

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 I

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)

How to cite this book chapter:

Spikins, P., 2022. *Hidden Depths: the origins of human connection*. Pp. 17–70. York: White Rose University Press. DOI: <https://doi.org/10.22599/HiddenDepths.b>. License: CC BY-NC 4.0

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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](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

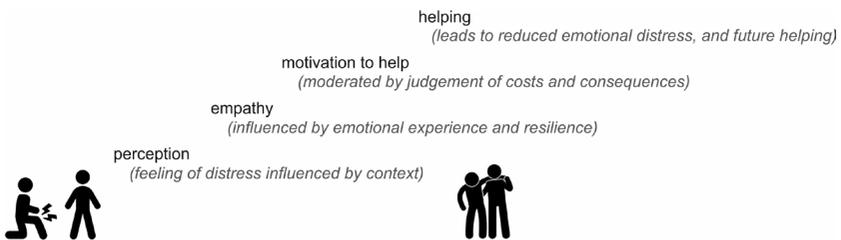


Figure 1.2: Illustration of emotional and cognitive responses leading from empathy to helping behaviour. Penny Spikins, CC BY-NC 4.0.

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

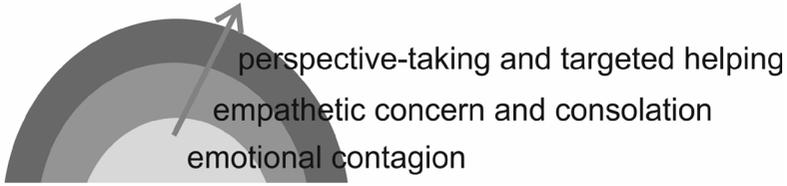


Figure 1.3: Levels (or shells) of empathetic abilities we experience from our earliest infancy to later childhood, and share with some other social animals. Penny Spikins, CC BY-NC 4.0.

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 Bousou, 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 evolved (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](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 Tāi 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

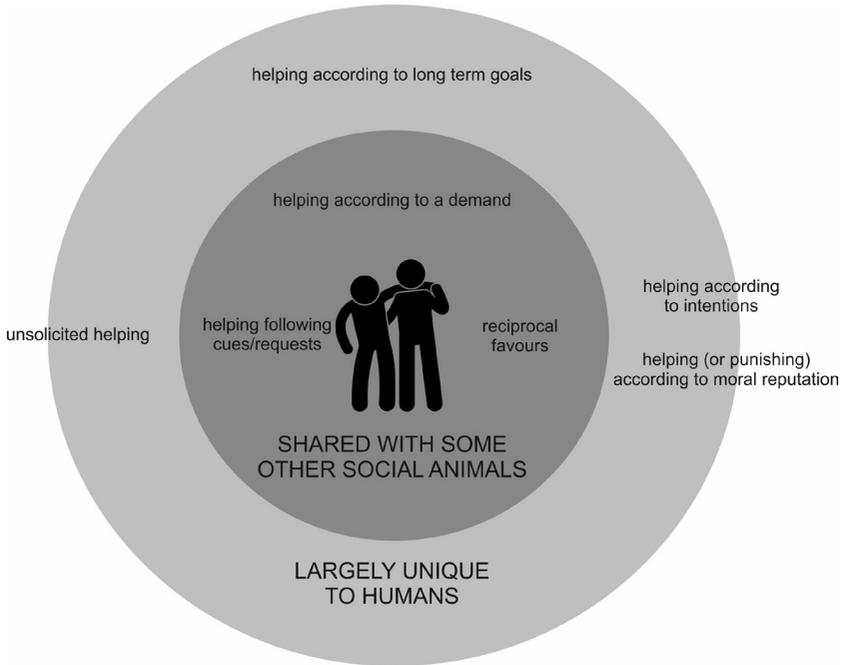


Figure 1.5: Increasingly complex cognitive empathy seen in humans compared to some other social animals. Penny Spikins, CC BY-NC 4.0.

