimate social relationships where deception or a lack of genuine motivations cannot be 'pulled off' for long (Boehm 2012). Even so, even in such highly intimate contexts there will be occasional deception or self-oriented motivations. Serious selfishness or exploitation is strongly resisted, even to the point of assassination (Boehm 2012). However, in modern hunter-gatherer contexts, many people can 'get away with' a low level of individualistic motivations or deception at certain times. Peterson described, for example, how the Australian Pintupi uphold the common hunter-gatherer ethic of food sharing, yet tolerate a certain level of hiding food to prevent others from asking for it (Peterson 1993). Likewise, Hadza men consume more food away from campsites, where they are not seen, rather than visibly eating something that might be shared (Berbesque et al. 2016). Equally, whilst people may not always *feel like* helping others' infants, sharing food or caring for the ill, unlike other animals we recognise that social reputation is affected by not seeming generous of time or effort. Moreover, even in the most collaborative of setting there will still be some people whose attachment insecurities will influence how genuinely they are about others' wellbeing. The modern Inuit, for example, acknowledge that orphans tend to be more competitive (and less genuinely motivated by others' needs) than those who have experienced a more secure upbringing (Briggs 1970).

These limitations mean that we can rarely place too much emphasis on any isolated example of helping behaviour. Broader patterns remain reliable, nonetheless. Genuine motivations are far more prevalent than calculated ones, and the most parsimonious (and simplest) explanation is that of an immediate uncalculated response, meaning it is reasonable to infer genuine compassion when we see widespread evidence for care of the injured (Flack and de Waal 2000). This does not mean that there are no exceptions. Capacities to be cunning, deceptive and calculated in response to others' needs clearly evolved in a constant and complex dynamic alongside those to convince others of genuine intentions, to detect deception and to punish cheats (de Quervain et al. 2004); see Chapter 3. These will certainly be present in cognitively modern humans and quite possibly much earlier. Sustained care for others, and other prosocial collaborative behaviours such as widespread food sharing, can only be sustained where the majority of individuals are genuinely altruistic, based on shared emotional responses to those in need (Egas and Riedl 2008). Nonetheless, a certain realism about human nature suggests that some will always be 'cheating' and no one is genuinely compassionate all of the time.

These potential complex variations imply that we should be careful not to make interpretations based on any single instance of probable care, though broad patterns occurring over long periods of time, as outlined above, withstand scrutiny. Moreover, these broad patterns of interdependence and response to vulnerability are reflected in other areas of the archaeological record.

Other realms of material evidence for helping those in need

We have focused here on evidence for care for illness and injury. However, whilst survival from injuries is the most obvious realm of evidence for care and compassion, it also fits within other realms of evidence.

In broad terms, evidence for extended helping of those with illnesses and injuries fits with other lines of evidence for key social changes. These include evidence for extended childhoods, implying collaborative infant care, as well as evidence for the hunting and sharing of large game, requiring collaborative effort. These different elements of responses to needs and vulnerabilities imply emotional attunement, sharing and generosity were emerging as a response to increasing interdependence from at least 2 million years ago (Smith et al. 2012; Whiten and Erdal 2012).

There are also more specific lines of evidence indicating closer emotional relationships and empathetic responses. The most obvious are mortuary practices. There is potentially some evidence of mortuary ritual as early as 3 million years ago, though evidence becomes more frequent after half a million years ago (Pettitt 2013). In some cases, it is hard to avoid the sense of emotional connection in life shown by the care afforded to the deceased. One example of such is the careful burial of a Neanderthal child at Dederiyeh Cave, Syria, with a flint flake carefully placed on their heart and stone above their head, likely as a collective response to a sense of loss (Spikins et al. 2014). As we have seen in Chapter 2, affective empathy for the living is often linked to particular grief-like attitudes at death, shown in species as widely separated as jays (Iglesias, McElreath, and Patricelli 2012), dingoes (Appleby, Smith, and Jones 2013) and chimpanzees (Biro et al. 2010).

A response to vulnerability is also evident beyond relationships with other people. Later in the archaeological record we see direct evidence for something we might see as animal companions, in the form of animals such as dogs buried with people or as if they were people (Morey 2010) (discussed in more detail in Chapter 6). However, even around the time of early *Homo* groups, animals were more than just an objectified food source. Handaxes made from elephant bone, found from about 1.4 million years ago, for example, are less practical than their stone counterparts and suggest that elephants had some particular meaning (Barkai 2021; Zutovski and Barkai 2015). Humans might even have recognised their empathy and capacity to care for others. By the time of archaic humans, such as Neanderthals, several different types of artefacts suggest a more complex relationship with animals, including the use of raptor talons and feathers presumably as decoration (Romandini et al. 2014).

It is also particularly notable that the earliest examples of what we term 'art' show the characteristic *infant-like* proportions that prompt empathetic responses today. The Makapansgat pebble, for example, not created by humans but carried several kilometres by an australopithecine to the site of Makapansgat in South Africa, has baby-like face proportions. Similarly, the Berekhat Ram figurine from Israel, dated to 250,000–700,000bp, has infant proportions, and the first construction of a human face, the Roche-Cotard mask, made by Neanderthals and dated to 33,000bp, also has infant-like proportions. This form suggests that, whatever their appeal as 'art', a response to vulnerability was also important in the creation and use of these objects (Spikins et al. 2014). These may be evidence of the sensitivity that is critical to human attachment and learning. Attachment processes and a drive to care for objects may even be an unrecognised part of how much handled items of Upper Palaeolithic portable art may have provided comfort, much like treasured jewellery today (Bell and Spikins 2018), discussed in Chapter 5.

The effects of a drive to care for things in the world around us can be felt in far more varied spheres than we might imagine.

Implications: a long evolutionary history of human vulnerability, compassion and interdependence

There are a number of implications arising from evidence for care for illness and injury and its association with other changes taking place during human origins.

Care for adults who are vulnerable, over either the short or the long term, affects the whole structure of communities (see Figure 2.12). On a biological level, care for injury and illness changes the parameters over which selection pressures operate. Assisted childbirth, for example, increases infant survival and changes pressures on female pelvis size and shape, whilst support to allow bone breakage can reduce selective pressures on robusticity (see, for example, Stieglitz et al. 2020). On an economic and ecological level, recovery from injury allows humans to move into niches with high injury risks, such as those involving hunting dangerous animals (Spikins et al. 2019). Socially, care for vulnerable adults leads to increasing life expectancy, generating older individuals able to provide extra care for infants or support parents, and able to pass on important knowledge and skills (Spikins

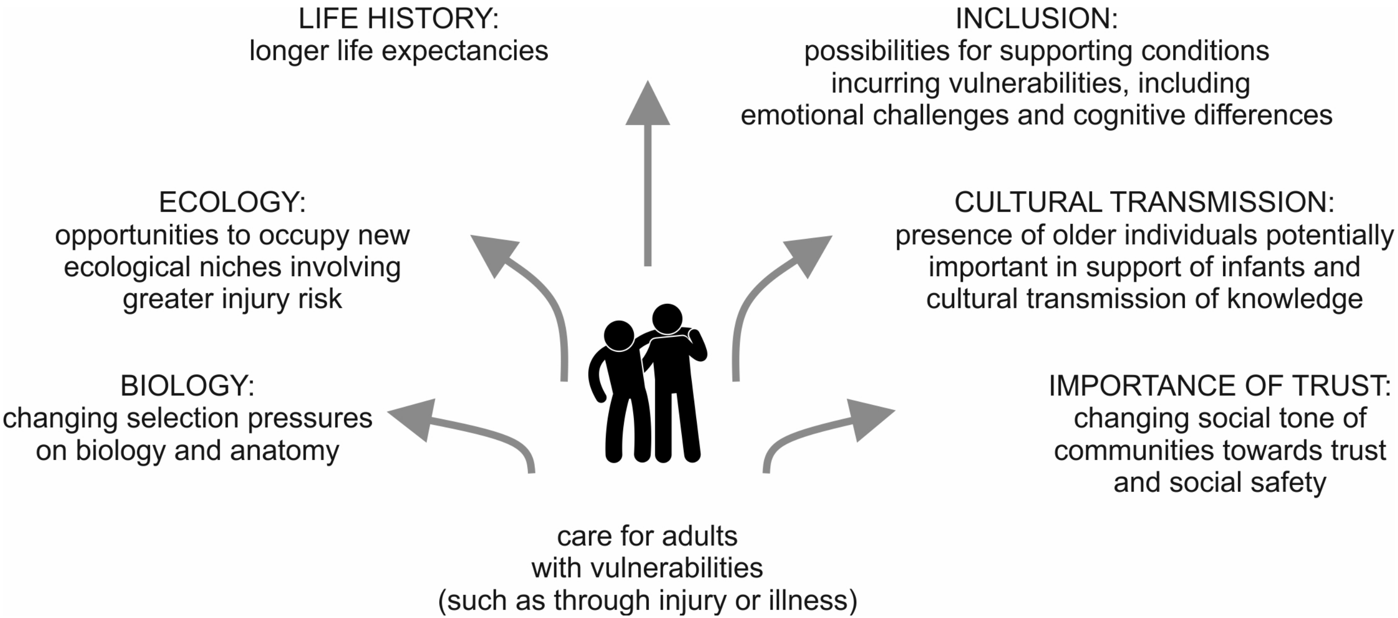

Figure 2.12: Implications of care for adults with vulnerabilities for other human traits. Penny Spikins, CC BY-NC 4.0.

et al. 2019). Older men amongst the Aché of Paraguay, for example, have a much higher rate of hunting efficiency, despite being less physically strong than their younger counterparts, as hunting requires much skill, learnt over many years or even decades (Koster et al. 2020; Walker et al. 2002). Being able to support occasional vulnerabilities also opens up possibilities of supporting individuals with conditions incurring occasional dependencies on others, including emotional challenges or cognitive differences (discussed in Chapter 3). Care also makes trust important to facilitate give and take, and opens up the possibility of developing communities with a sense of social safety (also discussed in Chapter 3).

Care for vulnerable adults also changes how we view our evolutionary past and suggests that we need to reappraise our narrative of human independence to one of interdependence, vulnerability and response. A fundamental interdependence, of which care for others' health and a reliance on others for our own is only part, seems to have been part of our evolutionary history from as far back as 2 million years ago. Much as we might like to portray an image of ourselves as physically invulnerable and independent, the average human from at least 2 million years ago onwards is likely to have suffered a range of illnesses and injuries, many of which required help from others. Almost all skeletal remains demonstrate a range of such pathologies (Trinkaus 2018b). Moreover, shared resilience comes with compromises in terms of individual emotional vulnerability – susceptibility to others distress and a desire to help, and a certain other-focused emotional sensitivity.

We can see these interdependencies and vulnerabilities today. A fundamental dependence on others for survival is evident in modern hunting and gathering societies. For these societies, survival itself depends on willing care from others at times of need. Amongst the Aché of Paraguay, adult males are typically provisioned or cared for by others for 21% of potential hunting days when unable to hunt due to injury or illness (Gurven et al. 2000; Hill and Hurtado 2009), for example, and similar rates have been recorded amongst the Efe of the Ituri forest (Bailey 1991). Seventy-five per cent of adults amongst the Tsimane were unable to get out of bed at least once in a three-month period, for example due to being incapacitated by illness or injury (Hill and Hurtado 2009), and this period of illness lasted more than three days in over 90% of cases (Gurven et al. 2012). It is also common to experience longer periods of incapacitation and care. Eighty-five per cent of men in the Arroya Bandera Aché had been ill or injured for at least a month over a seven-year period and would not have survived without care from others (Hill and Hurtado 2009). Willing care, regardless of the probability of survival, makes a significant difference to recovery. Healthcare provisioning significantly reduced juvenile mortality amongst the Shiwiar forager-horticulturalists, with half of the adults being incapacitated and unable to find food for themselves for at least a month (Sugiyama 2001; Sugiyama 2004).

Sharing health by caring and provisioning the ill and injured is only one aspect of a life fundamentally based on sharing in these societies. Sharing of food resources has a function for survival, minimising any individual's risk of starving themselves or being unable to provide for infants, and enhances survival of the whole group in similar ways (Ringen, Duda, and Jaeggi 2019). Most hunter-gatherers hunt collaboratively, and share the proceeds with other members of the group that they live with, and not just their kin, according to their needs. This means that, though some individuals tend to benefit more than others, overall everyone benefits from being buffered from days when they fail to bring home enough food for themselves or their family (Chapais 2013). The vulnerable consistently receive more food than the most able (Wood and Marlowe 2013). Meat, in particular, is shared both within families and between them, according to needs rather than previous contributions or status and despite how hungry the giver may be (Dyble et al. 2016; Wood and Marlowe 2013). Sharing food, however, is also about promoting harmony in social relationships (Lavi and Friesem 2019) and demonstrating self-control on others' behalves (Green and Spikins 2020).

A reliance on other people may not be as obvious in modern industrialised societies as it is in modern foragers but it is no less significant. We are all physically vulnerable at different stages of our lives, from infancy, pregnancy and childbirth, illness or injury and old age. More than this, we are also emotionally vulnerable (discussed in Part 2), and susceptible to loneliness, anxiety or the effects of unfairness or exclusion. The origin of these vulnerabilities lies in those societies that first depended on each other to survive. The more mutual survival depends on motivations to respond to others' vulnerabilities and others' response to our own needs, the greater human sensitivities to others' welfare must become.

It might seem surprising that changes in emotional motivations seem to predate changes in complex cognition, particularly as we like to believe that our human intelligence sets us apart from other animals. As we have seen, it was after 2 million years ago that humans developed new and highly effective types of collaboration, effectively working 'like a single predatory organism' in their new hunting niche (Whiten and Erdal 2012). It is easy to assume, working from our own ideological norms, that this collaboration was built primarily on strategic goals, better communication or abilities to plan. However, in reality, moving into a new ecological niche was much more about sharing, mutual vulnerability and a human response to vulnerability.

That there is clearly no simple progression of more recognisably human-like forms might also be surprising. Yet the anatomical record demonstrates alternative pathways, from those of the paranthropines to that of *Homo naledi*, and we cannot help but wonder what other branches of 'human' remain to be discovered or, indeed, perhaps might never be found.

Further, whilst it seems reasonable to conclude that a sensitivity to others and emotional motivations to help are perhaps the most significant development in our evolutionary past, does it follow, however, that this capacity elevates humans above other animals? Given that a widespread willingness to respond to vulnerable infants in the group, to share risks and food, and to care for the ill and injured is shared, at least with African wild dogs if not other social animals besides, this seems difficult to argue. Perhaps those traits such as complex language or cultural learning that mark us out as different are *less critical* to our origins than those that might be distinctive for an ape, but link us to other species rather than dividing us from them. Perhaps, as Anderson notes, '"we" (or at least those of "us" of a Western cultural tradition) urgently need to overcome the still lingering idea that being human means rising above our worldly, and indeed our animal existence' (Anderson 2019: 66).

There are, of course, many questions remaining. It is difficult to determine how dependent the earliest societies were on care for vulnerable adults for their survival, for example. Certainly, such care may have been part of their abilities to confront predators and hunt dangerous animals whilst living with the consequences in terms of injury risks. Care for vulnerable adults almost certainly played a role at some point in our evolutionary past in allowing longer lifespans and the involvement of grandparents in infant care, as well as in the cultural transmission of knowledge, but whether this happened early in our evolutionary origins or rather later remains to be explored. We may imagine that care extended across a range of vulnerabilities, including not only physical vulnerabilities but also emotional or mental health issues. However, the latter typically leave no surviving trace in skeletal remains, making this difficult to determine. It also seems likely that care played a social role as well as a practical one, not only forging strong bonds but also promoting a sense of safety and trust that is essential to a human willingness to act in others' interests. This is, equally, a harder area to assess from the material record (discussed in Chapter 3). Care for adults made vulnerable through illness or injury is also likely to be intimately related to care of vulnerable young or vulnerable elderly, though how these types of care are related to each other remains to be understood. In modern hunting-gathering societies, bone fractures increase substantially with age. More elderly members of groups are less physically able to take on some foraging tasks, for example, but nonetheless bring important knowledge and skills in less physically demanding areas such as in tool making (Stieglitz et al. 2020). It is not only care for adults with temporary vulnerabilities but motivations to care for anyone who is vulnerable that will have transformed societies in important and, as yet, not fully understood ways.

Moreover, there is much to reflect on. We cannot help but wonder whether a new narrative of human 'success', as based not on individual performance or intellect but on emotional connection, human vulnerability and response, might cast some of our modern assumptions about human 'value' in terms of competition or intellectual merit in a new light.

Conclusions

That care for adults who were vulnerable through injury or illness was a significant feature of our evolutionary origins is rarely, if ever, mentioned in accounts of our human origins. Our own discomfort with vulnerability may partly explain this apparent paradox. In many modern industrialised cultures, a focus on being independent and competitive can make any dependence on others feel deeply uncomfortable. However, extensive evidence for care for illness and injury, of which Shanidar 1 is only one example, suggests that our early ancestors were people who cared deeply for each other, and were prepared to go to great lengths on each other's behalf. These were populations for whom vulnerabilities and sharing responses from others were common.

As we have seen in Chapter 1, there are adaptive explanations for increasing significance of emotional dispositions towards helping others and responding to vulnerability. As well as being fundamental to being human, the archaeological record for an increasing prevalence and intensity of care suggests that changes in emotional dispositions were far more key to social transformation than has been assumed. An apparently simple response, to care for others in need or distress, becomes in humans an integral part of how societies work, the so-called 'glue' that holds us together. Rather than our intellectual capacity for language or technological skills making us human, our emotional connections to others and tendencies to respond to their vulnerabilities may have been more important.

Extended tendencies to focus on others, and be emotionally motivated to act on their behalf, did not come without costs. Collaboration based on emotional motivations comes at an individual cost of sensitivity to others' distress. Furthermore, in an evolutionary context, the more interdependent social communities became, and the greater investments made to helping others, the more important it will have been to know who one could trust – whose motivations were genuine, and whose were not. Here began our worries and anxieties about what others think about us, and who we can trust (explored in Chapter 3).

Key points

- After 2 million years ago, we see evidence for care for vulnerable adult humans who suffer illness or injury. This seems to be part of a critical process of transformation in emotional motivations within early members of the genus *Homo* and which includes motivations to help others in other realms such as hunting, food sharing and infant care.

- This significant transformation towards greater interdependence and emotional motivations to respond to vulnerability may represent a shift in response to ecological opportunities or changes, and shares similarities with the emotional responses to other group members seen in animals such as social carnivores.

- More extended periods of care, and more complex cognitive planning and knowledge involved in long-term care, appear later in human evolution, particularly in archaic humans. If any differences are apparent between care in archaic and modern humans, they are subtle and probably related to cultural context rather than emotional responses.

- Care for vulnerable adults has potentially significant implications for biology, subsistence practices, social relationships, cultures and the emotional connections within communities. The importance of such care also suggests a reappraisal of our assumptions about key driving factors in our evolutionary past.

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CHAPTER 3

Trust, Emotional Commitments and Reputation

Abstract

How did our uniquely human commitments to our loved ones develop, and why are we so concerned about what feelings lie underneath what other people do? In this chapter, we consider the origins of our long-term emotional connections based on trust, and how they lead to uniquely human sensitivities to what motivates other people and how they feel about us.

As we have seen in Chapters 1 and 2, new types of emotional connections, and new ways of collaborating to survive, emerged in early humans after 2 million years ago. This was a time when changes in emotional dispositions led to a greater willingness to share with, and care for, a wider set of individuals. Archaeological evidence demonstrates care for vulnerable adults, within the contexts of both food sharing and of collaborative care for increasingly dependent offspring.

(Abstract continued on next page)

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(Abstract continued from previous page)

The emergence of strong emotional bonds based on high levels of give and take at this time laid the basis for human trust, emotional commitments and love. Yet these long-term emotional connections also seem to have come at a price. The importance of knowing who to trust brought with it pressures to be acutely focused on displaying our genuine intentions (or hiding our less genuine ones), and on identifying the genuine emotional motivations of others. Considering the importance of relationships based on trust, and with this emotional astuteness about *who could be trusted*, may yield important insights into many debates about our origins. These include the cultural transmission of ideas, the explanations for an increasing concern with symmetry and the aesthetics of form in stone tools after 2 million years ago, and the mechanisms behind how people who thought differently may have been integrated into human populations.

Long-term relationships based on trust and a sensitivity to the emotional connections underlying people's words or actions may have been much more important in our distant past than we have previously recognised.

Figure 3.1: Our sensitivity to others' feelings and to who they are as a person prompts us to feel transported into the mind and feelings of the artist who created these lions from Chauvet cave, France, around 30,000 years ago. Image from replica at Brno Museum Anthropos (Czech Republic). Public domain, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Lions_painting,_Chauvet_Cave_(museum_replica).jpg.

Introduction

Many highly evocative examples of European Ice Age art affect us emotionally. Simply experiencing the depictions of lions at Chauvet cave (Figure 3.1) seems to transport us to the time, place and mind of the artist who created them, for example. Realistic depictions like these appear after 50,000 years ago, not only in Europe but as far afield as Indonesia. Debates about the meaning of such depictions have continued for well over a hundred years. However, beyond the specific meaning of any one painting or artefact, such art also tells us about a uniquely human sensitivity to how others feel. Even though all we are looking at is stone and paint, or even, perhaps, just an image on the screen or paper, we feel intimately emotionally connected to the artist, despite the many thousands of years between us. We feel that we are in some way in the moment, and in the mind, of whoever painted this picture. We get a sense that the artist knew how we would feel in viewing this image, at least on some level, despite the thousands of years and widely different cultures and experiences between us. We also have some sense of how they themselves felt when remembering these lions.

Our emotional brains are finely attuned to identifying not just what people believe but how they feel and the *emotions behind why they do what they do*. Yet, despite the complexity of these judgements, we scarcely notice we make them. Every story, action and item of gossip is subject to our unthinking judgement about its implications in terms of what people feel, and what they might feel about us. We cannot help being driven to try to understand what they mean about whether people are trustworthy or not, whether they are on our side, and even what their emotional motivations mean about the world as a whole. Because of this sensitivity, we are also almost inescapably drawn to infer the emotions behind art, a topic we return to in more depth in Chapter 5.

Why should it matter to be so attuned to others' feelings and motivations?

Some of the explanations for our acute sensitivities to other people's feelings lie in changes in recent human evolution over the last 300,000 years (discussed in Part 2). However, the origins of our attention to what lies behind other people's actions seem to lie much further back in time. The interdependence within groups of early humans, as far back as 2 million years ago, reflected in their willingness to care for adults with vulnerabilities (discussed in Chapter 2), seems to have triggered important changes in emotional connections. We hardly imagine our distant ancestors as *trustworthy*. However, so much of what kept groups alive may have depended on trust, whether that was raising vulnerable offspring and protecting them from harm, finding food together or tackling dangerous animals (Spikins 2019). Only by caring deeply about others would early humans have been motivated to help them when they were ill, share food with them, or risk their own lives to defend them from predators. Such willingness to help risks exploitation, however, perhaps from an individual's ally or mate who might abandon them in a time of need. Abilities *to make the right choices about* *people* and to correctly judge others' motivations and emotional commitments towards us will have been increasingly important.

The significance of trust to our evolutionary history may tell us something important about why we are so acutely attuned to what other people feel about us, and why it is not just social connections that we need to thrive today but shared emotional commitments marked by genuine care and trust.

Trust and a sensitivity to emotional motivations in human evolutionary origins

Our human drive to understand the emotions behind other people's actions

When we consider how human minds and societies developed, we have traditionally paid a lot of attention to the significance of our strategic social thinking or cognitive empathy (see, for example, Dunbar 2003; Noonan et al. 2018), explained in Chapter 1. We often hear about the 'social brain' or theory of mind, how unusually adept we humans are at understanding what others believe and what they are rationally thinking, and how good we are at the social understanding needed to maintain many social contacts. However, the importance of our affective empathy, or emotional attunement to others' feelings, and how we use it to understand how they feel about us, is often forgotten. This attunement to how others feel and why they feel this, rather than simply to what they think or believe, may have been far more important in our evolutionary past than we have recognised.

Clues exist today. Looking around us we can see a surprisingly complex attention and attunement to the hidden depths of other people's emotional lives.

We are much more sensitive to the emotions of people around us than we often imagine. As we have discussed in Chapter 1, how others around us feel affects us deeply. We are acutely sensitive to heroism, cruelty or even everyday kindness or harshness, for example (Keltner and Haidt 2003; Piper, Saslow, and Saturn 2015). Even just hearing about acts of genuine compassion or heroism can influence how we treat others around us and what we believe about the world. Acts of generosity tend to spread to people down the line, as people feel differently after hearing about or witnessing them and 'pay it forwards' (Fowler and Christakis 2010). Moreover, we have extraordinary levels of biological attunement to each other – the heart rate and gamma brain wave oscillations of mothers and babies and couples even coordinate in tune with each other, as well as their emotions and movements (Feldman 2017).

More than this sensitivity, however, we pay great attention to what other people feel *about us*, or even *might feel about us*, and what their feelings might mean. We have remarkable abilities to make highly accurate inferences about other people's intentions, even on the basis of the tiniest of facial expressions or slightest of other indications of what feelings are happening 'behind the scenes' in others' minds.

There have even been many changes to the human face since our split with other apes which reflect our need to display our feelings and identify the feelings of others. These include the emergence of blushing and crying as signs of genuine emotions (Evans 2002), as well as changes in face shape and appearance (Bastir 2018; Godinho, Spikins, and O'Higgins 2018; Lacruz et al. 2019). We share a distinctive ability to both express and identify in others subtle expressions of vulnerability, sympathy or recognition through movements of our eyebrows, for example, discussed in more detail in Part 2.

Often without realising it, we constantly track the feelings and intentions of the people around us, and how they might behave (Thornton, Weaverdyck, and Tamir 2019). We may think we pay attention to what people do but, in fact, the hidden world of their feelings is often more important to us. Research confirms that we are much less swayed by the outcomes of people's actions then we are by the emotional intentions behind them, for example (Yudkin, Prosser, and Crockett 2018). We may feel more positively inclined towards an elderly person who kindly gives sweets to a child than to someone wealthy who gives substantial funds to a major charity, even though the outcome in the former case may not be all that positive and, in the latter, may make a substantial contribution to people's lives. We even feel more comfortable talking to a stranger who displays their caring nature through owning a pet dog than we would if they were by themselves, for example (McNicholas and Collis 2000). By this small acknowledgement of their emotional need for a pet, they seem more trustworthy. Our complex pictures of the emotional motivations of other people even extends to how they treat not only other people or even animals but also inanimate things (discussed in Chapter 5).

The efforts our brains make, behind the scenes, to keep track of others' feelings and what they might mean extend into having profound effects on our long-term relationships. We may love our children unconditionally, or at least aspire to, but, in our adult relationships, how our friends, partners or other people important in our lives feel about us matters deeply. We keep extraordinary track of the motivations of people close to us through a constant set of mathematically founded assessments of their 'trust metric', or the extent to which we understand that they will act in our interests above theirs, for example (Gottman 2011). However much we value rationality in our business world, amongst our partners and friends we are unimpressed if they are not prepared to be irrationally driven to sometimes put our needs above their own when it matters for us (Jordan et al. 2016; Manapat, Nowak, and Rand 2013). Further, many micro judgements lie at the heart of long-term relationships. In these relationships, as we trust someone more, we become increasingly more willing to be generous, and more comfortable with giving to another person without expecting anything in return (Manapat, Nowak, and Rand 2013).

We start to make these judgements about what motivates other people from an early age, and they become so routine that we barely notice them. As we have seen in Chapter 1, these judgements begin in early childhood, when we are no longer duped by apparently kind acts but become much more aware of what feelings lie behind what other people do, and why they matter. This is the point when, even as young children, we help others *discriminately*, deciding how much effort to put in to help, or even whether to put in any at all, according to our estimate of the person needing help. From childhood, it is not sufficient just to track what others do. We also need to know what their underlying emotional motivations are. Even in the playground, we often make decisions to resist bullies and help those genuinely in need which may not be in our own immediate short-term interest.

We cannot help but wonder why we should devote quite so much time and effort to understanding what emotions lie underneath others' behaviour, and what they might mean.

We do share a certain sensitivity to others' motivations with many highly social animals. Chimpanzees, for example, can remember favours that have been done to them for at least six months (Schino and Aureli 2010). Domestic dogs make judgements about people who have either helped or refused to help their owners, and will not accept food from the latter (Chijiiwa et al. 2015). Being a social animal involves being astute about how your fellows are behaving and how it might affect you. It also involves being able to handle emotions rather than immediately act on them, such as through overcoming the frustrations of having to share food, or controlling impulses to be aggressive (Green and Spikins 2020; Marshall-Pescini, Virányi, and Range 2015). However, our seeming obsession is different. Only humans build up a complex picture of the emotional motivations of people around us on the basis of a whole myriad of behaviours, not just those we see in front of us but also stretching into the past.

The unique problems faced by early humans may give us important insights into why trust became so important, and why we care so much about what lies behind what other people do and how they feel about us.

Why early human interdependence made a good reputation matter

As we have seen in Chapters 1 and 2, early humans from about 2 million years ago survived dangerous predators, brought up vulnerable young and found food because they *depended on each other*. Archaeological evidence demonstrates an increasing tendency to care for ill or injured adults as well as increasingly vulnerable and dependent children, alongside collaborative hunting of increasingly large and dangerous animals and sharing of food resources.

Early human groups at this point took a different pathway from other apes, as we discussed in Chapter 1. Non-human apes may be socially clever, but they are largely self-focused, with their main emotional bonds being between mothers and their offspring. However, early human communities needed to be far more collaborative to survive, and changes in emotional connections are likely to have played a key role in enabling this. By being willing to be generous to others in their group, and to depend on others' generosity in turn, they will have been able to reduce their individual risks at a time of increasing environmental unpredictability (Grove 2011). Sharing hunting risks, food, infant care and caring for the ill and injured made human groups far more resilient to the vagaries of resource shortfalls, injuries or individual misfortune (Gurven and Jaeggi 2015). It was also in these collaborative contexts, where caring for others was key to bringing up vulnerable young, to finding and sharing food, and to looking after vulnerable adults, that the strength of our human emotional connections, and even love, emerged.

Two key transformations had to take place. Firstly, collaboration had to happen across the whole group, rather than just with particular allies as we see with chimpanzees (Figure 3.2). This meant that being a valuable and trusted group member began to matter (Tomasello and Vaish 2013). Secondly, the depth of collaborations, and the extent of give and take anyone might expect from others, had to increase. From calculated exchanges typical of other apes, early humans had to develop much more in-depth commitments, such as in taking risks to find resources or to defend the group from predators, or in shared care for vulnerable young (Figure 3.3).

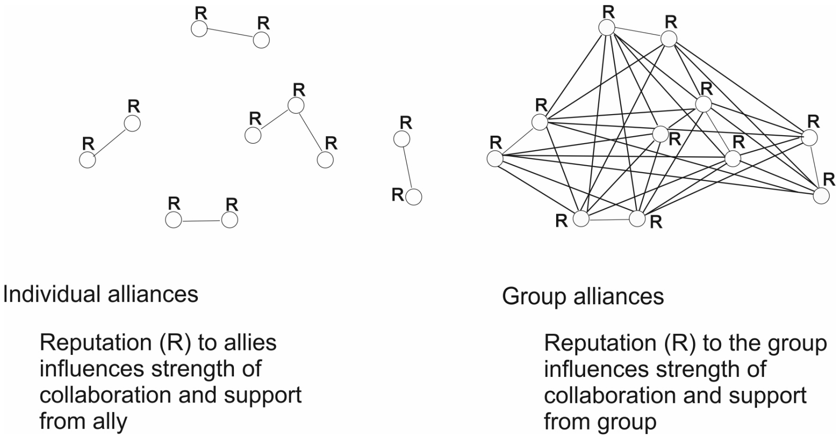
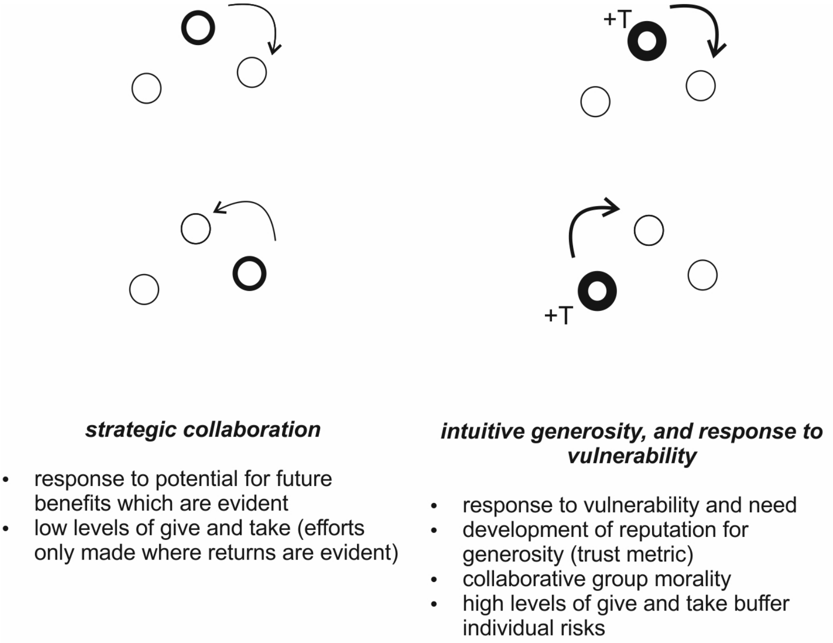


Figure 3.2: Judgements of reputation within peer-to-peer alliances are relatively simple (left) whereas within collaborative groups judgements of reputation with regard to many potential allies or even the group as a whole are far more complex (right). Penny Spikins, CC BY-NC 4.0.



strategic collaboration

- response to potential for future benefits which are evident
- low levels of give and take (efforts only made where returns are evident)

intuitive generosity, and response to vulnerability

- response to vulnerability and need
- development of reputation for generosity (trust metric)
- collaborative group morality
- high levels of give and take buffer individual risks

Figure 3.3: Relationships based on strategic selfish motivations (left) show lower levels of give and take (denoted by thinner lines) and lack trust (denoted by T) than those based on genuine caring and mutual generosity (right). Penny Spikins, CC BY-NC 4.0.

These transformations brought new levels of collaboration but, also, new problems. As we have seen in Chapter 1, whilst it makes simple adaptive sense to help out members of one's family, helping out non-family members depends on mutual generosity and some kind of assurance that one's efforts will be repaid, if not by that person then by someone else. Ancestral apes would be fully capable of deception, opening up possibilities for exploitation. The more interdependent people became, and the more survival depended on extensive 'give and take', so the more serious would be the consequences of being exploited. There are many situations where a small amount of help from someone who genuinely cares can make a big difference to survival, of which temporary illness or injury is just one example. But how could such help be ensured? Without laws or formal repercussions, what would stop a friend, mate or ally from abandoning someone with a serious injury in time of need?

Emotional commitments, fuelled by trust and abilities to discern who is or is not genuine, solve this problem (Spikins 2019). Genuine emotions act like an insurance policy, forcing other people to pay a price in terms of emotional pain if they do not act in the best interests of someone they care about. In this sense, emotions handcuff people to act on others' behaviours before their own, and vice versa should the situation be reversed. We all experience this most acutely when we talk about the effects of love, or scientifically phrased 'strong emotional bonds'. Love motivates us to sacrifice ourselves for someone else, and when something bad happens to them or we let them down *love hurts*. The extremes of joy and pain through our emotional connection to people we love create strong bonds, resilience to life's challenges and high levels of give and take. However, our tendencies to care can also be exploited, and the more we care about other people the more we are willing to sacrifice and the more we might lose. The more attuned we can be to identifying genuine motivations from fake ones, and at displaying our own genuine intentions, the better we can be at developing relationships based on mutual trust and so the better we are protected from deception or cheating. For this reason, early human interdependence brought with it selective pressures on displaying and identifying genuine emotions and tracking others' reputations, with genuinely caring about others working almost like a type of currency to ensure willing generosity from them in turn (Hoffman, Yoeli, and Nowak 2015; Jordan et al. 2016; Rand and Nowak 2013; Spikins 2015a).

The more important collaboration became to survival, and the more interdependent human groups became, the more important relationships based on trust and long-term emotional commitments were. This, in turn, meant that having, displaying and being able to identify genuine kindness became more important also. The potential for exploitation also became greater, of course. The need to express and identify genuine motivations, and the possibility of cheating and exploitation, can almost be seen like the escalation of an arms race, to which we credit both our capacities for love and our all-too-present concerns with who to trust and what others feel about us.

We can see the role of reputation affecting other people's emotional willingness to help all around us even today. Examples abound in modern hunter-gatherers, as well as in our own society. Amongst the Martu of the Australian Western Desert, for example, the most genuinely generous hunters are the ones that are most favoured as hunting partners (Bird and Power 2015) and, amongst the Aché of Paraguay, the most genuinely generous hunters were most willingly looked after when ill or elderly (Gurven et al. 2000). It is easy to imagine that these judgements might simply be about actions but instead they rest on judgements of genuine feeling. Amongst the Jo'huansi of the northern Kalahari, for example, too large a gift is treated with suspicion – it might indicate that someone wishes to ingratiate themselves, rather than genuinely caring (Wiessner 2002). Our intuitive judgements about the feelings behind people's actions even affect who we find attractive. Even in Western industrialised societies, more altruistic men tend to be rated as more physically and sexually attractive and desirable as dates than those who are less altruistic (Jensen-Campbell, Graziano, and West 1995), and more genuinely altruistic people also have higher mating success over the long term (Arnocky et al. 2016). It is not *what people do* that matters in highly collaborative human groups but the hidden depths of *the emotional motivations underlying why they do it*.

We tend to imagine that early humans were cunning rather than kind but, perhaps surprisingly, in a climate of trust within small cohesive societies, genuinely caring about others can be a more successful strategy than just being socially clever. We may imagine that collaboration depended on being socially clever, but social astuteness alone does not foster effective collaboration. Strategic social thinking can add 'fuel to the fire' of competition, promoting unethical behaviour (Pierce et al. 2013) and enabling manipulation. Emotional motivations to care about others' wellbeing can be far more important to how people work together effectively than being socially clever (Smith et al. 2017; Stellar et al. 2017). Our willingness to punish those who cheat or who are exploitative also acts like a measure of 'policing' people who are manipulative or purely self-interested (discussed in Chapter 1). Moreover, it is not always an advantage to have more complex social thinking or theory of mind abilities. Higher levels of perspective-taking contribute to anxiety about what others are thinking and have been associated with psychosis (Brosnan et al. 2010). Further, when it comes to making friends, we are often more willing to trust people who do not delve too deeply into what others are thinking about them (Jordan et al. 2016; Spikins, Wright, and Hodgson 2016). Being too socially intelligent can backfire if others are focused on your trustworthiness and suspicious of social astuteness. We may imagine a ‘successful’ early human as rather a self-centred and even cutthroat type of person, successful perhaps through their Machiavellian tactics, but such ideas are purely our own assumptions (Winder and Winder 2015). The nature of collaboration argues that being kind may have mattered much more to success than being cunning.

Trust, emotional commitments and the price to pay for caring about reputation

Collaboration based on emotional commitments, rather than on simple agreements or loose alliances, may have been even more key to human evolutionary success than we imagine. Relationships based on trust meant that collaborative groups could hunt larger and more dangerous prey, as individuals would be willing to risk their lives for others and also to care for injured adults. It also meant that vulnerable young could take longer to reach adulthood, given the security of many adults to care for them, and so could learn more in the process.

However, there was a price to pay for a dependence on such relationships. Firstly, depending on the generosity of one’s socially astute peers for one’s own survival meant that the social and emotional world got a great deal more complicated. Secondly, an awareness of one’s reputation in others’ eyes brought with it emotional vulnerabilities that continue to plague us today.

There are costs in terms of brain power needed to keep track of who to trust. It takes a lot of cognitive effort to fully understand others’ emotional motivations, or their emotional reputation, as this depends on building up a picture over many different moments, not just one individual instance. Without building up our understanding of someone else, we are easily duped by behaviours that appear to be helpful but may hide selfish or harmful intentions. Moreover, whilst chimpanzees only need to track peer-to-peer relationships (single sets of allies), people are also concerned with others’ group morality, the extent to which they want to contribute to the wellbeing of the whole group (Tomasello and Vaish 2013). Understanding what someone’s behaviour might mean about their intentions towards you is already complicated enough, but understanding what their behaviour means about their intentions and motivations with regard to the whole social group is even more complex.

There is good reason to argue that it was the *heightening stakes* on making the right decisions about who to trust that prompted selective pressures on a better understanding of what other people think or feel, including about each other (Hoffman, Yoeli, and Nowak 2015; Rand and Nowak 2013; Spikins 2015a). Quite simply, early humans needed to understand a great deal about what others thought and felt, not only about them but about everyone else, and to get better at building up a picture of others' feelings and actions over many instances. Moreover, these kinds of pressures may have been key to driving accelerated human intelligence and, as we have noted in Chapter 2, it may not be so surprising that even the smallest brained species of early human add enlarged brain areas responsible for social and emotional processing.

These heightened stakes also set the scene for painful emotions such as guilt or shame, which prompt us to adhere to moral norms. After all, painful though such feelings may be, people tend to trust us more when we are visibly guilty or ashamed for our transgressions. Our emotional self-punishment is difficult to fake, and provides some reliable evidence to others that we would find it hard to exploit them. These feelings hardly make our own lives easier, though, and can often become debilitating. The importance of reputation within our social relationships means that we are left with deep-seated concerns and vulnerabilities around what people think about us, and who to trust, making us vulnerable to shame and depression. It may be a price worth paying for deep-seated connections, kindness and support in hard times, but it is not an easy one.

The significance of trust, emotional commitments and a concern with reputation to key issues in human origins

The importance of trust, emotional commitments and reputation to early human collaboration may give us new insights into some of the key questions about our early origins.

Being kind rather than being cunning

We often base our interpretations on the assumption that people who were socially clever were the most successful in our evolutionary past, rather than those who were emotionally kind or good at forging relationships based on trust.

It is not difficult to see why we have made this assumption. Our preconceptions about what must have been important for success may have played a role (discussed in the introduction to this volume). Moreover, drawing a straight line between our nearest relatives, chimpanzees, and ourselves may be another influence. As we have seen in Chapter 1, imagining our ancestors as existing part way along a continuum between non-human ape and modern human easily prompts us to ignore the importance of interdependence, emotionally based collaboration, and response to vulnerability to how early humans survived.

There are also other reasons why being socially clever, rather than kind, has been emphasised in our evolutionary origins. Evidence from changes in the size and shape of the human brain through time seem to point in the direction of increasingly large, and so socially challenging, human groups rather than small and cohesive ones. Social understanding or theory of mind abilities are key to keeping track of many individuals within the type of large-scale social network such as we imagine characterised an early human past (Lewis et al. 2011; Noonan et al. 2018). Increases in prefrontal (neocortex) size through human evolution, alongside comparisons with other species, were taken to imply a progression towards increasingly large human social networks (Lehmann and Dunbar 2009). On this basis, it appeared that selection pressures on the 'social brain' and so our abilities to manage complex social situations, drove expansions in human intelligence.

There are problems with the idea of increasingly socially intelligent humans adapted to ever larger social networks, however. Whilst neocortex size does increase throughout human evolution, this may not be primarily indicative of increasing group sizes, and with this the need to negotiate relationships with many people, but rather of a need to forge closer and more trusting relationships with a few.

Firstly, the relationship between neocortex size and group sizes has been called into question, with clear correlations difficult to identify (Lindenfors, Wartel, and Lind 2021; Miller, Barton, and Nunn 2019). Secondly, there is little archaeological evidence for either large groups or large social networks prior to 300,000 years ago, and archaeological and genetic evidence more clearly support small close-knit groups rather than large complex social communities, as discussed in Part 2. An increasing neocortex size may have more to do with emotional understanding and social emotional relationships than with simply being socially complex. Theory of mind (understanding what other people think) and emotional understanding (affective empathy) use somewhat different parts of the brain (Stietz et al. 2019) but both involve increasing activity in the neocortex.

Social networks and social intelligence, in terms of keeping track of many people, may be a much less significant factor in our evolutionary history than we imagine. We can 'keep track of' many different relationships without these relationships necessarily having any real depth or significance in our lives. Some 'relationships' that involve theory of mind and perspective-taking do not involve any meaningful emotional interaction. For example, chimpanzees use their social abilities to pay close attention to the calls of neighbouring groups and what they mean about their politics (Sapolsky 2017), paying more attention to socially surprising sounds (such as submission by a dominant individual to a lower-ranking one) (Figure 3.4). Ravens use their social intelligence in the same way (Massen et al. 2014). In each case, this demands social cognitive complexity. In similar ways, in modern societies we use our social competence to keep track of relationships between pretend characters, which feel like they are real but are similarly not a meaningful part of an alliance network (Lather and Moyer-Guse 2011). None of these relationships provides allies who are there when needed.

If we redress the balance and take on board the significance of trust, emotional commitments and reputation to our human origins, we may contribute to several key debates – from early cultural transmission knowledge to the explanations for a concern with aesthetics to the mechanisms promoting inclusion of different minds into early societies.

Reflecting on the cultural transmission of knowledge

Most authors agree that the capacity to pass on knowledge from one generation to another, or cultural transmission, is a significant evolutionary step in our origins. However, in terms of explaining this important transformation,

Figure 3.4: A group of chimpanzees at Kibale National Park, Uganda, stop near the boundary between groups and listen carefully to the calls within their neighbouring group for several minutes before moving on. Photo copyright John Mitani, reproduced with permission.

we have tended to focus on the role of capacities for social communication, including language.

There has been a tendency to assume that teaching and learning are primarily about effective communication. From this perspective, passing on knowledge from one generation to another comes about through being able to communicate that knowledge effectively, both technically in terms of language and socially in terms of understanding of how others think. However, cultural transmission of important innovations and knowledge may be one example of the often-underestimated role of trust and emotional commitments. Emotional dispositions and abilities may be more critical to learning and teaching of skills than we imagine.

Abilities to teach new skills to others (particularly stone tool production) have been related to perspective-taking capacities (Shipton 2010). However, emotional motivations towards others' wellbeing may be as much, if not more important, in learning. There is good reason to suggest that motivations to teach skills and a sense of safety needed to learn are most dependent on emotional connections, rather than cognitive skills. Those social species that are most collaborative and most emotionally motivated to care about offspring seem most disposed to teach skills to their young, rather than those that are most socially or cognitively clever. We might expect our nearest relatives, the chimpanzees, with the highest non-human theory of mind abilities, to be the most adept at teaching skills to the young. However, young chimpanzees typically learn only by copying adult behaviour rather than by being actively taught. It is amongst far more distantly related collaboratively breeding tamarins that we see evidence of teaching, including vocalisations, amending food transfers according to skills and sculpting of behaviours (Snowdon 2011). Cooperatively breeding meerkats may not technically be clever but they teach foraging skills to the young, such as by stunning scorpions to allow young to learn how to kill them (Thornton and McAuliffe 2006). Moreover, bonding hormones play a key role in this activity. Increasing levels of oxytocin in meerkats cause increased efforts to teach skills (Madden and Clutton-Brock 2011). On a phylogenetic level, teaching appears to be more associated with cooperative breeding and emotional motivations to care for other group members than theory of mind (Thornton and McAuliffe 2015).

Changes in emotional dispositions as early humans become more collaborative may have had a far greater impact on facilities to learn new skills and pass on cultures than we think. We have tended to assume that more complex technology associated with the origins of *Homo*, which must have been taught across generations, was a product of increasing social understanding, more complex theory of mind abilities, and so abilities to teach others, for example. Changing emotional dispositions, affecting motivations to share knowledge, may have been equally, if not more, important.

Reflecting on the influence of emotional reputation on attention to the aesthetics of artefact form

The importance of emotional commitments may also cast light on questions of the earliest concern with aesthetics and symmetry.

Of all artefacts, it is perhaps stone tools that we most tend to associate with being purely functional. However, even these artefacts may demonstrate quite how sensitive our complex emotional brains were, even as far back as nearly 2 million years ago.

It is handaxes, or bifaces, in particular that have attracted attention for their potential to inform us about early human emotional capacities. Handaxes begin to appear in the archaeological record after 2 million years ago, alongside increased meat eating. They were almost certainly largely used to butcher meat, remaining in use for over a million years. Research into the form of handaxes or bifaces argues that these carefully formed stone tools may demonstrate a certain sensitivity to reputation in their construction (Green and Spikins 2020; Spikins 2012). Attention has been drawn to these artefacts as they demonstrate a concern with symmetry and the aesthetics of form in their construction, usually complying with what appears to be a mental template of what a finished tool ought to look like in terms of a typical teardrop symmetrical shape (Figure 3.5).

Figure 3.5: Photograph of a handaxe or biface from Olduvai, dated to around 1.2 million years ago, illustrating attention to symmetry and the pleasing aesthetic form of these artefacts (on display in the British Museum). Johnbod, CC BY-SA 3.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Olduvai_handaxeDSCF6959.jpg.

Two particular characteristics of bifaces suggest that they may have played an important role as signals of genuine emotional motivation. Firstly, by imposing an aesthetically pleasing symmetry on an artefact that may be used by others, early humans may have been demonstrating their other-focus – the extent to which the feelings and wellbeing of those around them demonstrably mattered to them. Secondly, early humans may also have been signalling their abilities at inhibitory control, or overcoming frustration (Green and Spikins 2020; Spikins 2012). Certainly, it is far more difficult to impose a preconceived form on a stone tool than simply to create a sharp edge. Imposing the classic teardrop shape of a biface a flint core demands considerable inhibitory control (or what we might more prosaically call patience or self-control).

Both of these capacities are plausibly important to collaborative social relationships and liable to others' judgements. Any species that becomes more socially collaborative also needs to develop increased inhibitory control – the capacity to withstand motivations to act, particularly in one's own interests. We use inhibitory control, or patience, when we share food rather than 'giving in' to the temptation to eat it all ourselves. Being able to act prosocially in response to others' needs demands not only empathy but also inhibitory control – our capacity to handle emotions. When we see someone in pain, for example, we feel an empathetic response, particularly if we care about them. Without being able to exert some self-control over our emotions, our own empathetic feelings can be overwhelming. Feeling empathy only leads to compassionate helping behaviour if we can handle difficult emotions and overcome tendencies to simply act impulsively.

Evolved capacities for impulse control (self-control/inhibitory control), or more prosaically patience, vary between different species, as well as according to any animal's experiences. Sometimes, evolved selective pressures to handle emotional impulses arise simply from the type of resources different animals exploit. Predators need inhibitory control to resist temptations to 'pounce' until the right moment, for example. There can also be subtle pressures that influence differences between closely related species. Amongst New World monkeys, for example, common marmosets depend on exploiting sap that oozes slowly from trees and are more 'patient' than cotton top tamarins, which more predominantly exploit quick-moving insects, requiring greater impulsivity (Stevens, Hallinan, and Hauser 2005).

For highly social animals, getting along with others often demands a need to withstand immediate impulses, such as desires to snatch food from others, to hit back or even to run away. Social-living primates, such as our nearest relatives, chimpanzees and bonobos, typically show high levels of self-control, for example. Chimpanzees and bonobos are able to wait for a greater food reward rather than impulsively take what is immediately on offer, suggesting comparable abilities in our shared ancestor (Rosati et al. 2007). Social carnivores are particularly adept at impulse control as they depend so intimately on high levels of collaboration for survival (Marshall-Pescini, Virányi, and Range 2015). Wolves are able to share food, which entails withstanding the frustrations of being hungry themselves in order that those they care about can eat (Dale et al. 2017). Moreover, although conflicts erupt often in wolf packs, actual violence is rare, with impulse control allowing wolves to focus more on a reprimand and typically stop short of actual serious harm (Marshall-Pescini et al. 2017). In social mammals, play performs an important function in fostering emotional regulation, providing an arena to safely practise frustrations (Bekoff 2001; Linsey and Colwell 2003; Palagi et al. 2016). In chimpanzees and bonobos (Palagi 2006) and wolves (Cordoni 2009), as well as in humans, social play extends into adulthood.

Self-control in humans shares similar features to that in other animals (Miller et al. 2010). However, we also have extra levels of emotional regulation. We can also draw on our conscious self-awareness of how we feel, and our capacities to label (or 'tame') our feelings, as well as being able to use conscious strategies to resist temptation (Hobson 2002). By bringing our emotions into awareness, sharing them with others, and rationalising and reframing our emotional experience, we can use our gut feelings as well as our rational thinking to make decisions (Damasio and Dolan 1999).

Capacities for self-control and emotional regulation have far-reaching influences on human lives, affecting social relationships, achievement, and propensity to anxiety and depression (de Ridder et al. 2012; Joormann and Gotlib 2010; Tangney, Baumeister, and Boone 2004), and predicting academic performance better than IQ (Duckworth and Seligman 2005). Higher-level controls on impulses also make it possible to delay gratification over considerable timescales, for example saving money today for a pension many decades in the future. More than this, however, our abilities to withstand being carried away by our emotions allow us to translate the intensity of feelings we have for those we love to help them in pain, loss and grief.

Though it takes extra effort and inhibitory control to overcome the frustrations involved in imposing symmetry on the form of a biface, given the significance of demonstrating one's genuine motivations, this 'costly signalling' would almost certainly pay off in terms of fostering stronger social bonds (Spikins 2012). In modern, highly collaborative societies, material displays of genuine generosity and inhibitory control in giving away food even when hungry have been shown to have rewards in later life through the willingness of others to help at times of illness or infirmity (Gurven et al. 2000). Conversely, material displays of impulsivity, at least in adults, are typically treated with a certain disdain and loss of status, as seen amongst the Inuit (Briggs 1970). Almost everything we do betrays how we feel, and the way in which we create and use objects around us is no different. Whilst we tend to focus on how more complex stone tools, such as handaxes, gave early humans who used them a technological advantage over other hominins, their ability to display subtle messages about generosity or trust may have been equally if not more important. Not only can subtle messages in the creation and use of material things send signals about positive reputation; they may also perform a role as signs of comfort, safety and familiarity that might promote physiological safeness and increase confidence to explore (discussed in Chapter 7).

Of course, there may be far more to handaxe symmetry than simply displaying positive emotional capacities to others who were sensitive to such indicators. Certainly, an irrational concern with the aesthetic form of bifaces has been a source of much debate (Gowlett 2011; Gowlett 2020; Hayden and Villeneuve 2009; Hodgson 2015; Kohn and Mithen 1999; Lycett 2008; McNabb and Cole 2015; Nowell and Chang 2009; Wynn and Gowlett 2018). Nonetheless, much like cave art many thousands of years later, it is clear that these subtle signs of inner emotions can have powerful influence.

A sensitivity to moral reputation may also be part of social processes that fostered the inclusion of diverse cognitive styles in the evolutionary past.

Reflecting on a sensitivity to emotional motivations and the integration of different minds

An understanding of the significance of relationships based on trust and of judgements of reputation may also contribute to our understanding of the mechanisms driving inclusion of people with different minds within societies.

As we discussed in the introduction to this volume, all too often we impose an idea on the past of there being a simple progression in human evolution from one individual being to another, when the real story is far more complex. We know that human populations are not really many examples of a single 'ideal' mind but are made up of many different minds that work together, but we easily forget this when we discuss our evolutionary past. The concept of a progressively better individual through time tends to easily suppress our understanding of the significance of diversity to human evolutionary success.

One particularly important example of how the interaction between different minds may have contributed to our evolutionary history comes from research on autism. Few people fit into the mould of having what we might think of as a 'normal' mind, and the differences associated with autism present us with one of the most interesting, important and hotly debated areas of cognitive difference.

Definitions of autism have changed over the years. Nonetheless, there is a general consensus that people who we say have an autism spectrum condition (ASC) tend to display a constellation of traits related to how they perceive the world and their social perception. Individuals with ASC tend to lie at the extreme of perceiving and thinking in terms of high levels of detail (Happé and Frith 2006), and in terms of rules and systems rather than intuitive understandings (Baron-Cohen and Lombardo 2017). Their strategic social thinking is limited, and they tend to have only low levels of theory of mind (being more likely to fail at the level of second-order theory of mind, i.e. 'Y believes that X believes this'; Baron-Cohen 1989). Whilst, in the earliest cases of autism, the term implied a highly debilitating condition, today only about 30% of cases of ASCs are associated with intellectual impairment (Iossifov et al. 2014). Autism without intellectual impairment is more common, and is often seen as more of a difference than a disability, bringing with it both talents and vulnerabilities (for a more detailed review, see Spikins 2009; Spikins, Scott, and Wright 2017; Spikins, Wright, and Hodgson 2016; Wright, Spikins, and Pearson 2020).

For many years, it was assumed that autism was simply a disorder, and that autistic individuals would not have survived in the societies of the far-distant past (Bednarik 2013; Bednarik 2016; Pickard, Pickard, and Bonsall 2011). However, relatively recently genetic evidence has proved that this assumption was wrong. Some of the variants of genes associated with traits related to autism are present across primates, being identified in macaques, for example (Yoshida et al. 2016). Autistic traits have also been recorded in chimpanzees (Faughn et al. 2015). Autism seems to be an essential part of that evolvability of the human gene, that is, its capacity to adapt. Moreover, autism has been subject to positive selection (Polimanti and Gelernter 2017) and there also seems to be a proliferation of genes associated with autism in relatively recent evolution (Nuttle et al. 2016). Not only were individuals with ASC present in the past, but there appears to sometimes have been certain advantages to the condition.

We will probably never identify any individual archaeological artefact made by someone who we would now identify with ASC. However, there are some clues as to the involvement in Palaeolithic societies.

How individuals with ASC interact with the material world around us today show subtle differences (Spikins, Scott, and Wright 2017; Spikins, Wright, and Scott 2017; Wright et al. 2021). A far greater percentage of individuals with ASC today have extraordinary talents in realistic depiction as a direct result of their enhanced detail focus, for example (Spikins, Scott, and Wright 2017). Extraordinarily talented autistic artists are well known; however, a tendency to show greater talent in realistic depiction is seen across the whole population of individuals with ASC. Furthermore, individuals with ASC tend to be drawn to creating and owning highly technological objects and ones made with a high degree of precision, a trait that enhances their abilities to produce highly specialised technology (Spikins and Wright 2016; Spikins, Wright, and Hodgson 2016).

A focus on technology and detail may have been particularly important to the ability of past hunting and gathering populations to survive in cold and highly risky environments. As we see in the modern Inuit today, complex technology is essential for survival in such situations. In these particular contexts, of which Ice Age Europe is a particularly good example, the skills associated with autism may have been particularly valued. Similarities between highly realistic depictions in European Upper Palaeolithic art and that of talented autistic artists today are probably explained by the involvement of autistic individuals in producing some of the art but also,

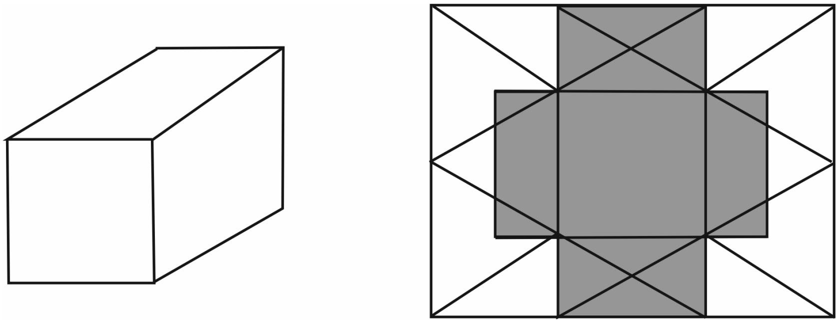


Figure 3.6: Example of an embedded figure test. Individuals with ASC have superior abilities at identifying the shape on the left within that on the right. Penny Spikins, CC BY-NC 4.0.

perhaps more importantly, influencing the style of art (Spikins, Scott, and Wright 2017).

Given that we know that autistic individuals were present in the Palaeolithic past, and able to make a contribution, the question then becomes: why and how were autistic individuals integrated into past societies?

There are many potential advantages to the inclusion of individuals with autistic talents. ASCs are associated with elevated abilities in various domains. These include visual perception (perception of detail, identifying hidden figures; see Figure 3.6), focus, pitch, smell and taste detection, as well as social skills such as an unemotional response to crisis and concern with fairness (see Spikins, Wright, and Hodgson 2016).

Many autistic people have remarkable talents in particular domains. In studies of over 250 autistic individuals, Meilleur, Jelenic and Mottron (2015) found that over 60% had some special skills. These 'savant talents' occur in several realms, including computational (listed as 'easily able to multiply two numbers in the millions together in head; can tell the elevation of both the sun and the moon at any time on any date without reference to any book'), calendrical ('could tell people what day of the week their birthday would occur and what day of the week they were born on'), memory ('a few years ago, he was bought a book which was read to him; this year we read it to him again after over a year – if we stopped he would finish the rest of the sentence quite accurately') and visuospatial abilities ('successful in painting portraits of friends, friends' children and selling them') (Howlin et al. 2009).

Strategic social thinking is not always important to being successful. In a study of 840 Cambridge University students, around 2% scored in an autism quotient range suggestive of having ASC (Baron-Cohen et al. 2001). As Baron-Cohen comments,

> None of those meeting criteria complained of any current unhappiness. Indeed, many of them reported that within a University setting their desire not to be sociable, together with their desire to pursue their narrow or repetitive interests (typically mathematics and computing) was not considered odd, and was even valued. (Baron-Cohen et al. 2001: 12)

Our own research has demonstrated the same pattern in students at York (Spikins, Wright, and Hodgson 2016), as well as how the different perception and skills of autistic individuals are reflected in unique forms of art (Spikins, Scott, and Wright 2017), particular preferences for cherished possessions (Spikins, Wright, and Scott 2017), and certain attributes of the built environment (Schofield et al. 2020). Rather than there being a single human mind, society is in reality a *balance of minds*.

Although there may be challenges to the integration of autistic individuals, it is not difficult to see that some of these abilities could be a real advantage in realms such as hunting, medicine or technology. Such advantages might even particularly be important in cases of environmental unpredictability, when being able to quickly develop new technologies or exploit new resources may have been vital to survival. Technological abilities may even have provided the potential for specialised roles, such as around the production of elaborate and highly detailed technologies.

Were autistic individuals integrated into prehistoric societies *because of* their talents? An understanding of the significance of emotional motivations adds a new perspective to this debate. As we have seen above, when we make judgements of others, we tend to focus on the emotional motivations behind their actions – whether they intended to help others or not. An explanation for the integration of autism should probably look beyond simply behaviours and abilities to emotional motivations, and the motivations of autistic individuals to make a contribution to group wellbeing, albeit perhaps in subtly different realms.

Motivations to help others are not affected by ASC per se (that is to say, individuals with ASC are as likely to be motivated to act for the common good as are individuals who are neurotypical). Whilst empathy for complex emotions may be impaired in autism, empathy for pain remains intact (Hadjikhani et al. 2014). Most autistic individuals are highly motivated to make a contribution, albeit often in particular realms such as law or medicine or justice (Spikins 2009; Spikins, Wright, and Hodgson 2016). For this reason, the emergence of group judgements based on genuine emotional motivations (collaborative morality) and around contributions to the group interests seem likely to have been an important part of the process whereby autistic individuals became an essential part of the balance of human societies.

Particular roles for autistic individuals may have been most evident in the later phases of human evolution (discussed in Part 2), potentially as part of a process that includes occupation of high latitudes, and larger group sizes in which specialised roles become more sustainable. However, the inclusion of autism is discussed here as the primary driver for this process seems not to be strategic skills that autistic individuals may possess, but rather their shared human capacity to think about the wellbeing of the group above their own.

There is almost certainly more to understand, and disentangling the mechanisms and reasons behind the inclusion of autism into human societies may continue well into the future. There are, after all, a number of complexities to this issue. It would be rather convenient for our understanding if genes simply mapped onto autism, and yet this quite clearly is not the case. The actual situation is frustratingly complex. Not only are there over a thousand genes that show some association with autism but also the relationship between gene variants and autistic traits is certainly not a simple one. Moreover, there are complex issues such as epigenetic factors, that is, the potential effects of environmental conditions on the expression of particular genes. Neither is the presence of any particular difference within populations necessarily any indication that it was selectively advantageous; simply not making a difference can be enough, as is often the case with hair or eye colour. As we shall see throughout this volume, we can construct a speculative explanation for why evolutionary changes took place, but may never entirely understand whether our perfectly plausible explanation is the right one. At best, we hope we are getting nearer to the truth.

We can be confident that autism is not outside of the human evolutionary story but is very much part of what makes us human. Certainly, the condition deserves to be seen in terms of its positive attributes, as well as the challenges it may impose (Wright, Spikins, and Pearson 2020).

Rethinking our societies of the past as ones in which feelings, motivations and sensitivities to others were centre stage may help us better understand the changes taking place.

Further questions

Many questions remain. We have seen through the three chapters in Part 1 of this volume that ecological changes after 2 million years ago, and opportunities to move into new niches involving greater meat eating and collaborative hunting, placed new selection pressures on human emotional responses. Increasing interdependence placed selective pressures on group members to care more deeply about each other, and in long-term ways.

As a result, we share emotional motivations to share with and care for others in our group with other highly social and collaborative animals. However, for all the similarities, our human emotional connections, in particular our long-term commitments and the importance of trust in our relationships, are markedly different to those of other animals. We can recognise that our human reliance on emotional commitments has its roots in the complex social brain of an ape placed under pressure to collaborate in more in-depth ways. Yet there is also much more to understand about the timing and mechanisms underlying the significance of trust and reputation to human emotional connections.

There is also more to understand about who is cared for, trusted and included. Here we have focused on the inclusion of different minds within close kin and living groups. But what about the inclusion of strangers or people who are different or unfamiliar in other ways? To address this question, in Chapters 4 and 5 we turn our attention to the evolution of increasing tolerance towards those outside of our familiar living groups. Beyond the question of other people, however, lies that of other animals, or of even things with which we develop strong emotional connections. These are topics we turn to in Chapters 6 and 7.

What about competing pressures towards self-interest? It would be foolish to portray human societies as wholly driven by motivations of generosity and trust. Rather, there seems to be a balance, both at an individual and a social level, between pressures towards self-interest or exploitation of others, and those towards generosity, sharing or compassion. A complex dynamic exists between our emotional desires to share and care and those to hold and control (Gilbert 2021). In climates of trust, it may pay to be genuinely kind, but there are highly competitive climates in which it pays to be cunning or exploitative. Both contexts may have existed in a certain equilibrium within past societies, or even have been expressed differently in alternative evolutionary pathways in the past. The developmental influences on this dynamic, and its implications for the future, are discussed in more detail in Chapter 5.

There are also many other issues that remain to be explored and for which this discussion is merely a starting point. Our capacities for emotional commitments themselves bring their own constraints, for example. Close-knit collaboration brings a cost in terms of tendencies to look inwards rather than out, and may have restricted the capacity of human groups to make large-scale connections until at least 300,000 years ago. Different evolutionary branches with different types of emotional connections are likely to have existed, as explored in Part 3. Moreover, emotional commitments have a darker side. The same loyalties and a willingness to take risks on behalf of others and to make great sacrifices for the sake of the group can also motivate some of the darker elements of human nature, including wars, feuds and vendettas. There is some evidence that conflicts may even have been important in human dispersal events after 100,000 years ago, for example (Spikins 2015b).

For all that love and trust are some of our human characteristics that we most applaud, there is much more that might be said about the negative side of human loyalties. The drives to defend loved ones and to make sacrifices on the behalf of others play an important role in much of human war and suffering (Spikins 2015a). We may have only scratched the surface of what might be discussed, discovered or explored.

Wired for trust?

Perhaps we have at least begun a journey towards uncovering evidence for the significance of kindness, trust and emotional commitments in our shared origins. Our understanding of our long evolutionary history of living in close-knit communities connected by warmth, trust and interdependence may also cause us to begin to reflect on the mismatch between today's societies and our evolved make-up. In this light, we may be less surprised that an education system based on competition, judgement and a focus on quantifying merit fuels an epidemic of mental ill health amongst the young. Equally, the causes of high rates of depression in the context of rising inequality and declining social trust may be easier to explain. In beginning to resolve these issues, and to develop the type of society structures that promote better emotional connections and support the caring side of our natures, we might be helped by a more accurate narrative of what made humans successful as a species than one that emphasises cunning and self-interest above caring and community.

Conclusions

Our acute sensitivity to the feelings underlying other people's actions seems most likely to stem from increasing pressures on early humans to be ever better at judging who they could safely trust. From here, we began a journey towards extraordinary attunement to others' emotions and concerns as to how we might appear to others.

A focus on changes in our emotional brain, rather than on more strategic social intelligence, explains how strong bonds relying on mutual generosity fostered survival through challenging environments. It also provides insights into archaeological questions of changes in teaching and learning, the integration of different minds, and attention to the aesthetics of stone tools. Rather than intelligence or social understanding, it may have been changing emotional motivations that allowed more effective collaboration and made changes in intelligence, social complexity and cultural transmission possible.

Other changes taking place over the last 300,000 years, alongside pressures to look beyond familiar local allies, added further fuel to changes in social sensitivity, needs for belonging, and motivations to be likeable, as discussed in Part 2.

Key points

- Changes in affective empathy and in our emotional attunement to others may have been a more significant factor in human social evolution than developments in social thinking skills. Furthermore, rather than strategic social astuteness, displaying genuine emotional motivations towards others and being sensitive to genuine emotions in those around us may have played a greater role in evolutionary success than we imagine.

- Archaeological evidence suggests that a *sensitivity to moral reputation*, the pattern of emotional motivations towards others someone expresses over time, emerged after 2 million years ago, as seen in a concern for symmetry and aesthetics in stone tool form. Furthermore, later developments in the significance of genuine emotional motivations to group wellbeing, and collaborative morality, may have provided a basis for the cultural transmission of knowledge and for the inclusion of different minds within human populations.

- Our human emotional minds developed through compromises between strengths and vulnerabilities. Collaboration based on trust and emotional commitments came at the cost of individual sensitivities to what others think or feel about us.

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Part 2

Tolerance, Sensitivity and Emotional Vulnerability

In Part 2, we consider the development of human *tolerance*, or changes in social approach/avoidance behaviours. We consider how and why we became capable of extending compassion outwards beyond our close kin and living group, showing tolerance and generosity towards neighbouring groups and distant friends, and the implications of this for human social sensitivity and emotional vulnerability.

We begin in Chapter 4 with the evolutionary basis for our physiological and hormonal responses to unfamiliar people, before continuing in Chapter 5 to consider the issue of increasing human friendliness and social sensitivity or human 'self-domestication'. In Chapter 6, we consider how new social sensitivities and emotional vulnerabilities changed human relationships with animals, particularly focusing on our increasingly close relationships with wolves and their descendants, domestic dogs. In Chapter 7, we consider how and why significant objects came to play an important emotional role in our lives. We particularly focus our attention on key changes taking place relatively late in our evolutionary history, alongside the emergence of anatomically and cognitively modern humans after 300,000 years ago.

What enables us to form strong relationships beyond our immediate family? How did we become friendly towards strangers? What made large-scale regional connections and the emergence of human *communities* possible? And what were the implications of human tolerance for our social relationships and emotional lives?

CHAPTER 4

The Evolutionary Basis for Human Tolerance – Physiological Responses

Abstract

For most animals, unfamiliar members of other groups present more of a threat than an opportunity, and are best avoided or even attacked. In contrast, our attitudes are markedly different. There is no denying that we are capable of being hostile to people we do not know, particularly if we feel anxious or threatened. However, compared to other animals, we are unusually open to new relationships, and form strong bonds with individuals outside our family group.

Although we tend to focus on the 'thinking' part of our minds, or our cognitive appraisal of social situations, our physiological responses and emotional reactions play a central role in how we build and maintain relationships. Subtle changes in 'gut feelings' can have an important influence on our attitudes to people around us, particularly to unfamiliar outsiders or people we have not seen for some time.

An understanding of how different hormones affect social behaviour in other species, as well as in humans, provides insights into the type of changes that led to increasing human 'friendliness'. Genetic and

(Abstract continued on next page)

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(Abstract continued from previous page)

anatomical evidence documents subtle changes in neuroendocrine function in recent human evolution after 300,000 years ago that appear to have played an important role in increasing tolerance of unfamiliarity, and abilities to forge new external bonds. Being able to make external connections, and form new relationships based on give and take despite lengthy periods apart, seems to have been important to our success as a species. Friends in distant communities may often have been important to survival by providing resources or help that could buffer the effects of crises and resource shortfalls. We find that it is genuine emotional commitments to distant friends, rather than strategic alliances, that allow modern hunter-gatherers to survive in times of crisis.

Changes in emotional dispositions towards being less aggressive and more tolerant of unfamiliar individuals might seem to be progress, but we should be cautious in thinking in these terms. Increased ‘friendliness’ is not without its disadvantages. It also brings downsides in terms of social sensitivities and emotional vulnerabilities that influence much of human behaviour.

Figure 4.1: Male bonobo at Lola ya Bonobo, Democratic Republic of Congo. Evanmaclean, Public domain, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Male_Bonobo_Lola_ya_Bonobo_2008.jpg.

Introduction

In 2017, researchers working with bonobos at LuiKotale, Democratic Republic of Congo (DRC), documented an apparently unusual encounter between two different communities of bonobos (Figure 4.1 shows an adult male bonobo, or pygmy chimpanzee, *Pan paniscus*). Generally, most animals are distrustful of other groups or are even aggressive towards them. They defend the boundaries of their resources, or at least take great pains to avoid other communities. This only makes evolutionary sense. After all, other communities are made up of individuals with whom they will share few, if any, kin relations and it makes little sense to do anything to benefit these potential 'competitors'. In this case, however, not only were bonobos tolerant of each other's company but, more than this, they shared food (Fruth and Hohmann 2018).

Bonobos can be aggressive (though only rarely violent) at the boundaries between communities. However, they can also be tolerant, so this peaceful interaction was not in itself unusual. On this occasion, however, bonobos from the eastern community (10 adult females, five adult males and infants) joined several members of the western community (12 adult females, three adult males and infants) (Fruth and Hohmann 2018: 96–97). What happened next was very much worthy of note. One of the western males, a bonobo called Camillo, caught a forest antelope (a duiker) and over the next half an hour responded to appeals from the bonobos from both communities to share the meat, which was widely shared between them. During this time, one of the females from the west community and one from the east groomed each other, and an eastern male and western female mated. Such behaviours would be unthinkable in chimpanzees, and yet these bonobos were capable of remarkable tolerance to individuals who were effectively 'outsiders'. Furthermore, further cases of tolerant interactions emerged over subsequent research, often taking place where resources were plentiful (Lucchesi et al. 2020). Peaceful interactions can even occur over several days. These interactions enabled resources at borders to be exploited, rather than avoided, and gave opportunities for intercommunity mating to occur. Moreover, peaceful interactions avoid the risks of injury or even death recorded in intercommunity attacks in chimpanzees.

We might imagine that it pays to defend our community boundaries and be intolerant towards strangers but, in many cases, collaboration can pay off more (Spikins et al. 2021). Of course, human collaboration across community boundaries is much more extensive than that of bonobos. Modern foragers depend on relationships with other communities for access to resources, such as raw materials for stone tools, medicines or salt (Pisor and Surbeck 2019), and survival in times of famine often depends on being able to visit and depend on distant allies (Wiessner 2002). However, bonobos may give us at least some insight into the earliest beginnings of human tolerance.

Intergroup tolerance in the human evolutionary past

We saw in Chapters 1 and 2 that human social relationships within social groups in our distant past were highly collaborative, but what were intercommunity relationships like?

Early humans were certainly highly social, with relationships that revolved around ready responses to vulnerable group members, collaborative infant care and sharing of food and other resources. However, these responses may have focused almost exclusively on kin and living groups. There is good reason to argue that early humans may have been rather socially insular and, at best, only very weakly socially connected across large communities and regions.

It is not uncommon to *assume* that early human societies must have been connected within large social networks, much like we might recognise today. All modern societies, from industrialised societies to those living by hunting and gathering, are linked by social networks that connect many people and large regions. We easily assume early human societies resembled some watered-down version of what we know. Moreover, our nearest relatives live in relatively large connected communities. Fission–fusion societies, like those of chimpanzees, are made up of communities of 50–150 individuals that come together and separate into smaller parties at different times, and these are often seen as a model for our early ancestors. Inspiration for ideas about early human social groups also comes from multilevel animal societies that join together seasonally and are made up of individuals with different levels of kin relations. An example of this is seen in elephants, where individuals are related to key older matriarchs (Wittemyer, Douglas-Hamilton, and Getz 2005). We tend to expect these kinds of socially complex societies in our early ancestors, because we see ourselves as socially complex. Furthermore, evidence from changes in cranial shapes through human origins seemed to support ideas of large early human communities. Increases in neocortex sizes, associated with increasingly complex social understanding, have been interpreted as implying large social networks in the distant past. However, as we have seen in Chapter 3, a relationship between neocortex size and group size has been called into question. There are also other explanations for increasing neocortex sizes related to keeping track of other groups, or to more complex types of within-group relationships such as those associated with trust and emotional commitments.

Evidence from movements of raw materials, the sizes of archaeological sites, inbreeding deformities and genetics, argue that early human social groups were surprisingly constrained in size and insular in scope, with interactions beyond the local group relatively rare. In reality, evidence for intercommunity interactions does not become widespread until much later in human evolution, and at least after 300,000 years ago.

One area of evidence is from the movements of raw materials used to make stone tools. If we look at raw material movements, we see that these largely come from local areas, often within four kilometres, and most likely reflect exploitation by a local group until at least 1.2 million years ago (Marwick 2003). Even by 300,000 years ago, evidence for raw material movements beyond what we might expect to see in local catchments is rare (Layton, O'Hara, and Bilsborough 2012). There are even apparently unexploited boundaries between territories seen in the raw material transport networks of archaic humans in the Near East (Belfer-Cohen and Hovers 2020). These unexploited areas appear to be symptomatic of a desire to avoid other groups.

The sizes of archaeological sites throughout most of human evolution also accord with small, constrained groups. Analysis of faunal remains at FLK Zinj (level 22) at Olduvai dating to around 1.8 million years ago suggest that a group of around 18–28 individuals occupied the site, for example (Domínguez-Rodrigo and Cobo-Sánchez 2017). This relatively small number of individuals matches evidence from footprints at Ileret around 1.5 million years ago that suggests a similar size of social-living group (Dingwall et al. 2013).

Most tellingly, evidence of skeletal material showing deformities related to inbreeding are seen from as early as 1.5 million years ago, and remain common throughout most of the Palaeolithic record (Trinkaus 2018). Even in later phases of human evolution, such as from 1 million to 250,000 years ago, evidence from skeletal abnormalities is common (Ríos et al. 2019; Ríos et al. 2015; Trinkaus 2018). Moreover, genetics (Castellano et al. 2014) supports the notion of high rates of inbreeding in archaic humans, which would be unlikely to occur where social groups were fluid and connected. Genetic evidence for much greater interactions and mating between groups is limited to the Upper Palaeolithic (starting around 100,000 years ago in Africa and 70,000 years ago in the rest of the world) (Sikora et al. 2017).

It seems unlikely that there was *no* interaction between communities in early humans. Distributions of similar artefacts suggest that something like ‘cultures’ existed in archaic humans after around 300,000 years ago, at least (Ruebens 2013). However, similar ways of doing things might not imply community connections on a wider scale – similar behaviours could be maintained though limited mating network interactions, for example. It is certainly possible that movements between communities were limited to those related to mating networks and quite possibly also restricted to females (Lalueza-Fox et al. 2011). Though we tend to assume that early hominins lived lives connected within large social networks, probably based on our own experiences and concepts that they must have been highly ‘social’ in modern terms, there is no good evidence to support this idea prior to the emergence of our own species after around 300,000 years ago.

Given that the evidence doesn’t support the notion of large-scale regionally connected human communities before 300,000 years ago, what were community relationships like? There is a lot that we do not know. It is not clear if what we might call a community (a set of individuals who know each other well) was simply a small group of early humans who foraged together, or made up of several small groups that foraged together or apart at different times. Nonetheless, it is unlikely that group sizes were as large as those of chimpanzees or bonobos, particularly as an ecological niche involving a dependence on meat eating will have significantly constrained population densities. Certainly, for most of our distant evolutionary past, our ancestors seem to have been living in social landscapes in which they were ‘thin on the ground’ (Churchill 2014), making encounters between different communities rare to begin with. There is no reason to imagine aggressive or violent interactions between different communities. Rather, the motivations and willingness to extend social relationships outside of familiar kin and community members seem to have still been largely lacking until after around 300,000 years ago. We could perhaps imagine rare intercommunity interactions a little like those recorded in bonobos, which can be aggressive, avoidant or sometimes cooperative.

It is only after 300,000 years ago, beginning in Africa, that a novel openness to new relationships, and the capacities and needs to connect to an extended social group, appear to have emerged (Dunbar, Gamble, and Gowlett 2014). From bounded groups with constrained mobility and limited contacts between each other we see the emergence of fluid connections across large social landscapes. In these new social contexts, supportive alliances provided a social buffer for resource shortfalls and people maintained connections with a wide number of allies (Coward and Gamble 2008; d'Errico and Stringer 2011; Foley and Gamble 2009; Spikins et al. 2021). Raw materials and finished artefacts that might previously have only come within a predicted home range were now drawn from well outside this range, sometimes even over thousands of kilometres, suggesting both higher levels of mobility and a degree of intergroup exchange (Féblot-Augustins 2009; Layton, O'Hara, and Bilsborough 2012; Marwick 2003).

The explanation for this transformation in intergroup connectivity remains enigmatic. Explanations have largely focused on changes in social intelligence and capacities to remember an extended set of group members (Dunbar, Gamble, and Gowlett 2014; Gamble 2008; Gamble, Gowlett, and Dunbar 2011), or the ways in which cultural objects might be able to symbolise identities (Coward 2015; Gamble 1998). However, changes in emotional dispositions towards unfamiliar individuals may have been playing an important role in these changes. Changes in our biology may also have played a role in changing how we *were able to feel* about outsiders.

Here we explore the role of our physiological reactions in our reactions to unfamiliar individuals, and the ways in which these reactions may have changed throughout our evolutionary past.

The evolutionary background to human physiological reactions to unfamiliar people

When we discuss our physiological and emotional reactions to unfamiliar people, it is usually around the negative elements of other biases against people who look different from ourselves.

It is clear that we have evolved emotional reactions to people who are different, which are, at best, unhelpful and, at worst, dangerous. When encountering strangers, it is sadly all too common to make immediate assumptions about people. We may judge people by a visible physical disability or be less trusting of people of different skin colour to ourselves, for example. We even react with greater empathy when viewing someone in pain who has the same skin tone as ourselves (Sapolsky 2017). Our immediate intuitive emotional reactions can be at odds with our principles.

These reactions are certainly unwelcome. However, in an evolutionary context, they are perhaps not entirely surprising. As we have seen, in most animals, individuals who are not close relatives or who do not belong to the same social group are usually best avoided. It is not unusual for typical responses to unfamiliar individuals to be either fear or aggression. Though we discussed the highly collaborative, and even tender, nature of wolves within their group in Chapter 1, fearful aggression to outsiders is typical (see Figure 4.2). In a moment, they can swap from carer to killer (de Bruin, Ganswindt, and Roux 2016). Even in multilevel societies of animals that live in close proximity, of which baboons are perhaps the best example, there will be close-knit subgroups that do their best to have little to do with the larger population other than to simply put up with their presence (Städele

Figure 4.2: A wolf showing fearful aggression. Denali National Park and Preserve, CC BY 2.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Wolf_Snarl_(5300989527).jpg.

et al. 2015). In animals that live in hierarchically organised kin groups that separate and rejoin, genuine intergroup collaboration between non-kin is rare, and there are no emotional bonds with non-relatives in neighbouring groups. This makes clear sense as neighbouring groups are most likely to be competitors, presenting a threat to one's own resources or even the possibility of violent aggression.

More complex perceptual biases against 'out-groups' also exist in primates. Out-group bias, a tendency to view members of other groups as a whole as lesser or even dangerous, has been recorded in monkeys, for example. As with humans, their preconceived biases towards members of out-groups make it harder for them to associate out-groups with positive things or in-groups with negative ones. Rhesus macaques shown pairings of members of their own or a neighbouring group and images of fruit (which they like) or spiders (which they do not like) stared longest at the 'discordant' pairing of their own group members with spiders, or neighbouring group members and fruit. This implies that their own group members were associated more with nice things (fruit) and other group members with nasty things (spiders) (Mahajan et al. 2011; Sapolsky 2017: 389). Abilities to identify with one social group in contrast with another seem to predate the split between *Pan* and *Homo* lineages and so are likely to have existed in our distant hominin ancestor (Moffett 2013). Moreover, chimpanzee 'pant hoots' show a distinctive group identity (Crockford et al. 2004) and vocalisation of early hominins are likely to have been similar. In the far-distant past, there was good reason to be suspicious of 'outsiders' and, despite our modern friendliness, this suspicion can leave its mark, with people typically using top-down cognitive appraisal (discussed in Chapter 1) to counteract effects of visible differences (Sapolsky 2017). Given this evolutionary context, the occasional sharing across community boundaries seen in bonobos seems even more remarkable.

Overcoming these reactions, and being able to effectively collaborate with other communities in a sustained way that goes beyond the occasional tolerance seen in bonobos, will have been a major challenge for human societies. The formation of new collaborative social alliances will have depended, firstly, on individuals being friendly enough to enable encounters, rather than being fearful or aggressive, and, secondly, on their being open to treating less-familiar individuals a lot like family members, even though their habits, behaviour or ideas may have seemed foreign (Wiessner 2002: 22). Whilst we typically explain changes in the archaeological record involving new patterns of mobility, new alliances and greater cultural connectivity after 300,000 years ago in terms of changes in cognitive capacities or cultural change, changes in emotional motivations may be far more significant than we have imagined (Spikins et al. 2021).

What might have happened, and why?

To address these questions, we need to build up a better understanding of how our neurobiology affects how we relate to other people, and how evolutionary pressures can create long-term changes in hormonal and emotional reactions.

Neurobiology, emotional responses and social behaviour

We might feel that our physiological responses are rather too basic, or biological, to have played an important role in something as complex as changes in human social relationships. However, whilst our physiological reactions in social situations might not determine what we do, they can have a significant influence. Brain, chemical and hormonal systems which moderate *avoidance* (such as fear) can prompt us to keep away from certain people, whilst others that moderate our *approach* behaviour (such as caring responses) make us want to be closer, for example.

Social behaviour in mammals in general is mediated through hormonal and, in turn, physiological responses to particular social situations. As a result, one of the main ways in which social behaviour changes between species is through genetic changes influencing hormone pathways – that is, how the neurobiology of our brains influences us physiologically in any particular social situation or our ‘gut feelings’ (Narvaez 2014; Narvaez et al. 2013; Zink and Meyer-Lindenberg 2012). Certain social situations may make us anxious or afraid, others make us excited, and yet others make us feel calm, connected and secure. Changes over time in the selective advantages and disadvantages of different social behaviours, including behaviours towards individuals who are rarely seen or unfamiliar, are strongly influenced by 'gut feelings' under the control of hormonal responses. Of course, how we behave is about far more than simple biological responses. As discussed in Chapter 1, our perceptions of a social situation influence our hormonal responses and, in turn, our physiological reactions, after which we also have a top-down control over what we think and how we behave. However, how *we feel* can have significant effects on our behaviour towards other people.

Discussions of physiological and hormonal changes in human evolution have been limited, with attention particularly focused on changes in androgens (such as testosterone) and potential effects on reactive aggression (Wrangham 2014; Wrangham 2018). Reduced aggression doubtless played an important role in allowing humans to form external social alliances and intergroup collaboration. However, changes in other key emotional dispositions affecting how we interact socially seem likely to have also played an important role. Rather than any one single response to non-kin or unfamiliar individuals, a capacity and motivation to forge distant social alliances seems likely to have been built on several subtle but important changes in some of the hormonal responses that influence social behaviour (Figure 4.3). Genetic evidence suggests that particular hormones that play an important role in affecting capacities for tolerance include those associated with stress reactivity, such as cortisol, those associated with changes in motivations towards aggression or competition, such as androgens, those associated with reward-seeking behaviour, such as dopamine, and those associated with social bonding, such as oxytocin, vasopressin and beta endorphins (Hare 2017; Theofanopoulou, Andirko, and Boeckx 2018; Theofanopoulou et al. 2017). Each of these hormonal changes appears to have had an important role to play in setting the emotional scene that enabled humans to develop large-scale collaborative social alliances.

The relationship between genes, hormones and emotional responses, and how these evolve, is a fast-moving area and the influence of hormones on physiology and emotional reactions is complex. In some cases, we see similar behavioural changes in different species from either an increase or a decrease in the same hormone in the bloodstream, for example (de Bruin, Ganswindt, and Roux 2016; Trumble, Jaeggi, and Gurven 2015). This is because responses to hormones are mediated by not only levels in

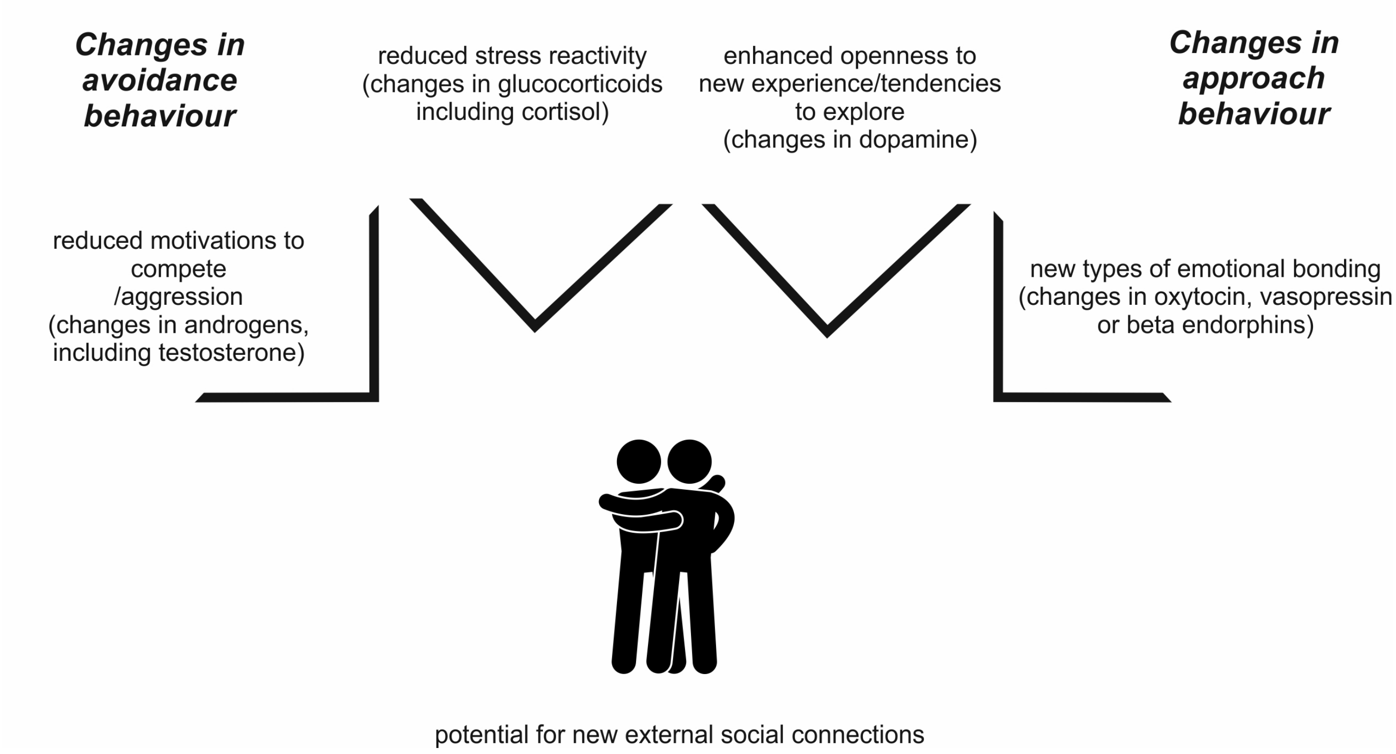

Figure 4.3: Changes in emotional dispositions involved in moving from constrained social groupings to large-scale social alliances. Penny Spikins, CC BY-NC 4.0.

the bloodstream but also receptiveness to different hormones, and how hormones react together. This means that we can at best only really talk about changes in the pathways of particular hormone systems. Moreover, similar behavioural patterns or changes can take place through differing hormonal changes. Monogamy in different species of lemur is controlled by subtly different hormones, and these are different again from those controlling monogamy in prairie voles, for example (Grebe et al. 2021). Nonetheless, there are some simplifications that can at least help us to understand how evolved hormonal responses may have influenced human emotions and behaviours in the past.

What is clear is that subtle changes in emotional reactions, which can often occur quickly on evolutionary scales, can have far-reaching consequences on both avoidance behaviours and approach behaviours.

The physiology of changes in avoidance behaviour – how changes in hormones might make us less competitive or fearful

Often our emotional responses to particular situations tend to push us away from other people. It goes without saying that we usually avoid people or social situations if they make us feel aggressive or fearful. In the former case, behaviour may be influenced by hormones that control competition and aggression, such as androgens, and, in the latter case, by hormones that influence stress reactivity, such as cortisol.

Competition and aggression – the role of androgens

Readily aggressive reactions might deter any would-be ally we might encounter. However, there is no doubt that they solved particular adaptive problems in the evolutionary past – defending resources or our families, for example. It is no surprise that particular hormones, including androgens such as testosterone, exist to play an important role in influencing our gut feelings towards competition or aggression.

We know that variations in testosterone influence human social behaviour, so it only makes sense to conclude that changes in testosterone pathways over time would also change social behaviours on a larger scale. Tendencies in humans to collaborate or compete with strangers in economic games show a relationship with individual variations in testosterone levels, for example. Those who tend to be most collaborative tend to have lower levels of testosterone than those who are more likely to adopt a selfish strategy (Eisenegger et al. 2017; Mehta et al. 2017). This is important, as long-term collaborations tend to depend on individuals being prepared to be generous rather than immediately selfish. Those with typically tolerant and collaborative personalities are also associated with lower levels of testosterone than individuals who display traits of narcissism such as extreme selfishness and self-centredness (Pfattheicher 2016). Moreover, in an evolutionary context, reduced levels of testosterone are associated with increased levels of paternal care in species such as social carnivores (de Bruin, Ganswindt, and Roux 2016). We might reasonably expect selection pressures on testosterone to have been significant in changes in the balance of competition or collaboration in human evolution.

Androgens such as testosterone are particularly interesting within an evolutionary context as they have an influence on physical characteristics which is potentially identifiable in past skeletal material. Androgen hormones control the development of male reproductive tissues, and bone and body mass. 'Extra' muscle and body size are costly but, where male competition for mates is highest, these extra energetic costs beyond that which would be optimal otherwise are worth paying to increase reproductive success (Muller 2017). Thus, 'sexual dimorphism', the difference in body size between males and females, gives us important clues as to the level of male competition driving pressures to be aggressive to other males within and between groups. Sexual dimorphism shows a relationship with male aggression in non-human apes. Gorillas, for example, live in groups comprising a single male and several females. Male gorillas show some of the most extreme reactions to potentially competing males, reacting aggressively to males within their group as they reach adolescence and to any adult males that might approach near to their group. They are also amongst the most highly sexually dimorphic of primates, with male gorillas larger than females by a factor of 1.6–1.7 (Plavcan and van Schaik 1997). It pays off for males to invest in the costly extra efforts of body size, well beyond that which might relate directly to resource availability, as extra power may make a big difference in reproductive success. Male gibbons, in contrast, live in largely monogamous pair bonds, which means they compete far less with each other, and thus male and female gibbons are of a similar size.

Sexual dimorphism in ancestral humans gives us some insights into how human male aggression may have changed through time. On the basis of fossil evidence, australopithecines show some level of sexual dimorphism, perhaps not entirely dissimilar to chimpanzees, whilst sexual dimorphism appears to reduce in early *Homo*, including the small-bodied *Homo naledi* (Garvin et al. 2017). However, making interpretations of fragmentary fossils is plagued with difficulties, not just because only parts of the body are represented and it is rare to be able to identify males and females separately but also because different specimens tend to be compared across a large geographical area where environment may be influencing size (Plavcan 2012; Plavcan et al. 2005). Most notably, it remains unclear where one 'species' ends and another begins in both time and space, making it easy to interpret a high degree of dimorphism between individuals that are actually of different species. It would be unwise to be overly specific about estimates. Nonetheless, assuming our nearest relatives, chimpanzees, with a sexual dimorphism ratio of around 1:1.3, are broadly similar to ancestral apes, it does seem that sexual dimorphism reduces through the hominin lineage. Modern human males are slightly larger than females on average, by a factor of around 1.1–1.2, making them more similar in size than estimates for earlier species (Michael Plavcan 2012). In the broadest terms, it seems that male–male competition has reduced.

Other evidence for androgen levels in an evolutionary context comes from 2D:4D digit ratios – the difference in size between our second and fourth fingers. 2D:4D digit ratios in modern contexts show a relationship with foetal testosterone levels (Pearce et al. 2018). The ratios in both early humans and Neanderthals are higher than those of modern humans, which may suggest a reduction in testosterone in more recent phases of human evolution (Nelson and Shultz 2010; Nelson et al. 2011). Moreover, changes in testosterone are also implicated in research into key genes that changed with the origins of modern humans (Theofanopoulou et al. 2017).

Differences in rates of aggressive conflicts and in testosterone pathways between closely related primate species also provide important insights into the potential role of testosterone in intergroup relationships.

Chimpanzees are renowned for their tendencies to get into aggressive conflict with other groups, in contrast to more common patterns of avoidance in primates as a whole. Testosterone levels rise from infancy onwards, and control the large body size of male chimpanzees compared to females. Testosterone also has an effect on an individual level, with individual differences in testosterone levels associated with the rate of aggressive attacks on others (Anestis 2006). Moreover, on a group level, chimpanzees experience peaks in testosterone in territorial boundary patrols, which then play a role in their aggressive attacks (Sobolewski, Brown, and Mitani 2012). Chimpanzee males at Kibale patrol the limits of their territories, for example, forming coalitions to defend the boundaries of their territories and attacking when they outnumber their opponents, with attacks on individuals from neighbouring territories sometimes being fatal (Watts et al. 2006; Wilson et al. 2014). The most famous and much debated example of chimpanzee violence even led to an entire chimpanzee group at Gombe being apparently systematically attacked by a neighbouring group of which they had previously been a part (Goodall 1986). Aggressors only attack when they outnumber their opponents, so face little risk to themselves and will tend to benefit in terms of increased access to resources (Mitani, Watts, and Amsler 2010; Wilson, Wallauer, and Pusey 2004; Wilson et al. 2014). This territorial aggression commonly leads to territorial advantages, explaining why intragroup aggression may have been advantageous in the past (Crofoot and Wrangham 2010).

It is tempting to draw a link between chimpanzee aggression, testosterone and human violence (Wrangham and Peterson 1996). Testosterone also influences human aggression, after all. Competitors in team games also show a surge of testosterone, even when competitions are not physical, and particularly amongst the winners (Trumble, Jaeggi, and Gurven 2015), suggesting similar positive feelings of solidarity in opposition to the ‘enemy’. We probably sometimes feel a similar rush of excitement, and antipathy towards ‘them’ when watching or playing team games, as do chimpanzees on border patrol. The mechanisms of territorial aggression amongst chimpanzees have even been compared to particular cases of human intergroup aggression, such as that of violent youth gangs, for example (Wrangham and Wilson 2006). It has been suggested that cases of violent ‘raiding’ in hunter-gatherers reflect the same kinds of adaptive advantages to such behaviours, such as taking over the resources of another group, as those observed in non-human primates (Pandit et al. 2016).

The apparent similarities may be superficial, however. Cases of human feuding tend to be skewed towards adolescent and young adult males, who are much more impulsive than adults, given that emotional regulation abilities are not fully mature until their mid-twenties (Sapolsky 2017). Moreover, it is clear that hunter-gatherer raiding is motivated by complex beliefs, loyalties and commitments (Boehm 2000; Boehm 2011). Perhaps even more significantly, hunter-gatherer raiding is set within a context in which there is also collaboration between groups (Boesch et al. 2008). Rates of intergroup violence in modern hunter-gatherers tend to be low (Fry and Söderberg 2013), and substantially lower than in chimpanzees (Wrangham, Wilson, and Muller 2006). Moreover, lethal intergroup aggression is relatively rare in hunter-gatherers and only seen in certain contexts (Lee 2014), and organised conflict appears to be restricted to late in an evolutionary context (Kissel and Kim 2018). Our top-down cognitive control usually makes it easier to rationalise whatever emotions we may feel, and to choose how to act.

The effects of testosterone on social behaviour are far more complex than they might immediately appear. Testosterone can promote parochial altruism and generosity on behalf of one's own group, whilst also promoting out-group aggression, for example (Diekhof, Wittmer, and Reimers 2014). It is probably best thought of not as a hormone controlling aggression but as one influencing motivations to compete, which may play out in complex ways (Sapolsky 2012). Social norms play an important role in mediating how testosterone affects aggression in chimpanzees as well as humans, for example. Within different chimpanzee groups, there are notable differences in attitudes to other groups, particularly being influenced by the role of females. There are lower rates of fatal intergroup attacks and far fewer records of infants being attacked at Taï forest than at Kibale or Gombe, for example. This seems to be because female chimpanzees at Taï forest are more likely to be involved in intergroup encounters, which changes the dynamic of intergroup aggression. Furthermore, Taï forest chimpanzees tend to spring to the defence of an individual being attacked or taken prisoner, even at their own risk (Boesch et al. 2008). Males might feel equally aggressive but learn that attacks are unlikely to be successful (Fuxjager, Trainor, and Marler 2016).

Perhaps the most remarkable influence of social context is that testosterone has even been linked to increased generosity in humans, where a reputation for generosity is considered a mark of status and thus something worth competing for (Diekhof, Wittmer, and Reimers 2014). Moreover, aggression in adulthood is most clearly affected by early trauma rather than testosterone (Fragkaki, Cima, and Granic 2018), and cultural norms have a far more significant effect on aggression than genetics (Shackelford and Hansen 2015). The structure of social relationships can even influence whether other groups feel like competitors. Unlike in modern industrialised contexts, testosterone levels amongst the Tsimane hunter-gatherers do not rise in group competitions, as patterns of mobility mean that groups are made up of a complex mix of kin and non-kin (Trumble et al. 2012) – there are plenty of close friends and relatives in other groups to moderate any competitive feelings towards them. There are many social norms and rules within modern hunter-gatherers that constrain the potential for violence. The complex and interconnected net of social relationships amongst recent hunter-gatherers, in which each individual maintains a set of close friendships beyond their own kin, almost certainly plays a role in preventing out-group biases from developing.

Bonobos provide perhaps the most significant insight into how the evolution of differing hormonal pathways *can* nonetheless influence behaviour (discussed in more detail in Chapter 8). Bonobos are just as closely related to humans as chimpanzees are, and share a common ancestor with them that lived around 1.7 million years ago. Despite this close evolutionary relationship, bonobos have androgen responses that are different from those of chimpanzees and contrast quite markedly in their attitudes towards other groups, as well as in their levels of within-group aggression. In contrast to the rising levels of androgens seen in chimpanzees, levels of androgens in bonobos stay at similar levels from infancy to adulthood (Hare, Wobber, and Wrangham 2012; Wobber et al. 2010; Wobber et al. 2013), with implications for levels of both internal and external aggressive conflict.