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 Gavrillets 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](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

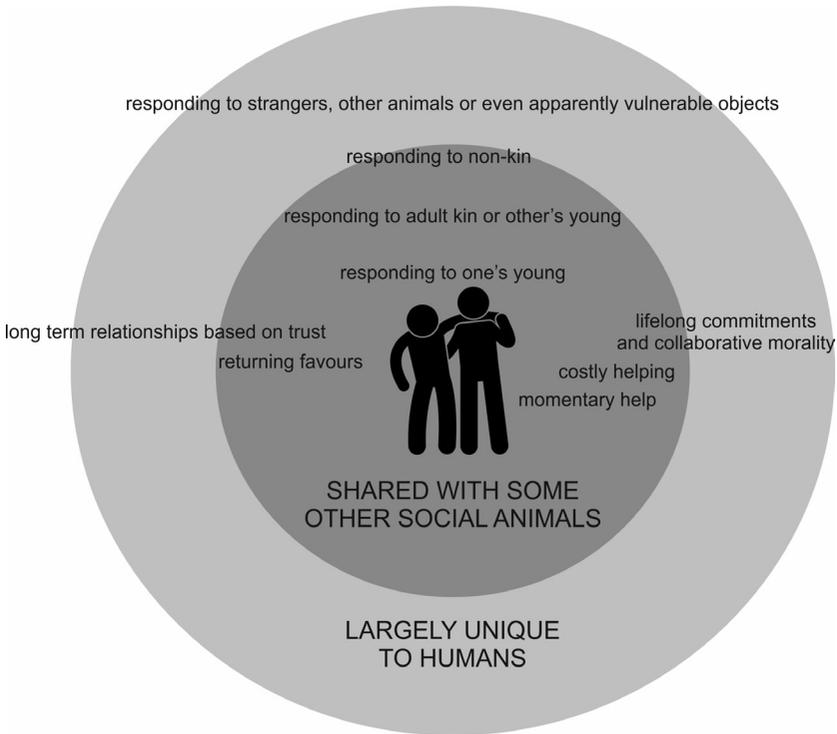


Figure 1.7: Increasingly extensive affective empathy seen in humans compared to some other social animals. Penny Spikins, CC BY-NC 4.0.

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

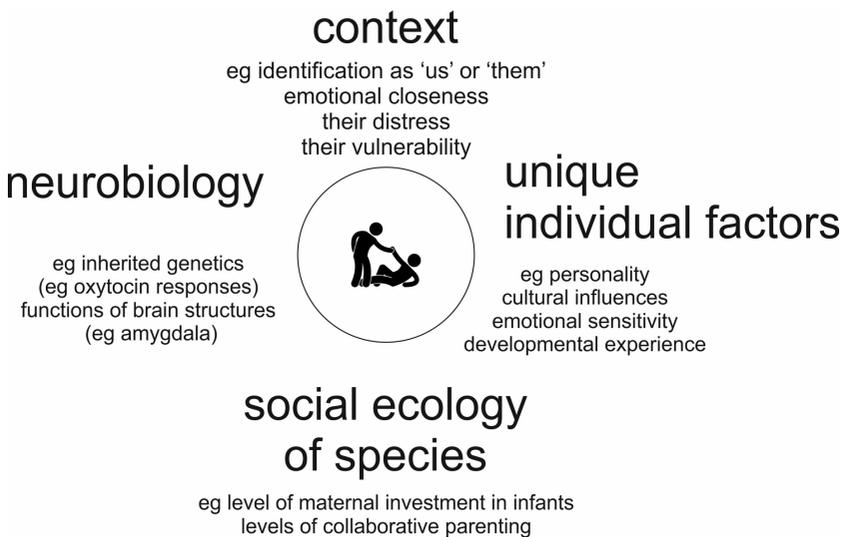


Figure 1.8: Some of the factors associated with variations in caring motivations and behaviours. Penny Spikins, CC BY-NC 4.0.