Differences between androgen responses in chimpanzees and bonobos undoubtedly help explain the capacities for intergroup collaboration in bonobos, as described at the introduction to this chapter. In contrast with common chimpanzees, intergroup encounters at the borders of bonobo groups are far less aggressive. Fruth and Hohmann (2018) estimated that intergroup encounters occur around one to three times a year amongst groups at LuiKotale, DRC, and sometimes involve threat displays, although actual aggression or violence is very rare. However, importantly, neighbouring groups sometimes forage together. Groups come into contact more often when fruit trees at their shared boundaries are ripe, for example, with both groups exploiting the same fruit trees (Sakamaki et al. 2018). Most remarkable of all is the recorded instance of bonobos sharing food at the borders between groups, described in the introduction to this chapter. These individuals were clearly comfortable sharing with those from other communities, something that Fruth and Hohmann commented would be 'unthinkable' in chimpanzees (Fruth and Hohmann 2018: 99). It seems likely that differences in androgen levels between chimpanzees and bonobos had a major influence in the distinctions in intergroup behaviour between the two species. These might help us understand, therefore, how reduced tendencies towards aggression may also have played a part in changes in sociality in recent human evolution (Wrangham 2014; Wrangham 2018).

Whilst aggressive or competitive responses can certainly lead to avoidance, the same is also true of fearful or stressed responses to social situations.

Fear, stress reactivity and cortisol

Although changing androgen levels have received the most attention, in some cases it is reduced stress reactivity, rather than changing motivations towards aggression or competition, that seem to play the biggest role in reduced aggression.

Being fearful or stressed in the presence of someone who is different or unfamiliar, and thus being motivated to avoid them, makes evolutionary sense for most animals. From an evolutionary perspective, there is every reason to be distrustful, if not overtly aggressive, to outsiders. Firstly, and most obviously, individuals of one's own species who are not members of your own living group are generally not kin, and thus most likely, at the very least, to be competitors for scarce resources. Other members of one's own species may even present a threat to survival if likely to become aggressive and attack. Furthermore, they may also compete for mating opportunities. From the perspective of the potential threat that they may present, it is not too surprising that few species share the potential openness to unfamiliar members of other groups displayed by humans. Most animals endeavour to avoid other groups, such as by territorial displays or vocalisations, or resort to aggressive encounters. It makes sense to take efforts to demarcate the limits of where your group lives, such as by vocalisations or threat displays, and minimise interactions with other groups and warn unfamiliar individuals not to approach. Howler monkeys (genus *Alouatta* of the subfamily Alouattinae), for example, demarcate their territory through sound in an attempt to avoid other groups as much as possible.

For most animals, unfamiliar individuals, or even those they have not seen for some time, are a source of fear and stress, stimulating the production of glucocorticoid hormones such as cortisol and what we traditionally refer to as 'flight or fight' responses. A gut feeling to run away is thus a fairly common response to unusual situations or strangers, in most animals, and makes such feelings in people who we see as being 'socially anxious' all the more understandable. It even makes sense to try to avoid some of the individuals within one's own group. In highly social animals that live in dominance hierarchies we see the production of glucocorticoids in response to the stresses of managing relationships with higher ranking individuals, who may be aggressive. It made more evolutionary sense to be stressed and motivated to avoid the danger of conflicts with individuals of higher rank than not to be stressed by their presence. Low-ranking baboons, for example, tend to have such high glucocorticoid levels that being in a constant state of stress affects their immune function (Archie, Altmann, and Alberts 2012). The kind of stresses they feel are not so different from humans today whose social systems make them fearful and whose immune systems can be equally affected (Snyder-Mackler 2020).

Evolutionary reductions in stress reactivity can constrain fearful reactions and so promote approach behaviour. Reduced stress reactivity may be more important in changes in tolerance in domestic dogs than any changes in androgens, for example (Miklosi 2014). Cortisol levels are a key element to tameness in domesticated species, and cortisol levels are three to five times lower in 'tame' domesticated foxes than in wild ones (Trut, Oskina, and Kharlamova 2009), discussed in Chapter 5. Reductions in cortisol are also key to tolerance in humans. Studies show that human aggression has no simple relationship to testosterone but also appears to be mediated by stress reactivity through cortisol (Montoya et al. 2012). Increased tolerance in humans is thus likely to be a much more complex issue than simply reductions in androgens. The type of increased friendliness that promotes close interactions with unfamiliar individuals seems to involve not just reductions in aggression but also reduced fear through reduced stress reactivity.

There are interesting similarities in reduced stress reactivity between humans and domesticated animals, particularly dogs. Humans and dogs are much less stressed by the presence of strangers than is typical for other species, for example. Securely attached infants and dogs will both prefer to interact with a stranger than to stay with their owner/caregiver (Feuerbacher and Wynne 2017). Dogs *and* people even often prefer social interaction or praise to the immediate basics of survival such as food (Cook et al. 2016). For dogs, this hypersociality helps free-ranging animals to survive by approaching people for food. Street dogs in Moscow, for example, find enough resources to survive by forging relationships with new guardians who them feed them or by begging effectively from passers-by, including on the subway, showing remarkable tolerance for the potential stress of unfamiliar humans (Figure 4.4) (Poyarkov, Vereshchagin, and Bogomolov 2011). For humans, a capacity and motivation to form new external friendships is critical to the formation of large-scale networks of connection (Migliano et al. 2016).

New social relationships can themselves be a means of further reducing a stress response. The presence of allies lowers the levels of stress in low-ranking baboons (Silk et al. 2010) and this same process occurs in both dogs and humans (Heinrichs et al. 2003), not only with their own species but through human–dog bonds (Buttner 2016). Human stress responses can even be reduced by the presence of imagined allies, or their proxies in terms of cherished objects, which can act like compensatory attachments to repair these rifts. Dogs and other animals (Kurdek 2008), beliefs in spiritual beings (Lenfesty and Fikes 2017), and even treasured possessions (Bell and Spikins 2018; Keefer, Landau, and Sullivan 2014; Keefer et al. 2012), can act like parents or attachment figures, making us feel more secure (discussed in Chapters 6 and 7).

Making new social allies and friendships is not just about better tolerating the presence of unfamiliar individuals, however. It depends, however, on motivations to seek out new people, experiences and situations. We need to be *drawn to* friends, unfamiliar people or even animals to form new relationships and even new types of relationships. For this reason, we need to also

Figure 4.4: A Moscow free-roaming dog riding the Metro. A remarkable change in stress reactivity allows domesticated dogs to tolerate unfamiliar humans at close quarters. Here a street dog travelling independently on the Moscow subway is surrounded by people. Adam Baker, CC BY 2.0 via Wikimedia Commons: https://en.wikipedia.org/wiki/Street_dogs_in_Moscow#/media/File:Street_Dog_Riding_the_Subway.jpg.

understand why changes in hormones affecting *approach behaviour* may be implicated in recent changes in human evolution.

The physiology of changes in approach behaviour – how changes in hormones might make us more 'friendly'

Goal seeking exploration and novelty – the influence of dopamine

Dopamine has received much attention recently as the hormone potentially involved in addictive behaviours through activating motivation systems. Dopamine, like serotonin, oxytocin, vasopressin and even testosterone, is one of the hormones which provide us with pleasurable feelings that motivate how we behave. It is the neurotransmitter involved in *pleasurably rewarding* our motivations to seek things out and pursue goals, and is produced by the mesolimbic pathway (or 'reward pathway') in the brain, which connects the more ancient midbrain to the forebrain.

In common with other animals, dopamine motivates us to seek out food or sex. However, dopamine release has also been co-opted through human evolution to motivate our behaviours in a wide variety of complex social contexts (Sapolsky 2017). As we have seen in Chapters 1 and 2, dopamine plays a key role in the 'buzz' we get from helping others (Rilling 2011). Dopamine rewards encourage us to collaborate with others or give to charity, as well as to punish cheats or feel good about the downfall of someone we dislike (Takahashi et al. 2009). We even experience dopamine-related pleasure as an aesthetic response, such as to particularly moving music (Salimpoor et al. 2013), or even to cultural objects such as sports cars (Knutson et al. 2007).

Changes in dopamine are also likely to have been key to seeking out new relationships. As outlined in Part 1, changes in emotional responses are likely to have been important in transformations in social relationships occurring after 2 million years ago. There are suggestions that these changes may have included changes in dopamine as a result of an increase in available fats through increased meat eating (DeLouize et al. 2017). Nonetheless, this hormone may have been most significant in more recent periods. Dopamine influences whether novelty and risk are perceived as pleasurable, and so plays a particularly significant role in adolescent novelty seeking and risk-taking. Changes in dopamine with sexual maturity play a key role in motivating mobility to maintain mating networks in social animals, for example. As Sapolsky explains, the lowered dopamine levels of subadult male baboons prompt them to seek similar 'thrills' in the novelty of neighbouring groups, as individuals in their own groups seem dull in comparison (Sapolsky 2017). As a whole, adolescents feel less dopamine-based pleasures for small rewards and much greater dopamine-based responses to larger rewards than do adults (Vaidya et al. 2013) – sensible options are less rewarding and, with self-control not yet fully mature, risk-taking and impulsivity become ever more likely (Padmanabhan and Luna 2014; Steinberg 2008).

Dopamine can play an important role in directing different behaviour between males and females. It is changes in dopamine and reward-seeking behaviour that allow individuals to overcome their reluctance to associate with members of other groups in the context of mating. At sub-adulthood, males or females (depending which sex moves, usually only one) experience novelty and risk as pleasurable, largely through changes in dopamine and actively seek out members of other groups. We can see this process in male baboons. As a male baboon matures, their feel-good dopamine reward through novelty reduces, and they begin to seek higher and higher levels of novelty to feel any kind of thrill. When neighbouring groups meet, the males will threaten each other and then the groups will retreat, but the adolescent males may linger far longer, appreciating the novelty of the other group. Slowly, the individual will spend more time with the other group, until eventually they transfer groups (Sapolsky 2017: 162). Changing hormones at adolescence have changed how males *feel* about other groups.

In chimpanzees, it is the females who repeat this same process of being drawn to the novelty and excitement of neighbouring groups. Female chimpanzees typically move when they reach adolescence and sexual maturity.

The tolerance shown to males and females from other groups also varies. Whilst chimpanzee males and infants are typically the focus of aggressive and often fatal encounters, females, particularly those in oestrus, are almost never attacked. Even once they have moved to another group, female chimpanzees may still form relationships with individuals in other groups. Around 10% of infants in the Taï forest result from matings with males who are not members of their own group (Boesch et al. 2008).

Generalisations about the structure of social communities may not necessarily describe how all members behave when we take age and sex into account. Whilst we may imagine a landscape of entirely bounded groups in chimpanzees, and a certain level of fearfulness of potential aggressive encounters, this characterisation holds less clearly for subadult females. Female chimpanzees are far more free to move between groups than males, and it is the movement of females that ensures sustainable mating networks (Boesch et al. 2008). The 'female perspective' on mobility is an important one. The intensity of lethal intergroup aggression, and the extent of support for victims of attacks and for 'prisoners', varies with the role of females in intergroup interactions. Where females are more involved in intergroup interactions, as at the Taï forest, there is substantially less violence (Boesch et al. 2008). The role of females also seems to be key to the lack of intergroup conflict and the potential for intergroup collaboration in bonobos (Furuichi 2011). Female primates are no stranger to defensiveness and even violence when protecting their young (Hrdy 2011). However, a transition to tolerance for out-groups seems far less of a leap from a female perspective than it appears from a male one. Females may stay within their own group most of the time, but at least sometimes venturing to associate with other groups is more appealing than scary.

Dopamine affects modern human males and females in similar ways. Whilst culture and conscious choices play an important influence, modern human adolescents are also disproportionately driven to experience increased drives to risk-taking and novelty by hormonal influences on dopaminergic activity in the brain in ways not dissimilar to other mammals. The same hormones also affect their ability to evaluate risk (Kelley, Schochet, and Landry 2004). Amongst the Baka, for example, adolescent males travel great distances to learn new skills from acknowledged specialists, typically motivated by seeking to impress potential partners. In doing so, they play an important role in transmitting knowledge and forging social networks.

How dopamine changes at adolescence affected mobility in *pre*-modern humans remains a matter for debate. Evidence for movements of males and females in australopithecines on the basis of strontium isotope analysis shows the smaller individuals having a non-local signature. Given that the smaller individuals are likely to be female, this suggests primarily females making movements out of the local area (Copeland et al. 2011). The genetic relationships between a Neanderthal group buried under a rockfall at El Sidrón in northern Spain also potentially suggests that Neanderthals were patrilocal, as the group consisted of three brothers with unrelated females and their infants (Lalueza-Fox et al. 2011). It is tempting to suggest that, prior to modern humans, with their distinctive pattern of high mobility and movements by both males and females, archaic and earlier humans showed a chimpanzee-like gender-based mobility pattern, though more evidence would be needed to confirm that this was the case. It is nonetheless notable that archaic and earlier humans show high levels of inbreeding (Trinkaus 2018), suggesting that drives to seek out unfamiliar others, even in relation to mating networks, were somewhat constrained. In contrast, the emergence of modern humans is associated with entirely new levels of mobility, and genetic diversity (Apicella et al. 2012; Templeton 2015). Both a greater propensity to explore and a lack of constraint on gender would have had an important influence on levels of interbreeding.

Changes in the effects of dopamine may be one of the mechanisms by which selection pressures created increased tameness/friendliness during the most recent phase of human evolution after around 300,000 years ago (Cagan and Blass 2016; Theofanopoulou et al. 2017). Whilst we might imagine that reduced aggression is key to such processes (through reduced androgens), *friendliness* depends on connection and openness to novel experience. It is, thus, dopamine which encourages approach behaviour, and dopamine receptor D4 gene (DRD4) is associated with gazing towards humans in domestic dogs for example (Hori et al. 2013). Dopamine has also been associated with maternal bonding (Atzil 2017) and abilities to develop social networks (Pearce et al. 2017).

Increases in the presence of particular dopamine variants may even be implicated in human dispersals after 100,000 years ago. One particular dopamine receptor variant, the 7R (seven repeats or the long allele version) form of dopamine DRD4, is particularly interesting. The 7R variant is associated with relative unresponsiveness to dopamine (i.e. greater thrills are needed for the same response) and is associated with a host of behaviours, including extraversion, exploratory behaviour, novelty seeking, promiscuity, less sensitive parenting, impulsivity and susceptibility to ADHD (Bakermans-Kranenburg and van Ijzendoorn 2006; Chen et al. 1999; Garcia et al. 2010). Polymorphisms in DRD4 predate the dispersal of modern humans out of Africa after 60,000 years ago (Chang et al. 1996; Chen et al. 1999; Ding et al. 2002; Kidd, Pakstis, and Yun 2014). Modern populations that undertake long migrations tend to have greater proportions than more sedentary populations of individuals with long alleles of the DRD4 gene, associated with novelty seeking and hyperactivity (Chen et al. 1999). Moreover, populations farthest from the African origin have the highest rates of the 7R variant associated with impulsivity and novelty seeking. The Ticuna, Surul and Karitiana, occupying the Amazon Basin, have a roughly 70% incidence of 7R variant; the Guihiba and Quechua of northern South America have an incidence of around 55%; and the Maya in Central America have an incidence of around 40%, with lower incidences in more northern populations of the Americas, for example (Ding et al. 2002; Matthews and Butler 2011; Sapolsky 2017). Individuals more prone to novelty seeking may be more likely to find the prospect of new regions alluring, and the familiar as boring, as well as being less prone to stress in novel situations. How they behave will, of course, be influenced by culture, and what is novelty seeking and risk-taking in one society might seem tame in another. Equally, as with many subtle hormonal distinctions, differences bring both advantages and disadvantages. There will be contexts in which it may be beneficial to be more prone to novelty seeking, and in others where it is less so. Risk-taking, and a desire for novelty, might be beneficial overall in yielding rewards in terms of accessing new resources, or might be a disadvantage due to an increased mortality risk.

Genetic variation in DRD4 alleles has other interesting characteristics. It is also one of the best examples of gene–culture interaction, in that the behaviours associated with dopamine-related genes *depend* on cultural context. Long (2R or 7R) allele variants bring an elevated sensitivity to the experience of parenting. That is, securely attached individuals with 7R variants will be more generous than average, whilst the insecurely attached will be less so, for example (Bakermans-Kranenburg and van Ijzendoorn 2011). Moreover, individuals with the long allele variants seem to be more sensitive to cultural influences (Tompson et al. 2018). Such individuals tend to be more individualistic in individualistic cultures and more interdependent in collectivistic ones, to such an extent that the differences between the two cultures on these characteristics disappear if individuals with the long allele variant are excluded from analysis (Kitayama et al. 2014). Like many adaptive variations, there is no simple 'better form', as being more sensitive to one's social context is rather a double-edged sword – such sensitivity also brings a vulnerability to insecure or unsupportive environments.

As well as dopamine, as we have seen in Chapter 1, other hormones also play a key role in maintaining strong relationships. Oxytocin, often called the 'cuddle hormone', is the most famous, but vasopressin, beta endorphins and serotonin also play important roles in making our closet relationships feel comforting and rewarding.

Bonding hormones

As we have seen in Chapter 1, bonding hormones play an important role in social bonding, motivating generosity, care for the vulnerable and altruism within close-knit social groups. Selection on neuroendocrine pathways, including oxytocin and serotonin, are associated with differences in social behaviour between chimpanzees and bonobos, for example (Kovalaskas, Rilling, and Lindo 2020). Changes in oxytocin and beta endorphins are likely to have played a role in the expansion of compassion towards a broader set of group members that we saw occurring between 2 and 1.5 million years ago (Feldman 2017; Gordon et al. 2010). Oxytocin, in particular, is involved in social touch, grooming, and behaviours that facilitate strong emotional bonds, motivate generosity and altruism, and reduce stress (Snowdon 2011).

The role of oxytocin in intergroup collaboration is rather more complicated. Given a long evolutionary history as a motivator of nurturance behaviour in mammalian mothers, oxytocin provokes both nurturance of the young and their defence, including defensive aggression (Snowdon 2011; Ziegler and Crockford 2017). Oxytocin thus has a role in promoting defence from outsiders. As we have seen in Chapter 1, oxytocin is known as the 'tend and defend' hormone (Ziegler and Crockford 2017). In this way, oxytocin can thus play a role in increasing intergroup conflict, through promoting emotional commitments, and aggression and conflict where external groups are seen as a threat (De Dreu et al. 2011; Ne'eman et al. 2016). Competitive aggression may be motivated by testosterone; however, oxytocin is implicated in what we might better see as emotional commitments and motivations to defend vulnerable young. Defending justice by punishing cheats has a similar reward system in humans (de Quervain et al. 2004). The influence of oxytocin is further complicated by apparent differences between human males and females, with some evidence that females are more likely to often 'tend and befriend', seeking emotional support from others at times of stress, than necessarily defend from a perceived attack (Taylor et al. 2000).

Differences between individuals in particular oxytocin receptor genes provide interesting insights. Certain gene variants (G allele of a common variant (rs53576)) confer advantages in interpreting social cues, empathising with others and building trust. Individuals with these genes are in many ways more prosocial (Dannlowski et al. 2016). They are better able to read emotions from facial expressions (Dannlowski et al. 2016) and to build stronger and more trusting and supportive relationships as adults than those with the A allele (Chen et al. 2011). However, such potential advantages come at a price. In situations in which there is a lack of parental warmth, individuals with the socially sensitive G allele are more susceptible to depression (McQuaid et al. 2013), and other mental health conditions (Dannlowski et al. 2016), and they suffer more in conditions of social isolation (McQuaid et al. 2015). Differing empathy between individuals mirrors, in some ways, the effects that increasing prosociality and tolerance have had on increasingly social sensitive humans in the later stages of human evolution.

Bonding hormones such as oxytocin may play a key role in the formation of those important few friendships with high levels of trust, in which we know people are there for us when we need them, rather than forming extensive social networks (Pearce et al. 2017). Once avoidance or stress responses, which might trigger us to see unfamiliar individuals as outsiders, are overcome (see above), humans' empathy towards strangers triggers oxytocin release and subsequent generosity (Barraza and Zak 2009). Longitudinal studies following humans from infancy to adulthood describe oxytocin involvement in the transfer of attachment from parents to friends and romantic partners (Feldman et al. 2013). Close friendships are thus a particular form of bond, extending from maternal attachment and romantic attachments (Feldman et al. 2013). Oxytocin increases following contact with friends (Feldman 2017). Changes in oxytocin late in human evolution (Theofanopoulou, Andirko, and Boeckx 2018) may thus relate to new capacities to form close friendships. In the case of domesticated dogs, for example, changes in oxytocin-related bonding have brought them new abilities to form close bonds with their owners (Kis et al. 2014; Kis et al. 2017). Oxytocin and similar bonding hormones also play a role in how networks are maintained, through motivations towards mutual generosity, feelings of gratitude, and desires to maintain contact and improve the wellbeing of distant friends (Algoe and Way 2014; vanOyen Witvliet et al. 2018).

Other related hormone changes are also significant, and attention has also particularly been drawn to changes in serotonin pathways. Serotonin is another hormone influencing our mood and social behaviour that is likely to have been subject to selection pressures in human evolution. It plays a role in influencing attachment styles (Gillath 2008) and propensities to obey or challenge social rules (Gelfand 2011; Mrazeket al. 2013). A particular polymorphism of serotonin influences social sensitivity and, with it, susceptibility to supportive or unsupportive environments within modern populations. Alleles within the 5-HTT linked polymorphic region confer greater plasticity to the effects of childhood mistreatment. One form is associated with greater empathetic perspective-taking in supportive environments but also brings disadvantage in terms of a higher risk of traits such as depression or impulsivity in unsupportive or traumatic childhood environments (Flasbeck et al. 2019). As a result, those of us inheriting a tendency to be more socially sensitive, under the influence of genetic differences influencing the hormone serotonin, are both more severely affected by negative social experiences and more buoyed up by positive ones (Assary et al. 2020). The former have even been dubbed 'orchids' – so empathetic and highly tuned to the emotional and social tone of their environment that they are more deeply affected than others by cruelty, neglect or isolation, particularly in childhood, whilst the latter dubbed 'dandelions' are more resilient and better able to thrive regardless of their environment (Boyce 2016). Orchids do particularly well in supportive social environments, understanding others more fully and forming close social relationships, and particularly benefiting from the confidence and emotional wellbeing that such environments foster. However, they are more likely to do badly where such support is lacking. There seems to be an evolutionary balance between these alternative strategies – one (orchids) that is particularly successful in supportive environments and another (dandelions) more resilient to harsh social context. This polymorphism even influences our propensity to be prone to feeling nostalgic (Luo 2019) and, so, our tendencies to derive comfort from past (rather than present) experiences. Variations in serotonin pathways within populations provide a good example of how increasing social sensitivity is not simply an advantage but also sometimes a disadvantage depending on context.

Other subtle genetic differences within populations that influence hormonal responses have also been identified. One particular arginine-vasopressin allele, EVPR1A (rs 1117 4811), which is found at high frequency in modern humans, is linked to prosocial phenotypes while the ancestral allele is associated with antisocial phenotypes, for example (Theofanopoulou, Andirko, and Boeckx 2018).

As more genetic studies are undertaken, we are likely to have an even better understanding of the influence of these genetic changes on neurochemical responses. However, it is always wise to be somewhat cautious not to over-interpret genetic evidence. On the level of differences within populations we need to be particularly careful. There *are* differences *within* populations that are strongly influenced by inherited genetics, such as autism or dyslexia, that should not be ignored and which challenge us to be better at understanding *different but equal* perceptions of the world (discussed in Chapter 3). However, we should not imagine that people with particular serotonin polymorphisms or particular oxytocin receptor genes or any other genetic difference affecting hormonal mechanisms could or should be identified as different. Such influences are only felt at population level and not at the individual, and are far less significant than culture, background or individual choice in how people behave. To begin to separate people according to these subtle genetic differences would be folly.

Where an understanding of the evolution and function of hormones and their influence on behaviour is useful is around the 'big picture' patterns of changes in human evolution. Understanding the role and function of these key hormones, and how changes may have affected human 'gut feelings' to unfamiliar or non-kin others, gives us some insights into how selection pressures acting on these hormone systems may have played a role in evolutionary transformations in human social behaviour.

Selective pressures on human tolerance

What mechanisms drove changes in human tolerance? It has often been assumed that changes seen in those human neuroendocrine responses that affect approach–avoidance behaviours must be a result of social selection pressures. These have variously been argued to derive from selection for cooperative and non-aggressive mates or allies (Hare 2017), or even active social control of aggressive males and reactive aggression (Wrangham 2018; Wrangham 2019a; Wrangham 2019b). The more important it was to demonstrate one's collaborative motivations, the less popular more aggressive individuals might be, with group level controls perhaps exerting a strong influence moderating bullying, dominating or aggressive behaviour (Boehm 2012; Boehm 2015). There are also other potential mechanisms. As explained in Chapter 3, collaborative morality also places selective pressures on group-focused motivations and behaviours, in turn promoting more tolerant and inclusive traits.

Social influences on tolerance inevitably played some role in human evolutionary changes. However, there are other explanations. Amongst non-human apes and other primates, the ecological context plays a key role in determining those situations in which friendly encounters between different groups are advantageous rather than disadvantageous. Bonobos, for example, are more friendly at the boundaries between communities where there are abundant resources and opportunities to learn about how to exploit unfamiliar environments (Lucchesi et al. 2020). Bonobos have similar characteristics of physiological changes in approach behaviours as do humans and, in their case, the sharing of food boundaries rather than aggressive confrontation is an advantage (as we have seen at the start of this chapter). As human societies became more dependent on a wide variety of resources, not only food and water but also flint, raw materials for tools and other resources used for even medicines, competition over resources may have become more disadvantageous (Pisor and Surbeck 2019). Moreover, increasingly challenging environments, caused by increasing aridification, alongside increasingly unpredictable resources, may have placed greater pressures on collaboration in certain regions of Africa after around 300,000 years ago at the emergence of our species (Spikins et al. 2021). Whilst much debated, the question of the relative roles of internal social selection pressures and external ecological influences remains unresolved.

It remains an open question whether internal social selection processes, which may have taken many different forms, ecological pressures acting on particularly human resource requirements, or indeed a combination of many factors, pushed certain hominins towards increasing friendliness, whilst other species may have taken a different pathway (as discussed in Chapters 8 and 9).

Conclusions

We would be wrong to see the suspicion of unfamiliar individuals, which is so typical of most 'wild' animals, as equally natural to humans. Life in highly collaborative societies, discussed in Part 1, is likely to have set in place pressures for humans to simply be less aggressive than their distant ancestors. However, the changes in emotional dispositions that paved the way for the formation of recognisably human tolerance to unfamiliar individuals seem to have occurred relatively late in our evolutionary history. These changes were probably more complex than simply related to reduced aggression, and seem to have involved different hormonal pathways influencing aggression, fear, excitement and anticipation and bonding. Though internal social processes may have played a part in these transformations, ecological factors may also have had an important role.

Changes in genetics and anatomy in the recent evolutionary past, after 300,000 years ago, argue that being more tolerant was increasingly important during this period. Changes in neuroendocrine pathways are likely to have played a key role in shaping both changes in approach and avoidance behaviours. Such changes bring both advantages and disadvantages, however. Whilst tolerance brought with it capacities to approach unfamiliar individuals and things, increased openness to new experiences, and increased social sensitivity, it also brought emotional vulnerabilities (discussed in Chapter 5).

Key points

- Most animals tend to avoid unfamiliar individuals belonging to other kin groups, or are even aggressive towards them.

- Neuroendocrine responses influence systems of hormones that govern avoidance or approach behaviours, such as through feelings of safety and security, feelings of threat or desires to explore.

- Evolved physiological changes, such as reduced stress responses towards unfamiliar individuals, can be advantageous in situations where intergroup collaboration may be an advantage.

- Evolutionary changes affecting reductions in avoidance behaviours (such as through changes in androgens or stress reactivity) and enhancements of approach behaviours (such as changes in dopamine or bonding hormones) are implicated in changes in tolerance in recent human evolution.

- An increasing external tolerance or approachability in human responses towards unfamiliar individuals brings both advantages and disadvantages, including not only the possibilities of formation of large-scale social networks but also social sensitivities and emotional vulnerabilities.

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CHAPTER 5

The Evolutionary Basis for Human Tolerance: human ‘self-domestication’?

Abstract

The idea that humans could be ‘self-domesticated’ is certainly rather strange and unlikely-sounding, perhaps not entirely out of keeping with something we might expect to find in a science fiction novel. However, there is good evidence that changes in emotional tendencies and capacities in recent human evolution (after 300,000 years ago) followed some similar pathways to those seen in domesticated species. Furthermore, these changes are not necessarily limited to animals that have been deliberately domesticated by humans, with some of these developments also seen in bonobos, which, alongside chimpanzees, are our nearest living relatives. Though questions and debates remain about why and how these changes might have occurred, genetic and anatomical evidence, alongside changes in the archaeological record, support the notion that changes similar to domestication were occurring in humans.

The concept that the evolution of human emotional tendencies and capacities may have followed similar changes in increasing tolerance

(Abstract continued on next page)

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seen in domestic animals is a challenging one. Rather than elevating modern humans above other animals, it would imply that some of the most crucial adaptations in our recent evolutionary past are shared with many other species. Moreover, with many traits changing under simple and single selection pressures, it contradicts any notion that human capacities are necessarily 'adaptive'. Many of our social traits may simply be emerging alongside key changes but have no adaptive role, or even be a disadvantage.

There are also added complexities. Increasing tolerance associated with self-domestication has largely been viewed as an entirely progressive development in the recent human past, opening up possibilities for more tolerant and connected communities to emerge and, in turn, enabling communities to become more resilient to resource shortfalls. However, there are costs and disadvantages to these changes in emotions, particularly at the individual level, which are rarely considered. Heightened sensitivities to social and cultural context, and *hypersociability*, bring increased vulnerabilities to disrupted emotional wellbeing in unsupportive contexts, as well as the types of challenges we associate with a certain eagerness to please. The emotional challenges that self-domestication brought may have been part of processes leading to compensatory mechanisms, such as attachment fluidity and tendencies to be driven to find additional emotional support and comfort outside of human relationships (discussed in Chapters 6 and 7).

Figure 5.1: A Russian domesticated red fox with 'Georgian white' fur colour (2015). Keyfedewa at English Wikipedia, CC BY 3.0 via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Georgian_white_Russian_domesticated_Red_Fox.jpg.

Introduction

Since 1959, and continuing today, a fascinating experiment into the domestication of a wild species has been taking place in Novosibirsk in Siberia. This experiment provided remarkable evidence for how quickly behavioural physiological and external changes can take place under selection for friendliness or tameness.

Dmitry Belyayev and, later, Lyudmila Trut directed experiments with the breeding of hundreds of farmed silver foxes (a subtype of red fox, *Vulpes vulpes*, with black fur). In each generation, the foxes that were most tolerant of humans were bred with each other to create increasingly 'tame' foxes (see Figure 5.1). Changes happened remarkably quickly. Foxes were notably more tame after only two generations, with floppy ears and changes in pigmentation occurring after 10 generations. Farmed foxes could be 'tamed' after about 30–35 generations of selection and eventually became keen to interact with humans. This experiment remains the most remarkable example of rapid domestication of a wild animal yet recorded.

‘Tame’ foxes, in comparison to non-domesticated foxes, showed a range of cognitive, behavioural and physical differences from their wild counterparts. They showed a reduced fear response to new situations, and an increased friendliness to humans, from as young as one month old. They approached people and licked their faces, whining and barking to attract human attention. They were also better able to ‘read’ human expressions and were as successful as puppies at finding hidden food on the basis of human clues (Belyaev, Plyusnina, and Trut 1985; Belyaev and Trut 1975; Hare et al. 2005; Trut, Oskina, and Kharlamova 2009). As well as physiological changes, in many cases foxes showed a change in appearance, with changed pigmentation (black and white patterning), shorter tails, more upward ‘waggy’ tails, floppy ears, and underbite and overbite (dental abnormalities). They also showed a shortening and widening of the skull and changes in oestrus (some females began mating twice a year and so producing more litters). Neuroendocrine changes included a down-regulation of hypothalamic–pituitary–adrenal (HPA) axis activity and reduced basal and stress reactive cortisol levels (stress reactivity and fear response), higher serotonin levels, and changes in dopamine and norepinephrine (Belyaev, Plyusnina, and Trut 1985; Belyaev and Trut 1975; Hare et al. 2005; Trut, Oskina, and Kharlamova 2009). Though foxes had only been selected on the basis of their lack of aggression, these other traits seem to come as part of the wider package of ‘domestication’.

These foxes, in effect, became more like dogs in both physical appearance and in temperament, being eager to please and enjoying human affection, and many were sold as pets.

Though no experiments have ever quite matched those with silver foxes, there are other cases of similar changes under pressures for tameness, reduced aggression or tolerance in other animals. Rats selected for tameness show similar changes in face shape, for example (Singh et al. 2017). Even less forcefully directed selection pressures can create similar changes. A long-term study for over 14 years of free-living wild house mice in Switzerland exposed to human handling as pups also demonstrated changes associated with domestication, including a reduction in snout length and change in pigmentation (Geiger, Sánchez-Villagra, and Lindholm 2018). What was particularly interesting about this latter study is that, in this case, mice were not being actively selected for aggression, simply being passively exposed to greater interaction with humans. They were always able to come and go as they wished, through holes in the barn used for the experiment. In a sense, then, perhaps these mice had 'self-domesticated' in response to a new adaptive niche in which food and freedom from predators was readily available as long as they could tolerate handling from humans. The same types of changes in snout length and braincase size, and in levels of sexual dimorphism, are even seen between rural and urban red foxes (*Vulpes vulpes*) in the UK, which match the changes occurring under 'domestication syndrome' (Parsons et al. 2020).

Perhaps most remarkably of all, similar genetic changes and changes in anatomy have been seen in recent human evolution. Similar morphological changes seen in the human face shape to those in 'domesticated' species in recent human evolution, and similarities in neurophysiological changes, make a strong argument for our having followed a similar evolutionary pathway, leading to our increasing friendliness and tolerance to unfamiliar individuals.

Human self-domestication?

The parallels between changes seen in Siberian silver foxes, other domesticated species such as dogs, and those in recent human evolution are perhaps surprising.

Similar genetic changes are implicated in both modern humans and domestic dogs, as well as in other domesticated species. These include signals of positive selection in specific genes including RNPC3, FAM172A, PLAC8L1, GRIK3 and BRA (Theofanopoulou et al. 2017). These key pathways influence neural crest cells (Wilkins, Wrangham, and Tecumseh Fitch 2014) and, in turn, hormone systems, as well as other aspects of cognition, biology and behaviour. Similarities across species seem to be explained by high-level genetic controls of many elements of responses – in effect, single changes may cascade down. In this way, cascading sets of changes influencing 'gut feelings' towards unfamiliar individuals explain an association between increasing friendliness or tameness with anatomical changes, particularly to the shape of the face (Singh et al. 2017).

Adaptive changes under pressures for increased tolerance are also reflected in human anatomical and physical changes. Anatomical changes, such as in face shape in humans occurring between 300,000 to 30,000 years ago, follow a similar trajectory to changes seen in other animals under domestication (Hare 2017; Hare, Wobber, and Wrangham 2012; Theofanopoulou, Gastaldon, and O'Rourke 2017; Theofanopoulou et al. 2017). Over the last 300,000 years, humans have experienced a flattening of their faces (Cieri et al. 2014; Godinho, Spikins, and O'Higgins 2018), reduction in cranial volume (Hare 2017), and reduced tooth size (Brace, Rosenberg, and Hunt 1987), as well as changes to the shape of the brain and the jaw (Theofanopoulou et al. 2017), which is seen in domesticated dogs; see Figure 5.2. The same changes are also seen in other 'domesticated animals' (such as sheep and cows), wild animals artificially selected for tameness such as rats (Singh et al. 2017) or ferrets (Hernádi et al. 2012) or 'self-domesticated' animals such as bonobos (Hare, Wobber, and Wrangham 2012). These include: changes in pigmentation; shorter face/muzzles; smaller teeth; smaller cranial capacities (and brain size reduction); a more juvenile-like appearance and temperament; reduction of sexual dimorphism and more frequent oestrous cycles, and so longer period of fertility, as well as (specific to species) floppy and reduced ears and curlier tails.

Many people argue that recent changes in physiology affecting avoidance behaviours and approach behaviours, as outlined above, warrant describing humans as a 'self-domesticated' species. Whether we should really term humans 'self-domesticated' is a matter of debate, and there are certainly a number of unknowns around what self-domestication really is or how it comes about.

It is not clear if the idea of humans becoming *self-domesticated* fully fits the changes taking place in recent human evolution. Some argue that these recent physiological changes are also in some way distinctive from those seen in 'domesticated' species, such as by affecting development in different ways. As a theory it is, after all, somewhat difficult to test (Sanchez-Vallagra 2019). As we shall see in Chapter 8, for archaic and modern humans, the generalisations *close-knit* and *approachable* may be more useful terms than an oversimplification into 'wild' and 'tame'.

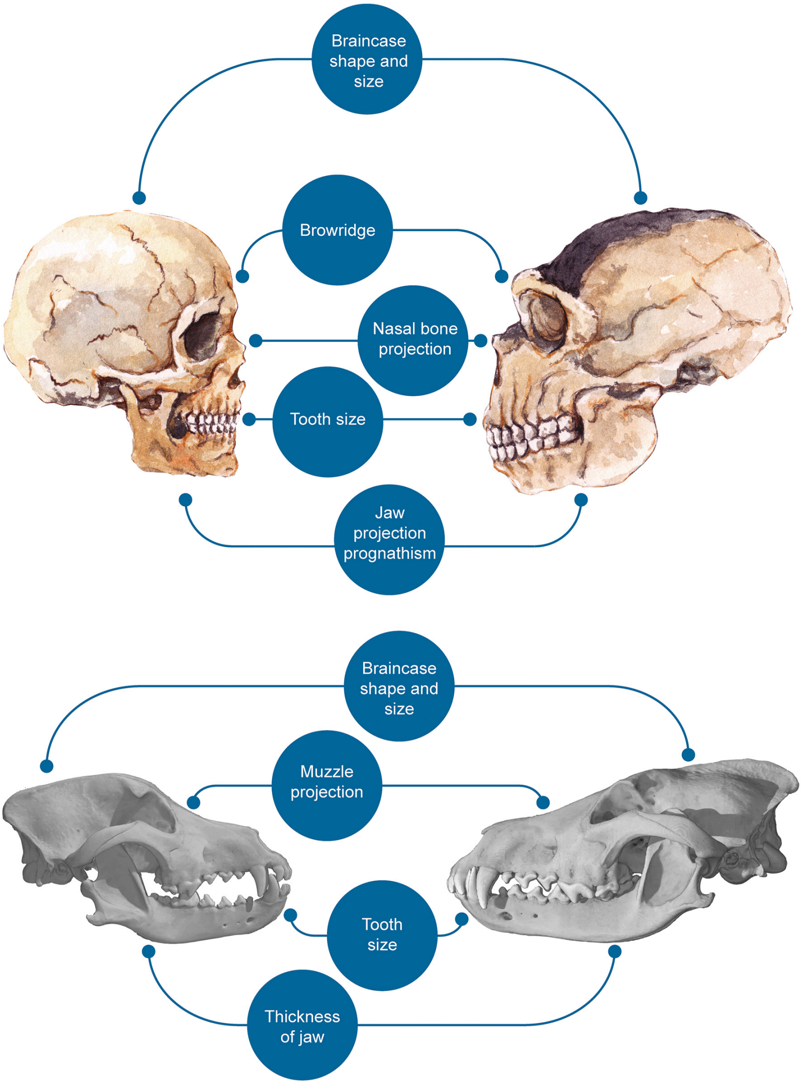

Figure 5.2: Salient craniofacial differences between modern humans (top left) and Neanderthals (top right), and between dogs (bottom left) and wolves (bottom right). The pattern of recent cranio-facial changes in modern humans (above) shows a remarkable similarity to that of domesticated animals such as dogs (below). CC BY 4.0, reproduced from: Theofanopoulou C, Gastaldon S, O'Rourke T, Samuels BD, Martins PT, et al. (2018), *Self-Domestication in Homo sapiens: Insights from Comparative Genomics*, PLoS One. Available at: https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0185306.

The process of domestication is often far more complex than it might appear. There may be many traits that change under single selection pressures, and many different selection pressures that might lead to similar changes (as discussed in Chapter 4). Reduced antisocial reactions to unfamiliar social situations can come about not only through the reduction in aggression but through a reduction in stress reactivity. The relationships that dogs develop with humans (discussed in more detail in Chapter 7) involve new types of approach behaviour that are equally, if not more, important than any reductions in aggression. There have been suggestions that it may not have been selection against aggression that was key to the Siberian experiment, as many of the adaptations shown by the Siberian silver foxes may have occurred prior to the experiment as a result of adaptations to the stresses of the farm environment in previous generations (Lord et al. 2020).

Whatever we decide to call changes in tolerance in human evolution, there is also debate over why and how this may have occurred (discussed in Chapter 4). Different theories have been put forward, ranging from selection for increased prosociality and friendliness (Hare 2017) to selection for reduced reactive aggression (Wrangham 2019), to the effects of secure food resources on female choice for less aggressive males (Gleeson and Kushnick 2018), to the pressures of ecological changes affecting the adaptive advantage of sharing between communities (Spikins et al. 2021). Others argue that alternative selection pressures, such as for self-control, were responsible (Shilton et al. 2020). We often tend to assume that it was unique internal social pressures that drove human self-domestication. However, it is equally possible that external ecological drivers played a key role (Spikins et al. 2021).

Despite the limitations of the term ‘self-domestication’, and that we are as yet in the early days of understanding how and why these changes take place, there are certainly important parallels in the ways in which hormones, physiology and anatomy change in human evolution that demonstrate similar changes to those seen in domesticated or self-domesticated species (Hare 2017; Wrangham 2014; Wrangham 2019). Many of the changes we see as humans become more externally socially tolerant share similarities with how other animals also react to selection pressures to become more friendly, less aggressive or more ‘tame’.

Implications

The implications of humans following a similar pathway of changes in physiology, hormone systems and behaviours to domesticated species (such as dogs) and self-domesticated species (such as bonobos) are profound.

The rate of change seen in experimental and even semi-wild conditions demonstrates that marked changes in emotional capacities and tendencies, or perhaps *temperament*, could have occurred relatively rapidly in evolutionary terms. Extensive changes in behaviour under pressures to reduce aggression or increase approachability can result from even quite subtle changes in physiology, which can take place even over only a few generations. We should not necessarily expect changes in approach or avoidance behaviours to occur over the timescales of hundreds of thousands of years that we often associate with significant evolutionary changes.

The scope of changes occurring under a single selection pressure, from reduced aggression, approachability and eagerness to please to facial shape and pigmentation, also tells us something important. It is easy to assume that human traits evolved *for a reason*, and yet this diversity of traits associated with self-domestication demonstrate the folly of assuming adaptedness of human traits. It can be easy to assume that, if we can create a plausible story about how some aspect of our bodies or brains might have been adaptive, this should explain its existence. However, many, if not most, human traits probably emerged through the complex associations between different genes that came along for the ride when others were selected for, and might even have been a disadvantage.

Complex social emotions are one particular example of our tendency to assume adaptedness. Complex social emotions, created through an interplay of both affective and cognitive empathy (discussed in Chapter 1), are important motivators of our behaviour. We feel social emotions, such as guilt or gratitude, because of our understanding of what other people think or feel about us, and our understanding of what is expected of us or them. These social emotions tend to motivate us to behave in prosocial ways that help others. We can make a plausible argument for why gratitude may have been selected for, starting with reciprocal relationships, which we see in non-human primates, and becoming a basis for strong alliances based on give and take (Allen 2018). Certainly, gratitude plays an important function in our positive social relationships, encouraging support and mutual collaboration (Smith et al. 2017; Wood et al. 2010). Certain genes even predispose people to a greater likelihood of experiencing gratitude (vanOyen Witvliet et al. 2018). However, despite the advantages and link to particular genes, gratitude might equally simply be a side effect of changes in affective and cognitive empathy occurring for other reasons. Other complex social emotions, such as shame, do not even seem to serve even a useful function, with feelings of shame strongly associated with depression and motivating an unhelpful withdrawal from relationships (Gilbert 2000).

We prefer an ordered world, and a meaning to most elements of our existence, but nature does not always provide it.

Perhaps most significantly, the idea that many key changes in our social tendencies could align us with other animals, rather than elevating us above them, challenges our notion of human exceptionalism. We do not feel entirely comfortable with the notion that we might feel ‘friendly’ to strangers or eager to please others in ways not unlike those of pet dogs. However, appreciating that we are perhaps more animal than we think might be important for many reasons, not least of all in recognising that we are part of nature, and vulnerable to ecological changes as much as any other species.

The advantages of increasing tolerance

There is good reason to think that changes associated with increasing tolerance played a key role in the success and expansion of modern humans as a species.

Increasing tolerance has been argued to be associated with important developments such as reduced aggression and greater egalitarianism through levelling mechanisms (Wrangham 2019), increased collaboration (Hare 2017), more sophisticated language and communication (Thomas and Kirby 2018), enhanced self-awareness and creativity (Zwir et al. 2021), enhanced emotional expressivity in faces (Godinho et al. 2018), and even changes in body cognition, allowing more sophisticated tool use (Bruner and Gleeson 2019). Certainly, a new tolerance and capacity for external social focus to human communities would have allowed connections to form between living groups and kin groups. At the same time, a reduction in stress reactivity accompanied by increased novelty seeking will have motivated the maintenance of distant social connections, reduced inbreeding, and created regional connected communities. Such connected communities, in turn, reduce the risks imposed by local resource shortfalls (Pisor and Surbeck 2019; Spikins et al. 2021). Forming external allies provides the possibility of creating large-scale resilient networks that buffer effects of ecological changes and, moreover, allow knowledge and culture to spread. Moreover, a certain playfulness, or attraction to novelty, may also at least partly explain extensive dispersions, and attraction towards new ways of doing things (discussed in Chapter 4).

Archaeological evidence supports a picture of many of these important changes in social behaviour appearing initially in Africa after 300,000 years ago and leading to a remarkable global expansion of 'modern humans'.

From around 300,000 years ago, certain populations of humans started to show changes in the crania, such as reductions in brow ridges and other changes in facial form that we associate with increasing tolerance (as discussed in Chapter 6) (Bergström 2021; Stringer and Galway-Witham 2017). At Jebel Irhoud in Morocco, for example, some of the human fossils dating to around 315,000 years ago have more modern human-like features, including a flatter face and much reduced brow ridge (Hublin et al. 2017; Richter et al. 2017). Across Africa, we see a diverse range of archaic and more modern-like characteristics in various fossils (Bräuer 2015). Crania from Omo 1 and Herto in Ethiopia with a more modern cranial shape appear around 195,000 and 165,000 years ago, respectively. These more modern forms are contemporary with a diverse set of other types of human, from robust descendants of *Homo erectus* to small-brained *Homo naledi*, following different evolutionary pathways (discussed in Part 3).

A combination of increasingly challenging and increasingly fragmented environments seems to have driven particular selection pressures on both physical and social characteristics. In this period, we also see material evidence for increased mobility in certain regions of Africa in the form of raw materials travelling further away from the source until their eventual discard. These extended distances of raw material transport may reflect more external-focusing social behaviours in human populations, and a greater ease with which longer-distance movements across many territories could take place. At around 300,000 years ago in the Olorgesailie basin in South Kenya, at a time of increasingly variable environments and periods of resource stress (Potts et al. 2018), we see raw material being procured from a wider area. From typically local raw material distance transfers of around five kilometres, we see new movements of obsidian of around 25 to 50 kilometres, and up to 95 kilometres in certain cases, implying interactions with neighbouring groups (Brooks et al. 2018). The distances over which materials are transported also increase in other regions. Middle Stone Age populations in the Kalahari imported preferred silcrete raw material from up to 295 kilometres, particularly during drier periods (Nash et al. 2013; Nash et al. 2016). Certain populations seem to be more mobile, and better able to negotiate moving through areas usually occupied by particular groups, or even exchanges with them.

Ecological factors play at least some role in these changes. Many environments become more challenging for survival in Africa after half a million years ago. Increasingly, aridification is evident in East Africa, and is associated with extinctions in the South Kenya Rift between 500,000 and 400,000 years ago (Owen et al. 2018). Alternating periods of arid and wetter conditions affected southern African environments, placing pressures on human populations in dry periods and prompting dispersions along wetter corridors (Kutzbach et al. 2020). Across the whole continent, highly diverse ecological contexts, the expansion and contraction of the Sahara, basin structure and variable topography provide a unique environment (Foley 2018) in which distinct subdivided populations seem to have emerged and periodically connected (Bergström 2021; Galway-Witham, Cole, and Stringer 2019; Scerri et al. 2018).

Increasingly harsh environments, environmental unpredictability and landscape diversity may have been significant factors in changing the selective advantages and disadvantages of dispositions towards unfamiliar individuals. Unpredictable environments will have led to an increased frequency of shortfalls in resources. Diverse and fragmented landscapes reduce the synchronicity of shortfalls, however, as different groups would not all have experienced shortfalls at the same time (Campenni, Cronk, and Aktipis 2017). Moreover, optimum conditions for peaceful interaction between groups occur in the most fragmented landscapes, as these are the contexts in which populations can control their interaction and maintain their own integrity (Rutherford et al. 2014). For human societies, pressures to share will have been exacerbated by a reliance on a far greater variety of resources – not only food and water but also flint raw materials for making tools, other resources such as salt (Pisor and Surbeck 2017) or even medicines (Spikins et al. 2021). Initially, changes in disposition towards unfamiliar individuals may simply have meant that interactions at the boundaries between living groups become more friendly and collaborative in nature, encouraging shared resource exploitation in these particular locations. Through time, the nature of intergroup collaboration could have become more sophisticated and, in turn, more effective in reducing the impact of unpredictable resources and frequent shortfalls (discussed in Spikins et al. 2021).

Increasing mobility and interaction is also evident from genetic evidence. For example, excursions of populations out of Africa into Europe led to interbreeding with early Neanderthals around 200,000 to 400,000 years ago (Posth et al. 2016). A modern human jawbone found at Misliya cave in Israel suggests modern humans were in the Near East by 180,000 years ago (Hershkovitz et al. 2018), whilst tooth remains in China also place modern humans there at least 100,000 years ago (Liu, Wu, and Xing 2016). Similarly, archaeological evidence places humans in Saudi Arabia at Jebel Faya as early as 125,000 years ago (Armitage et al. 2011; deMenocal and Stringer 2016; Groucutt et al. 2018). There is also evidence of greater movements within Africa, with climate changes also seeming to play a role in these patterns of migration (Lamb et al. 2018; Petraglia, Breeze, and Groucutt 2019; Rito et al. 2019; Timmermann and Friedrich 2016).

It is only following these anatomical and behavioural changes that we see the successful expansion of modern humans out of Africa, eventually replacing (with some low levels of interbreeding) previous archaic species and expanding into previously unoccupied regions, such as the far northern latitudes, the Americas and Australia (Bergström et al. 2021). Although there may be many questions about the timing and mechanisms of this ‘global diaspora’, it seems highly plausible that changes in social tolerance played a key role in these developments. Whilst there may also have been changes in cognition or culture during this period, changes in social tolerance (as discussed in Chapter 4) created connected communities, providing genetic diversity, resilience to resource shortfalls and the cultural transmission of innovations (Spikins 2021).

All of these developments fit a clear picture of human ‘progress’. Even the way we phrase changes, in terms of *archaic* or *modern* species (with no commonly accepted alternatives available), imposes a clear concept of progression toward ourselves as the better or ‘modern’ form. However, there is another side to the changes taking place. Increasing tolerance also brings emotional vulnerabilities. In making us more connected to the feelings of everyone around us, and not just our close kin, developments in potential connectedness and social awareness also bring increased vulnerability to feelings of insecurity when connections are not available, anxieties over what others think or feel about us, and even the predisposition towards other debilitating emotional disorders.