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

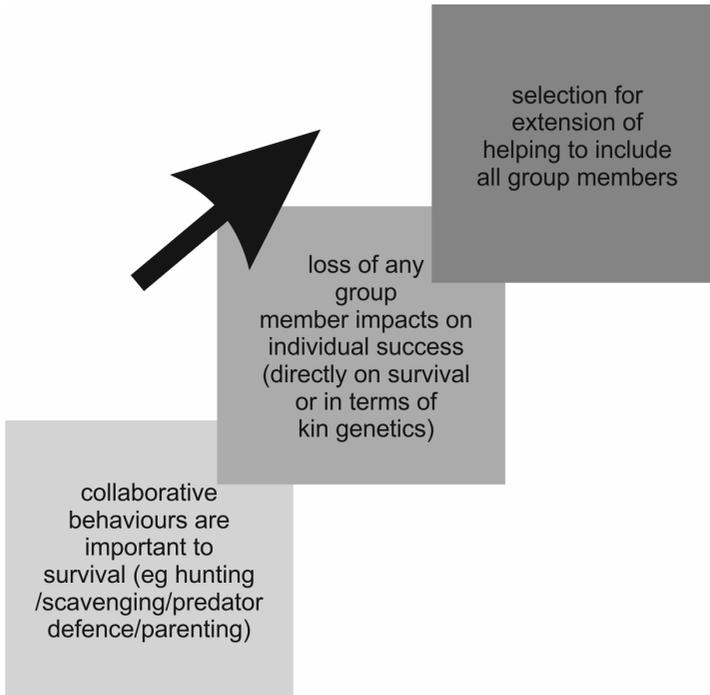


Figure 1.9: Selection pressures acting in highly collaborative social mammals, and particularly social carnivores, towards the extension of empathy to all group members. Penny Spikins, CC BY-NC 4.0.

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

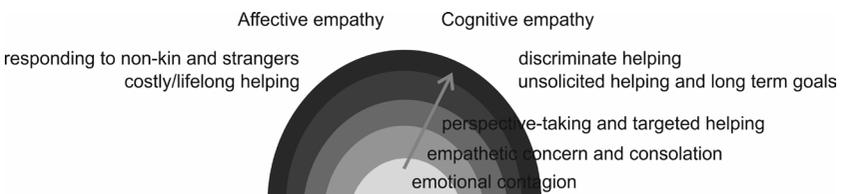


Figure 1.10: Additional levels of uniquely human developments in affective and cognitive empathy building on capacities shared with some social animals. Penny Spikins, CC BY-NC 4.0.

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.

References

- Abraham, Eyal, and Ruth Feldman. 2018. 'The Neurobiology of Human Allo-maternal Care; Implications for Fathering, Coparenting, and Children's Social Development.' *Physiology & Behavior* 193 (Pt A): 25–34.
- Algoe, Sara B., and Baldwin M. Way. 2014. 'Evidence for a Role of the Oxytocin System, Indexed by Genetic Variation in CD38, in the Social Bonding Effects of Expressed Gratitude.' *Social Cognitive and Affective Neuroscience* 9 (12): 1855–61.
- Allen, Summer. 2018. 'The Science of Gratitude.' Available at: https://ggsc.berkeley.edu/images/uploads/GGSC-JTF_White_Paper-Gratitude-FINAL.pdf?_ga=2.217126422.1217948920.1544632649-1208319986.1540629117. Accessed 01/06/21.
- Anderson, James R., Alasdair Gillies, and Louise C. Lock. 2010. 'Pan Thanatology.' *Current Biology: CB* 20 (8): R349–51.
- Appleby, Rob, Bradley Smith, and Darryl Jones. 2013. 'Observations of a Free-Ranging Adult Female Dingo (Canis Dingo) and Littermates' Responses to the Death of a Pup.' *Behavioural Processes* 96 (June): 42–46.
- Aureli, F., S. D. Preston, and F. B. De Waal. 1999. 'Heart Rate Responses to Social Interactions in Free-Moving Rhesus Macaques (Macaca Mulatta): A Pilot Study.' *Journal of Comparative Psychology* 113 (1): 59–65.
- Bales, Karen L., William A. Mason, Ciprian Catana, Simon R. Cherry, and Sally P. Mendoza. 2007. 'Neural Correlates of Pair-Bonding in a Monogamous Primate.' *Brain Research* 1184 (December): 245–53.
- Barber-Meyer, Shannon M., L. David Mech, Wesley E. Newton, and Bridget L. Borg. 2016. 'Differential Wolf-Pack-Size Persistence and the Role of Risk When Hunting Dangerous Prey.' *Behaviour* 153 (12): 1473–87.
- Barraza, Jorge A., and Paul J. Zak. 2009. 'Empathy toward Strangers Triggers Oxytocin Release and Subsequent Generosity.' *Annals of the New York Academy of Sciences* 1167 (June): 182–89.
- Bartal, Inbal Ben-Ami, Jean Decety, and Peggy Mason. 2011. 'Empathy and Pro-Social Behavior in Rats.' *Science* 334 (6061): 1427–30.
- Baumgartner, Thomas, Markus Heinrichs, Aline Vonlanthen, Urs Fischbacher, and Ernst Fehr. 2008. 'Oxytocin Shapes the Neural Circuitry of Trust and Trust Adaptation in Humans.' *Neuron* 58 (4): 639–50.
- Bearzi, Giovanni, Dan Kerem, Nathan B. Furey, Robert L. Pitman, Luke Rendell, and Randall R. Reeves. 2018. 'Whale and Dolphin Behavioural Responses to Dead Conspecifics.' *Zoology* 128 (June): 1–15.