The constraints and disadvantages of increasing tolerance

As we have seen in Chapter 4, evolutionary changes affecting key hormonal responses and associated with increased social tolerance in recent human evolution affect many different realms of social behaviour. Changes in hormones affecting aggressive responses and stress reactivity increase tendencies and capacities to approach unfamiliar others, whilst those in exploratory and bonding hormones influence an increased social and emotional sensitivity.

Rather than a simple success story, increasing tolerance is best seen as more of a complex set of compromises, advantages, disadvantages and constraints. Some attention has been paid to this other side of the story in a focus on how new types of aggression, associated with labelling of outgroups as subhuman, might be associated with human self-domestication (Hare and Woods 2021). However, this alternative form of aggression remains difficult to identify in archaeological evidence, and emotional commitments to defend one’s group against perceived others predate this transition (discussed in Chapter 3). Perhaps even more important is another disadvantage brought by tolerance, in this case potentially overlooked owing to our discomfort with vulnerability (discussed in the introduction to this volume). This comes from emotional vulnerabilities we continue to suffer today.

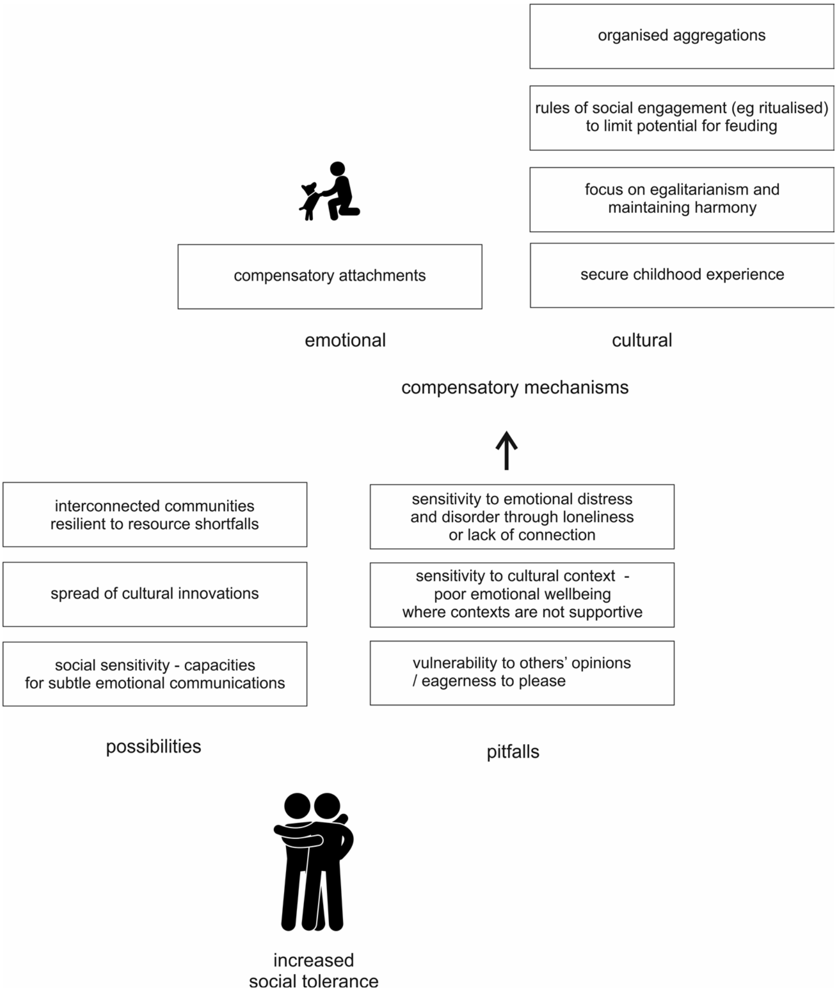

Figure 5.3: Representation of new styles of community connection developing in recent human evolution through neuroendocrine changes, leading to greater external tolerance and approachability. Penny Spikins, CC BY-NC 4.0.

Alongside the potentials that increased tolerance brings come pitfalls at both an individual and a community level, as well as a need for individual and cultural responses to emotional vulnerabilities (see Figure 5.3).

Most obviously, direct effects of recent genetic changes influence human vulnerability to specific emotional and cognitive disorders. Recent changes in neurological plasticity are associated with the emergence of a greater number of deleterious alleles, bringing heightened susceptibility to the appearance of abnormalities, particularly those affecting cognition (Castellano et al. 2014; Cruz, Vilà, and Webster 2008; Theofanopoulou et al. 2017).

Most effects on our emotional vulnerability are more subtle, however. *Social understanding and being socially sensitive* is, perhaps, best seen as being more of a double-edged sword than a straightforward strength. In domesticated and self-domesticated species, we see better abilities to pick up human social cues, but at the same time as an increased eagerness for human social contact and a vulnerability to insecure attachments, for example. Like these other species, our neurological sensitivity to our social surroundings has come at the price of a greater vulnerability (Sherwood and Gómez-Robles 2017). Both dogs and humans are susceptible to attachment insecurity, for example (Bradshaw 2017). Without socially supportive environments and positive social interactions, both also suffer emotional distress and susceptibility to disorder. Heightened social sensitivities allow for sensitivity to social and cultural context in development, but also bring with them other effects.

This is even more evident when we consider contrasts in social sensitivity within human populations. Individuals found to have *enhanced* social capacities show a greater vulnerability to the effects of harsh social contexts (Assary et al. 2020). These include those associated with enhanced oxytocin-related sensitivities to facial expressions (Marsh 2019) and serotonin-related sensitivities to social experience (Flasbeck et al. 2019), which elevate abilities to make friends easily and thrive in socially supportive contexts. In unsupportive contexts, these socially adept individuals suffer tendencies to depression and other emotional disorders (Dannlowski et al. 2016; McQuaid et al. 2013), as well as sensitivity to feelings of isolation (McQuaid et al. 2015). Taking an adaptive pathway towards increasing social sensitivity brings with it a notable cost, in terms of emotional wellbeing, which is felt in contexts where there is any lack of caring social support.

Because of recent changes in human evolution, we are all remarkably sensitive to the effects of loneliness, which has an even more pronounced effect on health than obvious physical onslaughts such as smoking (Holt-Lunstad et al. 2015; Leigh-Hunt et al. 2017). Compared with other apes, we also have a far greater desire, and need, for closeness and touch (Bzdok and Dunbar 2020; Hewlett et al. 2019). People who are simply playing an online game, cyberball, even feel acute pain similar to that of physical pain when they are excluded from playing with other contributors (Hartgerink et al. 2015). We are uniquely sensitive to signs of judgements from others, criticisms, or potential loss of status, and are all too prone to remodel these criticisms on ourselves, leading to tendencies towards anxiety or depression (Gilbert et al. 2009). Our drive to connect and belong, which forged large-scale human communities, brought with it heavy individual costs when our longed-for connections are missing.

In order to thrive emotionally we need extensive emotional connections, not only in childhood but throughout our lives. Without socially supportive environments through childhood, or what is perhaps best known as a loving home, we find it hard to handle our complex emotions. Around 25% of people in modern industrialised societies have some level of attachment disorder, or emotional insecurity though insecure attachment to their caregivers as infants or which develops in adulthood (Mikulincer and Shaver 2017), for example, with far-reaching effects. Insecure attachments affect not only trust and the quality of close emotional relationships but also many other aspects of our lives, such as our physiological reactions to challenging situations, our abilities to handle difficult feelings, our risks of suffering emotional disorders, our confidence to explore and even our physical health (Table 5.1).

This effect of emotional insecurity is not limited to childhood; it can also create changes in emotional wellbeing in adults. Even ideological indicators that our environment is not supportive can affect our sense of social and emotional security. Ideals of individualistic competition drive us to self-criticism and damaging levels of perfectionism, for example (Curran and Hill 2017). Subtle cultural effects are even so pervasive that a fascinating, if rather worrying, example of how sensitive we are to social context, even as adults, comes from research into how studying traditional self-interested economics affects social relationships. Economics is a discipline that, traditionally, particularly focused on the concept of individual rational self-interest and thus students felt surrounded by rationally self-interested (rather than

PHYSIOLOGICAL
Attachment insecurity leads to: – increased distress at stressful events (Mikulincer and Florian 1998) – greater physiological reaction to betrayal (Lawler-Row et al. 2006) – increased cortisol levels (Jaremka et al. 2013) – increased feelings of pain (Davies et al. 2009) – impairments in immune system function (Gouin and MacNeil 2019; Jaremka et al. 2013)
COGNITIVE/EMOTIONAL
Attachment insecurity leads to: – reduced abilities to regulate emotions (Mikulincer and Shaver 2018) – reduced ability to suppress negative thoughts (Gillath et al. 2005) – greater propensity to depression and anxiety (Bejinaru 2017) – reduced confidence to explore new situations and new relationships (Feeney and Van Vleet 2010) – reduced creative problem-solving (Mikulincer, Shaver, and Rom 2011) – increased reaction of amygdala to threats (Norman et al. 2015) – impaired prefrontal cortex development (Insel and Winslow 2011; Strathearn 2018)
SOCIAL DYNAMICS
Attachment insecurity leads to: – reduced compassionate helping (Gillath, Shaver, and Mikulincer 2005; Mikulincer et al. 2005) – a negative (vs positive) slant on others motivations (Mikulincer and Shaver 2005) – increased negative orientation towards out-groups (Mikulincer and Shaver 2001; Saleem et al. 2015) – greater conflict and violence in romantic relationships (Mikulincer and Shaver 2005) – reduced tendencies to forgive offences or betrayal (Lawler-Row et al. 2006)

Table 5.1: Effects of attachment insecurity on human physiology, cognition, emotions and social dynamics.

caring) social actors in their imagined worlds during their degree. Marwell and Ames (1981), Frank et al. (1993), and more recently Bauman and Rose (2011), explored these effects in now-famous studies. They found that, as they progressed through their degree, undergraduates in economics became less able to share and develop relationships based on trust, and less willing to contribute to the public good. Effectively, they changed their internal emotional schema towards social relationships, arguably becoming better prepared to survive in their perception of a self-oriented social environment around them. Despite thinking of ourselves to be individual independent beings, resilient to the opinions or attitudes of others around us, we are surprisingly vulnerable to the emotional tone of the social context we have experienced in the past and the one we live in today.

It is not difficult to see that human social sensitivities affect not only individuals but also communities. Individually, we are acutely emotionally vulnerable to our social context. As infants and children, we may benefit from a supportive context and become generous, trusting, confident to explore and emotionally resilient as adults. Alternatively, we may be affected by a lack of support and become less generous, less trusting and lacking in confidence, with effects even felt at the level of our feelings, or pain, or the functioning of our immune system. As adults, the same sensitivities continue to operate, leading us to thrive in supportive social groups and communities where there are supportive ideologies, and suffer in competitive or socially harsh groups, communities or ideologies. However, a larger-cultural-scale supportive community will tend to be populated with individuals who are more generous and collaborative, creating greater resilience through give and take, whilst, in unsupportive contexts, there will be a less collaborative ethic.

Compensatory mechanisms

Societies that have coped stably for thousands of years with the challenges posed by our emotional vulnerability show a number of adaptations that support both individual and collective wellbeing. Modern hunting and gathering societies, in particular, provide a good example. In such societies, people are equally concerned as in industrialised contexts about what others think or feel about them (Wiessner 2014) and, whilst attachment disorders may be rarer, they nonetheless still exist (Briggs 1970). However, over many thousands of years, such communities have learnt ways of providing emotional support that can counteract many of our vulnerabilities.

For one thing, the emotional investment in infants is distributed amongst several different individuals who willingly give time and effort towards care of infants and children, providing many alternative sources of emotional support, and making shortfalls in emotionally supportive care much less likely. Children form strong bonds with unrelated adults, as well as with relatives (Hewlett and Lamb 2005; Hewlett, Lamb, and Leyendecker 2000). Amongst some groups, such as the Bayaka, infants will spend as long in the arms of their fathers as in their mothers', and are often cared for by many other family members and non-kin (Hewlett, Lamb, and Leyendecker 2000). Moreover, learning is situated in an emotional context in which adults care about children's emotional wellbeing and understanding of the world (Boyette and Hewlett 2017). Furthermore, at a cultural scale, great efforts are made to promote harmony and constrain dominance (Boehm 2012), with constant communication within social groups, as well as great efforts to support social connections between groups through regular aggregations, rituals and celebrations (McDonald and Veth 2012). Rules and rituals also exist to prevent the escalation of conflicts. Many would link modern psychological distress with a loss of the sharing and caring ethic of hunter-gatherer communities (Gilbert 2021). These communities, so often seen as somehow 'primitive', have learnt what works to make societies and individuals resilient over thousands of years of living with our evolved emotional vulnerabilities.

We may think of our emotional vulnerabilities, and the risks they bring of pain and suffering, as weaknesses, but they exist through being essential to a shared communal strength and resilience against hard times. Connected communities would probably not have been possible without emotional vulnerabilities driving a need to connect to others and to belong to a larger community, the desires to feel valued, or concerns about reputation. As we explore in Chapters 8 and 9, other pathways with equally viable, albeit less connected, ways of living also existed. However, modern human ancestors built on motivations to care for others (discussed in Chapters 1 and 2) with recent changes in tolerance, adding further drives for new types of emotional connection. Because we need to belong and make wide social connections, we seek out others beyond our local group when, without such needs, we might be content with our local kin. Because we are driven to explore, we like to meet new and different peoples. Because we are sensitive to others' judgements, we seek to fulfil social roles and be accepted and respected. Because we are prone to loneliness, we seek extensive networks of friends and allies. Even expressions of vulnerability themselves promote trust and social connection (Evans and Krueger 2009; Strohkorb Sebo, Traeger, and Jung 2018). Furthermore, changes in human face shapes over the last 100,000 years allow much greater expression of emotions that make us vulnerable, such as insecurity or sympathy (Godinho, Spikins and O'Higgins 2018).

Our emotional vulnerabilities may also explain some of our uniquely human compensatory mechanisms. Whilst our desires to feel socially connected, and our need for affection, make us vulnerable to any lack of social support, they seem to have also provoked new ways of generating a feeling of belonging and connection to compensate for this vulnerability.

Human abilities to compensate for our emotional vulnerabilities through new types of support go well beyond those seen in other animals. Animal orphans, such as infant chimpanzees, sometimes form attachments to new parents, and in some cases these parents may even be a different species. However, for humans, *compensatory attachments* are widespread and go well beyond any replacement parent. We form much more common and in-depth attachments to non-human animals, which often play an important role in our lives. Yet, compensatory attachments that bolster our emotional wellbeing go well beyond other living beings and extend to spiritual beings, or even objects. As children, we often have imaginary friends or personified objects (such as a favourite teddy bear), with their own characters and personalities, for example, with personified objects being found across many different cultures. As adults, it is common to believe in an invisible and intangible god (Mackendrick 2012). Like imaginary companions, beliefs in spiritual beings often come to the fore at times of loneliness or anxiety, and comforting spiritual beings can have a significant impact on emotional wellbeing (Lenfesty and Fikes 2017). Compensatory attachments of other kinds, such as to pets or objects, come to the fore in adults in response to social isolation or loneliness (Niemyjska and Drat-Ruszczak 2013). Perhaps rather surprisingly, many people find greater comfort from their pets than their relatives (Serpell 2016), or feel closer to their god than to their friends (Niemyjska and Drat-Ruszczak 2013). Pets (Kurdek 2008) and objects (Bell and Spikins 2018b; Keefer and Landau 2014; Keefer et al. 2012) can act as psychological attachment figures. Much like a parent, they function in the same way to bolster confidence and wellbeing at times of insecurity. These compensatory attachments are extraordinarily rare, if even ever recorded, in other animals.

Whilst most sources of emotional support remain invisible archaeologically, some forms of compensatory attachments leave certain visible traces of their existence. In the following chapters, we will explore two examples. Firstly, in Chapter 6, we will consider a new attachment to cherished personal possessions, appearing after 100,000 years ago. Secondly, in Chapter 7, we will consider a new attachment to particular social animals, dogs, which appeared in the same period.

Like the Siberian foxes described at the start of this chapter, subtle changes in emotional responses in our ancestors had far-reaching effects on our lives.

Conclusions

Despite sounding rather bizarre as a concept, the notion that human emotional capacities and tendencies have travelled along similar pathways to those of domesticated species, such as dogs, or 'self-domesticated' species, such as bonobos, is broadly supported by genetic and anatomical evidence.

Quite why and how this transformation took place remains hotly debated. There are plausible arguments around internal causes, such as general pressures towards increasing friendliness throughout human evolution or selection pressures against reactive aggression, as well as external effects of ecological changes. Whatever the precise explanation, that these changes bring us closer to other animals, rather than further away, is significant to our perspectives of 'progress' in human origins.

Transformations in tolerance and friendliness appear to have been key to enabling connected communities to emerge, providing resilience to resource shortfalls through sharing beyond local groups. In turn, connected communities allow for innovations to spread rapidly, enabling quick technological responses to environmental changes. However, increasing social tolerance also brings disadvantages. Social sensitivity during development leaves individuals vulnerable to unsupportive contexts, with insecure attachments having widespread effects in many different realms of social life and even physical health. Compensatory cultural mechanisms to facilitate social connections such as aggregations may have partly mitigated these vulnerabilities. Equally, compensatory attachments to non-human beings may also have provided emotional comfort at times of stress.

Key points

- Human emotional capacities and tendencies towards increased tolerance in recent human evolution (after 300,000 years ago) seem to have followed similar paths to those seen in domesticated and self-domesticated species, with similar changes seen in anatomical and genetic evidence.

- The reasons for human 'self-domestication', as well as precisely what this means, remain debated.

- At the scale of human communities, increases in social tolerance provide the basis for the emergence of large-scale interconnected societies, which are resilient to resource shortfalls and are technologically responsive to ecological changes.

- At the scale of individuals, increased tolerance brings remarkable emotional sensitivities, but also vulnerabilities to the effects of insecure or unsupportive development.

- Compensatory attachments beyond those to other people may have emerged to provide additional emotional support at times of stress.

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CHAPTER 6

Comforting Things: cherished possessions as sources of social comfort and security, from the Palaeolithic to the present

Abstract

All around us, almost all the time, we see objects with no obvious function that seem to play an important role in our lives. This apparently bizarre obsession with non-functional objects is one of the most obvious differences between ourselves and other animals. Our lives are filled with all kinds of objects, not just those with a practical function but a whole range of mementos such as photographs, or treasured childhood toys, or necklaces or bracelets whose special place in our hearts has little to do with physical appearance. Although many non-industrialised societies are far less materialistic, even constantly mobile hunting and gathering populations create and attach meaning to objects such as beads, figurines or amulets, which do not have any immediate practical function.

(Abstract continued on next page)

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(Abstract continued from previous page)

Here, we consider the extent to which new emotional vulnerabilities may explain our apparently bizarre emotional attachment to certain treasured things and provide an explanation for the creation, significance and movement of many non-functional things in the archaeological record. We draw together evidence for an often-overlooked characteristic of cherished possessions – their capacity to provide comfort and a sense of connection and counteract loneliness. We then consider the characteristics of those kinds of objects that particularly inspire a sense of comfort and security in our own societies and the extent to which these characteristics can also be found in archaeological artefacts from the Upper Palaeolithic. There will have been many other aspects of meaning that are important in the creation and use of non-functional things by Palaeolithic societies. Nonetheless, the significance of new emotional vulnerabilities, and compensatory attachments to objects, appears to provide important insights. By moving away from the concept that our own species – modern humans – must have had a superior mind to other humans, we can begin to better understand how new vulnerabilities may have been integral to community resilience.

Understanding how we came to rely on cherished objects to bring us a sense of emotional security also leads to a better understanding of our human vulnerabilities and our need for warmth and social connection.

Figure 6.1: The treasured and now very shabby teddy bear belonging to Aileen Rogers and found on the body of her father, known as the Rogers teddy bear (1910–1915, housed in the Canadian War Museum). Artefact number 20040015-001 in the Canadian War Museum. For online catalogue with further details, see https://www.warmuseum.ca/collections/artifact/1368588. Photo copyright Canadian War Museum, all right reserved. Used with permission.

Introduction

In the early years of the 20th century, a Canadian girl called Aileen Rogers owned an unremarkable teddy bear. When Aileen was 10 years old, in 1916, her father, Lieutenant Lawrence Browning Rogers of the 5th Canadian Mounted Rifles, joined the army and was sent to the Western Front. He served as a medic in the trenches of the First World War. Aileen wanted to make her father feel better about being so far away and, hoping to keep him safe, she sent him her precious teddy bear in a care package. Lawrence treasured the bear and always carried it with him every day. He wrote in a letter:

> Tell Aileen I still have the Teddy Bear and I will try to hang on to it for her. It is dirty and his hind legs are kind of loose but he is still with me.

Tragically, Lawrence was killed at Passchendaele in 1917 when tending the wounded, and the bear (who by that time had lost both legs and his eyes) was found with him and returned home. Its story gives us a profound sense of the love shared by Lawrence and his daughter, represented in her gift of the bear to him and how he always carried it with him. This small and very bedraggled teddy bear would later become one of the most significant artefacts in the Canadian War Museum (Figure 6.1).

By sending her father her teddy bear, Aileen sacrificed her own source of emotional support to give something similar to her father. For Lawrence, holding this bear close made his daughter somehow nearer to him (Bell and Spikins 2018; Spikins 2015). Our heart goes out to Aileen, and to her father, Lawrence, who so cared about his daughter that he carried the bear with him everywhere. This small object tells us a great deal about human love, loss and vulnerability.

Examples of objects with a similar power to comfort us are all around us today, as much as they were a hundred years ago. In March 2020, as the UK went into lockdown at the start of the COVID-19 crisis, for example, treasured objects seemed to take on a particular importance for many people, despite contributing nothing obvious in practical terms. During this period, an unusual and generally very low-budget programme became surprisingly popular. Around 7 million people watched *The Repair Shop*, a programme based on the careful repair of cherished but largely valueless possessions brought in by members of the public. Many were regularly brought to tears. Credited with being one of the best programmes on television, *The Repair Shop* carefully cared for an assortment of treasured but broken and battered heirlooms, including stools and seats, teddy bears and varied toys, paintings, boxes and cases, which were restored and returned to their owners.

Why would *The Repair Shop* be so popular, and especially at the time of national crisis? Of course, there may be many different reasons, including nostalgia, escapism and a desire to find alternatives to throwaway culture. However, amongst these explanations, we cannot help but recognise that, as humans, we are unique in becoming remarkably attached to all kinds of valueless or impractical objects, and these attachments seem to become even more important at certain times. Our emotional relationships to treasured objects are not easily explained. This ability to form apparently one-way connections to entirely inanimate things, which cannot repay our emotional investments as people who care about us might be able to, might seem to be more of a weakness than a strength. We suffer at the loss of treasured personal possessions, and can invest tremendous time and effort in protecting and caring for these entirely non-human companions in our lives.

Our capacities to find emotional comfort in cherished possessions are unique, and nothing entirely the same seems to exist in other animals. However, these tendencies have been rather overlooked as an area of evolutionary research, and emotion is only just beginning to feature in archaeological or evolutionary discussions of past minds (Stade and Gamble 2019). We have focused, instead, on elevated cognitive capacities – how our increasingly complex human technology developed, how our aesthetic sense emerged or how artefacts may act as indicators of status or identity.

It is a little difficult to explain quite why the power of objects to give us a sense of social safety, and soothe, reassure and comfort us, should be somewhat sidelined. Of course, as we have seen, emotions tend to be thought of as overly complex, connected to bodily processes rather than mind, and are even seen as a somewhat woolly area of research in general (see the introduction to this volume). More than this, however, part of our reticence towards dealing with our emotional connection to cherished social objects may lie in our discomfort with our own vulnerability, particularly within a narrative of our own distant origins. We prefer to see our distant ancestors as entirely independent and invulnerable (as discussed in Chapter 2). Any tendency to seek out certain cherished possessions to provide us with reassurance thus makes us feel somewhat uncomfortable in demonstrating an apparently irrational need for such support.

There is certainly a sense of vulnerability about our connection to cherished things. Indeed, we can be so attached to certain objects that we grieve deeply if they are broken. We may even find it difficult to let go of things and start to hoard objects, as each small letting-go feels too great a loss to bear. Whilst our cherished personal possessions reflect the strength of our emotional connections to each other, it can also feel as though they bring us only a step away from hoarding things irrationally, and that to be irrational is dysfunctional. *Emotional vulnerability* such as this is rarely recognised as part of our evolutionary story.

How can an understanding of our emotional brain, and evolutionary changes in physiological responses affecting tolerance and social sensitivity, as discussed in Chapters 4 and 5, help us to understand the emergence of apparently impractical cherished possessions? Might new emotional vulnerabilities and new needs for connection and support explain a rise in cherished personal possessions with the emergence of modern humans?

The appearance of widespread non-functional objects in the archaeological record

That there seems to have been a proliferation of objects of art and adornment after the emergence of modern humans has been an accepted feature of the archaeological record for decades. There certainly seems to be a relationship between the origins of our own species in Africa after 300,000 years ago (discussed in Chapter 5) and the later appearance of widespread non-functional objects, such as beads or small portable figurines, after 100,000 years ago, with a particular proliferation after 45,000 years ago. This proliferation has traditionally been seen as an explosion of symbolism, reflecting new 'modern' capacities of thinking and expression to such an extent that it has been seen as the major 'origin myth' of our species (Hopkinson 2013).

Apparently non-functional artefacts, often seen as early art or symbolism, certainly existed well before 100,000 years ago. Etched shells from Trinil in Java date to 500,000 years ago (Joordens et al. 2015), for example. The Berekhat Ram figurine from Israel, a natural stone whose human-like figures have been deliberately accentuated, dates to around 250,000 years ago (d'Errico and Nowell 2000). During the African Middle Stone Age, from around 400,000 to 300,000 years ago onwards, we see an increasing frequency of apparently symbolic artefacts at various locations (Coulson, Staurset, and Walker 2011; Kissel 2017; Kissel and Fuentes 2018) and evidence for a greater use of colouring materials such as ochres (Brooks et al. 2018).

What we see as 'symbolic' artefacts do, however, become much more prevalent after 100,000 years ago, which seems to indicate that objects that are not directly functional have taken on a new significance. As we have seen in Chapter 5, alongside changes in cranial and facial anatomy, we see extended movements of raw materials. This implies increased mobility and social connection in various places in Africa after 300,000 years ago, associated with the emergence of anatomically and cognitively 'modern' humans. We see the appearance of beads in North Africa after 100,000 years ago (Wadley 2021), for example, with particularly notable finds including 13 similar shells of *Nassarius gibbosulus* found at Taforalt in Morocco dating to 82,000 years ago (Bouzouggar et al. 2007). At Blombos cave in South Africa, 41 marine shells (of *Nassarius kraussianus*), perforated for suspension and showing wear from this use, were recovered in deposits dating to around 72,000 years ago (d'Errico, Vanhaeren, and Barton 2009; d'Errico et al. 2005). Several artefacts that have been seen as clear examples of early art and date to the period 100,000 to 70,000 years ago, including ochre fragments with incised crosshatch lines, have been found at Blombos cave and surrounding sites (Henshilwood et al. 2018; Tylén et al. 2020). Burials with clear examples of grave goods are seen in the Near East around 100,000 years ago, such as that at Skhul V, with a wild boar mandible placed in the hands of the individual who is interred, and that at Quafzeh 11, in which an individual is buried with fallow deer antlers on their chest (Hovers et al. 2003; Wadley 2021). These burials, as well as finds of perforated marine shells (*Glycymeris*) that had travelled over 40 kilometres and also date to 100,000-year-old deposits at Quafzeh, are associated with an early migration of modern humans out of Africa (Bouzouggar et al. 2007). Shells used as ornamentation are also associated with burial at Border cave in South Africa around 70,000 years ago (d'Errico and Backwell 2016). At this latter site, a perforated Conus shell is found with a four- to six-month-old infant. Later in the archaeological record, marine shells and ostrich eggshell beads, which are identical to those created and exchanged by modern Jo'huansi, appear in the archaeological record at around 42,000 years ago at Border cave in South Africa (d'Errico et al. 2012). These remain in use until modern times. The widespread use of beads of various forms extends to early Upper Palaeolithic communities as far apart as China (Wei et al. 2016) and Siberia (Lbova 2021). Clearly, beads, art and other items of ornamentation are playing newly significant and increasingly essential roles in people's lives.

The most well-known proliferation of beads and other personal ornaments, as well as small figurines, is that seen in Europe, particularly after 45,000 years ago alongside the movements of modern humans into this region (Mellars 2005; Vanhaeren and d'Errico 2006). These beads are not only produced from naturally occurring shells but also created out of mammoth ivory and soapstone, often circulating over huge areas along extended networks of communication (Heckel 2018). It is also during this period that we see the only documented, potentially systematic production of personal ornaments by Neanderthals in the form of the somewhat contentious Châtelperronian industries of south-west France (Caron et al. 2011, Gravina et al. 2018). Though a Neanderthal's capacity for symbolism is not in doubt (discussed in Chapter 9), objects such as shell ornaments or portable art are extremely rare.

It is not difficult to see why a relationship between the emergence of our own species and the proliferation of symbolic ornamentation and art has always been seen in terms of a cognitive advance, albeit over a delayed timeframe from the first emergence of our species. Cognitive differences are known to exist between modern humans and archaic humans such as Neanderthals (Bruner 2021). Art and ornamentation provide a physical, and aesthetically remarkable, image of what makes a 'modern' mind, seen in terms of a symbolic revolution (Klein 2008). Furthermore, this apparent cognitive advance seems also to have made new relationships possible. Beads, used as personal ornamentation in necklaces or on clothing, have traditionally been interpreted as a mechanism by which connections between groups could be made and maintained – as demonstrations, perhaps, of ethnic identity (Gamble 1991; Gamble 1998).

Much of this progressive narrative does not entirely fall into place, however. That changes in both anatomy and mobility significantly predate the appearance of such personal ornamentation poses a notable issue. Furthermore, whilst capacities for elaborate symbolism are ubiquitous, there is a pronounced concentration of expression in very specific regions and periods. Though depictive art dating from after the arrival of modern humans is found in Indonesia (Aubert et al. 2014), portable art and personal ornamentation are particularly widespread with the arrival of modern humans in Europe. What initially appeared to be a clear distinction between the symbolic capacities of Neanderthals and those of the early members of our own species has been eroded in recent years (Hoffmann et al. 2018). Furthermore, personal ornamentation and art emerged in South Africa from 100,000 to 70,000 years ago but then declined, before emerging again after 50,000 years ago. This makes little sense if some critical cognitive threshold is meant to have been crossed.

Increasingly, there is a sense that there must be other explanations for the proliferation of symbolism than cognitive superiority, though it is not entirely clear what these might be. However, the changes in emotional tendencies discussed in Chapters 4 and 5 provide a potential explanation. Rather than a cause, personal ornamentation may instead potentially be a side effect of changes in emotions and increasing social connectivity. Likewise, rather than a proliferation of symbolism demonstrating some exceptional cognitive advance, such as understanding of symbolism, an ability to be creative, or an elevated sense of imagination, these capacities might have equally existed in earlier humans but without an emotional need for elaborately created non-functional objects. As discussed in Chapter 5, elevated friendliness and social sensitivity often brings with it an almost desperate need for comfort and social connection. Indeed, we only need to take the most casual of glances at our close companions, dogs (discussed in Chapter 7) to appreciate how changes associated with domestication affect needs for social context (and it may be no coincidence that dogs are unusual in also sometimes showing strong attachments to objects). This raises the question of whether new relationships with objects might be a reflection of emotional changes rather than of elevated capacities in symbolic thought. Increased intergroup tolerance brings with it emotional vulnerabilities, particularly an extraordinary sensitivity to social surroundings, greater needs for social connection, and elevated susceptibility to the effects of any lack of attachment security, social connection or loneliness. Rather than signs of a cognitive advance, the increasing prevalence of non-functional artefacts and their distribution within social networks after 100,000 years ago could perhaps be far better explained, at least in part, by new vulnerabilities occurring with increased intergroup tolerance.

New emotional relationships to objects?

As humans, we seem to be uniquely capable of forming unusual *compensatory attachments* whenever human relationships fail to provide everything we need. By reaching out past our close human relationships into realms of real, part-real or entirely imagined companionships, we seem able to cope better with emotional vulnerabilities. These *beyond-human relationships* reflect our ability to imagine other social worlds, and an acute social focus, and they also reflect our need for this type of connection. These unique relationships have not always been part of the human experience, however.

Might a proliferation of non-functional objects after 100,000 years ago be, at least in part, explained by new needs for sources of emotional support?

To address this question, we will initially consider the nature of compensatory attachments to objects and how these objects can make us feel comforted and secure both as children and as adults, as well as their common characteristics in modern society. We will then move on to consider cultural and individual variations in these objects and attachments. Lastly, we will consider the characteristics of the archaeological record, which might argue for the significance of so-called 'symbolic' material culture as a source of emotional comfort and support.

Compensatory attachments to objects in childhood

As we have seen in Chapter 1, our childhood experience can provide us with important insights into the key elements of our adult emotional responses. Children's emotional attachments often present us with a simplified form of what becomes important to adults and may help us to understand the possible role of personal ornaments, portable art or other things seen as symbolic objects which we find archaeologically.

As children, we will all have sought compensatory relationships to cope with the day-to-day experiences of being alone. These compensatory attachments are many and varied. It is typical in the modern Western industrialised context for children to form close relationships with pets, or become attached to a particular comforting object such as a blanket or teddy bear, for example. However, of all of their attachments, it is those that children make to the rather curious phenomenon of *imaginary friends* that provide us with perhaps the most revealing insight into both our capacities and our needs to find sources of emotional support, often in what might appear to be unusual ways. Often sidelined as an area of research, children's imaginary friends give us an extraordinary insight into our ideal companions and the role of our social imagination in bolstering rather fragile human securities.

Children's imaginary friends used to be thought of as a reflection of some kind of emotional issue or even weakness. However, we now recognise that they are, instead, an effective means of bolstering emotional resilience. Imaginary friends appear to us as children when they are most needed. We tend to develop imaginary friends in response to times of loneliness and social stress, and to help to improve our sense of connection, self-esteem and security (Hoff 2004). They tend to be supportive, providing companionship and emotional support, and improving self-esteem. Children with imaginary friends tend to have better theory of mind abilities, and be more social (Giménez-Dasí, Pons, and Bender 2016; Taylor et al. 2013), and even create more interesting and elaborate stories (Trionfi and Reese 2009). They straddle the world of reality and imagination and, whilst children are aware that imaginary friends do not really exist (Taylor and Mottweiler 2008), imaginary friends seem so real that they provide the emotional support of an ideal friend (Majors 2013).

The character of imaginary companions may provide us with some important insights into ideal supportive figures for children, and how these then may relate to material objects. These companions are clearly not just a fleeting sense of something or someone but are fully formed individuals with not only physical characteristics but also separate lives and opinions. Taylor et al. (Taylor et al. 2004: 1178) described several examples, such as a child's imaginary friend called *Alicia*, who was an invisible eight-year-old female dog, with green fur and blue eyes, who lived under the child's bed. The child liked Alicia's good sense of humour but did not like that no one else could see her. Another child's imaginary companion was called *Rose* and was an invisible female squirrel, nine years old, with brown fur and hazel eyes, who lived in a tree in the yard and slept in her imaginary house. Imaginary friends can be close companions when children are lonely, enabling them to be more socially confident. Ella, a child of 11, explained how her imaginary friend *Polly* helped her become more confident as, without her, she says, 'I'd probably feel like very shy, 'cos before when I was like 3 years old, I wouldn't talk to anyone and when I got my imaginary friend, I got, I built up my confidence and if she wasn't there I'd probably be quite shy now' (Majors 2013: 560). Polly emerged when Ella was four years old and her grandmother died (Majors 2013: 555).

Children's choice of imaginary friends reflects certain common patterns (see Table 6.1). They often mimic those types of relationships that are most reassuring to them, such as with friendly furry animals, with powerful animals that might protect them, or with friends with combinations of human and

Key characteristics of imaginary companions
Imaginary companions: – are supportive: they provide companionship, emotional support, nurturance and help to foster self-esteem (Hoff 2004; Taylor 2001) – cannot be created at will 'on demand', but will appear such as in times of loneliness – can be human, animal or a combination of the two, or fantasy animals (and often have human and animal traits) (Taylor, Carlson, and Gerow 2001) – are common (50–60% of children in modern contexts have imaginary friends, often several; Hoff 2004) – in animal form tend to be mammals (i.e. able to nurture), and often large mammals (for example, elephants or lions) (Hoff 2004; Taylor, Carlson, and Gerow 2001) – are associated with higher levels of theory of mind, creativity, achievement and absorption in children and the adults they become (Kidd, Rogers, and Rogers 2010; Wigger, Paxson, and Ryan 2013) – are known by their creators not to be 'real' (Taylor and Mottweiler 2008)

Table 6.1: Characteristics of imaginary companions.

animal features. Imaginary friends are most commonly human or animal, or a combination of the two, or even fantasy animals (Taylor et al. 2004: 1178). For example, one child's companion, called 'quack quack', was a duck with a human head and hands (Wigger, Paxson, and Ryan 2013). They tend to most often be mammals (perhaps unsurprising given a shared mammalian nurturance response) and particularly large mammals (for example, elephants or lions).

It is not surprising that medium-sized or large mammals are common imaginary friends. Being mammals, animals such as bears, elephants and horses share a common nurturing response with us. Also, given their size and intelligence, they seem to be more powerful caregivers or friends than rabbits or mice might be (Vanutelli and Balconi 2015). Furthermore, social and empathetic animals may be particularly comforting in ways that humans sometimes are not. Performance in a stressful test is enhanced more by the presence of a dog than a friend, for example (Allen et al. 1991). We might think that our friends could surely understand us better than an animal could. However, many of our stresses stem from worries about social judgements, and animals provide support that is more clearly non-judgemental. Medium-sized and large mammals seem popular choices as imaginary friends, therefore. They have the clearest abilities to protect, as well as befriend, and it seems no coincidence that the animals chosen as companions are those that seem most capable of understanding how we ourselves feel.

Children's personified objects share many common features with imaginary friends, perhaps not surprisingly. Personified objects, such as teddy bears, dolls or soft or hard animal toys, have personalities of their own and are seen as protectors (Morris, Reddy, and Bunting 1995). As such, these personified objects are typically imagined as comforting companions, similar to imaginary friends, albeit ones with a more tangible physical presence. So-called transitional objects, such as comfort blankets or teddy bears, even seem to play a crucial function in development, particularly in modern Western societies. They bridge a transition to independence and to being able to comfort oneself in the absence of a human caregiver (Winnicott 1953).

Whilst imaginary friends are protected from the distress of accidental loss, personified objects benefit from provoking a sense of touch and bringing a certain permanence to children's lives. Whilst our imagination conjures up an ideal personality in these objects, such as nurturing caregiver or fun-loving companion, our sense of touch at the same time responds to the warmth and softness of favourite personified objects such as teddy bears in a very bodily way, and the very constancy of such objects provides an additional sense of security. Given their power to heal distress, it is no surprise that certain personified objects take on such important emotional roles. Most parents in a modern Western industrialised context understand only too well the powerful attachment infants can form to personified objects.

Compensatory attachments to objects in adulthood

We might imagine that tendencies to derive support from personified objects are discarded as we grow to adulthood. However, it seems that, rather than disappearing entirely, compensatory attachments to things that once comforted us seem to simply change in form, and often become far less visible, perhaps as we feel somewhat embarrassed by the role in our lives. Where invisible or intangible companions are concerned, beliefs in spiritual beings show many similarities with childhood imaginary friends (Mackendrick 2012). Creating in our imagination an ideal caregiver has a powerful effect in relieving stress and in reducing depression, anxiety and other emotional disorders (Gilbert 2014; Rockliff et al. 2008). Where physical and tangible replacements for companions are concerned, animal spirits and amulets or talismans often take similar forms to the animals chosen as personified objects (Varner 2008). Many people continue to cherish their childhood teddy bears, and others transfer their source of security into other forms such as jewellery (Bell and Spikins 2018). In this context, it is perhaps not surprising that personified objects attain the significance seen in *The Repair Shop*. We learn as children that teddy bears or dolls can be companions that, despite being inert, feel like they are living beings who are on our side (Keefer et al. 2012; Keefer, Landau, and Sullivan 2014).

Although each object has its own story and set of beliefs surrounding it, the way in which attachment objects affect us emotionally is remarkably similar from teddy bears to cherished gifts to photographs. Like genuine caregivers, such cherished objects stimulate the soothing neuroendocrine responses that make us feel cared for. We reach for our keepsakes when suffering pain and separation (Niemyjska 2019) and they affect us in turn. Remarkably, simply touching a teddy bear makes us feel more secure and also in turn to become a nicer person to be around (Tai, Zheng, and Narayanan 2011). Cherished personal objects that affect us in this way contribute to our sense of *social safeness*, a warm, soothing emotional state that protects us from stress (Armstrong et al. 2021; Gilbert et al. 2008) and mitigates against feelings of loneliness (Best et al. 2021). Research even shows brain changes in people who are lonely over a long time period and find support outside of human relationships. In their brains, regions known as the default network seem to have been particularly strengthened so that the kind of mentalising, reminiscence and imagination used in personifying objects can 'fill the social void' (Spreng et al. 2020: 1).

Different types of objects may provide comfort in different ways to different people. In some cases, what feels comforting is that the object, such as a teddy bear, seems to have its own personality or soul, and is capable of befriending or even protecting us. In other cases, however, objects connect us to particular people in our lives. A photograph has the most immediate effect in making us feel like someone might almost be there with us, but often clothes, or things that loved ones touched or used, often seem to transport us to their presence in other ways. These kinds of object have a powerful effect on emotional wellbeing by stimulating our sense of attachment security (Table 6.2), a trait which seems to have become more vulnerable to being disrupted as a result of recent evolutionary changes (described in Chapters 4 and 5).

Differences within human populations even hint at evolutionary selective mechanisms acting on physiological and emotional capacities, which may have influenced capacities to find comfort in things. Though people in general tend to anthropomorphise objects at times of stress, those with more social imagination, and a greater tendency to anthropomorphise objects, are those who find the greatest comfort in certain things at times of stress or loneliness (Keefer 2016). They seem better at visualising a comforting presence. Certain people are also more prone to feel nostalgic through objects, apparently relating to differences in serotonin receptor genes that make them more sensitive to negative experiences and more driven, therefore, to find security in comforting things and memories (Luo et al. 2019). Broad

Improvements in attachment security
Priming attachment and promoting social safeness with reminders of caring relationships: – Thinking of attachments reduces noradrenergic stress response (Bryant and Chan 2015) and pain (Jakubiak and Feeney 2016). – Thinking of a romantic attachment figure reduces blood pressure, to the same extent as having a romantic partner in the room (Bourassa, Ruiz, and Sbarra 2019). – Thinking of attachments reduces painfulness of traumatic memories (Bryant and Foord 2016). – Priming attachment security reduces negative reactions to out-groups (Mikulincer and Shaver 2001; Saleem et al. 2015). – Priming attachment security reduces depression and anxiety (Carnelley et al. 2018). – Fostering abilities to feel a sense of social safeness reduces loneliness (Best 2021). – Repeated priming of attachment security by various means leads to more lasting secure attachment (Hudson and Fraley 2018).

Table 6.2: Ways in which objects can improve emotional wellbeing through fostering attachment security.

differences in social sensitivity, as we have seen in Chapter 5, also have a genetic component and affect widespread emotional vulnerabilities and potentials (Assary et al. 2020; Flasbeck et al. 2019).

Like dogs (Kurdek 2008), discussed in Chapter 7, or spiritual beings (Lenfesty and Morgan 2019; Niemyjska and Drat-Ruszczak 2013), cherished objects can even function emotionally like human attachment figures, giving us a sense of safety and promoting positive physiological effects (Keefer, Landau and Sullivan 2014; Keefer et al. 2012). These compensatory companionships can, in effect, reset our bodies away from competitive insecure and threat-based systems that damage not only our own health but also our social relationships, and towards more emotionally connected and healthy social schemas (Gilbert 2019). As we have seen in Chapters 4 and 5, these changes can affect our tolerance of differences or strangers, our willingness to explore, our sense of trust in our close relationships, and even our immune systems.

Are there common forms or features to cherished personal objects?

Disentangling which objects are emotionally significant as a source of social comfort can be challenging. Clearly, in modern Western societies with a focus on materialism, objects also fulfil many roles other than being comforting or useful, such as being signs of status or achievement, or providing some sense of comfort in familiarity without bringing with it a sense of supportive social connection. The boundaries between functional objects and those that provide comfort can also be fluid, and our grandfather's toolkit, belt or other practical items might be both useful and comforting, for example. Moreover, an old belt, a handmade box or cheap jewellery may carry real emotional significance for one person, yet appear to another to be of no value. We may not even acknowledge, or be able to articulate, why some particular object makes us feel cared for or socially supported.

Research into objects that provide comfort for adults in modern contexts does, however, provide some support for a continuity of common characteristics seen in children's personified objects to those that become significant objects for adults. Cherished possessions that provide a significant source of comfort often conform to certain forms, such as representing humans or animals and being easily portable (Bell and Spikins 2018); see Figure 6.2. Research on over 200 cherished personal objects (see Bell and Spikins 2018),

Figure 6.2: Examples of cherished personal possessions that can provide comfort. Left: Girl with teddy bear. Lisa Runnels, 2015, via Pixabay: https://pixabay.com/photos/girl-backside-woods-teddy-bear-961648/. Right: Brooch with photograph. Penny Spikins, CC BY-NC 4.0.

for example, revealed not only teddy bears kept by adults but other types of animals as well, such as a toy guinea pig recorded by a student as a constant stable presence reminding them of friends and family, or jewellery. Certain jewellery, including animal pendants, are described as providing comfort, much like speaking to parents or grandparents, and small animals, either as toys or figurines, are also described as being reminders of the feelings of being safe at home.

A common theme of continuity with childhood imaginary companions, described above, with common human or animal figures, albeit often in portable form, is evident. Objects that act like compensatory attachment figures also tend to be easily portable and show many signs of wear. Like our childhood caregiver, we want to be close to them, and touching them is important. Like imaginary friends, they also often take the form of modified animals, particularly large mammals, such as teddy bears or animal pendants. In this case, they are more likely to have 'a life of their own' as something similar to an attachment figure, rather than simply be intangible reminders of loved ones. Animals seem to have a certain power.

Any object can become meaningful and provide us with a sense of comfort, much like a caring attachment figure, but some types of objects – those representing animals, in particular, and which are able to be carried, held or worn – are more likely to fulfil this role.

Cultural variations

Culture and context affect the types of objects we may become attached to and, moreover, whether it is objects that we look to to provide us with comfort or if we seek support elsewhere, such as in companion animals (discussed in Chapter 7) or even in less tangible imaginary entities.

The role of cherished possessions is seen more clearly in some cultures, and at certain times. For example, whilst many people still believe that things like a preserved rabbit's foot could be 'lucky' (Thwaite 2020), historically there was a much greater function for charms and amulets and a belief that they had healing and protective properties. Nonetheless, common patterns of seeking support in *something* seem resilient, despite the differences in what seems the right sort of object to make us feel safe. The tendency for people hiding in shelters in the London Blitz of 1940–1941 to carry lucky charms, including rabbits' feet, has, perhaps, some similarities to the changing significance of personally meaningful objects seen during the COVID-19 crisis. Whilst, in both cases, many people sought comfort from touching cherished objects, the form of the objects chosen has changed through time.

There is also much individual variation within any culture. For some people, cherished possessions, with their power to make us feel safe, secure and socially connected, are essential to make life bearable, whilst for others they may come into focus only at certain times of crisis, if at all. They are not always significant, or significant for everyone. Whether some people worry about appearing vulnerable, find it difficult to reach out for support, are anxious about objects being lost or find a sense of social warmth and safety elsewhere, there tends to be considerable variation in the personal significance attached to cherished possessions. A certain emotional austerity in modern contexts can even lead some people to have a sense of disdain for such things. Nonetheless, whatever the cherished objects, whether a rabbit's foot in the London Blitz or a grandfather's toolbox in the COVID-19 crisis, things provide comfort, security and safety for some people everywhere. Charms or talismans, in the form of beads and animal figurines carried or worn by adults, are found widely across many different cultures (Varner 2008).

Attachments outside of human relationships seem to be more necessary, and the bonds between people and things stronger, in cultural or social contexts of less social connection and support or where caring figures are not constantly present (Bowlby 1969; Fortuna et al. 2014). This makes sense of the relative scarcity of such objects in hunting and gathering communities. Such societies typically create supportive contexts during childhood development and adulthood, high levels of attachment security, and constant close physical contact during infancy (Hewlett et al. 2000). These are also societies with beliefs that include ubiquitous spiritual beings, the presence of which reduce loneliness. Furthermore, the constraints imposed by a highly mobile lifestyle and the significance of sharing and giving that is so central to modern foraging societies (Lavi and Friesem 2019; Peterson 1993) mean that few things are owned. However, objects continue to be a source of emotional comfort in these societies, albeit in different ways than in industrialised contexts. Cherished possessions providing some kind of social comfort are most evident in childhood. Often, as is the case of the

Yamana of Tierra del Fuego, children's personified objects in hunting and gathering societies are made from perishable materials such as wood, skins or grasses (Gusinde 1986) and represent animals or people. Albeit crudely fashioned from organic materials, such birds, animals or human dolls are significant figures in children's lives. Only in very rare cases would any indication of these objects remain in the archaeological record (Langley 2020). Children's personified playthings, imagined to have their own thoughts, feelings and identities, are, however, found across all cultures (Hong and Townes 1976). For adults, highly portable items, such as beads, figurines or amulets, can be important emotionally (Wiessner 2014). For the Awá of Brazil, the act of making, using and carrying stone arrows is important for their sense of self (González-Ruibal et al. 2011). Whilst not practical, compared to alternative hunting weapons that are much more efficient, they are emotionally important, providing a sense of comforting familiarity, identity and tradition. In many other cases, objects are felt to be significant spiritually and have their own living identities. Even in hunting and gathering contexts, we see cherished possessions playing a role in many people's lives, albeit often being less visible or less relied upon than those we see in modern industrialised contexts.

The emotional role of cherished possessions, as well as animal companions or spiritual beings, in *keeping us sane* may be more important than we think. Objects are an example of non-human attachments that seem to play an important, and often unrecognised, role in supporting our emotional wellbeing, a role that is often left outside of our human evolutionary story.

Art in search of empathy – reappraising the proliferation of symbolic objects

Anyone who studies Upper Palaeolithic portable art and ornamentation quickly concludes that much about its precise meaning will remain lost in time. However, emotional insecurity can have far-reaching effects on us as individuals (such as limiting our capacities to explore, affecting our immune system or making us less trusting) and as communities (such as through hampering a sense of collaboration or willingness to forge relationships based on high levels of give and take), as discussed in Chapter 5, art and personal ornamentation may play an important role in counteracting these insecurities. That cherished objects can provide a sense of security, and even compensatory attachments where supportive others are lacking, may help us to understand some elements of 'symbolic' objects, particularly personal ornaments and portable art.

The timing of a proliferation of 'symbolic culture' after populations of modern humans spread into new regions may be explained in terms of newly evolved emotional vulnerabilities and new needs for support, rather than elevated symbolic capacities, imagination or creativity. After modern humans appear, the proliferation of such objects plausibly follows times of particular stress, for example. 'Symbolic' artefacts appear to particularly proliferate globally after the 'Adams event', 42,000 years ago, when we know that there were major environmental changes and extinction events, as well as decades of electrical storms, for example (Cooper et al. 2021). It seems at least plausible that people sought natural forms of comfort in creating animal-like objects. Moreover, further proliferation of such objects particularly appears as populations move into new and challenging regions of the globe. The emergence of elaborate art in Europe after 30,000 years ago also makes sense in terms of a particular context of elevated needs for social safeness, without any need to rely on narratives of European distinctiveness. Aurignacian beads number in their thousands, for example, and mark the progressive movement of modern humans across Europe (Mellars 2005; Vanhaeren and d'Errico 2006), when meeting existing archaic populations, as well as challenging environments, may have placed them under particular social stress. A proliferation of modern human personal ornamentation and art during the period of interaction between the two species has also been seen as a potential response to the presence of Neanderthals themselves (Greenbaum et al. 2018). That both species felt a greater need for compensatory attachments seems entirely plausible.

That what we see as an explosion of art and symbolism may be more related to a need to fill a void than to some elevated European capacity for imagination or innovation seems important. We like to see the European creators of elaborate and highly realistic art as uniquely talented, but an alternative perspective is one in which they were sensitive and emotionally vulnerable, within communities that faced challenges from their environments. Ice Age environments placed remarkable challenges on human communities, with often-radical shifts in climate leading to severe resource failures and localised extinctions. Moreover, people are likely to have been pushed into lower population densities or isolated refuges, where connections with others, and a sense of belonging, were difficult to sustain (Maier and Zimmermann

2017). Furthermore, and perhaps most importantly, there are indications of at least incipient or occasional hierarchisation in these societies (Pettitt 2020; Vanhaeren and d'Errico 2005; Wengrow and Graeber 2015). Depictive art is extremely rare in the most egalitarian of hunter-gatherer societies (Bird-David 2006), yet becomes more common in hierarchical societies where other people are competitors rather than allies, creating physiological arousal rather than safety. From this perspective, a drive for perfection may be motivated by insecure striving, and the widespread production and use of personal ornamentation, figurines and engraved objects a means of bolstering social security.

The form of portable art seen in European contexts also makes sense in terms of sources of emotional support and connection. As we have seen, children's imaginary friends take animal, human or combined forms, with a particular focus on large animals and on mammals as these companions naturally stimulate our sense of something which can protect us. These same forms tend to feel most comforting to us as adults, with easily portable objects that we can touch being most effective at making us feel secure. Whatever its cultural or individual meaning, portable art may have been important emotionally in terms of promoting a sense of safety and connection, particularly in difficult times. Similar motifs might, thus, naturally become prevalent in the more widely discussed cave art.

Some of the earliest and most famous of these portable art pieces come from south-west Germany, and date to not long after the arrival of modern humans into the region. Here, figurines of therianthropic (human-animal) forms or animals have been recovered. Particularly famous examples include a lion-headed figure from Hohlenstein-Stadel, dating to around 32,000 years ago (Kind et al. 2014; Piprani 2011); see Figure 6.3. Dating to the same period, at Hohle-Fels there are other, smaller pieces, including a waterbird, a smaller human-lion figurine, and a horse, for example (Conard 2003), and, at Vogelherd, a further horse figurine amongst other similar figurines (Dutkiewicz, Wolf, and Conard 2018). The form of portable art pieces seems significant, particularly as, amongst portable art pieces across Europe throughout the Upper Palaeolithic, large mammals tend to predominate (Figure 6.4). Characteristics of objects that may have had a spiritual meaning also seem to have tapped into shared human needs for compensatory attachment figures (see Table 6.3).

Figure 6.3: Lion-headed figure from Hohlenstein-Stadel, 40,000–35,000 years bp. Left: *Loewenmensch1*. Dagmar Hollmann, CC BY-SA 3.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Loewenmensch1.jpg. Right: *Loewenmensch2*. Thilo Parg, CC BY-SA 3.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Loewenmensch2.jpg.

Like both imaginary friends and personified objects, these objects, quite possibly held close and carried around for some time, typically represent those living beings that share a mammalian capacity to responding to our needs, and the size to viably protect and nurture us, such as mammoth, woolly rhino, felines, horse and bison. When we consider these famous examples, it is not hard to see how holding and touching such objects, and sensing a living and caring soul with them, might give a sense of comfort, stability and constancy.

We have appreciated for some time that personal objects, art and ornamentation can be important socially but, perhaps, ignored the emotional significance of such items. Attention has tended to focus on how non-functional items play a role in sharing and exchange systems in small-scale mobile societies, for example. That the exchange of gifts, like beads and personal ornaments, functions to sustain networks is clear in the

Figure 6.4: Small portable art figurines from Vogelherd cave, *c.* 35,000–30,000 years bp. Top: Horse. Museopedia, CC BY-SA 4.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Pferd_Vogelherd_Kopie.jpg. Middle: Cave lion. Hermann Junghans, CC BY-SA 3.0 DE, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:L%C3%B6we_Vogelherd-H%C3%B6hle.JPG. Bottom: Mammoth. Thilo Parg, CC BY-SA 3.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Vogelherd_Mammut_2006.jpg.

Similarities between the characteristics of Upper Palaeolithic portable figurines and personal objects that promote comfort and security in modern contexts:

- small size (portable close to the body or able to be suspended next to the skin)
- preferential selection of large or socially complex mammals as figurines/depictions (e.g. horse, elephant/mammoth, lion)
- rounded morphology (beyond that of the animal-human depicted): teddy bears have evolved to be more rounded through time, for example (Morris, Reddy, and Bunting 1995)
- signs of wear from frequent touch

Table 6.3: Similarities between the characteristics of Upper Palaeolithic portable figurines and personal objects that promote comfort and security in modern contexts.

anthropological context (Wiessner 2002). There is certainly a relationship between the exchange of items as gifts over many hundreds or thousands of kilometres and the maintenance of social networks (Ambrose 1998; Balme and Morse 2006; Dunbar, Gamble, and Gowlett 2014; Gamble, Gowlett, and Dunbar 2011). As Coward explains, since artefacts persist in time, they can be an aid to memory and a record of social relationships, acting as the scaffold for social understanding and making it possible to extend social networks (Coward 2016; Donald 2000; Jones 2007). However, the underlying emotional motivations behind the creation, exchange and use of cherished objects of art or ornamentation is rarely explored and may lie more in the realm of emotional comfort than in any calculated social exchange. Gifts such as beads, in ethnographic contexts, do cement social networks. However, they also play a far less socially strategic and more personal role in people's lives. More than simply representing identities, they make their wearers feel connected and safe (Morris and Preston-Whyte 1994). Personal ornamentation, such as beads, satisfy a feeling of needing touch and closeness, perhaps much like modern items like cherished necklaces or bracelets. Though the appearance of such objects may indicate new social capacities, they may also tell us about new vulnerabilities and emotional responses, and responses to social challenges.

A need for a sense of social safety does not answer all our questions about so-called art or symbolic objects, of course, and many existing interpretations have cast important insights into many other elements of their use. As we have seen in Chapter 3, archaeologists in recent years have increasingly appreciated the evolutionary basis by which the material culture around us influences how our minds work (Malafouris 2015). We have discussed and debated how material culture influences how we think (Knappett and Malafouris 2008), how material things can seem to be part of us (Coward 2010) and create our identities (Miller 2013), and even how material evidence reveals emotions, particularly those of grief (Tarlow 2012). It has become clear that objects can have 'agency', that is, a power to influence the world, almost like living things. Indeed, many ethnographically documented societies do not draw the rigid distinctions that we do between living things and inanimate objects (González-Ruibal 2012). These differing ontologies help us to understand the relationship between people and art (Ingold 2006; De Castro 2007). However, the concept of objects as a source of attachment, security or emotional comfort is rarely raised. Quite why this should be the case remains a mystery. Perhaps emotional insecurity seems too raw or too personal to contemplate, emotional attachments too much connected to bodily responses to seem sufficiently academic, or vulnerabilities too difficult to navigate. Whatever the reason, our emotional needs for social safeness and security, and our abilities to find this in compensatory attachments, including those to objects, are a much-understudied area.

There are also characteristics of portable art and ornamentation that do not entirely fit a role in terms of social safety. Portable art shares many characteristics with cave art, and yet the latter cannot be carried around to provide a sense of support and is even, in many cases, never seen again after its production. Even when we consider art that is portable, we can reflect that many such items may be shared rather than personal, though the connections this creates may themselves be part of the power of the items. Moreover, many such objects, including the lion-headed figure, were deliberately destroyed, something hard to bear in the context of emotional attachments, though perhaps demonstrating a certain ambiguity about the emotional power of such objects. Furthermore, it is entirely possible to argue, conversely, that some elevated social imagination is key to the way in which modern humans relate to their world, providing a new ability to create social safety through imagined relationships that may have been restricted prior to our own species. After all, we have seen that some children are more imaginative, more social, and more able than others to conjure imaginary friends, and some adults more prone to find solace in things, or other compensatory attachments, than others, and that these abilities have some genetic basis. Elevated social imagination may be prompted by the genetic changes occurring under self-domestication that we have discussed in Chapter 5. However, it seems at least plausible that new emotional needs and vulnerabilities are part of the explanation for the so-called symbolic explosion with modern humans.

Perhaps this is the right moment to turn ideas of a progressive elevated symbolic capacity of modern humans in general, and some elevated European capacity for the depictive art, on their heads. These may not have been people with some unique imagination or elevated symbolic capacities but, rather, sensitive and emotionally vulnerable populations reaching for objects as a source of support.

Conclusions

Our attachment to cherished possessions, and our capacity to derive comfort from them, are areas of human experience that are often ignored. However, when we consider these tendencies in more depth they give us an insight into several realms of our emotional lives – from our human sensitivity and need for connection to the flexibility of our attachment systems and ways in which we are able to seek out and find the social warmth and safeness we need. Faced with isolation or loneliness, from that caused by harsh environments or social stresses in the distant past, to wars and pandemics in modern times, we have remarkable ways of continuing to feel the social connections we need to thrive even in the absence of the people who care about us.

An understanding of our emotional vulnerabilities and responses suggests that Upper Palaeolithic portable art and ornamentation may be a product not only of our creativity but also of our need for a sense of social safety, connection and understanding. Much as we have experienced ourselves at times of war or crisis, portable items of Palaeolithic art and ornamentation reflect the responses of people who know what it is to be lonely and insecure about their role in the world. Reaching out to find a sense of connection and social safety in objects provides some social comfort. Moreover, this is not just about emotional wellbeing. When we feel more secure and socially safe, we are better people to be around, more open to new things, more tolerant of differences and perhaps just a little kinder than we would have been otherwise. In appreciating this, we should perhaps be less hasty to see anyone as overly sensitive when they feel attached to a precious heirloom, or to spend time caring for a treasured object.

Rather than demonstrating a human pinnacle of artistic talent, a proliferation of art and personal ornamentation alongside the global spread of modern humans may, rather, be a response to the need to accommodate new emotional vulnerabilities. Cherished objects seen as portable ornamentation or art, which become more common after 100,000 years ago and particularly prolific after 45,000 years ago, may be a product of new emotional vulnerabilities as much as, or even more than, cognitive advancements. The characteristics of objects which provide us with a sense of social connection and comfort in modern societies, and similarities to those of new regionally connected societies after 100,000 years ago, argue for a common role in providing comfort, alongside whatever other complex meaning they may hold. Hidden beneath the surface of our natural attraction to aesthetically pleasing things, it becomes evident that changing emotional capacities and vulnerabilities may prompt particular material objects to begin to play a new role in people's lives. As much as cherished personal possessions may be the most visible aspect of this in the archaeological record, it is reasonable to imagine whole realms of new compensatory attachments, including those towards imaginary or spiritual beings, as well as attachments to animals (explored in Chapter 7).

Many of the cherished personal objects left to us from the Upper Palaeolithic may, in some very human way, share similarities with the Rogers bear. Though we might not know *for whom* they provided reassurance or support or a sense of connection, we might nonetheless have the glimmerings of an understanding of how.

Key points

- We all share a capacity to find social comfort in things outside of close human social relationships, with cherished objects playing an important role in many of our lives. Compensatory attachments to these objects, as well as to other figures, imaginary, inanimate or non-human, can provide a sense of social safeness and security, and allow us to be more confident and resilient.

- The archaeological record shows a proliferation of 'symbolic objects' at times of particular stress, after 100,000 years ago, which can be explained as a response to physiological changes (discussed in Chapter 4 and 5). These changes enabled both greater external tolerance and approachability, and were also associated with elevated social and emotional sensitivities. Characteristics of compensatory attachment figures that provide emotional comfort in modern societies show similarities to new types of non-functional artefacts appearing at this time.

- New emotional vulnerabilities and sensitivities, rather than elevated and superior cognitive abilities, may explain a need to derive comfort from things and the proliferation of 'art' or 'symbolic' objects in the Upper Palaeolithic.

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CHAPTER 7

In the Company of Wolves: compensatory attachments and the human-dog bond

Abstract

Why are we able to form such an intense emotional bond with other animals, such as dogs, despite them being so different from ourselves in so many ways? In this chapter, we consider the human emotional vulnerabilities that drove our close relationships with canids. We explore how an understanding of compensatory attachments can provide a new perspective on the inclusion of wolves into human societies, and the significance of their dog descendants to our emotional wellbeing today.

We first explore the roles of dogs in present hunting and gathering societies, and the potential significance of bringing wolf companions into our emotional lives. We find that, whilst there are considerable cultural differences, dogs and people have a capacity to form remarkably strong bonds, and dogs can take up a sometimes uncomfortable position as *almost human*.

(Abstract continued on next page)

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(Abstract continued from previous page)

We then ask whether the domestication of wolves may have been more influenced by human emotional needs than we may have currently assumed. Whilst we tend to view the domestication of wolves as a process engineered by humans, and indicative of our particular elevated capabilities or intelligence, our emotional vulnerability and capacity to make compensatory attachment may have had a key role to play.

A closer consideration of our shared evolutionary history reveals that wolves and humans share a deep past of becoming incrementally closer to each other in terms of social emotional motivations. As we have seen in Part 1, selection pressures over the last 2 million years moved human emotional motivations closer to those of highly collaborative social carnivores such as wolves, whilst, as we have seen in Chapters 4 and 5, the period 300,000 to 30,000 years ago brought new capacities to make novel relationships, and new emotional vulnerabilities. During this period, the emotional motivations of wolves seem to have moved closer to those of humans through living in close proximity.

Wolf domestication is, perhaps, best seen as a two-way process in which each species moved to fill an emotional gap in each other's lives.

Figure 7.1: Artwork: *Sympathy*, *c*. 1878, Briton Rivière. Photo: Tate. Used with permission.

Introduction

Why have we developed such close relationships with many species of animals, and with dogs in particular?

Across human cultures and historical periods, there is often a recognition that animals can play an important emotional role in our lives. Dogs and humans can share a remarkably close emotional bond, as shown in this late 19th-century painting by Briton Riviere entitled *Sympathy*, *c*. 1878 (Figure 7.1). Despite our evolutionary separation, we seem to understand each other.

We find dogs almost everywhere that there are people. As early explorers came across indigenous peoples on almost every continent, they also encountered their dogs (Figure 7.2). The explorers themselves were all too familiar with dogs as hunting aids, working animals or companions, and the presence of dogs in people's lives, even in the farthest reaches of the world, went largely unnoticed. Yet here is an entirely different species, living alongside and in close relationships with people. That we would develop such a close relationship with a descendant of wolves is truly remarkable, and not necessarily easy to explain.

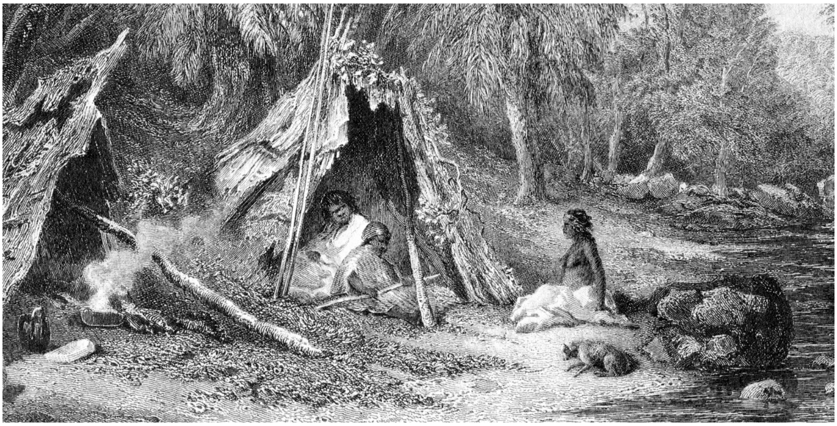

Figure 7.2: Dogs were almost ubiquitous wherever colonists met indigenous hunting and gathering populations. This late 19th-century drawing of an indigenous Australian 'native encampment' shows a dog asleep in the foreground. *Native Encampment* (detail). Edwin Carton Booth, 1876. Image: Skinner Prout, Public domain, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Native_Encampment_by_Skinner_Prout,_from_Australia_(1876,_vol_II).jpg.

Not only did almost all the hunter-gatherer societies that explorers encountered share their lives with dogs but occasional accounts also demonstrated perhaps surprising levels of affection for them. This indicates that these dogs often played an emotional, rather than simply functional, role in the people's lives. The Swedish explorer Lumholtz, cited in Serpell (2016b), for example, recorded the remarkable level of affection that indigenous hunter-gatherers in Australia gave to their dogs (dingoes). He notes that the peoples he met treated their dogs:

> With greater care than they bestow on their own children. The dingo is an important member of the family; it sleeps in the huts and gets plenty to eat, not only of meat but also with fruit. Its master never strikes, but merely threatens it. He caresses it like a child, eats the fleas off it, and then kisses it on the snout. … When hunting, sometimes it refuses to go any further, and its owner has then to carry it on his shoulders, a luxury of which it is very fond. (Serpell 2016b: 302)

The anthropologist Betty Meehan later added support to this picture, commenting:

> It is clear that for some members of the Anbarra community, dogs and especially pups fulfilled an important emotional role. Every Anbarra person loved 'puppies', and, as far as we could interpret, treated them tenderly as if they were human babies. They forced food upon them, cuddled and talked to them, slept with them and carried them around. (Meehan, Jones, and Vincent 1999: 100)

Perhaps most tellingly, such accounts demonstrate that dogs could move into people's emotional lives where human social connections were sometimes not enough. Meehan continues to describe, for example, the case of a woman who was an older and less favoured wife who fought with her husband and sister and saw little of her son. She had an unusually large number of dogs (about 10), with whom she slept at night, often engaging in animated conversations with them. Her dogs were devoted to her and she, in turn, carefully fed and cared for them. She even made a small cloth shelter similar to those made when women were giving birth for one of the female dogs when she had a litter of puppies (Meehan, Jones, and Vincent 1999).

Stories of dogs transforming people's lives by being loyal companions and sources of emotional support are even more common in modern societies. Dogs are awarded medals for bravery in combat and for risking their lives to save their owners, and we even build statues to dogs who have shown extraordinary loyalty. They often take up a role as an ever-present source of affection and loyalty, and are seen as our 'best friend', with us through all adversity. Dogs traditionally play a role as the willing companions and source of emotional support for children (Figure 7.1) and, as adults, research has even shown that, in modern Western societies, only romantic partners are preferred above our pet dogs as a source of emotional support in times of stress (Hart and Yamamoto 2016; Meehan, Massavelli, and Pachana 2017). There are numerous accounts of how dogs have saved people from depression and loneliness, or isolation, or have transformed their lives in other ways. Most of us will have experienced some kind of close interaction with the descendants of tame wolves who now share our lives. Dogs play a significant role in people's lives across the world, whether living as close companions, as is typical in many modern industrial societies, as working dogs, or as free-ranging dogs associated with human settlements.

What can an understanding of the evolutionary background to human evolved emotional dispositions contribute to our understanding of how dogs came to take up such an important role in many of our lives? Might the emotional sensitivities and vulnerabilities we have discussed in Chapters 4 and 5 play a more important role in the emerging relationship between people and wolves during the Upper Palaeolithic than has previously been assumed?

Here, we first consider insights from ethnographic contexts before considering what we can learn from dogs in modern contexts. We reappraise the archaeological evidence for the 'domestication' of wolves to consider if human emotional vulnerabilities may have played a more significant role in bringing dogs into human lives than we generally appreciate.

Dogs in recent ethnographic contexts

As we have seen in Chapter 1, many hunter-gatherer groups keep a range of different animals as pets, including birds and monkeys, and it seems that these animals play a certain emotional role (Bradshaw 2017). They seem to stimulate similar types of reactions to those we have to our own infants, and some of our tendencies to care for animals may stem from the selective value of demonstrating a reputation as someone sensitive to the needs of the vulnerable (Bradshaw 2017) (see Chapter 4). However, dogs are unique in certain ways in the level of intimacy that they have with human lives (MacLean et al. 2017). It has been dogs who most clearly adapted themselves to suit life with humans, as well as humans who adapted ourselves to suit life with dogs. They are found sharing their lives with hunting and gathering peoples from Australia (Figure 7.2) to Tierra del Fuego (Figure 7.3), to East Africa (Figure 7.4).

Dogs as a form of technology

At first sight, the presence of dogs in ethnographically documented societies seems to be explained through their usefulness in various tasks. Certainly, we often see cases in which dogs perform some kind of useful function (Brougham 2018). Arctic hunter-gatherers depended on teams of dogs to get around their landscape, and to carry the tools they needed to hunt and the meat from animals they hunted, for example (Figure 7.5). Further to the south, in less extreme conditions, North American societies also used dogs as pack animals using travois (a type of sled using two poles; see Figure 7.6). Dogs can also help in hunting, in effect making up for the relatively ineffective senses we inherit as primates. They have a remarkable ability to track prey and are also adept at killing small animals. Women in Central Australian groups commonly used dogs to flush out small game,

Figure 7.3: This photograph, taken around 1930, shows dogs accompanying Selk'nam hunters in Tierra del Fuego. Unknown author. Public domain, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Selknam_cazando.jpg.

Figure 7.4: Modern Hadzabe of East Africa returning from a hunt with their dogs. *Hadazbe Returning from Hunt*. Andreas Lederer, CC BY 2.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Hadazbe_returning_from_hunt.jpg.

Figure 7.5: *Inuit coming down Tree River by sled*. J. J. O'Neill, CC BY-SA 4.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Inuit_coming_down_Tree_River_by_sled_(38571).jpg.

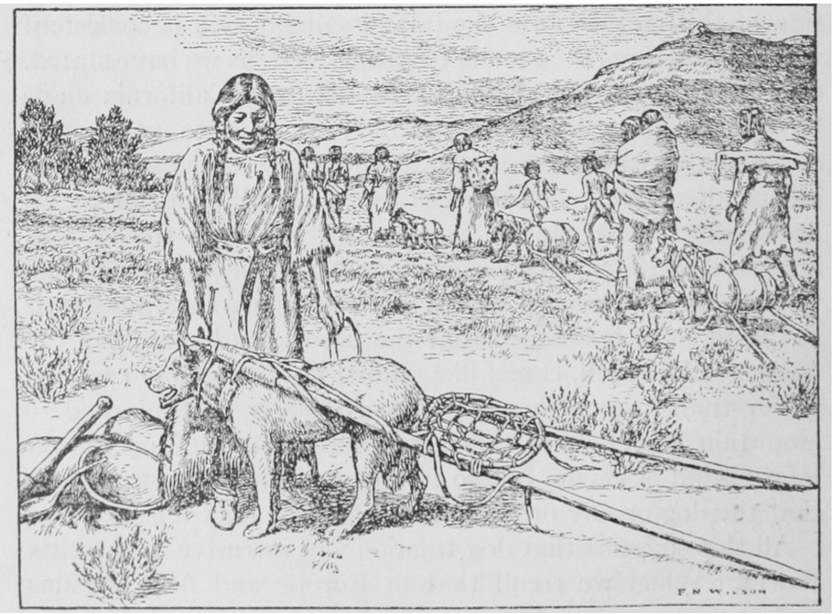

Figure 7.6: This depiction, published in 1917, shows indigenous North American hunter-gatherers of the Bison area travelling between encampments using dogs with travois to carry their loads. Clark Wissler, Public domain, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:The_American_Indian_Fig_11.jpg.

for example (Balme and O'Connor 2016). Hunters in lowland neotropics of South America increase their hunting efficiency when hunting medium or large rodents, such as agoutis or pacas, by using dogs to find and corner, or flush out, these animals (Koster 2008; Koster 2009). Moreover, dogs' highly attuned senses can be important in defence, such as acting as watchdogs in the event of intergroup feuding (Koster 2009). Many speculate that, in the Palaeolithic, dogs may have played a role in defence against the dangerous predators such as cave lions or hyenas that were common at the time (Germonpré, Fedorov, et al. 2017). Dogs are even used in some societies as a source of wool or furs (Germonpré et al. 2020). Some authors have even argued that domesticated wolves or proto-dogs played a key role in the decline of large carnivores during the Ice Age, as well as in the overhunting of large game, particularly mammoths (Germonpré, Fedorov, et al. 2017; Shipman 2015a; Shipman 2015b).

However, there is another side to the story.

Dogs as playing a role in emotional wellbeing

Ancient dogs may not have been as useful as we might imagine, nonetheless. The range of uses of dogs in recent ethnographic contexts may be a little misleading as these functions often depend on particular morphologies or traits that developed well after domestication and are specific to certain tasks, such as large robust physiques suited to carrying loads. Despite what we might imagine, unspecialised dogs are not always useful hunting aids. Dogs that live amongst forest-living hunter-gatherers in Central Africa, for example, only appreciably increase yields when hunting small animals such as pouched rats. They can actively interfere with more collaborative hunts of large game (Lupo 2017). Meehan, considering the use of dogs amongst the Ambarra of Australia, for example, concludes that most camp dogs were 'absolutely hopeless at hunting' (Meehan, Jones, and Vincent 1999: 102). This is an observation mirrored in other studies (Balme and O'Connor 2016; Smith and Litchfield 2009), though some argue that dogs may have been useful in hunting in some contexts (Koungoulos and Fillios 2020). It has been argued that the efficient hunting of large animals such as kangaroos would only have been possible in Australia through the introduction of highly bred and trained European dogs (Meehan, Jones, and Vincent 1999). Dogs may be useful when tracking and flushing out small game, but seem likely to have been a hindrance in hunting large game, which they may well have tended to scare away. Much of the usefulness of dogs for carrying loads may also be a result of later morphological changes following domestication. Wolves themselves are agile and nimble, rather than robust, with only distinctive stocky breeds used in carrying loads in North American contexts (Brougham 2018). Even some of the potential usefulness of dogs to alert us to dangers may have developed well after proto-dogs began to share their lives with humans. Though modern dogs bark frequently, for example, barking is very rare in wolves (Bradshaw 2017). Many societies, such as the Martu of Australia, have many dogs but make no use of them to hunt or for any other economic function (Lupo 2017).

Attitudes towards dogs in small-scale societies can reveal interesting insights into their potential relationship to humans in the distant past. However, the picture of human relationships to dogs in such contexts is complicated.

There are certainly examples of contexts in which dogs are treated with disdain and even abuse. Amongst many Central African populations, such as the Aka, dogs are often treated harshly (Lupo 2011). Even when considered useful in hunting, dogs may nonetheless not necessarily be treated with much respect (Serpell 2016). Many of the ways in which dogs are treated can also seem alien to our cultural perspective. Dogs may be a source of food, with the consumption of dogs recorded in both ethnographic and archaeological contexts, for example (Clutton-Brock 1995; Germonpré, Lázničková-Galetová, et al. 2017; Serpell 2016a). However, when we look more deeply, we can see that cultural beliefs about dogs can play a major role in our attitudes towards them. The Aka, for example, treat dogs harshly as they are seen as reincarnations of witches or sorcerers, and so dangerous (Lupo 2011). These reactions are not, therefore, particularly surprising. Believing dogs to be dangerous also leads to an equal lack of empathy in modern contexts (Jordan 1975; Serpell 2016a). As we have seen in Chapter 1, our tendency to empathise with anybody or any being is much influenced by our beliefs about them, and dogs are no different. Our modern Western sensibilities can also affect our understanding of what it might mean in emotional terms for dogs to be seen as food. Eating dogs can be a very practical response. That there were dogs that were eaten does not necessarily mean that there were not also dogs that were much loved, or even that dogs that were eaten were not mourned. In some cultures in which dogs are killed and eaten, this often happens in a ritual context as sacrifices who are mourned (Clutton-Brock 1995). Moreover, even where dogs are seen as simply a source of food, there are often certain dogs that are seen as being appropriate for being companions, whilst others are destined to be eaten (Serpell 2016).

Almost everywhere, dogs are recognised as sharing an intelligence and emotional capacities not unlike our own (Serpell 2016a).

Rather than their differences, it is their very similarity to humans that tends to be the root cause of some of the least empathetic treatment of dogs. Whilst dogs might seem similar to us in many emotional ways, they cannot behave according to human social rules or understandings. They lack any understanding of past or future, understand our language in only the very crudest of ways, and often behave in ways that are seen by human standards as immoral or disgusting (Serpell 2016b). They are, thus, often punished for behaviour that is simply following their instincts because of our own gut feelings that they *should have known better*. Being rather too much like humans also makes them easy scapegoats for displaced aggression (Singer

1978), and it is dogs that are the animals most frequently abused cross-culturally (Gray and Young 2011). For example, amongst the Matinen of Indonesia, whilst men form close relationships with their hunting dogs, carrying them around and even taking them to bed with them at night, women tend to treat them aggressively. This is interpreted as a displacement of their frustrations at gender inequalities that it is difficult to express overtly (Broch 2008). Dogs found in many archaeological contexts have been subject to aggression, as demonstrated from tooth loss and tooth fractures (Losey et al. 2014). Rather than not being similar enough to fit into human society, dogs can be *too close for comfort*.

For better or worse, dogs often occupy a liminal zone, in some respects animal but often seen as human-like. If they do not quite fit human ideals of how they ought to behave, or if cultural beliefs impose misplaced motivations on them, they can be subject to abuse.

The very humanness that can cause aggression towards them also makes them a frequent source of emotional support, however.

There are several ways in which dogs often play an important emotional role in recent hunter-gatherer contexts. Dogs are occasionally kept explicitly as companions, such as is recorded amongst the Iňupiaq (Germonpré et al. 2020). More commonly, however, dogs are frequent playthings and companions for children in almost all foraging contexts (Gray and Young 2011); see Figure 7.7. They are also often treated as infants, and, perhaps rather surprisingly from our cultural sensitivities, breastfeeding of puppies is common (Simoons and Baldwin 1982). These puppies, even as adult dogs, will be seen as sufficiently human-like, as having somehow taken on something important from a person, that the thought of eating them would be repugnant (Bradshaw 2017; Serpell 1987). Adult dogs can fill the place of close kin for whom one would have intense loyalties and go to great lengths to look after and protect, and who provide an important source of reassurance and emotional support. It is not unusual for dogs to be present and much cared for without seeming to perform any useful function. They may be cared for when ill or injured, provoke a distinct sense of grief at their passing, and are sometimes buried with their owners, or even individually (Serpell 2016b).

Amongst northern-latitude animistic traditions for which people, animals and objects all have a distinct spiritual essence, dogs can have a particular

Figure 7.7: Children, in particular in hunting and gathering contexts, often develop a close relationship with dogs, especially puppies. This photograph from the American Museum of Natural History shows Inuit children playing with their pet dogs, *c*. 1900. Internet Archive Book Images, no restrictions, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:The_American_Museum_journal_(c1900-(1918))_(18162508871).jpg.

position within human social relationships. Individual animals of other species, such as reindeer, are seen as more of a collective spirit, whilst dogs may reveal their individual soul (Losey et al. 2011). Rather than all dogs being almost human, however, it is rather more the case that *some dogs* reveal themselves to be human-like. Much like we may view other people with little regard, yet others as a means of achieving our own ends, and others we may care deeply for, dogs can occupy very different roles in the lives of humans. Those who were not seen to display a particularly human spirit may be discarded at death; others may be afforded a human-like burial in keeping with the human-like soul (Losey et al. 2011). Each dog, like each human, has their own individual identity.

Sometimes, dogs in ethnographically documented contexts are treated with what we might view as too much, rather than too little, affection, or at least with too great a leniency, being permitted to behave freely with few constraints despite the consequences. Perhaps surprisingly, dogs are almost never trained in the sense we might understand the word of being subject to positive or negative reinforcement, but rather they are expected to learn from imitation (Koster 2009), much as is typical of childhood social learning (Hewlett, Lamb, and Leyendecker 2000). This extreme level of tolerance towards dogs can be the cause of problems. Serpell describes, for example, how the Onges from the Andaman Islands are so loving towards their dogs that they have become a pest, far outnumbering the human population, creating constant flea infestations and common bites and keeping people awake at night with continuous barking and howling (Serpell 2016b, after Cipriani 1966).

The relationship between indigenous Australian hunter-gatherers and dingoes, an ancient lineage of dog unique to the region, is perhaps one of the most enlightening.

Dingoes are particularly significant because their evolutionary history and behaviours lie somewhere between wolves and modern free-ranging dogs (Crowther et al. 2014; Miklosi 2014), discussed in more detail in Chapter 8. Dingoes can hunt, parent and share food collaboratively, much as wolves do, yet are more tolerant of humans (Miklosi 2014). Dingoes are somewhat more like wolves in social terms than our other modern dogs, making them perhaps our best analogy for early proto-dogs. Their abilities to hold human gaze, important in bonding, lies for example between that of wolves and dogs (Johnston et al. 2017).

Given that their abilities to share goals and understand human emotional responses are somewhat reduced compared to 'domestic' dogs, that some of the closest relationships between humans and dogs are between indigenous Australian populations and dingoes is perhaps surprising. It is almost as if, by being less useful, they become more significant emotionally.

Perhaps more than any other dogs seen in ethnographic contexts, it is dingoes that were most clearly filling an emotional gap in people's lives. Whilst there is some evidence that, after European colonisation, imported domesticated dogs may have been useful hunting aids (Koungoulos and Fillios 2020), possibly even for large game such as kangaroos, the usefulness of dingoes in hunting is much less evident. Their use as a type of technology was limited. Dingoes mostly served a function as hunting aids for women hunting small game, and as 'blankets', and did not hunt large game or carry loads (Balme and O'Connor 2016; Smith and Litchfield 2009). In contrast, it is their role as companions and as a source of emotional support that is the most evident (Meehan, Jones, and Vincent 1999). Dingo puppies would commonly be breastfed and be companions and playthings for children, and treated with a great deal of affection (Balme and O'Connor 2016). Dingoes in Anbarra society in Arnhem Land provided a psychological defence against malevolent spirits, and played a particularly important role as companions for children and the elderly (Meehan, Jones, and Vincent 1999). Dingoes appear to have been treated 'almost as members of the family rather than as personal property' (Gunn, Whear, and Douglas 2010, after Berndt and Berndt 1988).

Despite their intimate relationship with people, dingoes were far from domesticated as we might understand the term. Adults were usually not deliberately fed but would scavenge for food, could suffer from diseases and could often be undernourished (Smith and Lichfield 2009). Their affiliation with people would often loosen as they became adult dogs, when they became less appealing to humans. Except in the case of a few favoured animals, adult dogs would usually return to free-ranging communities, which lived in more distant association with human groups (Gunn, Whear, and Douglas 2010). Only in a few rare circumstances were breeding adult populations integrated into indigenous communities (Smith and Licthfield 2009). This relationship with dingoes demonstrates how emotionally close people can come to animals that are effectively 'wild' without these groups being significantly dependent on each other, economically or practically.

Overall, it is clear that in hunting and gathering contexts, as in modern Western industrialised societies, dogs can play an important role in making the emotional context of childhood feel more supportive and in being a friend to adults when they feel they need one. Moreover, where there is a lack of connection or a sense of loneliness in human relationships, dogs can provide the emotional support to fill the gap. As we have seen in Chapter 5, this is not just important for individuals but for societies as a whole. Bolstering our sense of being socially safe through attachments to dogs makes individuals both more resilient, and better able to develop relationships based on trust and generosity, and also fosters more social collaboration at a community level.

Studies of the psychological significance of dogs in modern contexts can help us to understand the emotional role that they can play.

Dogs as sources of emotional support in modern industrialised contexts

What drives the remarkable intimacy between humans and dogs? Recent research in modern industrialised contexts has given us some important insights. We have discovered that dogs share many of our most critical emotional capacities. They are emotionally capable of forming strong bonds of love and affection, and can understand and empathise with many of our feelings (Albuquerque et al. 2016; Kis et al. 2017; Nagasawa et al. 2015; Turcsán et al. 2015). Dogs synchronise their stress levels with ours (Sundman et al. 2019), and even share a similar physiological reaction to crying babies (Yong and Ruffman 2014). A study of children in Spain, aged between six and 13, showed that they rated dogs as similar to humans on scores of cognitive and emotional capacities, such as intelligence and abilities to feel pain or happiness, for example (Menor-Campos, Hawkins, and Williams 2018). To them, dogs did not seem to be so different to humans.

Dogs can act in lieu of people as a source of emotional support in adults (as discussed in Chapter 5). They can even act in a way that is psychologically a little like parents as *attachment figures*. This means that, when we are with a dog with which we are emotionally attached, the release of opiates like oxytocin and beta endorphin make us feel safe and calm (Beetz et al. 2012; Kis, Ciobica, and Topál 2017; Kis et al. 2017). They make us feel loved and cared for, provide a 'safe haven' and give us the confidence and self-esteem to approach any difficulties we face (Kurdek 2008; MacLean and Hare 2015). Dogs can have a significant impact on improving emotional wellbeing (Brooks et al. 2018). As we have seen in Chapter 5, this is important not just for individuals but for societies as a whole, as bolstering our sense of social safety through the emotional support of dogs both makes individuals more resilient and fosters more social collaboration within communities. In Chapter 6, we discussed how a closer attachment to cherished objects seemed to have developed during the COVID-19 lockdown in the UK. Alongside many other pets, pet dogs were even more important, maintaining emotional wellbeing for many people (Ratschen et al. 2020; Shoesmith et al. 2021).

The support provided by dogs not only compensates for where social relationships may be deficient but also complements the support of people around us, even when supportive relationships are abundant. That dogs are not judgemental can sometimes mean that they are more effective means of emotional support in certain situations, for example. When having to complete a stressful or demanding task, it is often the company of a dog that is even more beneficial than that of a friend (Allen et al. 1991). That dogs share with us a beating heart and a capacity to care about us, to express affection and to show a certain level of empathy, can have a profound effect. Far from being a passive part of our lives or an object of functional use, dogs in modern societies certainly seem to be playing an important emotional role, and providing a means by which we are better able to cope with our own emotional vulnerabilities. They may fill a specific emotional void at the particular point it appears, but dogs also fulfil many of our basic emotional needs and respond to vulnerabilities that are part of our everyday lives. As we have seen in Chapter 5, dogs, or other sources of feelings of warmth, security and social safeness, do not just make us individually healthier but also make societies more collaborative and resilient. Much like comforting objects, discussed in Chapter 6, our close relationships with dogs in modern industrialised contexts tells us about a remarkable human capacity to find comfort, warmth and emotional safety outside of close human bonds. Much like our dependence on comforting objects today, our relationships with pet dogs also illustrates the additional needs for comfort and social support that our rather disconnected and isolated modern societies impose.

The process by which wolves came to be ‘tame’ is often seen as one that demonstrates the elevated intelligence of modern humans, and a new drive and capacity to control the environment, including animals, to our own ends. Could tame wolves or early dogs have, instead, been incorporated into human societies as a response to new emotional vulnerabilities?

Reappraising the domestication of wolves from the perspective of emotional vulnerabilities

Interpretation of the mechanisms underlying wolf domestication to date have tended to emphasise the practical or economic usefulness of either side of the wolf–human relationship. Wolves are seen as domesticated through being functionally useful for people (as described above) whose new elevated cognitive abilities paved the way for domestication, and people are seen as serving as a source of scraps of food to scavenge (Jung and Pörtl 2018).

A reappraisal of the archaeological evidence, in the context of our understanding of the evolution of our increasingly socially attuned and yet emotionally vulnerable minds, allows us to cast a new perspective on the so-called 'domestication' of wolves. Rather than elevated cognitive capacities, and economic drivers, it may have been human emotional vulnerabilities, alongside similar sensitivities in wolves themselves, that drove strong bonds between humans and wolves.

Archaeological evidence

Research into wolf domestication has tended to first focus on the *timing* of wolf domestication as the primary means of understanding how it occurred. The exact timing of the sustained domestication of wolves remains in debate, and the process almost certainly took many thousands of years. Genetic evidence, for example, suggests that there were very probably multiple points of domestication across Europe and Asia, as well as many instances of continued interbreeding between proto-dogs and wolves (Caspermeyer 2017; Godinho et al. 2011; Skoglund et al. 2015). In North America, for example, around half of grey wolves have a black coat coloration that came from interbreeding with populations of dogs arriving with humans into the continent (Bradshaw 2017). The earliest traceable *genetic ancestor* of modern dogs lived around 15,000 to 20,000 years ago (Cagan and Blass 2016; Druzhkova et al. 2013; Skoglund et al. 2015). However, the complexity of intermixing within the genetic record means that the first wolves came to live in close proximity to humans many thousands of years prior to this point (Freedman and Wayne 2017). Either earlier proto-dogs living in close proximity to humans left no direct descendants or the confusion created by high degrees of interbreeding with wolf populations makes their existence almost impossible to identify (Larson et al. 2012; Skoglund et al. 2015).

Potential evidence exists of morphological changes, typical of domestication (or, as we have seen in Chapter 4, something best described as *increasing tolerance or tameness*) occurring in wolves not long after modern humans entered Europe. Wolves, or perhaps even proto-dogs, dating to around 30,000 years ago in Europe, show a reduction in size and in snout length, for example (Germonpré, Lázničková-Galetová, and Sablin 2012). However, these interpretations remain somewhat contentious, as it may be difficult to differentiate such changes from morphologies that may have existed in contemporary wolf populations (Boudadi-Maligne and Escarguel 2014; Germonpré et al. 2015; Morey 2014). Nonetheless, a proto-dog from Razboinichya cave in Siberia, dated to 33,000 years ago and similar to those in Europe, also shares many features with modern dogs, rather than wolves (Druzhkova et al. 2013; Ovodov et al. 2011). Entirely conclusive evidence may be difficult to find, but there is certainly suggestive evidence that wolves took up close relationships with humans not long after modern humans arrived in Europe.

It is what archaeological evidence can tell us about the nature of the relationship between humans and dogs that is perhaps the most interesting.

Perhaps surprisingly, there seems to be limited evidence that dogs perform a functional role, though this evidence might, of course, be rather difficult to find. Neolithic dogs from Siberia may show certain signs of being used as load animals through osteoarthritic changes in the limbs (Losey et al. 2011). However, these results remain speculative. Equally, these are late examples and, as we have seen, load animals tend to be a rather specialised breed. Specialised forms of dog do not seem to appear until late in the archaeological record. The earliest possible example of a specific form of dog is that of Late Glacial small dogs found the south-west (Pont d'Ambon and Montespan) and north of France (Le Closeau), of which 49 examples date from 15,000 years ago onwards (Pionnier-Capitan et al. 2011). However, whether these dogs are notably smaller than wolves as a side effect of domestication or through some functional advantage of a smaller size that made life alongside humans more successful, such as for catching rodents or being less costly to feed, is difficult to determine.

Evidence for how people treated their dogs is more revealing. That the deaths of dogs or proto-dogs prompted certain rituals or practices gives us some indication of, at least, intense conflicting feelings towards dogs and, in many cases, what was likely to have been a sense of grief at their passing.

The act of burying a dog at death, or carrying out a particular ritual, much as we might for a human, almost certainly indicates an appreciation of the unique identity of dogs within human lives. Early proto-dogs or wolves, dating to around 30,000 years ago, found at Předmostí in the Czech Republic, for example, include one individual found with a large bone inserted between its jaws after death (Germonpré, Lázničková-Galetová, and Sablin 2012), potential evidence of a certain human drive to nurture this animal with food. Several contemporary proto-dogs also have holes that have been incised into the crania, which have been interpreted as a potential intention to allow their souls to be released into an afterlife (Germonpré, Lázničková-Galetová, and Sablin 2012).

Somewhat later in time, we see the appearance of dog burials. Dogs may have been buried as spiritual protectors or as beings with a human-like soul, and we may never entirely understand the motivations for interring dogs as if they were humans. It is not uncommon for certain groups, such as the Aka, who usually accord little respect or dignity to dogs, to nonetheless sometimes bury a particularly good hunting dog as a sign of respect for their contribution (Serpell 2016b). Nonetheless, many burials do appear to demonstrate the particularly significant role of dogs in people's lives, a little like that of a family member (Morey 2006).

Probably the earliest accepted dog burial is that of a dog buried within a double grave of a 50-year-old man, a 20- to 25-year-old woman, and another dog, at Bonn-Oberkassel in Germany around 14,000 years ago (Janssens et al. 2018; Morey 2010). The site was excavated over a hundred years ago, making the precise dating of this burial, and the details of placement of the people and the dog, rather uncertain. However, it is not details of stratigraphy or orientation of remains that are the most significant element of this burial. Instead, it is that the remains document probably one of the earliest cases of apparent care that seems to have been given to a dog during a lengthy period of illness. The dog, a juvenile who died at about 27 to 28 weeks, suffered from canine distemper, as well as periodontal disease (probably related to associated immune deficiency). It was severely ill from 19 weeks onwards, and would have been unlikely to survive without considerable care, which has been interpreted as an indication of a close emotional bond with the people who must have looked after it (Janssens et al. 2018).

Dog burials become more common from the end of the glacial period. More securely dated dog burials have been recovered at the North American sites of Koster and Stillwell II in Illinois dating from around 10,000 years ago (Perri et al. 2019). Here, three dogs were buried in clearly demarcated pits, with a certain level of care. Dogs must have accompanied some of the earliest colonists into the Americas (Perri et al. 2021).

The practice of burying certain dogs at death is seen in many contexts (Morey 2006). Some of the most famous dog burials date to the Holocene. Perhaps the most well known are those from the Late Mesolithic site of Skateholm in Sweden, dating to about 6,500 to 5,500bp. These burials seem to fit with the perception of dogs as remarkably human-like seen in animistic contexts (Larsson 1990). Within the large hunter-gatherer cemetery at Skateholm, there are 14 dog burials, each of which seems to indicate a dog with a certain status or personality who may have been significant at the time. In one case, a woman and dog were buried together, with the body of the dog situated above the women's legs. In another case, a single dog was buried alone, and was interred with more grave goods than other human burials, including flint flakes, red deer antler and a stone hammer. Red ochre was also often scattered over the dogs' corpses (Larsson 1990; Morey 2010).

Robert Losey has interpreted dog burials by Holocene foragers societies in the Cis-Baikal as signs of dogs that were seen as having human-like souls (Losey et al. 2011). Further potential evidence for care of an injured dog comes from this region, where a dog (or proto-dog/wolf) found at Ust'-Khaita and dated to around 12,000 years ago had suffered a puncture wound to the crania and scapula that had healed, possibly suggesting care from humans (Losey et al. 2013). In an animistic understanding of the world, typical of many hunting and gathering societies, certain dogs may have shown themselves to be human-like and, thus, a human-like treatment at death may also have seemed most appropriate. Perhaps for this reason, dog burials seem to be particularly associated with forager societies in the Cis-Baikal, rather than later pastoralists whose worldviews may have been less in keeping with attributing a human agency to animals (Losey et al. 2013). A dog at Pad'-Kalashnikova, dating to around 6,900 years ago, was individually buried in a sitting or crouched position, for example (Figure 7.8). Another, buried at Ust'-Belaia around 6,800 years ago, was buried wearing a

Figure 7.8: Prehistoric dog burial from Pad'-Kalashnikova. Image copyright Losey et al. (2013): https://doi.org/10.1371/journal.pone.0063740.g006. Shared under the Creative Commons Attribution Licence CC BY 4.0.

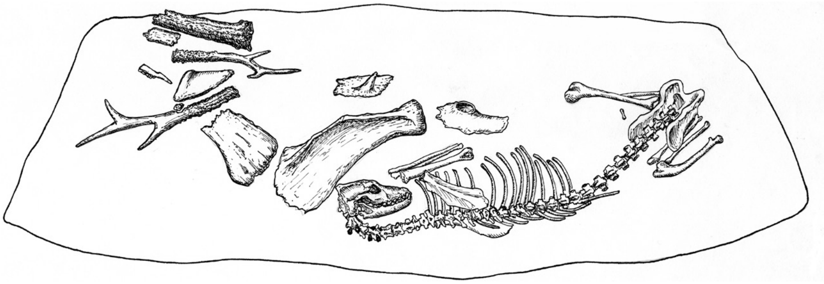

Figure 7.9: Prehistoric dog burial from Ust'-Belaia, Siberia. Image copyright Losey et al. (2013): https://doi.org/10.1371/journal.pone.0063740.g007. Shared under the Creative Commons Attribution Licence CC BY 4.0.

necklace of red deer teeth, as well as some antler and other faunal remains (Losey et al. 2013); see Figure 7.9.

Other burials apparently indicating much affection for dogs include that in a Natufian (pre- or early agricultural) context at Ein Mallaha, in Israel. Here, the 11,000- to 12,000-year-old burial of a puppy was associated with an elderly individual whose left wrist was partially under the forehead of the puppy, interpreted as denoting an affectionate relationship (Morey 2010).

Other canids also played an apparently emotionally significant role in people's lives, even if this did not lead to full domestication. There are even cases where foxes have been buried in a human-like way. An extinct fox was found buried alongside humans in the 2,000- to 3,000-year-old hunter-gatherer cemetery of Loma de los Muertos in Patagonia, for example, interpreted as indicating some particular emotional relationship, or recognition of the fox as somehow human-like (Prates 2014). Similarly, a burial of a red fox, dated to 14,000 years ago, was also found alongside human graves in a pre-Neolithic context at 'Uyun al-Hammam in Israel (Maher et al. 2011). These foxes may have been, at least in some understanding of the term, *friendly* towards humans. Whilst it is dogs who have particularly taken up a widespread role in our lives, canids in general share many emotional similarities and needs to humans as close relationships with foxes, as well as their ready domestication (discussed in Chapters 4 and 5) illustrate. There are often cases of orphaned foxes in recent times that develop a close relationship with humans. Clarence Birdseye, writing in 1955, described adopting an orphan wild Peruvian fox when living near Lima, for example, which he described as being 'as tame as any dog or cat' (Birdseye 1956). The fox, named Susie, lived with Clarence and his wife for over 18 months and was affectionate with them, calling for them when needing assistance, though always remaining nervous of strangers. Other burial evidence suggests an even wider range of animals in close relationship with people. Most famously, cats develop close relationships without being 'domesticated'. At the pre-pottery Neolithic site of Shillourokambus in Cyprus, an eight-month-old cat was buried with its presumed human owner around 9,500 years ago (Vigne et al. 2004).

Artefacts can also provide important clues to human–wolf relationships. The depiction of dogs or wolves, or the use of their bones, in personal ornaments may also indicate a close relationship to humans. Wolf or dog teeth are commonly suspended as jewellery in the Upper Palaeolithic, far more frequently than those of food animals such as reindeer, or even of other carnivores (Germonpré, Lázničková-Galetová, and Sablin 2012). Wolves often carry particular important meanings to people in North American mythology (Pierotti and Fogg 2017), and the teeth of dogs themselves might potentially have been worn in reflection of their significance, much like human teeth were also suspended as jewellery during the same period.

Across the prehistoric world, dogs are also sometimes depicted within art. At the pre-Neolithic site of Shuwaymis in Saudi Arabia, for example, a rock art frieze depicts people hunting horses with several dogs, some of which are on leads (Guagnin, Perri, and Petraglia 2018). However, in Upper Palaeolithic Europe, in contrast, dogs are conspicuous by their near complete absence. Like humans, dogs are rarely, if ever, depicted and, if they are, it is rather schematically, in contrast to the careful and evocative images made of animals such as horse and bison (Montañés 2018). Within the hundreds of images of other animals in the corpus of European Upper Palaeolithic art, only a few depictions of wolves exist. These include a cave art depiction of a wolf with a reindeer, dated to 11,000bp, at Altxerri in northern Spain (Sieveking 1979) and one at Font de Gaume in south-west France, dated to 17,000 years ago, as well as occasional depictions on plaquettes. This unwillingness to depict wolves or dogs, seen also in Australian Aboriginal art (Gunn, Whear, and Douglas 2010), may reflect an ideological discomfort with the imposition of otherness that depiction imposes (Bird-David 2006).

The timing and location of some of the earliest evidence of a close relationship between humans and dogs may also be a telling indicator of their role. As we have seen in Chapter 6, survival in Ice Age Europe and Siberia placed not only economic but also emotional pressures on human populations, conditions that also fostered a closer relationship to wolves. Whilst these relationships with wolves may have brought functional advantages such as load-carrying or hunting in cold northern climates, these are only likely to have developed well after early domestication. Furthermore, it is in those contexts in which we see early evidence of potential inequalities. Early Upper Palaeolithic (Gravettian and Epigravettian) sites in Central and Eastern Europe, for example, demonstrate differential burial types, specialisation in production and/or remains of monumental architecture, which may indicate some level of ranking, even if seasonal or occasional (Wengrow and Graeber 2015). It is possible that dogs were some type of prestige possession (Germonpré et al. 2020), although elevated stresses imposed by ranked hierarchies (discussed in Chapter 5), on top of existing emotional vulnerabilities, may perhaps better explain their incorporation into human communities.

Archaeologists have tended to focus on the functional elements of the transformation of wolves into domestic dogs and on the precise timing of domestication. Much of the archaeological evidence tells a rather different and perhaps more important story, however, of the emerging and complex emotional bond between humans and increasingly tame wolves as each adapted to each other (Losey, Nomokonova, and Fleming 2018).

Similar evolutionary pathways in dogs and humans

It perhaps is not difficult to see, on reflection, that human emotional vulnerabilities and need for compensatory attachments (discussed in Chapters 4 and 5) may be an important part of the explanation for why people drew animals such as wolves more closely into their lives. As we have seen, compensatory attachment figures such as dogs can fill a gap in people's lives. The emotional support and companionship they provide can, in bolstering a sense of emotional security, boost confidence, an ability to be social, abilities to explore, and resilience to depression, as well as affecting immune systems and health in many ways. Even when there is no emotional 'gap' in people's lives, dogs can give us a sense of belonging, friendship and, even, community. They can make us better people.

The roots of our close relationships lie far back beyond the transition we know as domestication. Important similarities exist between wolves/dogs and humans, despite the evolutionary distance, which may explain what drew humans and wolves to each other. A closer consideration reveals that the stage was set for a particularly close relationship well before the start of the Upper Palaeolithic. As we have seen in Chapter 1, between around 3 million and 1 million years ago, early humans moved into a similar niche to that already occupied by social carnivores. This transition was made possible through emotional changes, not simply changes in analytical thinking, bringing human emotional motivations more into line with those of highly collaborative social carnivores. From here came the roots of our social similarities with wolves. Our shared heritage as collaborative hunters gives us a remarkable loyalty to group members, inhibitory control over emotions, the drives to share food and care for infants and the vulnerable, a sense of justice, creative play (even as adults), social understanding, and strong motivations to collaborate toward shared goals. Wolves, like humans, are highly sensitive to the emotions of individuals around them, and care deeply about the wellbeing of everyone in their living group (Table 7.1).

As a result of shared heritage as highly social and collaborative hunters, people and wolves (as well as dogs) share:

- motivations to take risk on behalf of others and loyalty to other members of the group
- motivations to share (wolves share food fairly, though this capacity is lost in dogs) (Marshall-Pescini et al. 2017)
- inhibitory control (Marshall-Pescini, Virányi, and Range 2015)
- motivations to care for vulnerable young, even if not direct offspring (seen most clearly in collaborative parenting in wolves; however, dogs can be caring and protective of other young including human young)
- motivations to collaborate in a shared goal (Range and Virányi 2014)
- sense of fairness and justice (Essler, Marshall-Pescini, and Range 2017; Palagi et al. 2016; Pierce and Bekoff 2012)
- social imaginative play, even as adults (Bekoff 2001)
- social intelligence, including at least some rudimentary understanding of others' perspectives (Heberlein et al. 2016)
- sensitivity to facial expressions as indicators of emotion (Hobkirk 2019)

Table 7.1: Ancient shared emotional capacities and drives between humans and wolves (as well as dogs).

Other transformations in emotional motivations and the nature of social connections occurred later, and at somewhat different periods for modern humans and wolves. For humans, it was changes in tolerance, and human emotional dispositions more broadly, beginning in Africa after 300,000 years ago and described in Chapter 5, which paved the way for new relationships. At this stage, people seem to have become more confident in new situations and less stressed by unfamiliarity, whilst at the same time being more socially and emotionally sensitive. For dogs, it was only once humans reached Europe and Asia, where they interacted with wolves, that we see the same types of changes taking place as they interacted more closely with humans. A cascade of changes resulting from alterations in key genes provoked changes in proto-dogs to also make them more friendly to people, more open to new experiences, more sensitive to their social environment and, in turn, more vulnerable to a lack of social connection and support; see Table 7.2.

Whilst, of course, there are profound differences, important social and emotional changes took place within both modern humans and proto-dogs. The

As a result of a shared transition to increased tolerance/friendliness, humans and dogs both show:

- tendencies to seek out novelty (Gácsi et al. 2005; Miklosi 2014)
- abilities to follow subtle gestural and emotional clues (Hare and Tomasello 2005)
- hypersociability, e.g. infants motivated to explore new relationships with strangers (Shuldiner et al. 2017; Feuerbacher and Wynne 2017), and there are similar genetic underpinnings to human and dog hypersociability (vonHoldt et al. 2017)
- a period of socialisation in infancy, which guides orientations and expectations towards others in adulthood (Miklosi 2014)
- sensitivity/vulnerability to a lack of social support and emotional connection (Miklosi 2014)
- a tendency to look for help from others to solve problems (Miklósi et al. 2003; Gácsi et al. 2005)
- abilities to have a dual identity – relating in one way to one species and in different ways to another (Bradshaw 2017), including abilities to relate to humans/dogs as alternative attachment figures (Kis et al. 2014; Nagasawa et al. 2015; Thielke and Udell 2017)
- tendencies to seek compensatory attachments in objects (dogs can also have attachment objects) (unpublished survey, University of Bristol Veterinary school)
- attention to eye gaze, and abilities to form attachments and oxytocin-related bonds with other species (Kis et al. 2014; Kis et al. 2017; Nagasawa et al. 2015; Topál et al. 2005). Alongside these changes we also see changes in facial musculature allowing expressions of vulnerability (Raghanti 2019)

Table 7.2: Recent shared emotional capacities and drives between humans and dogs.

same capacities for relatively rapid evolutionary changes in the hypothalamic–pituitary–adrenal (HPA) axis existed in both species (Jung and Pörtl 2018). Within the broad characteristics already associated with domestication/self-domestication (including decreased aggression, increased gregariousness, modified adrenal gland function, changes in neurotransmitter levels, a prolonged juvenile period), dogs and humans share specific genetic changes (discussed Chapter 7), such as changes associated with hypersociability (vonHoldt et al. 2017). Moreover, dogs and humans appear to share two further evolutionary adaptations that facilitate their relationships with each other. Firstly, changes in particular parts of the brain affecting desires to please/conformity, focus on others versus self, and increased social sensitivity (the ventral striatum) seem to affect both species (Raghanti 2019). Secondly, changes in the eye muscles and expressivity around the eye (affecting abilities to show vulnerability or make 'puppy dog eyes') may also have affected both species (Godinho, Spikins, and O'Higgins 2018; Kaminski et al. 2019; Raghanti 2019).

Whilst so different in so many ways, some aspects of both human and dog emotional motivations and sensitivities have *converged* in evolutionary terms (Figure 7.10). Both at several million years ago, and more recently, both species have been those that took evolutionary pathways towards

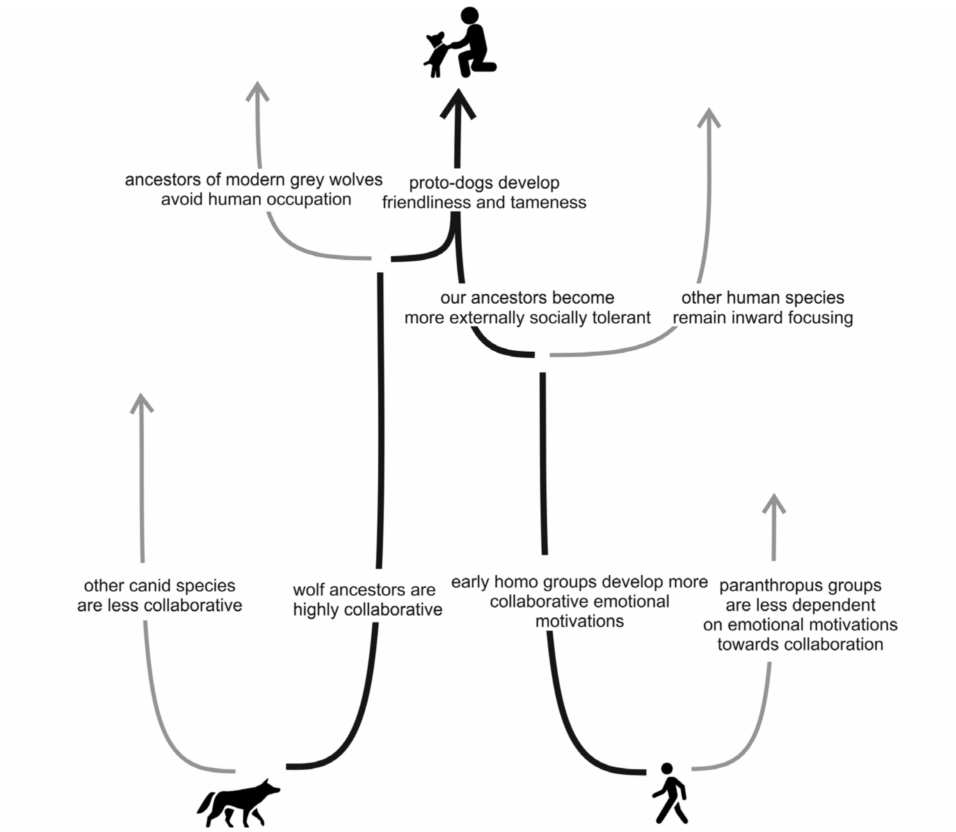

Figure 7.10: Illustration showing evolutionary convergence of elements of human and wolf–dog social emotional dispositions. Penny Spikins, CC BY-NC 4.0.

firstly increasing collaboration and secondly increased tolerance and approachability. Other species took different routes. Some hominin ancestors followed less-collaborative paths that were not dependent on collaborative hunting, whilst some canids became solitary hunters. Likewise, some archaic humans did not turn towards the external focus and emotional sensitivity of our own species but, rather, to an inward focus (discussed in Part 3), and some wolf ancestors became more avoidant of humans rather than tolerant of them. Our particular paths brought us together (discussed further in Chapter 8), whilst others led further apart.

Of course, it is not only dogs that have played an emotional role within human lives for a large part of our evolutionary past. Many people develop strong attachment and derive emotional support from many other animals, not only pets but also wild animals, which share our lives. Perhaps as far back as over a million years ago, animals came to mean something more to people than simply being a source of food. The creation of elephant bone handaxes, for example, suggests that some kind of meaning, or even symbolism, was attached to the use of elephant bones (Lev and Barkai 2015; Zutovski and Barkai 2015). The appearance and extinction of animals mattered to past humans in emotional terms (Halfon and Barkai 2020). By the time of archaic humans such as Neanderthals, some animals seem to hold important meanings. Neanderthals attached significance to certain birds, for example, probably using their feathers for adornment (Finlayson et al. 2012; Morin and Laroulandie 2012). People have interacted with many animals in different ways through our evolutionary past, and not simply as a source of food (Shipman 2010).

Dogs, however, share not only social similarities but also many of our emotional vulnerabilities. Like humans, they are highly sensitive to others' distress, affected themselves emotionally and driven to respond. They form strong attachments and, like humans, thrive in the context of loving and caring relationships, but are susceptible to a lack of closeness, affection and touch. They are susceptible to loneliness and sensitive to cruelty. Through our mutual demonstration and response to vulnerabilities, we develop relationships based on trust.

Why wolves, and later dogs, came to play such a key role in our lives makes sense within this larger evolutionary understanding of our shared emotional vulnerabilities.

How did wolves become close to humans?

When we discuss early wolves as 'hunting aids', almost like a new type of tool, we likely miss their significance in people's lives and, in turn, some of the key factors bringing wolves and people closer together.

The relationship between indigenous Australian groups and their dingoes may give us far more insights into the nature of early 'domestication' than when we look at modern, highly trainable dog breeds. Instead of economic benefits to either, there is evidence here of a genuine drawing together in emotional terms. Dingoes occupy a space that is neither 'tame' nor 'wild', frequently living outside of human settlements and not necessarily being fed by humans, perhaps not too different from the relationships early proto-dogs might have had with Upper Palaeolithic humans. Yet, at the same time, there is a remarkable intimacy to their relationships to people. Children play with puppies, and adult dingoes can form close relationships with certain people. It is certainly not too fanciful to imagine that the route to domestication lay with particularly sensitive people, perhaps isolated or hurt by trauma, who found friendship, companionship and emotional stability in similarly sensitive and emotionally vulnerable wolves.

What initially drew wolves closer to humans? Whilst there have been general assumptions that domestication began when more tolerant wolves learnt to scavenge from human settlements (Coppinger and Coppinger 2001), the observation that highly mobile foragers rarely produce anything like a waste dump calls this into question (Jung and Pörtl 2018). Instead, it seems most likely that the tamest of the wolves may have begged or scrounged for food, or lived independently, interacting with humans out of curiosity and companionship. Packs of Arctic wolves are tolerant of human proximity and interaction, for example (Smith and Litchfield 2009). As with dingoes, orphan wolf pups may have been the playthings of children, with some adult dogs then remaining attached to human groups. Wild wolves *can* form close relationships with people (see Figure 7.11), and can collaborate in shared goals. However, this relationship takes considerable time and effort, and shows little of the ease with which modern dogs integrate into human life. Wolves or early proto-dogs living within human groups probably became rather difficult to deal with, or even dangerous, as they got older. Most adult wolves may have entirely drifted away, or lived on

Figure 7.11: Wolves can be socialised to be friendly towards people. Photograph shows a socialised wolf enjoying affectionate contact. Vilmos Vincze from Hungary, CC BY 2.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:He_can_stand_stroking,_too..._(27205424372).jpg.

the outskirts of human groups, scrounging any food that became available, drifting back into lives as entirely wild wolves with only a few remaining in close relationships with humans.

With time, the changing socioecology of those wolves that became more integrated into human communities, or even simply scrounged for food, would have influenced the evolutionary selection pressures that they experienced (Marshall-Pescini et al. 2017). Being able to tolerate closeness to humans would have been an advantage, as would a certain openness to new experiences and new relationships, setting in train a sequence of genetic changes towards increasing friendliness. These increasingly friendly wolves would have been better able to develop a new kind of relationship with humans. Humans, in turn, may have begun to protect and care for adult wolves and their puppies within human settlements, with their descendants eventually becoming lineages that were more isolated from their wild counterparts.

The increased sensitivity to social support and emotional vulnerability of proto-dogs, which comes with increasing friendliness, will have matched similar vulnerabilities in humans. Proto-dogs could not only have been able to provide an additional source of affection and stimulation to infants, and a pleasing sense of reward for nurturance to adults, but also to plug an emotional gap left through an attachment system highly sensitive to any deficiencies in social surroundings (Kurdek 2008). It is not difficult to see how such proto-dogs could become an emotional safety net after the emergence of modern humans, who, as we have seen in Chapter 5, were now increasingly moving between new groups, encountering new people and living lives that sometimes failed to provide the supportive social relationships they craved. Moreover, as wolves themselves also changed, it may no longer have been viable emotionally to be a *lone wolf*, with human companionship preferable to loneliness for wolves isolated from a pack, much as wolf companionship well have been preferable to loneliness for humans feeling isolated or lonely themselves. In both species, their recent hypersociality may have enabled a new kind of relationship, but may also have driven each towards the other.

Increasingly friendly wolves will have been less dangerous companions, better able to understand humans, less stressed by human environment, and more likely to stay for longer within a human group (Morey and Jeger 2015). They may have begun not only to act differently but to look morphologically distinct, even while still showing some levels of interbreeding with their wilder relatives. Certainly, the genetic record suggests many thousands of years of interaction and hybridisation between tame and wild animals. Sustained domestication, demanding that humans protected wolves from being driven away or killed for food in times of famine, probably depended on genuine emotional attachments (Bradshaw 2011). At times and places where isolation and loneliness (such as from ecological conditions limiting contacts between human groups), or social stress (such as from more competitive and hierarchical social dynamics), became more pronounced, even closer attachments may have developed.

With time, proto-dogs will have become ever more emotionally attuned to humans, to the point at which they could seem almost disturbingly humanlike. For dogs, this would have meant both the potential for strong personal bonds with people, but also the possibility of becoming scapegoats for human relationships, and subject to aggression for the areas in which they failed to fulfil human expectations. Their capacity to share goals, and contentment with performing roles that were useful, such as hunting, defence and carrying loads, also allowed them to become a form of technology as well as a friend.

Rather than being a new technology first, and friends second, the story of wolf domestication may have been one in which nurturance and friendship came first, and in which emotional vulnerabilities of both species played a key role.

The journey shared between humans and wolves prompts not only further questions about that relationship but also leads to reflections about ourselves as supposedly independent from the natural world and the animals around us. When we consider the closeness of our relationship to dogs, and their wolf ancestors, we cannot help but reflect on the oddity of our human-focused narrative of human origins. Our social story is almost always taught as one in which human social relationships are the only ones of significance. However, it is clear that, throughout our evolutionary past, our hearts and minds have been intertwined with those of other animals, of which dogs are only one example. Children will have played with the young of other species, and adults will have developed relationships with wild animals that crossed their paths, or even ones that took residence in their settlements. The relationships we developed with wolves, and the dogs that they became, are just one example of this intimacy.

Our shared journeys also prompt us to reflect on the other pathways, and evolutionary journeys towards other species which were often equally viable, albeit less intimately connected. We explore one of these alternative pathways taken by humans in Part 3.

Conclusions

Though we tend to see human origins in a rather individualistic and independent way (as discussed in the introduction to this volume), it is clear that our evolutionary past has been one of a close connection to animals living around us. This relationship with the natural world is far more intimate than we tend to acknowledge. Ecology, and relationships to other animals, played an important role in the evolution of human compassion, as we have discussed in Part 1. However, human closeness and interdependence with other animals developed even further after 300,000 years ago, as discussed here. Where our relationship with wolves is concerned, even the line between 'human' and 'animal' itself becomes blurred. Members of this entirely different, and only very distantly related, species become our companions and friends, and even members of our communities. Of all the animals with which we share our lives, it is the descendants of wolves that seem to have by far the greatest capacities to affect us emotionally.

The so-called 'domestication' of wolves was more likely to have been a process in which both humans and ancestral wolves moved physically and emotionally closer to each other, rather than a one-sided imposition by humans for some economic gain. We often think of the creation of the 'domestic' dog as some kind of human achievement in which dogs have been co-opted to suit our needs, a little like cleverly adopting a new type of technology. However, insights from our understanding of the emotional brain, and the new emotional vulnerabilities that developed during the period 300,000 to 30,000 years ago, suggest, in contrast, that our shared emotional motivations may have had a much more important role to play than we might imagine, and that our emotional vulnerabilities, rather than our intellect, may have driven us together.

Key points

- Our evolutionary history is typically represented as one in which humans were independent from other animals, or even dominated nature. In reality, our evolutionary past has been about interdependence with the natural world. Moreover, other animals have played not just an economic role but important social and emotional roles in our lives.

- Of all the animals with which we interact or share our lives, it is dogs with which we show the strongest emotional bonds. Dogs can fill a gap in many of our emotional lives, particularly in modern industrialised contexts, providing important emotional support and companionship, as well as complementing existing human social relationships.

- We have traditionally assumed that the domestication of wolves occurred due to their functional usefulness as an aid in hunting, in defence or in carrying loads, and through elevated human ingenuity. However, these practical functions are largely dependent on specialised breeds or training, and are likely to have developed long after a close relationship between people and wolves emerged.

- Wolves and humans share a common background of evolutionary pressures on their emotions, despite the phylogenetic distance which separates us. The explanation for an increasing closeness between humans and wolves, and the so-called 'domestication' of the wolf, may lie in shared emotional needs and vulnerabilities between the two species.

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Part 3
What If? Exploring Different Human Pathways

In this part, we consider alternative pathways in human evolution, and how we might better understand the different humans we might have been. We focus on different adaptive pathways in emotional dispositions, and open up new possibilities, such as situating Neanderthals as *different* but *equal* within our evolutionary story. We also consider how the concept of branching pathways may help us to move away from progressive narratives and better understand human origins as a pattern of compromises and vulnerabilities as well as strengths.

CHAPTER 8

What If? The Evolutionary Basis for Different Pathways

Abstract

All too often, we see our evolutionary past as some inevitable ladder of progression. In considering our emotional connections, it is easy to imagine that the increased external friendliness and sensitivity seen in 'modern' humans represents some progressive or superior development from a more aggressive past. However, a close consideration of how external friendliness changes in closely related species reveals a far more complex picture, with advantages and disadvantages to different evolutionary pathways, each displaying a different type of prosocial or collaborative behaviour.

There are always many possible evolutionary pathways, affecting brains, bodies and behaviours. Here, however, we focus on simple contrasts in the adaptive routes followed within our nearest living relatives, chimpanzees and bonobos, and those within our closest friends, wolves and dogs. This brings some insights into how an increased openness, and the capacities to develop new external bonds, may have evolved. We reveal that each evolutionary pathway

(Abstract continued on next page)

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(Abstract continued from previous page)

brought both advantages and disadvantages, depending on context, rather than any specific pathway being a progression. Our similar physiological and behavioural adaptations under pressures to be more *tolerant* (discussed in Part 2) suggest that the same processes that occurred in these species also affected humans. An understanding of our evolutionary past as one of different alternative trajectories, and of possibilities and constraints along these, helps to frame our understanding of the process of human evolution, and the story of our origins.

Figure 8.1: Paths diverge in a wood. Photo by Beth Macdonald on Unsplash: https://unsplash.com/photos/P3rS8J1THi4?utm_source=unsplash&utm_medium=referral&utm_content=creditShareLink, with unrestricted use.

Introduction

The Road Not Taken

Two roads diverged in a yellow wood,
And sorry I could not travel both
And be one traveler, long I stood
And looked down one as far as I could
…
Two roads diverged in a wood, and I—
I took the one less travelled by,
And that has made all the difference

Robert Frost, 1916

If we look back on our lives, we can all think of key points at which there were different pathways to take, neither of which at the time seemed better or worse than the other but from which our choice made a significant difference to the rest of our lives. Robert Frost's poem 'The Road Not Taken' epitomises some of these moments, in which we stand as if at a forked point on a path (Figure 8.1), and wonder what each alternative entails. We often later create a story of why our particular choice was the better one (Orr 2015).

It would be easy to consider changes that take place along our evolutionary journey, and particularly with the emergence of modern humans, as a simple progression towards humans becoming increasingly better, more social, more sensitive and more collaborative. As we have seen in the introduction to this volume, we tend to prefer to think of our evolutionary past as a natural progression towards a better human being (Anderson 2019; Porr and Matthews 2017; Porr and Matthews 2019). The reality, however, is quite otherwise: our evolution has been a series of alternative pathways, each with different advantages and disadvantages – a far more complex and more interesting story.

Different versions of human, living alongside each other, seem like something that should be part of science fiction. However, we know that our single existence as the only human species stands out as unusual in our evolutionary past. Before the last 50,000 years, various different humans were around at the same time, and often in the same regions. Each had followed a different pathway, with each equally viable at the time.

Often, differences between species were driven by adaptations to different ecological conditions. The separation of distinct evolutionary pathways at times of intense environmental unpredictability mark many of the major changes in human evolution. Moreover, extinctions of human species closely match climate changes (Raia et al. 2020). As we have discussed in Part 1, around 2 million years ago members of the genus *Homo* took a path towards increasing reliance on hunted meat, and so intense collaboration and interdependence. However, other hominins, the paranthropines, specialised more on a plant-based diet, followed a different evolutionary pathway and lived successfully alongside members of the genus *Homo* for at least 1 million years. Other, equally viable alternatives clearly existed throughout human evolution. Their brains, bodies and social lives were probably *even stranger than fiction*. Often, the circumstances that drove different adaptations are difficult to determine. The small-brained *Homo naledi*, for example, managed to survive perfectly well amongst much larger-brained members of the genus *Homo*, around 250,000 years ago. Areas of their frontal cortex promoting a complex social understanding may have promoted collaborative behaviours (Holloway et al. 2018), whilst a smaller overall brain than other species would have been less energetically costly. Under different conditions, it might have been the descendants of these diminutive and small-brained humans, rather than larger-brained species of *Homo*, that took our place today. In short, there have been many different pathways in our evolutionary history. Both our tendencies to want to see our origins as a single story of progression and a lack of evidence tend to obscure their existence.

The differences between other closely related species of highly social animals can sometimes provide clues as to the differences between alternative species of human, not only physically but also in their minds, feelings and behaviours. Considering non-human animals can also be helpful because, whilst we find it hard not to impose a ladder of progression on humans, we readily understand that the differing adaptations that different animals show to their circumstances are comparatively neither better nor worse. The primate order is full of such examples. Closely related species can adapt to behave in quite notably different ways in response to subtle changes in their environments working with their existing evolutionary history. Fat-tailed dwarf lemurs (*Cheirogaleus medius*) in Madagascar hibernate to survive resource shortages, for example, whilst other lemurs live in different environments or adapt to resource shortages in different ways. These paths can also sometimes converge, not only genetically, when species interbreed, but also behaviourally. Similar challenges often provoke similar responses in different species, or at least responses that do the same job but in different ways. Differing hormonal changes seems to underlie monogamous relationships in differing species of lemur as a result of different evolutionary trajectories, for example (Grebe et al. 2021).

Other examples come from social mammals much more distantly related to us, as we have seen in Chapters 1, 4 and 5. A fascinating example of subtly differing pathways is provided by African wild dogs (*Lycaon pictus*) and grey wolves (*Canis lupus*). These closely related social canids are both highly collaborative and share very similar social structures. They hunt together, raise offspring collaboratively, take risks to defend each other, and share food. Nonetheless, these two different species show subtle differences that reflect slightly different ecological conditions, existing adaptations, or even just chance. African wild dogs' social communication focuses particularly on vocalisations, notably coughs, and on ear movements, whereas wolves are somewhat more dependent on facial expressions. African wild dogs (as discussed in Chapter 1) are the most internally socially cohesive of all canids, supporting the ill and injured. It might be easy to decide that they are the most social, and most collaborative. However, they are also more territorial and defensive towards outsiders than wolves can be. Neither one nor the other is 'better', or even more social, but these apparently very similar species are simply collaborative in a different way. Whilst we might prefer a simple story of one species being *better* than another, other highly social animals demonstrate that the reality is far more complex.

We particularly struggle to apply these understandings to humans. Often, we seem only able to think about ladders of progression, and see all humans that show differences from ourselves as inferior. Moreover, even though we know that different branches of recent humans have converged, blurring the distinction between what we think of as our own species and other contemporaries, we prefer to focus our attention on 'our' ancestors, and elevate these people above others. Even using the term 'modern humans' for people alive today, and their ancestors evolving in Africa from 300,000 years ago, is problematic, implying some sense of betterness or progression. *Homo sapiens* is no better than other, now extinct species of humans (what makes our species more wise?). We just do not have a widely understood and accepted term for ourselves that does not imply superiority.

Finds evidencing the increasingly diverse species of humans living after 300,000 years ago, and contemporary with the ancestors of modern humans, have pushed the beginnings of a reappraisal. One suggestion has been to see human evolution not as a ladder but as a braided stream (in which all humans flow or evolve in the same direction along parallel paths). This may be an improvement on a simple ladder but it is far from without problems. The reality is that different species of humans, like other animals, often adapt in *different* directions. One fascinating example is the possibility that Neanderthals hibernated (Bartsiokas and Arsuaga 2020). This is far from a ridiculous suggestion as Neanderthals may have adapted to resource shortfalls much like the fat-tailed dwarf lemur. It would, however, be an adaptation that meant Neanderthals travelled along a notably different direction than modern humans did, not only in physiology but also, in turn, in its effects on social behaviour. The possibility raises all kinds of questions around how hibernation might have been managed within an essentially human society. It seems more like science fiction, yet these very 'what if' questions around adaptations that seem radically unfamiliar are important to ask. Of course, the idea of branching pathways proposed here, which may sometimes coalesce, and sometimes lead in very different but equally viable directions, still oversimplifies what might be better thought of as a multidimensional set of pathways in which there are different domains of adaptation.

However we choose to represent our recent evolutionary trajectory, and here we think in terms of different pathways, the key issue is that of understanding differences without imposing value judgements. This seems to be a particular challenge with mind or emotion. As we have seen in Chapter 3, there are real differences in mind within our populations, all too often seen as inferiorities, making the challenge of understanding differences without a value judgement all the more important. Developing our understanding of how the emotional dispositions of closely related species can be different, with advantages and disadvantages according to context, and even equally social or collaborative, albeit in different ways, may be one way to help us rise to these challenges.

Here we draw on our knowledge of different branches of emotional dispositions taken by closely related species to better understand the different pathways that may have been taken by humans in the past. In the case of non-human animals, it can be easier to acknowledge that subtly different branches may be neither better nor worse, more nor less social, and nor more or less collaborative than either other, but are rather differently social or differently collaborative. Understanding the emotional and behavioural changes occurring in recent human evolution as being alternative pathways affecting emotional connections may help us understand many of the differences between archaic humans, such as Neanderthals, and modern humans.

Each point of divergence along the different evolutionary paths offers many different possible directions of travel, which may result in different divergent aspects of brain, biology or behaviour. Here we focus particularly on the different pathways in emotional connections brought about by changes in tolerance (discussed in Part 2) and their implications for our understanding of human origins. In Chapter 9, we then apply this understanding to interpretations of our close cousins, Neanderthals.

Alternative evolutionary pathways in other species

How different pathways towards or away from external tolerance or 'friendliness' play out in closely related species can provide us with useful insights into the advantages and costs of these alternatives in our own evolution, and the ecological and social context from which increasing externally social humans emerged.

In particular, the changes we see in bonobos, in contrast to their close relatives chimpanzees, and dogs, in contrast to their close relatives wolves, provide us with potential analogies for similar pathways in our own evolution. In both cases, we see how, in closely related species, changes in ecology and demography have driven changes in neuroendocrine function. In each case, particular social and ecological contexts have driven changes in emotional preferences, capacities and vulnerabilities and enabled new types of relationships to emerge. Whilst, typically, dogs and bonobos are seen as 'friendlier', we argue that neither pathway can easily be identified as better or worse, or more or less social or collaborative, but, in contrast, demonstrate subtly different adaptations and subtly different types of collaboration.

Contrasts in tolerance between chimpanzees and bonobos

Chimpanzees and bonobos are closely related and share many common characteristics. In fact, many people might struggle to tell them apart. Both chimpanzees and bonobos share cognitive and emotional capacities to build strong reciprocal alliances within their group, including to non-kin, and, in both, there is a certain amount of mobility between groups, mostly by females. However, there are notable differences in the levels of aggression, both within and between groups, as discussed in Chapter 4. Only bonobos can *feel comfortable* enough, when meeting other groups, to be generous to unfamiliar individuals and to share food (Lucchesi et al. 2020).

Differences in social behaviours between these two species may relate not only to random genetic drift through the geographic isolation of bonobos but also to how their distinctive ecological circumstances influence the advantages and disadvantages of different social behaviours (Gruber and Clay 2016). Bonobos benefit from living in environments with more stable and reliable resources than those occupied by most chimpanzees. This has several implications. Firstly, female bonobos carrying young do not have to travel as far to find enough food, and so have more energy to spend in alliance formation, which in turn affects the ability of males to form aggressive alliances. Secondly, more stable and reliable resources lead to reduced female competition (Clay, Furuichi, and de Waal 2016). Furthermore, less widely distributed resources also mean that bonobos travel in larger groups, making it much less likely that any individuals or small groups would be vulnerable to attack (Furuichi 2009; Wilson et al. 2014). In effect, these subtle differences mean that female bonobos gain less from competition and more from collaboration than do female chimpanzees, and that intergroup aggression is less potentially advantageous. Effectively, larger subgroups made up of several individuals are not 'worth' attacking, given little probability of success, and stronger female coalitions would also be more likely to defend against attacks. Both of these factors significantly reduce the potential advantages of entering into intergroup conflict (Furuichi 2009; Pandit et al. 2016). Being better at collaboration was more likely to pay off, in evolutionary terms, for bonobos than it was for chimpanzees. More tolerant and collaborative encounters also occur where resources are most plentiful (Lucchesi et al. 2020).

At least partly as a result of different ecological contexts, bonobos and chimpanzees thus followed different evolutionary pathways in relation to the levels of tolerance after their split 1.7 million years ago (Figures 8.2 and 8.3).

As selective pressures to collaborate increase, and pressures to compete aggressively are reduced, testosterone production in bonobos, in contrast to chimpanzees, also begins to decline. As discussed in Chapter 4, the effect of these variations is seen in differences in androgen pathways, and so in reduced aggression and greater potential for intergroup interaction in bonobos (Hare, Wobber, and Wrangham 2012). However, as we have seen in Chapter 2, selection pressures acting to change hormone systems tend to have broad effects. Differences in testosterone thus also have wide effects beyond the specific behaviours being selected for (Hare, Wobber, and Wrangham 2012). Reduced testosterone not only leads to bonobos

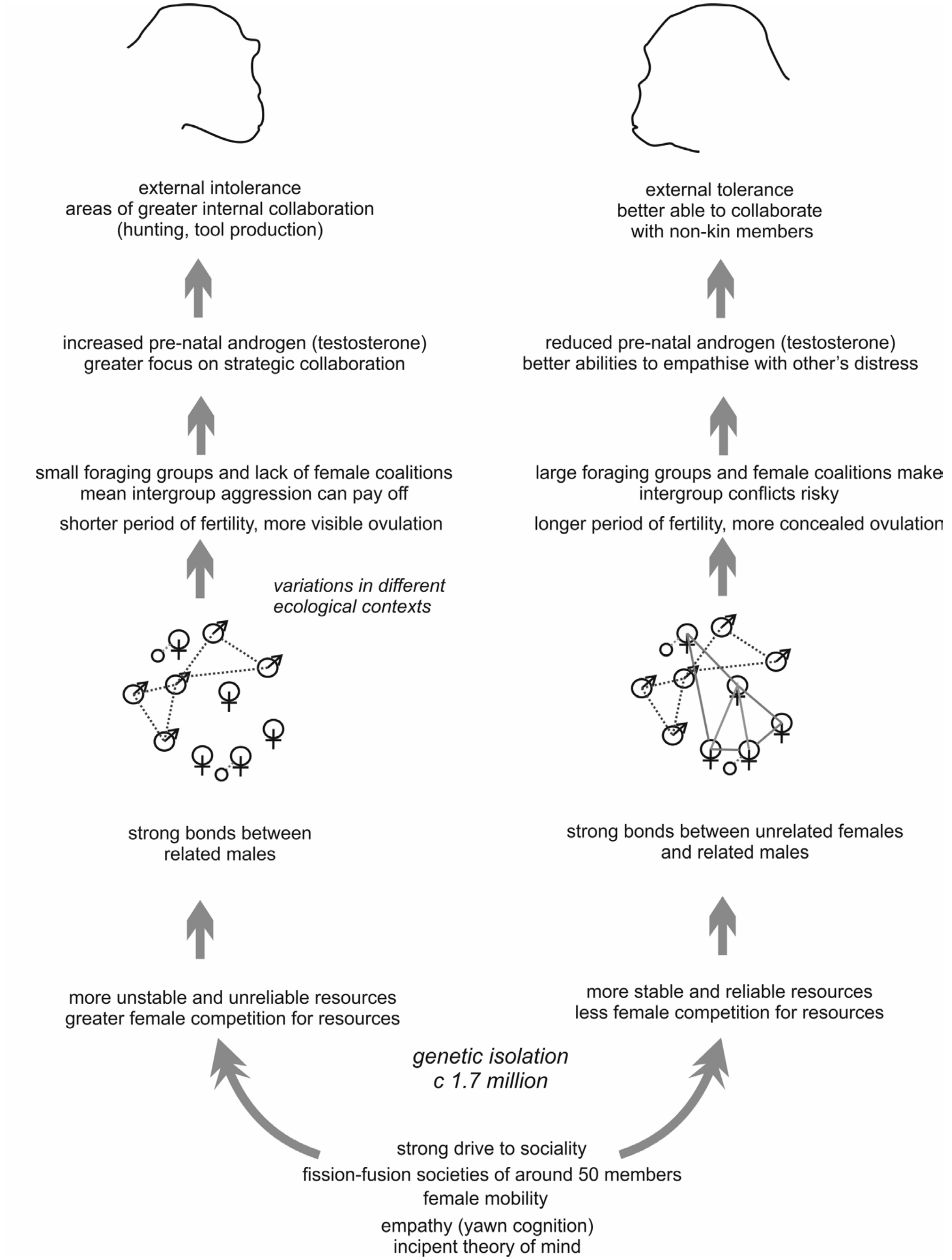

Figure 8.2: Ecological contexts influencing differences in social behaviour between chimpanzees and bonobos. Penny Spikins, CC BY-NC 4.0.

Figure 8.3: Male chimpanzee (left), showing marked brow ridge, and male bonobo (right). Rennett Stowe (chimpanzee image) and natataek (bonobo image), respectively, CC BY-SA 3.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Composite_image_of_male_chimpanzee_(left)_and_male_bonobo_(right).jpg.

retaining aspects of juvenile behaviour but also affects wider elements of behaviour, physiology and physical appearance. Bonobos have flatter faces, with reduced brow ridges in comparison to chimpanzees, as well as a more juvenile face shape. They also have reduced cranial capacity and depigmentation of their lips and tail tuft (Hare 2017). Bonobos are also less aggressive and more prosocial to non-kin within their group than chimpanzees are (Tan and Hare 2017), and in a wider range of different contexts. Laboratory experiments have even demonstrated that bonobos are simply more willing to be altruistic to strangers and to give food away accordingly (Tan and Hare 2013).

Research into bonobo and chimpanzee physiology, neurology and behaviour continues to reveal potentially important differences. There are also some suggestions that changes in other hormones may have had a role to play in the differences between chimpanzees and bonobos. Bonobos show a greater socio-emotional competence, and are more ready to provide consolation to others in distress (Clay and de Waal 2013), and to offer to help without it being solicited (Tan, Ariely, and Hare 2017), suggesting that oxytocin-related empathetic responses to others are more prominent than in common chimpanzees. That they are more focused on eye contact than chimpanzees provides further evidence of a more empathetic orientation to their interactions (Hare, Wobber, and Wrangham 2012; Kano, Hirata, and Call 2015; Stimpson et al. 2016). Indeed, bonobos are so socially focused that they will even sometimes prefer social interaction and play rather than a food reward (Warneken 2018). Getting on peacefully with others seems to have been so important to their survival that motivations to be sociable and to play can even override more basic motivations to eat. As research continues, further subtle but important differences are likely to come to light.

Different evolutionary pathways bring both advantages and disadvantages, and the levels of social tolerance seen in bonobos seems to come with certain costs. In fact, rather than see bonobos as simply more 'prosocial' than chimpanzees, it may be more appropriate to view them as social in different ways. They may be more focused on empathy and reduced competition, though perhaps less focused on technology and strategic collaboration. Though bonobos are as able to make tools in a laboratory setting, their use of tools in the wild is far more restricted than that of chimpanzees, for example. They seem to be too socially focused to be able to find technological solutions to problems. Not only is tool making less evident in bonobos but collaborative hunting is also much rarer, and much less of their diet is based on hunted meat than that of chimpanzees (Layton, O'Hara, and Bilsborough 2012). This may be because collaborative hunting often involves rather more strategic collaboration than empathetic collaboration. Likewise, whilst chimpanzees are far more reluctant to give away food than bonobos are, they are *more* willing to help with tools (Krupenye, Tan, and Hare 2018). For bonobos, interactions with tools seem to turn into a social game. Rather than hand the experimenter a tool that is needed, bonobos are more likely to tease them (Krupenye, Tan, and Hare 2018).

Increased juvenile behaviour, and increased playfulness, is a common element of changes associated with increasing tolerance (Wrangham 2014). Whilst play behaviour is important in imagination and social bonding, it can come at the cost of achieving a goal for which technology is required.

Contrasts between two other closely related species, this time not *our closest relatives* but *our closest friends*, wolves and dogs, provide us with a further significant glimpse into how increasing tolerance may have emerged.

Whilst we look like other apes, and share many social and cognitive features, there are many emotional similarities we share with social carnivores (as discussed in Chapter 1).

Differences in out-group tolerance

- Intergroup encounters are often aggressive in chimpanzees, and are more passive in bonobos (Sakamaki et al. 2018; Sakamaki et al. 2015).
- Bonobos are known to share food at borders (Fruth and Hohmann 2018).
- Bonobos can be altruistic to strangers (Jingzhi Tan and Hare 2013).

Key ecological/structural differences

- More stable and reliable resources imply less female competition for resources in bonobos, added to which, females carrying young have less far to travel and more time to socialise (Clay, Furuichi, and de Waal 2016).
- Bonobos travel in larger parties. Intergroup conflict is thus less effective, as there are fewer opportunities for picking off individuals or small groups (Furuichi 2009; Wilson et al. 2014).

Differences in social structure

- Bonobos have stronger female associations (Furuichi 2011).
- Immigrant females bond first with females in bonobos (Sakamaki et al. 2015) but with males in chimpanzees (Boesch et al. 2008).
- Bonobos have longer periods of sexual swelling, ovulation is more hidden, and paternity is more disguised (Gruber, Clay, and Zuberbühler 2010).
- Bonobos respond more readily to the distress of others within their group (Clay and de Waal 2013).

Physiological differences

- In bonobos, testosterone stays at similar levels through development, but it rises in chimpanzees (Hare, Wobber, and Wrangham 2012; Stimpson et al. 2016; Wobber et al. 2010; Wobber et al. 2013).
- Prenatal androgen in bonobos affects the balance of empathising-systemising (MacLean 2016; MacLean et al. 2017).
- Bonobos show differences in vasopressin receptor genes, which may be implicated in differences in social bonding (Hopkins, Stimpson, and Sherwood 2017).
- Possible differences in bonobos related to oxytocin production (Hare and Woods 2017).

Continued.

Continued.

Social cognitive differences
Social interactions – Bonobos show a greater socio-emotional competence (Clay and de Waal 2013). – Bonobos are prosocial in wider range of different contexts than are chimpanzees (Krupenye, Tan, and Hare 2018). – Bonobos voluntarily hand over food to an experimenter more readily than chimpanzees; chimpanzees more readily help with tool use (Krupenye, Tan, and Hare 2018). – Bonobos make more eye contact than chimpanzees and their gaze attention is more drawn to faces compared to the rest of the body than that of chimpanzees (Kano, Hirata, and Call 2015). – Bonobos are more motivated (and able) to collaborate than chimpanzees (Hare et al. 2007). – There are differences in neuroanatomical structures between the two species (Staes et al. 2019) and differences in socio-emotional circuits (Issa et al. 2018).
Juvenile behaviour and play – Bonobos show delay in social inhibition and no reduced tolerance to others with age, whilst chimpanzees do not (Wobber, Wrangham, and Hare 2010). – Bonobos use tools in a play context more readily than chimpanzees (Gruber, Clay, and Zuberbühler 2010). – Bonobos will also sometimes prefer social interaction and play rather than a food reward (Warneken 2018).

Table 8.1: Contrasting behavioural ecology of chimpanzees and bonobos.

Contrasts in tolerance between wolves and dogs

In the transition towards becoming dogs, descendants of wolves took a step further in tolerance than bonobos. They not only became comfortable with forming bonds with outsiders, even other species (ourselves), but, more than this, they are *driven to do so*, and are particularly adept at forming new emotional bonds.

As discussed in Chapter 7, wolves and dogs are close relatives. Modern dogs are relatives of the grey wolf, whose ancestors' ranges overlapped with early human populations in Eurasia. Humans will certainly have come into contact with wolves well before 'domestication', at the very least as competitors for hunted prey. Carnivore gnawing is common on archaeological sites where human remains are found, and wolf bones themselves are found on archaeological sites such as at Boxgrove, England, around 400,000 years ago; Zhoukoudian in China, dated to 300,000 years ago; and La Lazaret, France, dated to 150,000 years ago, for example (Serpell 2016). However, evidence for an unusually close relationship between humans and wolves dates to after 40,000 years ago, and postdates the arrival of modern humans into Europe and Asia. At this point, interactions with humans led the ancestors of grey wolves along two different contrasting pathways. Whilst we tend to focus on the wolf ancestors of modern dogs, it is easy to forget that 'wild' wolves did not remain the same but also followed their own path. Whilst wolves who were attracted to the opportunities provided by human occupation ultimately became the ancestors of domestic dogs, other wolves, those who avoided humans, led to modern grey wolves.

The close, social interactions that began to emerge between ancestral dogs and humans were aided by a similarly complex social cognition (see Chapter 7). Like humans, wolves have complex rules about social behaviour and have a sense of 'fair play', with certain gestures such as play bows, which are honest signals that they will not harm others (Allen and Bekoff 2005; Palagi et al. 2016). Like non-human apes, and humans, wolves seem to have the rudiments of a theory of mind (Horowitz 2011; Udell, Dorey, and Wynne 2008; Udell, Dorey, and Wynne 2011). Wolves show yawn contagion (one wolf yawning prompts others to do the same), a sign of empathy (Romero et al. 2014), and communicate emotions through facial expression. Moreover, as we have seen in Chapter 1, wolves have high levels of within-group altruism (Jouventin, Christen, and Dobson 2016).

Once again, differing resource availability may have played an important role in influencing changes in social behaviours between wild wolves and ancestral dogs. Wild wolves exploit animal prey that is unpredictable and concentrated, making them dependent on collaborative hunting to survive. Wolves living near human settlements, in contrast, will have been exploiting a more predictable and widely dispersed resource. This favoured individual exploitation (Marshall-Pescini, Cafazzo, et al. 2017), whether it took the form of food scavenged from humans, food given to puppies or favourite adults by humans, or simply that a different suite of smaller prey was found near human settlements.

As a consequence of different resource characteristics, wolves living near human settlements seem to have become much less internally cohesive and more independent, even before any sustained interaction with humans (see Figure 8.4).

Typically, we compare wolves to dogs that are domestic pets. However, the contrast between wolves and modern free-ranging dogs, rather than with pet dogs (Figure 8.5), provides us with a useful comparison in natural social behaviour. Whilst wolves share the proceeds of a hunt fairly, provisioning others such as pups and lactating females, dogs only rarely share food. Although pack dogs sometimes hunt, they usually do so individually. Similar contrasts are seen in raising offspring. Wolves form often lifelong pair bonds, and also parent collaboratively, with other family members looking after the young whilst others hunt, and with pups dependent on adults for many months. Free-ranging dogs, on the other hand, tend to exhibit a very varied mating system, in which pair bonds are rare. They typically parent their offspring alone, are not provisioned, and pups have to be independent at a much earlier age (Marshall-Pescini, Cafazzo, et al. 2017). Free-ranging dogs even exhibit a novel genetic adaptation to digest starch which is not shared by wolves (Axelsson et al. 2013). The nature of emotional connections and social behaviour in wolves and free-ranging dogs has adapted, along each different pathway, to the distinctive constraints and opportunities each faced.

We might be forgiven for thinking of free-ranging dogs as less social, or less collaborative, than wolves since they are far less supportive of others in their pack. However, this would be far too simple a characterisation. Free-ranging dogs are much more outwardly tolerant than wolves. A need to tolerate proximity to humans may partly influence changes in pack dynamics in dogs. Wolves tend to be defensive or, even, aggressive towards other packs. However, free-ranging dogs are much more tolerant of outsiders. In some regions, previously pet dogs even commonly join free-ranging packs (Miklosi 2014). Packs themselves are also different in character. Wolf packs typically comprise a 'family' with a breeding pair and their relatives,

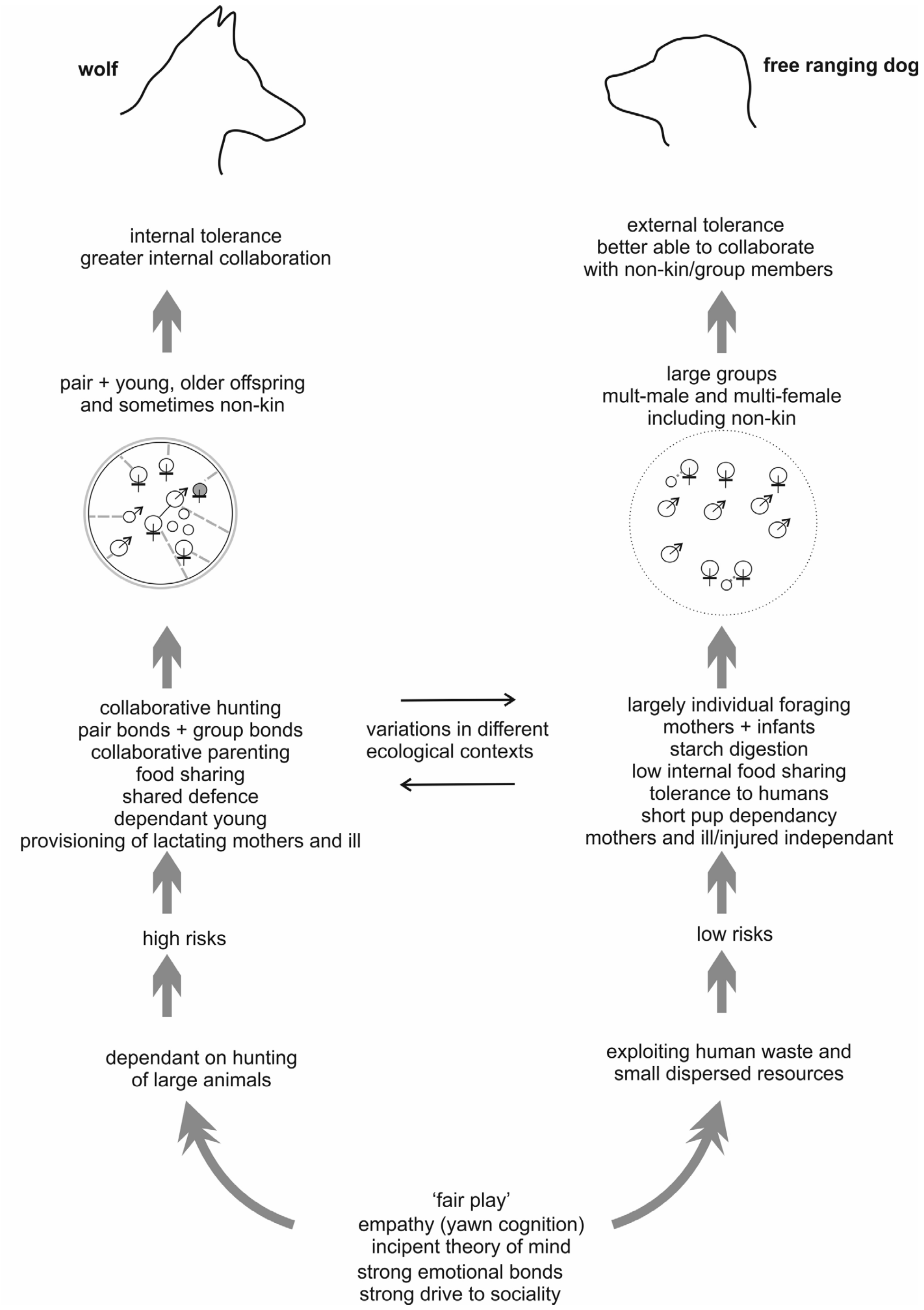

Figure 8.4: Ecological contexts influencing differences in social behaviour between wolves and free-ranging dogs. Penny Spikins, CC BY-NC 4.0.

Figure 8.5: Left: Eurasian Wolf showing long muzzle and short ears. Mas3cf, CC BY-SA 4.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/Canis_lupus#/media/File:Eurasian_wolf.JPG. Right: Free-ranging street dogs, showing shorter muzzle, flatter face and more pronounced ears, as well as changes in coat colouring. Andrew Currie from Toronto, Canada, CC BY-SA 2.0, via Wikimedia Commons: https://en.wikipedia.org/wiki/Free-ranging_dog#/media/File:Street_Dogs.jpg.

and non-kin only join packs when important members have been lost. Free-ranging dogs, on the other hand, maintain much larger pack sizes, and have a very fluid composition, made up predominantly of non-related animals. Free-ranging dogs can often form bonds with certain particular humans, and do so much more frequently and with greater ease than wolves.

Like the changes we have discussed above between chimpanzees and bonobos, these changes have been brought about by selective pressures acting on key genes affecting many aspects of biology and behaviour, and particularly on hormone systems (Dobney and Larson 2006; Trut, Oskina, and Kharlamova 2009; Wilkins, Wrangham, and Tecumseh Fitch 2014). Firstly, dogs have experienced a reduction in stress reactivity in comparison to wolves through changes in the hypothalamic–pituitary–adrenal (HPA) axis, adrenal glands and cortisol. In effect, unfamiliar dogs or people are simply less scary. Secondly, their abilities to form strong emotional bonds have changed, with changes in eye gaze-based bonding and oxytocin release (Buttner 2016). Close relationships with people can provoke a similar response in dogs themselves similar to that 'warm fuzzy feeling' we feel in our own human-to-human attachments (Nagasawa et al. 2015). A further effect of hormonal and wider genetic changes has been on the physical differences between wolves and dogs, which are more pronounced than those seen between chimpanzees and bonobos. Modern dog 'breeds' have been selected for certain physical and behavioural features. However, ancestral dogs, and certain 'wild' dogs, show common features in response to selection for increasing tolerance, notably shorter, flatter faces, reduced teeth size and reduced cranial capacity. Dogs' greater compliance/eagerness to please, lower aggression, and heightened social sensitivity may be brought about through changes in the ventral striatum, with changes in facial musculature allowing them to be more expressive, particularly when it comes to expressing vulnerability (Raghanti 2019).

A potentially interesting insight into the social behaviours of incipiently domesticated dogs comes from dingoes (Figure 8.6), discussed in relation to domestication in Chapter 7. Dingoes were separated from incipiently domesticated dogs around 6,000–8,000 years ago, and their group social behaviour seems to reflect that of incipient, rather than fully domesticated, dogs. In effect, they seem to represent some kind of middle ground between the outward-focused emotional connections of dogs and the inward-focused emotional connections of wolves. Rather than the disorganised group social

Figure 8.6: The Australian dingo has affinities with both wolves and free-ranging dogs, and is significant in sharing some elements of social behaviour with both. Jarrod Amoore from Sydney, Australia, derivative work: Mark Marathon, CC BY 2.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Dingo_walking.jpg.

behaviour seen in free-ranging dog packs, dingoes have a monogamous mating system, and hunt and parent collaboratively, sharing food resources between themselves in a more wolf-like social manner (Miklosi 2014). They also tend to defend their territory and their groups, in contrast to the more flexible social group patterns seen in free-ranging dogs. Dingoes are also far more tolerant of humans than wolves. They maintain eye contact more than wolves, though less than dogs (Johnston et al. 2017). Whilst showing a more cohesive internal social structure, dingoes are still able to form close relationships with humans, albeit being less biddable than fully domesticated dogs. Whilst we may make simple contrasts between chimpanzees and bonobos, or wolves and dogs, in terms of inward or outward focus of emotional connections there are clearly shades of adaptation in between, as well as other possibilities we may not have considered.

As with bonobos, the greater tolerance seen in dogs does appear to have come at a price, or at least as a *compromise* (see Table 8.2).

Dogs have also become more socially sensitive and, in turn, more emotionally vulnerable than wolves, largely as a side effect of the neuroendocrine changes promoting their enhanced tolerance (Miklosi 2014). A narrow window of reduced fear reactions in wolf pups allows them to orientate themselves to features of their social and physical environment that are not dangerous and can be trusted, such as other members of the wolf pack, though this window closes after two to three weeks. However, in dogs, this window is expanded by several weeks, providing an opportunity to 'socialise' with humans and thereafter view them as potential allies. This downside of this increasingly behavioural plasticity is that it also brings with it a vulnerability to the effects of an unsupportive emotional context. Dogs suffer in isolation and crave social contact far more than wolves (Bradshaw 2011; Serpell 2016). As discussed in Chapter 7, it is not difficult to see how our human social sensitivities and emotional vulnerabilities share many similarities with those of dogs.

In both chimpanzees/bonobos and wolves/dogs, we can see how subtle changes in ecology, combined with existing social patterns, can be related to different pathways in emotional connections – towards or away family or external connections. The different pathways may give us unique insights into differing human emotional connections and social systems in the past.

Interactions with non-kin and outsiders

- Aggression towards strangers is typical in wolves, although, occasionally, in exceptional circumstances, non-kin also join packs, such as when packs are missing key members (Miklosi 2014). Free-ranging dogs have a fluid group membership. The pack may defend itself from other packs. However, outsiders are often incorporated within packs, and dogs which have previously been 'pets' join free-ranging dog packs (Miklosi 2014).
- Wolf packs are typically made up of a breeding pair and their offspring (a 'family'), whilst free-ranging dog packs are typically made up of a large group of non-relatives.

Ecology

- Wolves largely depend on high-risk and unpredictable food resources (hunted animals), which requires collaboration, whilst free-ranging dogs depend on widely distributed but more dependable resources from human settlements, which they typically exploit as individuals. Feral dogs have been known to kill larger prey. However, they also typically do this as individuals (Miklosi 2014).
- Dogs have evolved an adaptation to digest starch (Axelsson et al. 2013).
- Wolves have a single breeding season, whilst dogs typically breed twice a year (Miklosi 2014).

Social structure

- Free-ranging dogs tend to live in larger groups than wolves, of varying size and in multi-male, multi-female communities. Wolves, in contrast, typically live in groups of around eight individuals, though there can be as many as 40 individuals in a pack. In some ecological conditions, wolves are mostly lone animals (Miklosi 2014).
- Free-ranging dogs have a fluid group membership, made up of non-kin, whilst wolves' packs are typically a 'family'.
- Free-ranging dogs match a linear hierarchy more clearly than wolf family structures. Whilst aggression is low when food is absent, aggression over food resources is common in free-ranging dogs (Miklosi 2014). Affiliative behaviours are common in wolves, which also display tactics to reduce tension through appeasing behaviour (such as looking away from a threatening approach).
- Wolves develop long-term pair bonds, whilst free-ranging dogs have a very flexible mating system and can display monogamy, polygny, polyandry and promiscuity (Pal 2003).

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Social structure
– Wolf pups are reliant on adults of their species for seven to eight months, dog pups for only up to three months (Miklosi 2014).
Differences in within-group collaboration
– Wolves share food, parent collaboratively, hunt collaboratively (often taking risks on behalf of the group), risk injury to defend the pack, provision pregnant and lactating females, and can provision the ill and injured. However, these behaviours are typically not seen in free-ranging dog packs (Miklosi 2014). – Dingoes, separated from incipiently domesticated dogs around 6,000–8,000 years ago, have a monogamous mating system, defend territories, hunt and parent collaboratively, and share food, possibly deriving from an ancestral wolf-like pattern (Miklosi 2014). – Conflict is observed more frequently in wolves than in free-ranging dogs. However, conflict is more likely to escalate to serious fighting in dogs (Marshall-Pescini, Cafazzo, et al. 2017). – Wolves outperform dogs in conspecific cooperation tasks (Marshall-Pescini, Schwarz, et al. 2017). – Wolves are more tolerant of proximity during feeding and do not monopolise food (Marshall-Pescini, Cafazzo, et al. 2017).
Neurophysiology
– Dogs show a delay in the fear-mediating responses as puppies, creating a longer period when fear responses to novelty are reduced (about three to 12 weeks), and during which socialisation with humans occurs (Buttner 2016; Topál et al. 2005). – Dogs show reduced stress reactivity through changes in the SAM (sympathetic–adrenomedullary) system affecting 'flight or fight responses', and HPA axis affecting adrenal glands and so influencing the action of hormones such as glucocorticoids (e.g. cortisol) (Buttner 2016; Saetre et al. 2004). – Dogs show an oxytocin-mediated attachment pathway with humans, engaging in mutual eye gaze from an early age (Buttner 2016; Kaminski et al. 2009), which stimulates oxytocin responses (Kis, Ciobica, and Topál 2017; Kis et al. 2014; Kis et al. 2017). – Dogs' social focus on humans means that they commonly prefer praise to a food reward (Cook et al. 2016).

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Forms of collaboration with humans
Emotional connection
– Dogs (but not wolves) have a long period of potential socialisation with humans during development, in which their fear response is much reduced in comparison to similar aged wolf puppies.
– Dogs (but not wolves) can develop a secure attachment to humans, acting emotionally like an attachment figure (Kurdek 2008), or better understood as close friend (Miklosi 2014), and providing emotional support (Miller et al. 2009). Humans, likewise, provide emotional support for dogs.
– Wolves take longer to be socialised with humans (though this can be achieved).
– Dogs have an oxytocin-based response to the human gaze (Kis, Ciobica, and Topál 2017; Kis et al. 2014; Kis et al. 2017; Thielke and Udell 2017). Dingoes establish eye contact more than wolves, but less than dogs (Johnston et al. 2017).
– Dogs approach a novel object in a shorter time than wolves (Marshall-Pescini, Cafazzo, et al. 2017).
Strategic collaboration
– Wolves and dogs can collaborate with humans by indicating where food is, and adapting to a more collaborative or competitive human (Heberlein et al. 2016).
– Dogs are more dependent/pay more attention to humans when moving together (dogs 'look back', whilst wolves do not) (Miklósi et al. 2003).
– Once socialised, wolves are even better at strategic collaboration, and better able to interpret human social clues (Udell, Dorey, and Wynne 2008).
– Wolves are better able to solve problems independently (Udell 2015).

Table 8.2: Contrasting behavioural ecology of wolves and free-ranging dogs.

Of course, it is easy to oversimplify. There are subtle but important differences, nonetheless, between changes occurring in wolves/dogs and those in chimpanzees/bonobos, and this will also have been the case with similar changes in different species of human. Whilst bonobos are principally less aggressive in both within-group and out-group contexts, dogs have taken tolerance much further, with a marked openness to new relationships including with ourselves. They also display more notable novel social and emotional competences. Clearly, there are common directions in changes in behaviour as a result of pressures towards increasing tolerance and common genetic changes as a result, but, nonetheless, each species also follows its own trajectory.

Different but equal human evolutionary pathways?

How do contrasts between different emotional connections in closely related chimpanzees/bonobos and wolves/dogs help us to understand different pathways in past humans?

As we have seen in Part 1, humans have been under strong selection pressures to be more internally prosocial from at least 2 million years ago. These pressures affected the strength of emotional bonds in close-knit groups, emotionally motivated to care for each other. However, selection pressures towards wider emotional connections outside the local group, and even beyond that to imagined beings (Chapter 5), other species (Chapter 7) or even objects (Chapter 6), appear to have come to the fore in much more recent human evolution, and most particularly in changes we see occurring after 300,000 years ago. As with chimpanzees/bonobos and wolves/dogs there are plausible ecological explanations for the different pathways (Spikins et al. 2021). These latter changes share many similarities with those seen in bonobos and in dogs. Rather than a case of one superior, more intelligent or even more 'social' route, different pathways are taken by different species under various selection pressures, with each pathway bringing both advantages and disadvantages. In each contrasting set of pathways we also see a move towards more infant-like (paedomorphic) features in the bonobo/dog/modern human sister species, associated with increased tolerance, greater intergroup interaction and increased social sensitivity.

These similarities have a genetic component in humans, much as they do in chimpanzees/bonobos and wolves/dogs (discussed in Chapter 5). There is some evidence for certain levels of convergent genetic evolution between humans and bonobos, for example. Genetic changes associated with increased prosociality are seen in both these species which are absent from the chimpanzee genome (Theofanopoulou, Andirko, and Boeckx 2018). These changes have been seen in terms of shared adaptive shifts towards 'tameness', 'friendliness', 'domestication' or 'self-domestication' (Hare 2017; Hare, Wobber, and Wrangham 2012; Hare and Woods 2017;

Theofanopoulou et al. 2017). Similarities to changes occurring in dogs are even more pronounced. In both humans and dogs, selection for 'tameness' has led to reduced stress reactivity brought about through changes in the HPA axis and reduction in production of stress hormones such as cortisol (Buttner 2016), whilst novel types of emotional bonding are the result of changes in oxytocin pathways (Herbeck et al. 2017; Theofanopoulou et al. 2017). This reduced stress reactivity may well play a more important role in encouraging friendly approach behaviour than any changes in androgens, particularly since social aggression in humans is more clearly related, in terms of hormonal reactions, to a complex relationship between testosterone and cortisol, rather than to testosterone alone (Montoya et al. 2012).

There are other significant changes. A willingness to explore new situations and openness to new relationships, mediated through dopamine, is also common to both dogs and humans. In both species, this openness is achieved through an increased sensitivity to social environment, with changes in similar genes affecting this new 'hypersociality' of both species (Shuldiner et al. 2017). An increase in juvenile-like behaviour in both species, associated with more paedomorphic (infant-like) facial anatomy, may also have led to increased playfulness and, perhaps, imagination (Fuentes 2017; Nowell 2016). These changes also affect eye gaze. Bonobos, for example, are more focused on eye contact than chimpanzees are (Kano, Hirata, and Call 2015), and similar changes may be happening in modern humans, given our extraordinary sensitivity to facial expressions round the eye area and the significance of our movable eyebrows (Godinho, Spikins, and O'Higgins 2018). In both humans and dogs, changes related to social bonding hormones such as oxytocin may have a particular effect on eye gaze (Decety 2015; Decety et al. 2012; Kis et al. 2017). Contrasts *within* human populations, between individuals with different alleles of oxytocin receptor genes, for example, illustrate that higher effective levels of oxytocin are associated with better abilities to read emotions in others (Dannlowski et al. 2016). These same alleles are also associated with lower stress in socially supportive contexts (Chen et al. 2011), and greater tendencies to make relationships, trust others and form strong bonds, all of which are likely to be selected for under conditions in which friendliness is selectively advantageous. As we have seen in Chapter 1, oxytocin is important in our close relationships, creating a sense of warmth, comfort and security (Gilbert 2015a; Gilbert 2015b). These stronger emotional bonds not only functionally cement social networks but also buffer us from other stresses.

For both humans and dogs, their elevated sensitivity to social environment, coupled with a greater capacity to form new social bonds, brings both new vulnerabilities as well as new ways to counteract them. Dogs are extraordinarily socially sensitive and have a long period of sensitivity to surrounding social cues, accompanied by increased emotional vulnerability to any lack of socially supported interaction (Miklósi 2014). In humans, as in dogs, a greater developmental (behavioural) plasticity has led to an enhanced ability to learn, and an increasing openness (Miklosi 2014). Recent evolution leading to modern humans, and along a separate pathway to other archaic species such as Neanderthals or Denisovans, has also contributed to our heightened neuroplasticity (Sherwood and Gómez-Robles 2017). Both species thus benefit from an increasingly sensitive and plastic brain, with an elevated capacity to adapt after birth and outside of that which is under direct genetic control. These changes bring elevated capacities to learn from our environment, particularly during development, such as, in the case of humans, potentially aiding in the acquisition of complex language and complex cultural norms.

Comparisons with the contrasting pathways taken by chimpanzees and bonobos, and by wolves and dogs, give us an opportunity to bring into focus contrasting pathways in humans. It is not difficult to see that, in many ways, modern humans have taken the more externally tolerant pathway, much like that taken by bonobos or dogs, whilst other human species followed a different direction (Figure 8.7). Similar changes in emotional dispositions in modern humans share many similarities with the different pathways recorded in chimpanzees and bonobos, and in wolves and dogs.

To think only of two contrasting pathways is, of course, an oversimplification. Like the example of dingoes, who share some characteristics with dogs and others with wolves, there will be pathways in between. Moreover, other pathways will have led in entirely different directions. Nonetheless, the concept of equal but different pathways in emotional connections can help us move beyond ideas of superiority or sameness in interpreting the social lives and behaviours of our close relatives such as Neanderthals, discussed in Chapter 9.

Changes in emotional capacities and dispositions at this point of divergence need only to have been subtle to have far-reaching effects on human

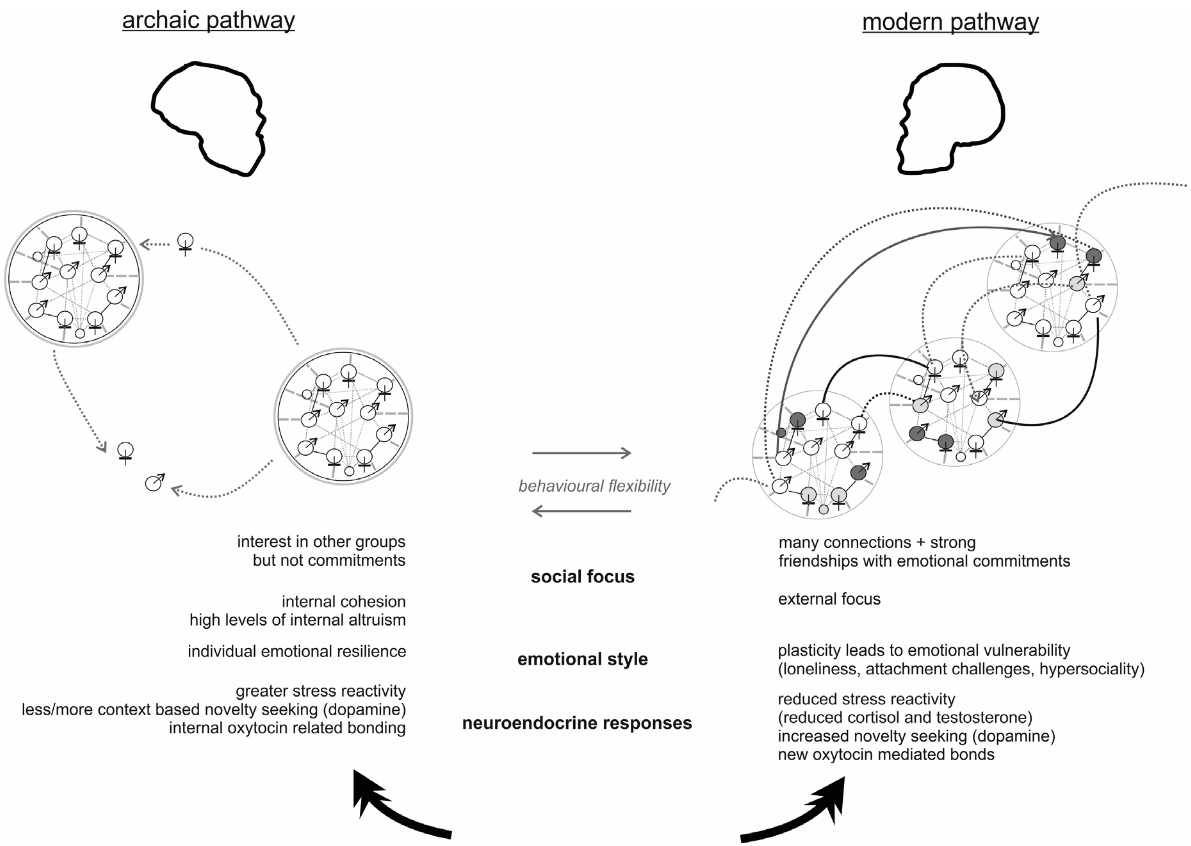

Figure 8.7: Potential changes in emotional dispositions along different pathways in human evolution 300,000 to 30,000 years ago. Penny Spikins, CC BY-NC 4.0.

social relationships. Extending our social network has far-reaching effects, for example. The number of people you might know and learn from, and who might be your potentially significant friends, increases dramatically if you are able to tolerate and approach unfamiliar individuals. Hill notes that, in recent hunting and gathering populations, individuals might reasonably expect to meet a thousand other people in their lifetime, compared to around 20 individuals in the lifetime of the chimpanzee (Hill et al. 2014). New types of mutually generous bonds with distant allies, maintained despite a gap of time and distance, also provide a remarkable degree of social buffering in times of shortfalls (as discussed in Chapter 5). These alliances can make a difference between death and survival. An elevated social sensitivity also allows cultural and social norms to become easily adopted, and for cultural ideas to spread, potentially helping innovations to buffer the effects of environmental changes and contributing to a large-scale social harmony. This elevated sensitivity may even have been instrumental in complex language abilities (Thomas and Kirby 2018). There is little doubt that this path, in the words of Robert Frost, '*made all the difference*'.

Though we should be wary of making comparisons which are too simplistic, there is much to learn from these differing pathways in *our closest living relatives* and *our closest friends* about our own evolutionary past.

As we have seen in wolves/dogs and in chimpanzees/bonobos, advantages brought by expanding the scope of social connectivity come with costs and compromises. The same evolved sensitivities that bring possibilities for high levels of cultural dynamism, extensive social connection and greater community resilience, come with elevated emotional needs and sensitivities. We all feel the costs of these evolved vulnerabilities in various ways.

At an individual level, as we have seen, we need close social support and emotional connection to thrive, and easily suffer in profound ways from loneliness or social isolation. We are liable to attachment disorders where genuinely caring relationships are lacking (discussed in Chapter 5) and, though we may have adapted new types of compensatory attachments (discussed in Chapters 6 and 7), even as adults we are easily weighed down by the fears, anxieties and even health effects that a lack of secure attachments bring. We want to belong, to help people, to feel significant and cared for. In emotionally supportive contexts, we reach out to help others and are sensitive to their feelings. When the structures we need to support our emotional capacities and needs are not there, however, not only do we easily slip into anxiety or depression but we often take what we can get in terms of human connection, even if what we turn to hurts ourselves or others. Sometimes a lack of connection leads us to damage ourselves if we sink into addictions and, at other times, it can harm others if we lose a sense of reality and sacrifice principles to belong to any group that gives any sense of connection, however unhealthy.

At the level of our societies, our capacity to connect with people who are unfamiliar can unravel, particularly when we are anxious or fearful. It has been argued that changes in oxytocin and, with them, propensities not only to *tend* but also to *defend*, might have elevated tendencies to dehumanisation (Hare and Woods 2021). However, much of our shared biological responses to the differences that can fuel racism or other negative attitudes are ones which we share with other apes (Sapolsky 2017), as discussed in Chapter 4. Furthermore, again as seen in Chapter 4, oxytocin can also prompt *befriending*, and changes in hormonal responses can have complex behavioural implications within a cultural context. Rather, tolerance itself, in bringing with it large-scale connected societies, may be laying the basis for the level of social interaction that makes dehumanisation an issue, where previously interactions with others were rare. Simply being prone to a range of social anxiety, fears and feelings of helplessness and isolation is quite enough to fuel hatreds. Moreover, our acute social sensitivity means we are highly liable to 'follow the crowd', and our need to belong can make us override our sensibilities about others' welfare. As the now-famous experiments of Stanley Milgram and Phillip Zimbardo have demonstrated, compliance with authority, rather than widespread individual evil, can make us cruel (Zimbardo 2011). Our modern industrialised societies seem some of the most alienating (Gilbert 2021). All too often, our emotionally vulnerable brains can be pushed too much to their limits by a lack of connection, and be so overwhelmed by the challenges of surviving without the right kinds of connection that there is little space for caring about other people or nature.

We can identify how our emotional vulnerabilities and needs for emotional connection were adaptive in the past. The evolutionary pathway our species followed can be judged a 'successful' one in terms of survival, expansion and population numbers. Amongst other changes, elevated tolerance and social connection provided a buffer to resource shortfalls, a means of sustaining social relationships in the absence of loved ones, and an ability to find close friendships outside of human relationships to bolster losses or make us better people. That this pathway was 'successful' in these terms does not take away the emotional suffering that human sensitivities, needs for connection and emotional vulnerability sometimes brings, or the potential damage that humans can inflict on themselves or nature. We are, after all, just one species of many, with emotional responses and behaviours that have been cobbled together from existing structures along adaptive pathways entailing many compromises.

Implications

A closer look at our evolutionary past reveals a rather different story from the one we are used to in which our species is portrayed as being better than any others, and perfectly adapted.

We have already seen from Chapter 4 that evolution is far less ordered and predictable than we might imagine. Species adapt according to immediate circumstances, regardless of which better options might exist elsewhere in the longer term. We are lumbered with the back problems that our ancestral bipedal locomotion brings, for example, as we are too far along this track to move to something that might place less stress on our lower back, such as four-legged locomotion. Painful emotions such as shame evolved to motivate us to do what is needed to belong to a group, but they are far from an ideal means to do so, bringing not only great unhappiness but tendencies to follow group behaviours no matter the cost, and propensities to depression (Gilbert 2021). We would not have designed ourselves this way. Added to which, even when there is selection for one gene that might bring advantageous traits, since many genes are associated with each other, many other traits come along with the ride. Moreover, the very mutations on which adaptations depend occur by chance and there are also all kinds of complex epigenetic factors that influence which genes are expressed in which particular contexts. The more deeply we look, the clearer it becomes that we are far from perfect, or even perfectly adapted. It can seem remarkable that we manage to negotiate life with our evolved minds, bodies and feelings as well as we do.

A new perspective on differing adaptive pathways in tolerance, explored in this chapter, adds to this picture by bringing into focus not only the advantages but also the compromises that have been brought by changes in emotional responses.

There are several implications.

Firstly, an understanding that each evolutionary pathway brings compromises affects our interpretations of the archaeological and human evolutionary record. Most obviously, we might revise some of our interpretations of our closest fossil relatives. An understanding of differing but equal pathways in tolerance provides explanations for previously enigmatic aspects of Neanderthal behaviour, for example. Rather than being inferior, or simply the same, as our own species, Neanderthals may have had different types of emotional connections, and a different focus to collaboration (explored in Chapter 9). We might also consider some of the many other species of human from which our pathway has diverged in the past, or who have been contemporaries. Diminutive species such as *Homo naledi*, which had small brains that nonetheless had enlargements in areas associated with social and emotional processing, might be considered to be following a pathway with a particular focus on strong emotional connections, for example. We can and should widen the scope of our interpretations to consider different ways of being emotionally human.

Perhaps even more importantly, there are implications for our understanding of ourselves. We are naturally able to care about others and to collaborate to make things better, not only for our kin and friends but also contributing to the wellbeing of our wider communities or people more generally. Yet there is a price to pay for these capacities in terms of emotional vulnerabilities and sensitivities, and this price is something that can be obscured by a reassuring narrative of superiority. It is all too easy to plan our lives and societies around an idea of ourselves as independent, and emotionally invulnerable, beings. An understanding that our evolutionary history has been one of compromises, in contrast, highlights the significance and challenges of our emotional vulnerabilities. We may be far more willing to give things up for others than a traditional view of ourselves as independent and self-oriented beings would suggest, as we have seen through widespread adherence to constraints on freedoms during the COVID-19 pandemic across the world. Yet recent times have also demonstrated that we are far more emotionally vulnerable, profoundly affected by our social and natural surroundings, prone to depression or anxiety through loneliness and a lack of belonging, or liable to be influenced by others, than we like to imagine.

Has our evolutionary story of superiority itself contributed to a disregard for the emotional costs that come with a lack of connection, perhaps even in this way adding to a sense of alienation in modern societies? It is difficult to know for sure. Nonetheless, perhaps a better understanding of our evolutionary history may help us to be more humble about our place in nature, and to recognise that we are vulnerable to the effects of social isolation or a lack of social safety. Only by creating supportive emotional connections can we be what we want to be.

Conclusions

We often think of human evolution as a progressive development of ever better forms of human, moving towards ourselves as some kind of pinnacle of evolutionary processes. There were, however, different pathways, and different types of human, many of which lie at the limits of our imagination.

Changes in tolerance and emotional connections in recent human evolution can easily be seen as advancements. However, when we consider how similar changes in tolerance play out within closely related species, those most closely related to us (chimpanzees and bonobos) and those most closely connected to our past ecological niche and present lives (wolves and dogs), it becomes clear that such changes present both potentials and pitfalls.

Studies of evolutionary changes in external social tolerance in closely related species cast insight into the types of changes that may have been taking place within recent human species. Particular ecological and social contexts may have allowed adaptations leading to external social alliances to become adaptive. As a result, one evolutionary pathway led to modern humans with new types of relationships and more extensive social networks. It would be too simplistic to see this as simply as an advancement or, even, as a more *prosocial* adaptation. Different evolutionary directions have both advantages and disadvantages, and it may, perhaps, be more appropriate to see the alternative pathways lying between early modern humans and other archaic humans as different types of sociality.

By following our particular evolutionary path, we have benefited from an increased openness to new relationships, reduced stress reactivity in the presence of unfamiliar others, reduced aggression, and capacities to build new bonds. However, these adaptations also brought costs in terms of individual emotional vulnerabilities and needs for supportive and caring social contexts. We can easily feel isolated and lack the right kind of emotional connection, making us prone to depression or anxiety. In modern industrialised contexts, where social isolation seems to be particularly widespread, and where we all too often lack a sense of social safety or relationships based on trust, these responses are particularly common. Perhaps, if we recognise that we are not some pinnacle of a process of increasing perfection, but rather the product of alternative paths, all with compromises, we might find it easier to understand why we have both the emotional capacities and the needs that we do.

If we are honest with ourselves, we would probably admit that our traditional story of human origins gives us a reassuring sense of entitlement, or at least a reassurance of things falling into place. A closer consideration of our evolutionary past reveals far less of a sense of direction, and far more of a story of the influence of chance, compromise and vulnerabilities. This may be a good point in human history to pause and reconsider our place in the world around this somewhat different story.

Key points

- Different species of human in the past did not follow a ladder of progression towards ourselves but travelled along different evolutionary pathways. For humans, as for other highly social animals, subtle changes in ecology can create different selective pressures affecting tolerance and the focus of emotional connections.

- Although changes taking place in modern humans, in contrast to archaic humans, after 300,000 years ago cannot be seen as simply a contrast between ‘wild’ and ‘tame’, there are, nonetheless, important parallels with similar changes taking place between both wolves and dogs, and chimpanzees and bonobos.

- A process of becoming more tolerant is not as simple as that of becoming more social or more collaborative, but rather one of greater social and emotional sensitivities, greater motivations to explore and to be playful, and social relationships with a more outward social focus at the potential expense of within-group collaboration.

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CHAPTER 9

Reframing Neanderthals

Abstract

Neanderthals have occupied a rather problematic position in our evolutionary history for many years. Neanderthals and modern humans share fundamental features of humanity, such as care for the vulnerable, yet differences in their use of symbolism, adoption of innovations and intergroup relationships have been hard to explain. Evidence suggests that Neanderthals lived in small living groups with only rare connections to outsiders and high levels of inbreeding, whilst modern human populations from their first arrival in Europe were highly interconnected and maintained connections between communities stretching over large regions. It has been tempting to interpret these differences in terms of an inferior social or intellectual cognition in Neanderthals. Subtle differences in emotional dispositions may, however, be a better explanation. A more inwardly focused or close-knit nature of Neanderthal communities, and a more outwardly focused or approachable nature of modern humans, can explain previously enigmatic elements of their archaeological record without recourse to ideas of progression or advancement.

(Abstract continued on next page)

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(Abstract continued from previous page)

Our understanding of Neanderthals as displaying subtly different emotional dispositions gives us an opportunity to think about human evolution differently. Rather than a ladder, or even a braided stream, here we argue that our evolutionary past is better conceptualised as a series of branching pathways which sometimes rejoin and sometimes follow different directions. Allowing past hominins to be different but equal opens up new lines of interpretation, as well as challenging us to understand that there is more than one way to be human.

Figure 9.1: Recent reconstruction of a Neanderthal woman. Neanderthals were no less human, yet their physical and behavioural distinctions challenge our understanding of our relationship to these close cousins. Neanderthal Saint-Césaire © Sculpture: Elisabeth Daynes/Photo: S. Entressangle. Used with permission.

Introduction

The role of Neanderthals in our evolutionary story has a long and chequered history from their first recognition (see Figure 9.1). In 1864, when William King considered the status of a Neanderthal cranium that had been discovered only a few years earlier in the Neander valley in Germany, he was challenged by its unusual appearance. Despite being essentially human-like and possessing a large brain, it was clear that this individual was distinctly robust, with a large brow ridge and notably long and low brain case (Figure 9.2). Here was a human, or human-like, being that was disturbingly different. In typical Victorian style, he concluded that this difference must relate to some inferiority on a perceived ladder of human progression. Furthermore, he decided that this being simply must have had an animal, rather than human, nature. He concluded:

> Considering that the Neanderthal skull is eminently simial, both in its general and particular characters, I feel myself constrained to believe that the thoughts and desires which once dwelt within it never soared beyond those of a brute. (King 1864: 96)

Figure 9.2: The cranium (known as Neanderthal 1) from the Neander valley that was derided as brutish by William King in 1864. Image of cast. Gunnar Creutz, CC BY-SA 4.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Homo_neanderthalensis_(cast_of_Neanderthal_1_skull cap)_at_G%C3%B6teborgs_Naturhistoriska_Museum_8790.jpg.

We may be alarmed by this ready assumption of brutishness to any different-looking human. However, for more than a century, the unfamiliar appearance of Neanderthals, coupled with pervasive ideas that our own species rose above others through some innate superiority, naturally led to Neanderthals being portrayed as lumbering and brutish (Madison 2020; McCluskey 2016; Peeters and Zwart 2020). Even as their close-relatedness to our own species became clear (to the point where we might at most consider them a subspecies), this relatedness often made them too close for comfort, leading to continued derision both in public portrayals as well as academic interpretations. The term 'Neanderthal' itself even became an insult, implying an aggressive and primitive nature.

Attitudes have changed over the last decade. New evidence for Neanderthal care for illness and injury, the production of art and mortuary practices have elevated our attitudes to the capacities of our nearest evolutionary cousins, whilst evidence for interbreeding and a contribution of Neanderthal DNA to our modern genome has made us increasingly uncomfortable about negative portrayals of people who are now seen as close family (Sykes 2020).

Neanderthals remain a challenge to approach and interpret, even within a more modern framework. Even though there has been notable interbreeding with our own species, so-called 'modern' humans (Hajdinjak et al. 2021; Lalueza-Fox 2021), Neanderthals have followed a largely different path to that of our own species for most of the last half a million years. They seem to have benefited from physical adaptations to their particular environments and ecology that are notably different, such as increased levels of brown fat (Sazzini et al. 2014) and adaptations to a high protein diet (Ben-Dor et al. 2016), and seem to have been better suited to short sprints rather than running for long periods (Higgins and Ruff 2011). They may even have undergone something similar to hibernation to escape resource shortages in winter months (Bartsiokas and Arsuaga 2020). Their brains also developed differently (Gunz et al. 2010). As well as evident robusticity and the presence of a notable brow ridge and different cranial shape (see Figure 9.3), Neanderthals show notable differences in adult visual cortex (Pearce, Stringer, and Dunbar 2013), parietal lobes (Pereira-Pedro et al. 2020) and cerebellum (Kochiyama et al. 2018). The archaeological record shows differences in technology and in symbolism, and most particularly in patterns of mobility, interaction and innovation (Spikins, Hitchens, and Neeham 2017).

Figure 9.3: Neanderthal (right) and modern human crania (left), showing distinctive differences in cranial shape, robusticity, and presence/absence of a brow ridge. Hairymuseummatt (original photo), DrMikeBaxter (derivative work), CC BY-SA 2.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Sapiens_neanderthal_comparison_en_black background.png.

In trying to explain why the material evidence for Neanderthal behaviour is different from that of the modern humans who replaced them, our attention has traditionally tended to focus on Neanderthal thinking skills. Particular attention has been paid to areas of Neanderthal cognition that might be seen as inferior to that of modern humans, in keeping with our assumption that our species ought to be cleverer than any others. Certainly, there is some evidence that Neanderthal thought and perception were different. There are a number of regions of modern human brains that seem to demonstrate potentially important differences from theirs (Bruner 2021). Differences in the parietal cortex may influence technical and visual cognition (Pereira-Pedro et al. 2020), for example, differences in the cerebellum may be significant in organisational skills (Kochiyama et al. 2018), and there may even be differences in body cognition (Bruner and Gleeson 2019). The idea that any differences, no matter how subtle, should imply human cognitive superiority seems somehow unsatisfactory, however (Hoffmann et al. 2018; Langbroek 2012; Zilhão 2014). Moreover, there tends to be little attempt to focus on where areas of Neanderthal cognition might have been superior. If we start by assuming that, in terms of their thinking skills, Neanderthals occupied a lower rung of an evolutionary ladder than modern humans, we tend to find what we are looking for. We then ascribe behavioural differences to their supposedly inferior thought.

The only alternative to a view of Neanderthals as necessarily inferior has tended to be portrayals and interpretations of Neanderthals as the same as our own species. Certainly, Neanderthals are no less human. Nonetheless, seeing Neanderthals as *the same* is, perhaps, too easy a solution to the challenge of approaching differences without assumptions of superiority and inferiority. Even a recent tendency to move away from an evolutionary model of a ladder by thinking of human evolution as a braided stream with different species of humans all going in the same direction, is far from perfect as it fails to allow for different evolutionary directions. No one likes to be seen as inferior, but equally we might doubt if any Neanderthal meeting a modern human would want to be seen as *just the same*.

The problem of how to approach and understand differences we see in past species who lived contemporaneously with each other, without imposing concepts of progression, has become even more pressing in recent years. Evidence has revealed that the relatively recent evolutionary past, and particularly the period between 300,000 and 30,000 years ago, was one in which there were a wealth of different human species, from those who were robust, such as the Denisovans and Neanderthals, to the tiny *Homo floresiensis* or *Homo luzonensis* or small-brained hominins such as *Homo naledi*, many of which lived in similar regions at the same time. It is far too easy to find ourselves assuming that our ancestors, the taller and more gracile forms amongst these unusual creatures, were better in every way, simply because we see ourselves as 'the survivors' of this remarkable proliferation of forms. The real story of what happens is likely to be far more complex.

Considering emotional dispositions may provide some insights. It may be possible to find explanations for differences in behaviours which do not depend on inferring that Neanderthals possessed an inferior cognitive capacity.

Different types of 'social'

Can contrasts in emotional dispositions between closely related species today help us reframe differences between Neanderthals and our own species?

We have seen how there can be subtle but important contrasts between quite closely related species that do not clearly divide into ideas of better or worse (Chapter 8). Contrasts between wolves and dogs, and those between chimpanzees and bonobos, are particularly relevant. In contrast to free-ranging dogs, wolves are much more willing to share food amongst the group and to collaborate in care of offspring, as well as to hunt collaboratively, for example. Free-ranging dogs, in contrast, rarely share or collaborate in offspring care, and the extent to which they collaborate in hunting is very limited. Yet, before we simply see wolves as *more social or more collaborative*, we must at the same time recognise that free-ranging dogs are far more open to external connections, and form packs of unrelated individuals that contrast with the largely kin groups we see in wolves. There seems to be a certain inward focus to wolf pack social relationships that contrasts with the outward focus we see in free-ranging dogs, and neither can simply be described as more social or more collaborative than the other. Different contrasts, which share some similarities, can also be drawn between chimpanzees and bonobos. Chimpanzees are far more effective collaborative hunters, and more prolific users of a wider variety of tools than bonobos. They cannot be seen as either more collaborative or more intelligent, however. Bonobos take a more outward focus to their community social relationships, and have a more intuitive emotional response to others within their communities.

These *differently social* distinctions are apparent between many closely related species. As we have seen in Chapter 8, African wild dogs and grey wolves seem very similar and are both highly collaborative, yet communicate their intentions in markedly different ways. We should not be surprised to find something similar to these subtle but important differences in types of social collaboration or communication when we consider differences between some closely related human species. Ideas that any one species is *superior* to a close relation – more collaborative, more social or more intelligent – tend to be over simplistic.

Different evolutionary branches bring differing advantages and disadvantages depending on context, and also bring compromises. Changes in emotional disposition are no different. Animals that become more externally socially tolerant, both under direct human influence and in the wild, show a greater social sensitivity and openness to new experiences (and, as we have seen, dogs have a longer period of openness to new experience as puppies than do wolves). However, social sensitivity brings with it a certain neediness. Whilst wolves famously 'don't look back' to their fellows or plead for support, and tend to solve problems independently, dogs immediately seek support, particularly from people, and look to others to how they should behave. Bonobos both reach out to help others much more willingly than chimpanzees do, and also seem to need and reach for closeness and affection more often. We cannot simply describe these different types of social behaviour as inferior or superior, or more or less complex. They are social behaviours that suit different contexts, and come along with compromises.

A better understanding of potential differences in emotional dispositions affecting social tolerance, social sensitivity and emotional vulnerability, as differences that cannot easily be placed within a ladder of progression, may help us understand different behaviours between different human species.

Here, we focus on how insights from understanding different pathways in emotional dispositions may help us to understand archaeological

Contrasts seen when comparing closely related species	**Comparing wolves and dogs**	**Comparing chimpanzees and bonobos**
Differing inward and outward focus to social relationships	Evident	Evident
Differing levels of group collaboration (hunting, sharing food, offspring care)	Evident	Evident
Differing willingness to include outsiders	Evident	Evident
Differing social sensitivity/ vulnerability	Evident	Evident
Differing individual independence	Evident	Unconfirmed
Differing facial expressivity	Evident	Unconfirmed

Table 9.1: Key contrasts in emotional dispositions and behaviours between closely related social species (discussed in more detail in Chapter 8), often simplified into a generalisation 'wild' versus 'tame'.

evidence for contrasting patterns of social behaviour between communities of Neanderthals and those of modern humans in Europe. We suggest that Neanderthals are best seen as differently emotional, and differently social. These differences, rather than some inferior cognition, can explain the differing structure of their communities, and different behaviours seen in the archaeological evidence.

Archaeological evidence for contrasting patterns of intergroup connection between Neanderthals and modern humans in Europe

Background

It is easy to forget that Neanderthals were a highly successful hominin. They lived in Europe from around 300,000 years ago, and descended from earlier species that had been living in the region since at least 1 million years ago. Whilst there were early incursions of so-called 'modern' humans from Africa into Europe (such as over 200,000 years ago in Greece; Harvati et al. 2019), their sustained occupation of the region has been quite recent, largely taking place after 40,000 years ago. Yet, after several thousand years of overlap and interbreeding, modern humans eventually occupied all of Europe and displaced Neanderthals.

The similarities between these two populations far exceed any distinctions. As we have seen in Chapter 2, Neanderthal communities were highly collaborative, showing strong altruistic motivations within their own groups, being willing to care for others for extended periods, and to risk their lives to bring back food (Spikins et al. 2018). Neanderthals, like modern humans, were very intelligent, highly socially complex beings who cared deeply for those around them. Both Neanderthal and modern humans share large brains, capacities for social complexity, learning and altruism. Furthermore, any genetic dividing line is far from clear cut, with a notable contribution of Neanderthal DNA to modern European and Asian populations, for example (Sankararaman et al. 2016). Many of the traditional interpretations of Neanderthals, which portrayed them as having inferior intelligence or being inferior in other ways, such as in their symbolic capacities, have eroded over recent years (Hoffmann et al. 2018; Langbroek 2012; Zilhão 2014).

Remaining distinctions, which are difficult to explain, are seen in patterns in the structure of Neanderthal and modern human social networks, social groups and communities. Explanations for these differences have tended to focus on the concept that Neanderthals were socially or cognitively less competent (see Pearce 2013). Insights into differing emotional dispositions between closely related species may provide alternative explanations.

Neanderthal community relationships

Like all members of the genus *Homo* (discussed in Part 1), Neanderthals were social beings, living in groups and thriving on emotional connection. When it came to contacts outside of family and living groups, it is clear that Neanderthal families did not live in isolated social bubbles. It seems reasonable to talk of Neanderthal communities, stretching beyond the confines of a single local living group (Sykes 2012). Similar artefacts found across large regions demonstrate that Neanderthals within some regions had a shared understanding of how certain things should be made. Regional styles are identified in Middle Palaeolithic lithic technology, for example (Ruebens 2013), as well in mortuary practices (Pettitt 2010). Individuals must have moved between groups at certain times.

Nonetheless, though there were some connections between Neanderthal groups, the scale of everyday social life seems to be small. Living groups seem to have been largely small and kin-based. At El Sidrón, in northern Spain, the skeletal remains of several individuals who were presumably a single group, victims of an unfortunate rock fall, were recovered. The group consisted of 13 Neanderthals: seven adults, three adolescents, two juveniles and one infant, of whom three of the adults were brothers, whilst the adult females were unrelated (Lalueza-Fox et al. 2011; Ríos et al. 2019). Intrasite spatial patterns also suggest that a small group of this size may have been typical (Spikins, Hitchens, and Needham 2017).

Archaeological evidence also suggests that interactions *between* groups, whilst they must have occurred occasionally to maintain mating networks, were infrequent. In many regions, raw materials used for making flint tools are moving only within the expected 'home range' (the area in which any single group might have travelled to find enough food). For example, raw materials within sites in the Southern Massif Central in France come predominantly from within the region itself, suggesting that there was little travel beyond this region (Fernandes, Raynal, and Moncel 2008). Raw materials for flint tools typically come from the most local source possible in this region – such as within five kilometres (Fernandes, Raynal, and Moncel 2008), with even only 20 kilometres away being exceptional.

Moncel commented:

> The data suggest highly mobile human groups, travelling in small territories on plateaus and valleys, along the Rhône corridor for daily subsistence. There is no evidence of human travel into the Massif Central Mountains to the west to collect raw materials; in fact any geographical obstacle appears to have stopped human movements along the south-eastern border of the Massif Central. (2011: 261)

This is not unusual for many European Middle Palaeolithic sites, such as in northern Italy (Spinapolice 2012) and the Swabian Alb (Conard, Bolus, and Münzel 2012), where raw materials predominantly come from within 10 kilometres. Across the whole of Europe, raw material movements are commonly small-scale, with those of more than 100 kilometres being exceptional (Féblot-Augustins 1993; Féblot-Augustins 1999; Féblot-Augustins 2009).

Raw materials are *sometimes* transported in a notable quantity from beyond what might be a typical home range. However, this only seems to occur where it seems to be a matter of necessity. In southern Italy, for example, the majority of flint raw material used in some of the sites in the Salento region comes from about 100–150 kilometres to the north. However, in this case, local raw materials are particularly poor quality and would have been difficult to use (Spinapolice 2012). Regular movements between home ranges may have been possible when required, without necessarily *being a welcome pleasure*.

There are frequent instances where a few examples of distant materials are recovered from Middle Palaeolithic sites, providing evidence of intergroup interactions or movements. For example, at Lezetxiki, in northern Spain, a marine shell that had travelled over 500 kilometres was recovered from Middle Palaeolithic deposits dating to 55,000–48,000bp (Arrizabalaga 2009), seemingly as a 'one off' transport (Spikins, Hitchens, and Needham

2017). A few well-used artefacts found at Cap Grand in south-west France had travelled over 400 kilometres (Slimak and Giraud 2007). Furthermore, flint from distant raw material outcrops has been found in certain Middle Palaeolithic assemblages at Amud cave in Israel, even though there seems to be no systematic exploitation of these raw materials (Ekshtain et al. 2017: 207). However, these occasional longer-distance movements fit within what we expect through *personal transport* (Kuhn 2012), that is, tools or raw materials that someone took with them, perhaps over a long period of time, and which ended up moving a longer distance from the source. The evidence for longer-distance movements outside of a group's typical range are consistent with what we might expect when external social connections were not common (Djindjian 2012). Such movements are not at all surprising, potentially occurring within mating networks and perhaps only as frequently, as we see in other social animals such as chimpanzees or bonobos. What we lack is any good evidence for *frequent* social interaction between groups.

There even seems to be marked constraints on significant movements across different home ranges in some regions. In the Middle Palaeolithic of the Levant, detailed studies of the transport of flint materials to the site of 'Ein Qashish suggest potential borders between groups where resources remain unexploited (Ekshtain et al. 2014; Ekshtain et al. 2017; Hovers 2018). This 'gap' in raw material procurement regions between what were probably neighbouring home ranges of different Neanderthal groups suggests that separate groups largely kept to the 'their side' of the border.

Genetic evidence adds to this picture of restricted intergroup movement. At El Sidrón, intergroup movements, such as they were, may have been constrained to a patrilocal pattern in which related males stayed in the group and females moved at maturity (Lalueza-Fox et al. 2011; Ríos et al. 2019). Other genetic evidence from the Altai Mountains in Siberia also supports the notion of females moving between groups whilst males stayed within their local group (Gibbons 2021). This would suggest that it was females who were creating patterns of long-distance transport, and maintaining cultural contacts. There is little to no archaeological evidence for sustained gatherings of communities any larger than local family or living groups (Spikins, Hitchens, and Needham 2017). Limited social connections are also associated with high levels of inbreeding. Half-sibling matings were common in the ancestry of the Altai individual (Prüfer et al. 2014), for example. Moreover, levels of developmental abnormalities, such as cleft palate at El Sidrón (Ríos et al. 2015), are higher than those typically seen in social primates (Trinkaus 2018), and may even have been a contributing factor to Neanderthal demise (Ríos et al. 2019).

A rather close-knit focus to Neanderthal social life may explain characteristics of their art. Neanderthals were clearly capable of symbolism, creating a range of symbolic material culture, from using decorative eagle features (Finlayson et al. 2012; Peresani et al. 2011) to cave art engravings (Rodríguez-Vidal et al. 2014). We see, as well, paintings and hand prints (Aubert, Brumm, and Huntley 2018; Hoffmann et al. 2018), incised and painted shells (Peresani et al. 2013) and even a facial representation (Marquet and Lorblanchet 2003), many of which clearly predate the arrival of moderns who cannot simply have been the inspiration for such creativity. Pigment use dates back to at least 200,000 years ago and is widespread, probably as a form of body decoration (Roebroeks et al. 2012), as do mortuary practices (Majkić et al. 2017; Pettitt 2011). However, Neanderthal art and symbolism is locally distinctive and there is not one but many varied forms of personal expression (see Figures 9.3 (Radovčić et al. 2015) and 9.4 (Rodríguez-Vidal et al. 2014)). In many cases, each example is entirely unique. It seems likely that the scale of Neanderthal social relationships had an impact on their style of cultural interactions, leading to a certain independence of local art styles rather than shared regional norms of expression.

Modern human communities replacing Neanderthals in Europe were similar to them in many ways, including finely tuned exploitation of their environments, care for the ill and injured, complex cultures and sophisticated technologies. However, their community connections were distinctly different in scale.

Modern human communities

We should be cautious of oversimplifying these different populations, particularly given variability in both Neanderthal and modern human occupation over vast realms of time and space. Nonetheless, it seems that the social lives of modern humans in Europe were distinctively different from those of Neanderthals in certain important characteristics.

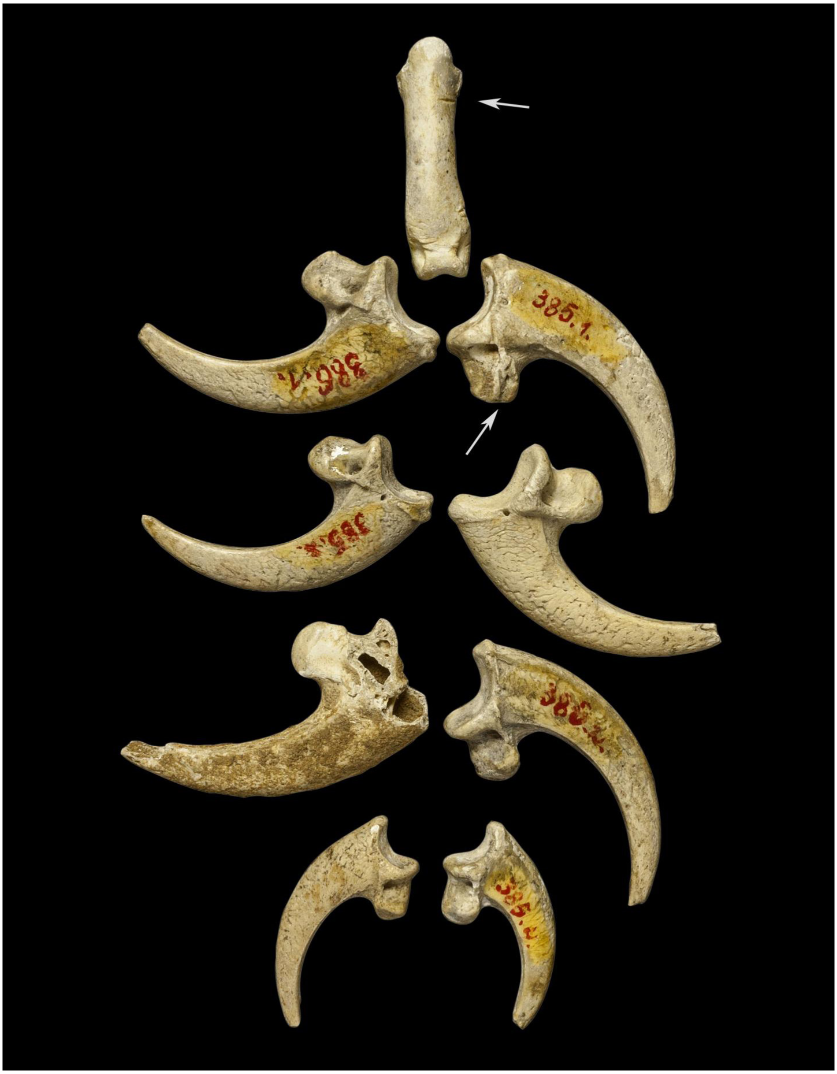

Figure 9.4: White-tailed eagle talons from the Krapina, dating to approximately 130,000 years ago. These talons are particularly significant as they seem to have been worn suspended as jewellery. Radovčić, Sršen, Radovčić, and Frayer. 2015. 'Evidence for Neandertal Jewelry: Modified White-Tailed Eagle Claws at Krapina.' PLoS ONE 10 (3): e0119802. DOI: https://dx.doi.org/10.1371/journal.pone.0119802. Luka Mjeda, Zagreb, CC BY 4.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Neandertal_Jewelry_(from_PLoS).jpg.

Figure 9.5: Neanderthal engraving in cross hatch shape found in Gorham's Cave, Gibraltar. AquilaGib (Stewart Finlayson, Gibraltar Museum), CC BY-SA 4.0, via Wikimedia Commons: https://commons.wikimedia.org/wiki/File:Neanderthal_Engraving_(Gorham%27s_Cave_Gibraltar).jpg.

From the first arrival of Upper Palaeolithic populations into and across Europe, their community relationships seem to be markedly different from those of the Neanderthals (see Table 9.1). They spread remarkably quickly into the region then occupied by Neanderthals around 40,000 years ago (Hoffecker 2009), soon reaching regions as far flung from their eastern entry through the Levant as southern Spain (Cortés-Sánchez et al. 2019) and Siberia (Douka et al. 2019). It is tempting to conclude that these populations were simply cleverer than previous ones, or more adaptable, but that many dispersals also failed, or were so risky as to be irrational rather than clever, argues that other distinctions were important. New motivations, and new types of social connection, are likely to have played an important role in motivations for this new level of mobility (see Spikins 2015).

The movements of raw materials and spread of art and personal ornamentation suggest that new large-scale alliances appeared quickly. From the very start of the occupation, identical Aurignacian beads were found over large regions and were transported across large distances along networks (Pettitt 2014; Vanhaeren and d'Errico 2006), for example. Marine shells commonly travelled over 200 kilometres, and some travelled over 1,000 kilometres. Unusual examples even include those that are made of human teeth, and are much worn, suggesting a close relationship with someone was being marked out and remembered (Spikins 2015a; White 2007). Large regions sharing similar styles of beads, and with transfers of beads across them, also suggest that people were re-enforcing a concept of 'us' that included whole communities (Vanhaeren and d'Errico 2006), much like those seen in hunter-gatherer ethnic communities today (Layton, O'Hara, and Bilsborough 2012). Indirect procurement, i.e. the deliberate travel over some distance typically outside of the home range in order to pick up raw materials for later use, or exchange of materials between groups, appears to have been common (Tomasso and Porraz 2016). Raw materials are typically brought from outside the area of a typical home range, with the transport of materials over 100 kilometres being common (Féblot-Augustins 2009). In some Gravettian sites, for example, more than 50% of the raw material comes from over 100 kilometres (Féblot-Augustins 2009). A drawing of a seal on a shale plaquette from the Late Magdalenian at Andernach-Martinsburg, found with marine shells and a whale bone fragment, over 1,000 kilometres from the coast, was probably made by an individual who had travelled that distance (Langley and Street 2013).

Genetic evidence also shows frequent movements and interaction between groups, beyond what would be purely functional (Fu et al. 2016). The genome sequences of Sunghir burials II, III and IV on the Russian Plain, dating to around 34,000 years ago, indicate extensive connections between groups and exogamous mating practices (Sikora et al. 2017).

There is even remarkable evidence from northern Spain for community aggregations. Collaborative hunting of mammoths at large mammoth megasites, such as Předmostí in the Czech Republic (with a minimum of 105 mammoths, dated to 26,000 years ago; Shipman 2015), is also likely to have needed collaborations between groups. Towards the end of the period at

Differences		
	European Neanderthals	**Upper Palaeolithic modern humans in Europe**
Population spread and migration	Archaeological evidence for slow spread of populations, typically in response to ecological changes and not crossing major ecological barriers (e.g. the Straits of Gibraltar) (Spikins 2015b)	Genetic and archaeological evidence for rapid population migration into new areas, and against ecological barriers (Cortés-Sánchez et al. 2019; Hoffecker 2009; Hublin 2015)
Mating networks	Genetic evidence for limited mating networks. Half-sibling matings common (Prüfer et al. 2014). High rates of inbreeding (Sánchez-Quinto and Lalueza-Fox 2015, Gibbons 2021), leading to high rates of developmental abnormalities (Trinkaus 2018), such as cleft palate at El Sidrón (Luis Ríos et al. 2015).	Mating networks large scale, and similar to modern hunter-gatherers (Fu et al. 2016; Pearce 2013)
Scale of movements within foraging areas	Raw material procurement: Raw materials typically transported within constrained territories (Djindjian 2012) (for example within the Vercors basin) (Fernandes, Raynal, and Moncel 2008; Pearce 2013) Isotope evidence: Short distances travelled over lifetime: example of Lakonis, Greece (Richards et al. 2008)	Raw material procurement: Apparently very large foraging areas (at least up to last glacial maximum; Djindjian 2012) and high mobility within these areas
Frequency of long-distance movements	Regionally longer-distance procurement rare, and in case of need (such as lithics imported into southern Italy) (Spinapolice 2012)	Regionally indirect procurement (to select optimal-quality flint) probably common (Tomasso and Porraz 2016)

Continued.

Continued.

Differences		
	European Neanderthals	**Upper Palaeolithic modern humans in Europe**
	Over large areas long-distance movements rare, and limited to certain contexts (e.g. the East European Plain) (Féblot-Augustins 1993; Féblot-Augustins 1999; Féblot-Augustins 2009)	Over large areas long-distance movements are common (Féblot-Augustins 1993; Féblot-Augustins 1999; Féblot-Augustins 2009). Whilst these may be a result of transfers of materials and finished products, there is also evidence of movement of individuals (Langley and Street 2013)
Use of art objects within social networks	Symbolism of many different forms, including cave art, but remains local	Material and finished personal ornaments in the early Upper Palaeolithic transported over long distances (marine shells or mammoth ivory typically travel over 200 kilometres, sometimes over 1000 kilometres)
Cultural resilience (maintenance of local cultural styles)		Highly conservative art styles over large regions

Table 9.2: Archaeological and related evidence for similarities and differences between Neanderthal and modern human large-scale social interactions.

the Magdalenian site of Altamira in northern Spain, many design elements were represented on engraved and decorated bone and antler artefacts that were not found together in surrounding sites (Conkey et al. 1980). Conkey concluded that this was an aggregation site, to which many surrounding groups, each with their separate distinctive design styles, had travelled (Conkey et al. 1980). With no particular reason for any concentration of resources at this site, this aggregation seems to have been fulfilling a social need, rather than an immediately practical one.

These social alliances seem to have played a key role in survival at times of resource shortfall, much as they do in modern hunting and gathering contexts (Whallon 2006).

There are certainly important survival advantages to regional connection and collaboration. Intergroup collaboration can make exploiting certain resources possible. Certain ethnographically and archaeologically documented populations join together to hunt particularly large or concentrated resources that might otherwise have been risky or impossible to hunt alone. The collaborative hunting of whales is a well-known case, as such hunting is difficult, if not impossible, without large numbers of people working together (Reeves and Smith 2006). Groups of Inuit coming together for collaborative whaling activities have been recorded from the late 18th century (see Figure 9.5). Hunting of bowhead whales has even been shown to be a major factor in the significant population expansion of Thule culture around ad 1000 (Wenzel 2009). Collaborative whale hunting is also known ethnographically elsewhere. Collaborative sperm whale hunters in Indonesia bring home more resources through their collaboration than they could through more individual fishing (Alvard and Nolin 2002), for example.

On the level of individuals, the most famous example of the survival significance of distant friendships is that of the Ju/'hoansi xaro network. The xaro is a network of gift-giving, visits and mutual friendships that buffers human communities from the effects of shortfalls and famines. Members of Ju/'-hoansi bands each forge alliances with non-kin or distantly related kin in other bands, giving them carefully made gifts and visiting them. It is these allies whom they turn to in times of local crisis (Wiessner 2002a; Wiessner 2002b). When food shortages following high winds destroyed much of the mongongo nuts in /Xai/xai province, for example, half of the population moved in with distant exchange partners, and would not have survived if this social support was not possible (Wiessner 2002a). These external allies can sometimes make a difference to survival, with such alliances even a matter of life and death.

Connected regional communities also favour survival in other ways. The best-studied effect of the emergence of social networks has been in allowing the spread of new ideas and innovations (Apicella et al. 2012; Fogarty 2018). Although they might live in small social groups, any individual in a similar hunting and gathering context is likely to interact with over a thousand other people over the course of their lifetime. Hill notes, for example, that, amongst the Hadza and the Aché, men are likely to have learnt how to produce tools from over 300 other individuals (Hill et al. 2014). An awareness of what is happening elsewhere, and an ability to pick up new ideas, can be important in allowing populations to adapt quickly to environmental changes (Derex, Perreault, and Boyd 2018; Foley and Gamble 2009; Muthukrishna and Henrich 2016). Connections thus foster rapid adaptability.

It would be easy to frame the contrast in communities as one between simple and complex, or even primitive and advanced, particularly since we associate the extensive social networks of the Upper Palaeolithic with the survival advantages of providing a social buffer for resource shortfalls. However, a closer consideration shows that, by focusing on the role of emotional dispositions in social tolerance, we reveal that *equal but different* may be a better way to understand such contrasts.

The structure of social networks and contrasting emotional dispositions in social tolerance

From our privileged position as the apparent survivors, it is easy to see networks of allies across connected Upper Palaeolithic communities as a sign of superiority. These populations appear socially and cognitively more complex, and better able to negotiate collaborations than Neanderthals. However, a focus on the economics of resilience to resource shortfalls may be hindering our understanding that the underlying mechanisms allowing their creation are not calculated or cognitive but emotional. Moreover, those capacities that allow the creation and maintenance of large-scale connections also carry costs. Considering the emotional basis underlying community connections in Neanderthals and modern humans allows a reframing away from inferior or superior.

The creation and maintenance of the regional communities and social networks seen in modern humans depend on a high level of social tolerance, on a strong drive to connect and, above all, on an individual emotional vulnerability that is both a strength and a weakness of these interconnected communities.

When we look in more depth at what drives regional collaborations in modern hunter-gatherers, we reveal the significance of emotional connections, rather than logical or calculated arrangements. Mutual generosity and trust, rather than calculated collaboration, is the basis for the collaborations to exploit resources. The coastal-living Yamana of Tierra del Fuego developed mutually generous alliances in order to exploit periodically beached whales, for example, which were a cause for many celebrations and shared rituals, such as the chiexaus and kina initiations (Chapman 1997; McEwan, Borrero, and Prieto 2014). Smoke signals were sent to invite as many other groups as possible to join in the feast, with this mutual give and take maintained by trust that this goodwill would be returned in the future (Gusinde 1986; Santos et al. 2015).

Where individual networks of friendships with distant allies are concerned, similar emotional motivations based on social tolerance, mutual generosity and trust are also key. The xaro has been seen in terms of networks of obligations, almost like a contract, but this would be a misunderstanding of the emotions underlying such networks. It is clear that people look forward to seeing xaro partners, and find preparing gifts a pleasure rather than a chore (Wiessner 2002a). Xaro partners 'hold each other in their hearts' (Wiessner 2002a: 27). Moreover, evening talk around campfires is not just about those people present at the time but also involves stories told about ties to distant people and remembered gatherings in the past (Wiessner 2014).

The value of connected communities lies not just in knowing a lot of people, as we might consider a social network today, but in caring about distant friends who also care about you. Migliano et al. demonstrated, for example, that networks amongst the Agta and Bayaka are made up of close relationships maintained over lifetimes with a few individuals (Migliano et al. 2016). In viewing networks of social alliances as economic systems, we can easily lose sight of the social and emotional capacities and motivations which they depend on. Yet it is clear that neither systems of obligation, nor simple agreements, work to ensure support in times of need. Relationships based on 'needs-based transfers' (responding to the vulnerability of those in need), rather than on systems of obligations, are those that ensure survival (Campenni, Cronk, and Aktipis 2017; Cronk et al. 2017; Smith et al. 2019). Strong emotional drives to make close friends outside our kin are motivators of human behaviour that provide mutual support everywhere (Cronk et al. 2017).

Networks of trusting relationships and close friendships are built on both a high level of social tolerance towards strangers, and also on certain social needs and emotional vulnerabilities to loneliness or lack of belonging. This individual vulnerability is also important to how social alliance networks are maintained as, without a strong emotional need to sustain and extend networks of social support to avoid a sense of isolation or loneliness, connections would fall out of use. Even when food supplies and the emergence of a cash economy made the Ju/'hoansi xaro network unnecessary, networks of social ties with distant friends were still kept up, even though fewer partners are typically involved (an average of seven rather than 15). These distant allies were socially and emotionally necessary, even if they did not perform a practical economic function (McCall 2000; Wiessner 2002a). Maintaining such relationships involves effort. The Jo-huansi spent about a third of the year visiting close friends in distant camps, and about 75 to 80 days making gifts to give them (Wiessner 2002a).

Opportunities to gather together are also important. A universal feature of modern hunter-gatherers, in all different environments, is that small living groups or bands will periodically join together as larger communities, or aggregations (Conkey et al. 1980; Kelly 2013). These gatherings are important in ensuring the sustainability of mating networks. However, they also fulfil a need to reconnect with old friends and develop new emotional connections, as well as for people to feel part of a larger community. Periodic gatherings seem to be as much about a human emotional need for meaningful social connection as they are a functional necessity. The times and places of aggregations usually coincide with a seasonal concentration of resources, but also provide an opportunity for important rituals to take place. Even where resources are more predictable and the risk of shortfalls less acute, alliances are still maintained.

Gatherings in modern ethnographically documented hunter-gatherers occurred even in the most difficult of conditions and despite notable costs. Gathering together is something people need to do. Even in the extraordinarily harsh conditions of the Western desert of Australia, in which population densities were as low as one person per 300km^2, the Martu still put considerable effort into coming together at aggregations, for example. In this highly arid region, it was typical to travel over 200 kilometres at least once a year to attend social gatherings (McDonald and Veth 2012). A 'tjabal' (the multitude) took place once or twice a year, particularly in winter, when seeds were abundant, and around reliable water sources in summer, for example (McDonald and Veth 2012). These social gatherings did not have a direct practical function but were nonetheless seen as vital. They were the focus for rituals, exchanges of goods and marriage arrangements, and general socialising that continued as long as resources and water allowed (typically a few weeks to a couple of months; McDonald and Veth 2012: 93). Moreover, these gatherings were also about extending friendships rather than reinforcing existing communities. There were no clear limits to the community who were allowed to attend and the attendance at aggregations amongst the Martu was flexible, sometimes including different dialect units and never the same set of individuals as previously. Hunter-gatherers commonly adapt their mobility patterns to maintain contact, even where this is costly (Grove 2018).

Oral histories within modern ethnographically documented groups confirm that it is emotional needs that underlie social connections. Gatherings and shared ceremonies are essential to maintaining emotional resilience and wellbeing. Coming together as a group and meeting distant friends provided a marked buffer to depression, anxiety and suicide (Danto and Walsh 2017).

Informants amongst the Cree commented:

> 'It was always through ceremonies and people talking to each other – Everybody would migrate as a whole, come from different places to get that and go back. You see … that was our form of communication and life. And we used ceremonies to do that.' 'It's not just something to talk about. It's a way of life, you know…' 'those are the things that made our people strong: ceremonies'. (Danto and Walsh 2017: 723)

Collaborative social networks can only be maintained through strong emotional desires to maintain friendships, and by extending genuine emotional motivations to help others' wellbeing well beyond kin and co-residents (Cronk et al. 2017; Fowler and Christakis 2010). Being socially astute or clever is not enough. Far from being a product of calculated strategy or cognitive complexity, connected social networks depend on emotional motivations. They depend on strong emotional needs and motivations to seek out friendships and to avoid loneliness or lack of belonging. Only these strong emotional motivations maintain networks of friendships in times of plenty, so that they also exist at times of need.

We have always assumed that large-scale regional connections in Upper Palaeolithic communities were brought about through new superior social capacities, and that 'we' modern humans are simply cleverer and more social than our predecessors. However, it is much more likely that new sensitivities, emotional vulnerabilities and new elevated needs for widespread emotional connections lay at the root of these new connected societies. Rather than a change in cognition, it is far more probable that a change in emotional dispositions towards an external focused tolerance, bringing with it individual emotional vulnerability, needs for connection and belonging, and tendencies to loneliness, explains the creation of Upper Palaeolithic social networks.

Rather than a concept of 'better' and more social Upper Palaeolithic communities, we might perhaps see the differences in behaviours observed in the archaeological record in a new light, reflecting the advantages and disadvantages of alternative evolutionary trajectories in the focus of emotional connections. As we have seen in Chapter 8, a more outward or inward emotional focus is suited to different contexts. Despite the lack of resilience at community level, there will have been benefits to the close-knit and inward-focused emotional connections of Neanderthals. An internal or close-knit emotional focus, and with this greater levels of internal social cohesion, can foster greater levels of give and take within the living group. Close-knit Neanderthal groups would have benefited from widespread care, willingness to take risks on behalf of the group, and individual emotional resilience (discussed in Chapter 2).

There are other practical advantages to close kit emotional dispositions. Limiting social mobility between groups can also reduce the energetic costs of such travel, which, as we have seen, can be extensive to maintain functioning friendships. For Neanderthals, the travel cost of maintaining social networks are likely to have been even greater than those of modern humans. Their robust body, for example, may have added at least 10% to the energetic costs of travel, even before we take into account low population densities, making distances between living groups much greater (Churchill 2014). Moreover, there is no need to manage challenging relationships outside of a largely kin-based social group. As we have seen in Chapters 4 and 5, avoidance of other groups can be an effective social strategy for avoiding aggressive encounters. The more pronounced brow ridge of the archaic population would have restricted subtle muscle movements around the eyes, limiting the movements that may have been important to how modern humans created affiliative gestures of recognition and sympathy, fostering trust (Godinho, Spikins, and O'Higgins 2018). Furthermore, individual emotional resilience, rather than emotional vulnerability to lack of social contact or to loneliness, fosters survival in conditions in which social support is lacking. Neanderthals may have benefited from being more emotionally resilient and from not needing to create costly compensatory attachments to animals or even things (Chapters 6 and 7) at times of social stress. Overall, their ecological situation and particular biology seem likely to have discouraged intercommunity tolerance in Neanderthals, whilst, in contrast, particular ecological conditions in regions of Africa may have particularly encouraged intercommunity tolerance amongst early modern humans (Spikins et al. 2021). The price of maintaining social connections, both in practical terms of the costs of travel and in emotional terms of the individual costs of emotional vulnerabilities to loneliness or lack of belonging, may not have been worth paying for Neanderthals. Rather than a social or cognitive inferiority, a close-knit focus and individual emotional resilience simply seems to have made more sense in the context in which Neanderthals survived.

Of course, we should always be cautious when we discuss differences between populations. Our human biology, whether Neanderthal or modern human, is only one of many influences on how we behave (discussed in Chapters 1, 4 and 5). Culture, upbringing and individual choice play a key role in who we are, and differences identified at a group level do not imply that any individual must be different on those terms. It is also easy to make simple assumptions about what differences in emotional disposition, identified from genetics and anatomy, mean. As we have seen in Chapter 8, we might imagine that wolves, with elevated androgen levels compared to 'tame' dogs, would suffer from higher levels of aggression and violence. The converse is true, with free-ranging dogs being more at risk from lethal attacks within their own less socially cohesive group than close-knit wolf packs. In the even more complex situation of human societies, as we have seen in Chapter 4, testosterone is more associated with competition to fit into social norms of respect than aggression *per se*. Thus, whilst genetics and anatomy, including not only cranial anatomy but also 2D:4D digit ratios (see Chapter 4 and Chapter 8), suggest that Neanderthals also had higher androgen levels than modern humans, this does not imply higher levels of violence. In fact, we only see clear evidence of intergroup conflict in modern humans rather than Neanderthals. Whilst external social tolerance may lead to generous collaboration between groups, greater levels of engagement between groups also carry risks of an escalation of conflict. Emotional dispositions have to be understood in context.

Reframing Neanderthals as emotionally *close-knit* and modern humans as emotionally *approachable*

Differing emotional dispositions explain contrasts in the structure of communities

The archaeological evidence discussed here, alongside the ecological, genetic and anatomical evidence discussed in Chapters 4, 5 and 8, suggests that a key distinction affecting differences in Neanderthal and modern human behaviour may be their differing emotional dispositions, and differing social tolerance. These differing dispositions are best seen as *different ways of being social*. Rather than seeing Neanderthals as cognitively inferior, or socially less complex, or resorting to shoehorning them into being *the same*, these seem to be societies that were more inward-collaborative and potentially individually independent, or *close-knit*. In contrast, the modern human pathway is one of being outward-focused and socially sensitive in emotional relationships, or being *approachable*. Each evolutionary pathway has both advantages and disadvantages in different contexts (Figure 9.6).

As we have seen in Part 2, archaeological evidence suggests a pattern in which modern humans became more socially sensitive and emotionally vulnerable, expressed in both material culture and relationships with animals. Neanderthals may have progressed some way along this path already, given their reduced brow ridge in contrast to early *Homo heidelbergensis*. However, in comparison to modern humans, Neanderthals seem to have a

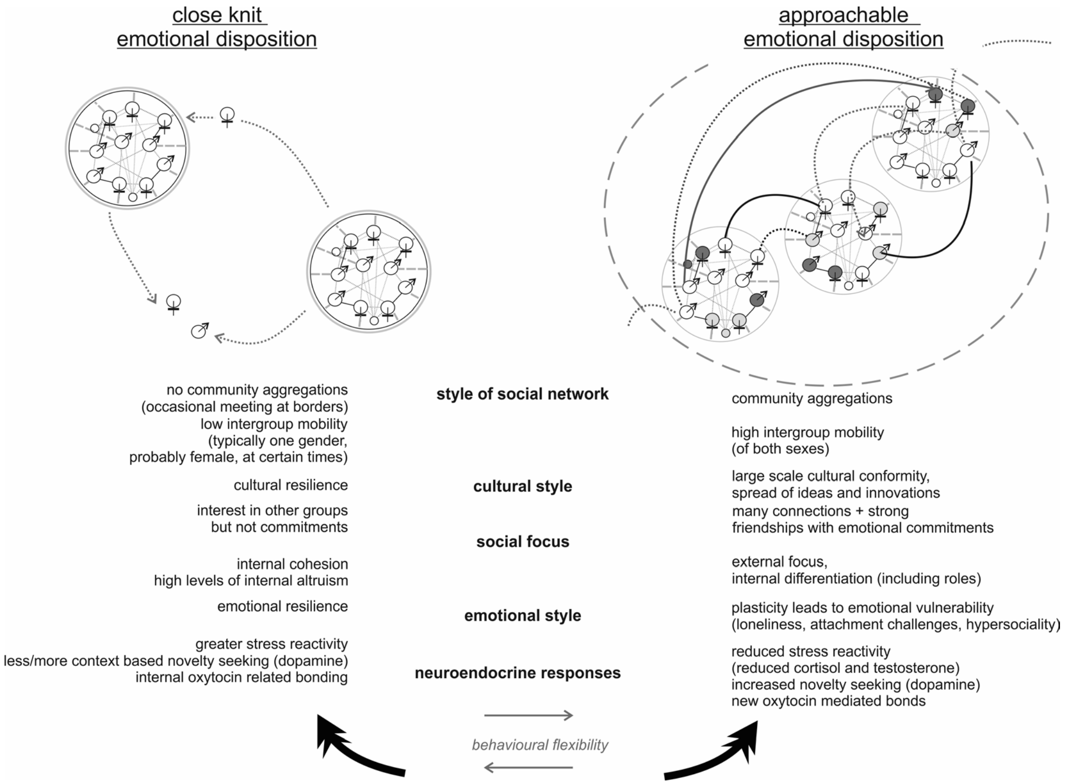

Figure 9.6: Simplified figure to illustrate contrasts between the close-knit emotional dispositions hypothesised to be characteristic of Neanderthals (left) and, in contrast, the approachable dispositions hypothesised to be characteristic of modern humans in Europe (right). The different line patterns between schematic living groups in the latter (right) denote different types and strengths of social connection (e.g. strong bonds with mutual generosity, casual friendships, family or ritual ties etc). The dashed outer circle (right) denotes a loosely defined regional community. Penny Spikins, CC BY-NC 4.0.

tendency to form close-knit groups, leading them to be highly internally collaborative yet more suspicious of unfamiliar individuals. As a result, we see differences in the relative constraints or openness of large-scale social interactions between the different species. Subtle but important differences in emotional dispositions would make the cultural character of Neanderthal communities distinctive from that of Upper Palaeolithic communities, without any implications for intelligence or social understanding.

Considering changes in emotional dispositions and the focus of emotional connections may better explain many of the differences previously attributed to intelligence, capacities for language or symbolism, or other ways in which modern populations have been seen as *more complex*.

Differing emotional dispositions explain previously enigmatic elements of the archaeological record

Understanding Neanderthal behaviour as reflecting a different, less externally socially tolerant but more internally socially collaborative pathway of human variation gives us a different perspective. This *different pathway* in which Neanderthals are *differently social* explains many characteristics which have been interpreted in terms of Neanderthals being on a lower rung of some cognitive ladder or less socially complex than the modern humans who replaced them.

Subtle changes in emotional dispositions, driven by changes in the pathways driving novelty and reward-seeking (through hormones such as dopamine), stress reactivity (cortisol), competitiveness (testosterone) and the nature of social bonds (oxytocin, vasopressin and beta endorphins), seen in genetic evidence (discussed in Chapter 8) and in line with Neanderthals being more internally cohesive, would have had subtle but important effects.

A reduced drive to seek out novelty, compared to that which is typical of modern humans (discussed in Chapter 6), explains the rather constrained nature of Neanderthal patterns of mobility. Unlike modern humans, it seems that Neanderthals may have felt no particular attraction to the novelty of strangers and, as a result, their external social relationships seem to have been oriented around the minimum practical needs. Interactions with neighbouring groups need not have been aggressive, and sometimes resources and materials travelled across the areas occupied by different living groups, particularly when such resources were important to survival. However, there may have seemed no particular pleasure in seeking out new friends. An elevated stress reactivity of internally cohesive Neanderthals, in comparison to the reduced stress reactivity of approachable modern humans (discussed in Chapters 4 and 5), is also likely to have made the experience of large groups, particularly of unfamiliar individuals, particularly stressful. This was a close-knit social life, without any big parties.

It is not surprising that Neanderthal art seems unimpressive in comparison to that of the Upper Palaeolithic when taken in the context of their inward-focusing sociality. Neanderthal art is far from elaborate or time-consuming, mostly requiring only a few minutes of attention. This contrasts markedly with displays of technological skills in Upper Palaeolithic contexts, not only in carefully produced artworks but even in flint tools such as elaborately made Solutrean foliate points (Sinclair 2015). This is, however, only what we expect within inward-focusing social contexts. There is, simply, little need to impress anyone. Whilst modern humans moved within vast networks where they needed to develop a social identity and reputation across large areas, Neanderthals would already be well known within their local group, without the need for any ostentatious display or for subtle eye movements to express affiliation to strangers (Godinho, Spikins, and O'Higgins 2018). Added to which, differences in dopamine production between archaic and modern humans may have made 'art' in aesthetics, depiction or music far less enticing to the average Neanderthal brain than it is to the modern human (see Chapter 4 and 5). Nature itself may have been enough of an aesthetic delight for Neanderthals, without needing to go to extreme lengths to produce something artificially beautiful. Furthermore, a relative lack of personal ornaments or cherished possessions also reflects this intimate focus on social life. Without loved ones ever being far away, there would be no need to rely on alternative sources of security. This greater inward focus makes sense of why Neanderthal children and adults show a relative lack of *personal* symbolic objects compared to those of the Upper Palaeolithic. As discussed in Chapter 6, whatever their meaning, such objects are likely to also have been part of compensatory attachments for modern humans, filling in when caring relationships come under threat. Whatever the ecological hardships, growing up as a Neanderthal child in a small inward-focused group will have encouraged emotional security. Neanderthals may have experimented out of curiosity, but most probably did not need 'art' in any of its forms.

The nature of social interactions in Neanderthals will also have affected how innovations may have begun or been adopted (Hovers and Belfer-Cohen 2006). Interactions with new ideas will have been much less frequent, constraining their spread. Certainly, at particular times, some individuals, particularly adolescents and young adults, must have been lured by novelty and sought out new connections in other groups. Nonetheless, distant travel by entire groups across the homelands of other groups may have been rare. Moreover, evidence suggests that even mating networks were constrained. Those individuals who move between groups may have been predominantly female, and external matings constrained by lack of connections (Luis Ríos et al. 2015). By implication, it would have been women who played a particularly significant role in Neanderthal social connections, not only in the maintenance of mating networks but in the spread of ideas and cultural connections across large areas of landscape. This is in no way surprising, as it is female primates who pass on mechanisms of producing and using tools. Chimpanzees largely depend on their mothers to learn how to make and use termite fishing sticks, for example. There is no reason to assume that males were any less competent than females in tool technology, simply that in a patrilocal context they are likely to have played a less significant role in the spread of shared knowledge and styles. Mobility constrained by gender, the comparative rarity of intergroup movements and a lack of regular aggregations will all have affected the potential for ideas and ways of doing things to spread.

In being more robust, and so having a greater energetic footprint per individual, Neanderthals already suffered from a relative demographic restriction to the size of their living groups and to their capacities to reproduce compared to modern humans in a similar ecological context. Fewer Neanderthals could survive on the same resources as modern humans, and it took more energetic costs for each child raised to adulthood. An additional, indirect effect may come from changes towards increasing tameness or friendliness on reproduction. An extended period of fertility is one of the notable side effects of increasing friendliness or tameness in other domesticated animals, including in the silver fox study (see Chapters 4 and 5). Genetic evidence suggests that the generational interval reduced in modern humans after 40,000 years ago (e.g. from around 30 to around 25 years between generations) (Macià et al. 2021). Whilst Neanderthals may have been able to give more care to each child, this increased child security would have come at a demographic cost. Modern human populations were able to bounce back more quickly after population declines (as shown from analysis of radiocarbon dated sites following Heinrich events; Bradtmöller et al. 2012).

The comparative failure of early modern human incursions into Europe can also be explained by their emotional dependence on social networks. Small groups of humans, unusually dependent on regional interactions not only for ecological resilience but also as part of their emotional support network, would be disadvantaged in comparison to inward-focused and independent Neanderthal populations. Whilst significant communities of modern humans, after 40,000 years ago, may have been more successful than Neanderthals at times of shortfalls, early incursions of modern populations into Europe or the Near East would in any case be at a competitive disadvantage if isolated.

Whilst the demise of Neanderthals is perhaps most likely to relate to either chance or subtle differences in biology, the possibility also exists that one influencing factor in Neanderthal demise was not that they were *vulnerable* but rather that, at least individually and emotionally, they *were not vulnerable enough*. Without emotionally needing to form social networks, or seek support in compensatory attachments, they will have had no need to go to great costs to maintain social contacts at a distance and, in lacking large social networks, may have been far more prone to resource shortfalls. That our relative survival may have come about through emotional vulnerability is a very different type of human evolutionary narrative.

Conclusions

The very presence of Neanderthals challenges us. We know that they were different from ourselves anatomically, with their increased robusticity, longer, lower crania and prominent brow ridges. Moreover, they were different physiologically and in their brain structures, even if these differences can be subtle and evident only at a population level. Furthermore, as argued here, they seem to have been emotionally different in terms of their levels of internal or external social tolerance, their social sensitivity and their emotional vulnerability. Such differences are hardly surprising since the line that led to Neanderthals diverged from that leading to our own species perhaps as far back as half a million years ago, albeit with some intermixing. It has been all too easy to fit this difference within a narrative in which 'we' modern humans boast superior intellect and social abilities.

Rather than seeing modern humans as socially or cognitively superior to our close Neanderthal cousins, it seems more appropriate to appreciate that there are different ways of being social. Different evolutionary pathways between *close-knit* and *approachable* emotional dispositions explains the distinctions we observe in the archaeological record of Neanderthal and modern human behaviours in Europe. Whilst the former dispositions led to strong internal bonds and high levels of individual emotional resilience, the latter led to the formation of large social networks, resilient to resource shortfalls but at the expense of individual emotional vulnerability and sensitivities to loneliness or a lack of belonging. Neanderthals were no less human and, like our own species, needed close emotional connections to survive and thrive. However, the focus of these connections seems to have differed.

If Neanderthals represent a humanity without our social loneliness, lack of belonging, or sensitivity to what others think, and with the unquestioning support and loyalty of a small social group, it is not surprising that we see interbreeding between these two lineages. Rather than a sign of Neanderthals being *the same* as modern humans, it might rather be a sign of *what was attractive about the differences*.

Key points

- Archaeological evidence for differences in mobility patterns and community interactions, alongside other lines of evidence (discussed in Chapter 8), suggest that Neanderthals and modern human communities show contrasting inward and outward social focus in their community relationships, described here as *internally cohesive* and *approachable* emotional dispositions.

- Contrasting behaviours may not indicate any inferiority or superiority but, rather, differing ways of being social.

- Differing emotional dispositions may also explain previously enigmatic aspects of the archaeological record, such as the characteristics of Neanderthal art.

- We are naturally tempted to impose concepts of progression when we consider our human evolutionary past. Accepting differences as neither better nor worse may be important in moving past these narratives.

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Conclusions

What have we learnt?

The origins of our uniquely human emotional connection are rarely central to any discussion, as we have seen in the Introduction. This is, perhaps, at least in part, because our human emotions are all too often seen as a weakness, particularly as they may prompt us to behave in ways that may seem against our rational self-interest. Certainly, our emotional connections to others can make us vulnerable in certain ways. Compassion may prompt us to expend precious effort helping others, our need for belonging makes us vulnerable to loneliness, and our emotional sensitivities make us prone to suffer in many different ways. However, rather than being weaknesses, we have seen that it is in these vulnerabilities that an unrecognised shared human strength lies. Only if we feel moved by others' pain or plight will we be motivated to respond to our vulnerable young or care for adults needing our help. Only if we feel moved by strangers, and care about their wellbeing, will we be motivated to extend our world to form communities, and to connect in new ways to animals and things around us. Only if we are sensitive to the animals, as well as the people around us, will we be able to make new emotional connections. Without our uniquely human emotional connections we would not have thrived as a species.

We have seen, throughout our discussions, that our human ancestors were more emotionally sensitive than our current interpretations of human origins allow for. Today, we know that we care deeply about the wellbeing

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of people close to us. As we have seen in Chapters 1 and 2 of Part 1, this remarkable depth of human motivation to help others comes from a very distant past, set within pressures to become more collaborative early on in our evolutionary history. We are also acutely aware of how others feel and think about us. As we have seen in Chapter 3 of Part 1, this sensitivity comes from the significance of relationships based on trust and the increasingly significant importance of our social moral reputation in others' eyes. We are also, above all, profoundly emotionally vulnerable. Not only are we vulnerable to emotional disorders, as we typically conceive of them, but, more than this, as we have seen in Part 2, we are sensitive to the damaging effects of loneliness and isolation. We only thrive in contexts of genuine care and connection, and seek out new forms of emotional connection whenever and wherever these may be lacking. As we have seen in Part 3, our peculiarly acute emotional sensitivities were in no way predestined but rather one option of many, a road that we might easily not have taken.

The significance of emotional vulnerabilities and sensitivities to the strength of our human connections is, in many ways, not a popular narrative. It would be far more comforting to see ourselves as individually resilient. However, the converse is perhaps a more realistic view. Our sensitivities and emotional vulnerabilities are not simply key to who we are as humans but are also a defining feature of our evolutionary success.

Through the chapters of this volume, we have also seen that changes in emotional capacities, rather than primarily intelligence or brain size, were far more significant to our evolutionary story than has been recognised, and were likely to have been a driving factor in two major transitions in human evolution.

Changes in emotional relationships within groups, rather than in rational thinking abilities, are, here, seen as key to the emergence of the genus *Homo*. This key transition occurred after 2 million years ago and involved movement into a new ecological niche dependent on collaborative hunting and collaborative infant care, as well as on care for illness and injury. Increasing brain size in this period is here argued to be an adaptation to the complexities of new relationships based on trust and emotional responses to vulnerability within a context of small and highly collaborative social groups, rather than some predetermined element of our hominin past. Furthermore, the driving factors behind key transformations are changes in emotional connections, allowing new commitments to both individuals and to whole groups. Moreover, this key transition is related to changes in emotional tendencies and capacities that brought early humans closer to highly collaborative social mammals, rather than elevating them above nature.

When it comes to the more recent transition around the emergence, and subsequent expansion, of our own species in Africa, after 300,000 years ago, it is once again changes in emotional capacities, rather than hard elements of cognition, that play the most significant role. New levels of intergroup tolerance make new types of connections between different groups possible, buffering local shortfalls in resources and providing a mechanism for the spread of innovations. Reduced stress reactions and heightened social sensitivity open up a window for new externally focused relationships whilst also bringing new vulnerabilities to loneliness or a lack of belonging. As in the earlier transition occurring after 2 million years ago, rather than being extraordinary, these changes in emotional dispositions are also seen in other highly social species.

Here, we argue that these two transitions were situated within changes in ecology, and responses common to other species, rather than some human exceptionalism. Adaptations in emotional disposition towards a broader response to vulnerability and emotional investments in the whole social group are argued to play a key role in changes in social relationships that occur in the emergence of genus *Homo*, much like similar adaptations in social carnivores. In turn, changes towards more externally tolerant emotional dispositions are key to the emergence of our own species, much like transformations seen in species that become more tame. Of course, complex technology, language and culture must have played a role in these transitions. Nonetheless, without the transformation in social relationships brought about through changes in emotional dispositions none of these developments would have been possible.

What makes this interpretation different?

This is not an interpretation that necessarily fits neatly within accepted narratives of human origins.

Firstly, this is no neat progression towards some pinnacle of adaptation. Changes occurred in a series of stops and starts. Some elements of what we recognise as our most human emotions appeared early in the evolutionary record: our response to vulnerabilities in those we love; our willingness to take risks on behalf of others; our sensitivity to the wellbeing and development of infants. Others occurred much later, and we argue here that what we recognise as our human capacities to extend care and altruism towards strangers, to develop caring connections across distant relationships, emerged much later and more recently.

Secondly, the past is here seen as a series of branches and connections rather than steps along a ladder. Whilst members of the genus *Homo* travelled their own emotionally collaborative branch, other hominins, such as the paranthropines, equally viable for over a million years, were less interdependent, and were less dependent on hunted or scavenged meat. Likewise, in their different ecological conditions in Eurasia, other archaic humans such as Neanderthals were under less selective pressure to focus outwards emotionally and, in turn, were perhaps even more committed to caring within their close-knit groups. By implication, our evolutionary past may have been different under different ecological situations. We might, for all we know, in a different evolutionary past have become less dependent on others around us for a sense of belonging or emotional support than we are today, be less interested in what lies outside our own small social group, or be different in all kinds of ways.

Thirdly, in this evolutionary history, changes in emotional capacities brought us *closer to*, rather than *further away from*, other animals. Changes, firstly, in our response to vulnerability and, secondly, in our friendliness toward strangers, are key to what makes us human. However, they do not make us further away from other animals or nature in general. Rather, these are shifts in focus, and ones that in many ways bring us closer to other animals.

Perhaps most significantly, an emphasis on our emotional minds as central to our evolutionary history is relatively new. No one would argue that language, technical intelligence or our highly complex culture are not significant in our evolutionary history, nor that they are not key elements that mark us as different from other animals. Yet these capacities have been given priority in our evolutionary story for far too long. Our emotional minds, and the role they play in our human connections, may be more important *to the better part of our natures* and, as such, deserve greater attention in our evolutionary story.

Some of this may feel challenging.

The emphasis we see here on the biological basis for emotional motivations and their influence on behaviour may feel uncomfortable, particularly amongst those who might argue that emotions are a product of culture and not biology. Here, again, no one would deny that conscious choice or accepted cultural norms play an important role in how we behave, or that rationality is key to how we think, or that emotions are affected deeply by individual and social circumstance. Our physiology, emotional capacities, thoughts and cultures interact with each other in complex ways. Emphasising the influence of the biological basis of our minds on who we are is not to see this as a predetermined genetic blueprint but to recognise that rational thought is grounded in physical experiences and incorporates feeling, and that the biological basis of our emotions play a role in who we are as humans.

The concept of distinct, and emotionally different, hominid branches as largely equal options, surviving or declining often through the vagaries of chance, can also feel disconcerting. Whilst we used to view Neanderthals as inferior, and now feel more uncomfortable in doing so, it has instead become fashionable to see them as so similar to ourselves as to be effectively the same. Responding to the challenge of difference by denying it is, however, too easy. The difference we outline here between Neanderthals and modern humans, related to emotional capacities and tendencies, may not be related to intelligence or culture. However, to consider this difference as about equally weighted options, much like those we see between relatives in canids or non-human primates may, nonetheless, create tension. Yet, the existence of different evolutionary branches and different possibilities for humans in the past seems important. It adds even greater weight to the argument that we need to be better at understanding not just how other *species* can be equal but different, rather than simply the same as ourselves, but how this holds true for other *people* around us as well.

A more nuanced appreciation of diversity is also key to the portrayal here of autism, and other elements of cognitive difference, not as disorders as much as adaptations to new collaborative moralities in which different individuals fulfil different roles. An autistic mind is different, but not better or worse, than a neurotypical one and this itself can be a challenging narrative, particularly where many see autistic individuals as less social, rather than differently social. The principle of *different but equal* can be difficult to accept where narratives of superiority often feel more comfortable.

When we are used to narratives of human origins that stress our superiority, it can be hard to view our emotional connections to each other as, in some ways, similar to those of animals that we share our lives with as inferiors, such as dogs. Yet it might be important to acknowledge that the same pressures towards interdependence in social carnivores that led to their close emotional bonds, willingness to defend each other, share risks in finding resources and share resources themselves, and care for vulnerable infants and adults, also played an important role in our evolutionary past. Equally, our profound sensitivities to each other's feelings, our need for affection and belonging, were also a response to similar pressures felt during domestication to forge close emotional bonds through vulnerability.

Whether we have succeeded in genuinely moving away from traditional ideas of human origins as about a progression towards some superior being, of course, remains to be seen. However, there can scarcely be a more important moment to reflect on our origins and what they mean for today.

Focusing on the significance of emotions, and with them on emotional vulnerabilities, allows us to question many developments typically portrayed as key human achievements. A reappraisal of the appearance of art, aggregations and the domestication of wolves situates humans in these processes as both remarkable and, at the same time, emotionally vulnerable and deeply influenced by biology. These reappraisals can be uncomfortable. The rise of elaborate art and personal ornamentation in Ice Age Europe is here interpreted, at least in part, as emerging through new emotional insecurities, a concept that may not mesh well with ideas of art as a symbol of elevated cognition and aesthetics. The rise of large-scale social networks associated with the emergence of our own species is not here seen as evidence of a new social ability but rather new needs for connection and belonging arising from new emotional vulnerabilities. This may be a difficult message, given how much more pleasing it feels to be seen as a species with unique and elevated levels of social intelligence rather than one uniquely socially needy. Likewise, that the 'domestication' of wolves is here argued to be a response to shared emotional needs and sensitivities between wolves and humans, rather than human innovative flair, presents ourselves in a more emotionally vulnerable light than is typical.

There can hardly be a more important time to recognise, in the face of climate change, that we are not elevated above other species, nor are we invulnerable. By highlighting what connects us to the rest of nature, and the complex paths of different but equal evolutionary options, we may be at least beginning this process. Those motivations that make us sacrifice for the good of others come not from some elevation above a natural world of competition but rather from a commonality with many highly social animals. Those motivations that make us reach out despite differences, or connect across borders, are equally rooted in a biology common to some other animals. At our best, we are part of nature.

The significance of our emotional sensitivities and vulnerabilities also makes more sense of our existence in a modern world. We have seen that our interdependence, and those connections we create through emotional vulnerabilities, rather than any individual independence, was key to making us human. Throughout our evolutionary history, humans increasingly needed each other more intensely, not just practically but also emotionally. This was key to the formation of close-knit collaborative groups and networks, not just an unfortunate side effect. By recognising the importance of emotions to our uniquely strong and wide-ranging connections and uniquely human means of collaboration, we must at the same time acknowledge the significance of our sensitivity to others' pain or distress, as well as that to loneliness or a lack of social recognition.

There is, of course, a lot more to find out. We cannot help but wonder about what different emotional biology may have characterised the many different hominin species in the past. As we add increasing complexity to our evolutionary tree, different types of social relationships, with perhaps no parallels today, may emerge. Equally, whilst we would be mistaken to pit culture against biology in our explanation of behaviours, we are left wondering about what relationships between these two realms motivated individuals in the past – to what extent any Neanderthal's motivations to care for the vulnerable were driven by how they felt or by how they were expected to behave, for example. There is also far more to know about interpersonal variability in emotional responses and capacities. It seems probable that, as much as today, some individuals in the past were deeply connected to objects that provided them with a sense of comfort or to animals that provided emotional support and companionship, whilst others felt little of these needs or responses. Some were without doubt more caring or more emotionally vulnerable than others. A perspective on past societies that integrates emotional variability may yet be to come.

There has been a simplification of many complex issues, and an overview of detailed evidence in order to achieve an understanding of the broad pattern of our human origins, and many of these arguments would benefit from greater depth. We have neither attempted to disaggregate different complex emotions, such as gratitude or shame, nor separated the nature of our close emotional connections into different ways we view love, such as romantic or parental, or close affection between friends. There is also much more that could be said about the relationship between emotions, bodies and touch. Furthermore, the details of this new narrative are bound to change with new findings, and some arguments presented here maybe overturned in future. However, I hope that the significance of our human emotional motivations towards others, and *the better part of our natures*, remains.

Why should this new version of our evolutionary past matter for the future?

Important insights gained from the hidden depths of our evolutionary past may help us navigate our futures.

The long timescales of our distant past give us new perspectives. Thinking of our evolutionary past as a testbed of what works to foster our shared survival against the odds shows that caring about others, and responding to their vulnerability, has been the most successful long-term strategy of all. This is most obvious in simple economics. People are most likely to survive where strong bonds provide the give and take that means that others are around to help in hard times. Less obviously, however, it is only in environments that are socially and emotionally supportive that we develop the levels of safety and confidence that prompt us to be motivated to help others. This matters for the future. As much as we need practical solutions to climate change, or other threats, we need these insights to develop social and emotional solutions as well.

This is not what we expected to find. We seem to find it easy to create stories about our evolutionary past to make ourselves feel superior or invulnerable but, on closer attention, these do not hold up to scrutiny. We like to think of ourselves as exceptional and above other living things. Yet this is far from the case. Like other animals, we are vulnerable to what happens in the world around us. Moreover, it clear that the processes that drove how our emotional connections evolved have much in common with those seen in other social animals. In many ways, we have travelled on a journey alongside these animals, not on an exceptional path away from them. We like to reassure ourselves of our intellectual superiority, perhaps imagining that this intellect will save us from whatever challenges we face. However, in the past, it has been our emotional bonds and our capacities to care for others that have fostered survival. We like to think of ourselves as independent. Yet, in reality, we are profoundly connected, not only in practical terms but also in how we feel. We may only rarely be entirely carried away by feelings such as compassion, guilt, sympathy or gratitude, yet they exert a surprisingly profound influence as an integrated part of our thinking. Even as infants, we quickly become aware of how others feel about us, and decide how to behave on the basis of our sensitivity towards others' feelings and how they might react. We are uniquely sensitive to the most subtle of facial expressions, to the barest hint of judgement or rejection, and to the slightest of social signs that others might approve or disapprove of us, for example. Viewing or experiencing courage, heroism or acts of supreme altruism elevates us, profoundly inspiring us to do things for a greater good. Yet, fear of failure, the concepts of honour or respect, and the prospect of loneliness drive us to all kinds of often unhealthy or dangerous extremes. We suffer in a very physiological sense if we cannot exercise our natural tendencies to care for others, and be cared for, and to belong and be appreciated. Indeed, we are only just beginning to recognise our profound need for genuine emotional connection, and not superficial social interactions, tweets or influence.

In the hidden depths of the distant archaeological record we can see that our emotional sensitivities, so long derided as weakness, are actually our greatest strengths, albeit strengths that needs nurturing. We are innately wired to care for living and non-living things, to seek emotional comfort and to reach out to form connections. When the going gets tough, we tend to help each other. But we were never meant to be individually resilient, and we struggle to find the courage to help others, to explore new ideas and to be creative without the genuine emotional connections we need. We cannot hope to become grounded, courageous and committed to shared goals unless we create the structures that foster supportive relationships and provide us with safe havens of comfort in nature, animals and even cherished things.

Today, we face some of the most serious challenges we have ever experienced. As well as the direct effects of climate change, bringing pressures on land and resources, and the impacts of new diseases, we also face entrenched hatreds, rising inequality and the emotional pressures brought about by experiencing ecological disintegration. However, it has been old narratives about who we are that played a role in creating many of the problems which we face. It is not difficult to see that cultures that elevate selfishness, inequality and exploitation of natural resources have been supported by ideas of innate human competitiveness, invulnerability and superiority over nature. If we can look beyond these assumptions and recognise a previously hidden past of connection, caring and sensitivity, we could harness the significance of these connections and vulnerabilities in creating resilient communities. We might begin to reframe who we are and, in turn, change the world that we create around us.

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