- Becker, Julia C., Lea Hartwich, and S. Alexander Haslam. 2021. 'Neoliberalism Can Reduce Well-Being by Promoting a Sense of Social Disconnection, Competition, and Loneliness.' *The British Journal of Social Psychology* 60 (3): 947–65.
- Bekoff, Marc. 2002. 'Empathy: Common Sense, Science Sense, Wolves, and Well-Being.' *The Behavioral and Brain Sciences* 25 (1): 26–27.
- Biro, Dora, Tatyana Humle, Kathelijne Koops, Claudia Sousa, Misato Hayashi, and Tetsuro Matsuzawa. 2010. 'Chimpanzee Mothers at Bossou, Guinea Carry the Mummified Remains of Their Dead Infants.' *Current Biology: CB* 20 (8): R351–52.
- Boehm, Christopher. 2000. 'Conflict and the Evolution of Social Control.' *Journal of Consciousness Studies* 7 (1–2): 79–101.
- Boesch, Christophe. 1992. 'New Elements of a Theory of Mind in Wild Chimpanzees.' *The Behavioral and Brain Sciences* 15 (1): 149–50.
- Boesch, Christophe, Camille Bolé, Nadin Eckhardt, and Hedwige Boesch. 2010. 'Altruism in Forest Chimpanzees: The Case of Adoption.' *PLoS One* 5 (1): e8901.
- Borrego, Natalia, and Michael Gaines. 2016. 'Social Carnivores Outperform Asocial Carnivores on an Innovative Problem.' *Animal Behaviour* 114 (April): 21–26.
- Brethel-Haurwitz, Kristin M., Katherine O'Connell, Elise M. Cardinale, Maria Stoianova, Sarah A. Stoycos, Leah M. Lozier, John W. VanMeter, and Abigail A. Marsh. 2017. 'Amygdala–Midbrain Connectivity Indicates a Role for the Mammalian Parental Care System in Human Altruism.' *Proceedings. Biological Sciences/The Royal Society* 284 (1865): 20171731.
- Burkart, J. M., S. B. Hrdy, and C. P. Van Schaik. 2009. 'Cooperative Breeding and Human Cognitive Evolution.' *Evolutionary Anthropology* 18 (5): 175–86.
- Call, Josep, and Michael Tomasello. 2008. 'Does the Chimpanzee Have a Theory of Mind? 30 Years Later.' *Trends in Cognitive Sciences* 12 (5): 187–92.
- Carter, C. Sue, Angela J. Grippo, Hossein Pournajafi-Nazarloo, Michael G. Ruscio, and Stephen W. Porges. 2008. 'Oxytocin, Vasopressin and Sociality.' *Progress in Brain Research* 170: 331–36.
- Carter, Gerald G., and Gerald S. Wilkinson. 2015. 'Social Benefits of Non-Kin Food Sharing by Female Vampire Bats.' *Proceedings. Biological Sciences/The Royal Society* 282 (1819). DOI: <https://doi.org/10.1098/rspb.2015.2524>.
- Cassidy, Kira A., and Richard T. McIntyre. 2016. 'Do Gray Wolves (*Canis Lupus*) Support Pack Mates during Aggressive Inter-Pack Interactions?' *Animal Cognition* 19 (5): 939–47.

- Clay, Zanna, and Frans B. M. De Waal. 2013. 'Bonobos Respond to Distress in Others: Consolation across the Age Spectrum.' *PLoS One* 8 (1): e55206.
- Clay, Zanna, Elisabetta Palagi, and Frans B. M. De Waal. 2018. 'Chapter 5 - Ethological Approaches to Empathy in Primates.' In: Ksenia Z. Meyza and Ewelina Knapska (eds.) *Neuronal Correlates of Empathy*: 53–66. Academic Press.
- Creel, Scott, and Nancy Marusha Creel. 2002. *The African Wild Dog: Behavior, Ecology, and Conservation*. Princeton University Press.
- Davenport, Lisa C. 2010. 'Aid to a Declining Matriarch in the Giant Otter (*Pteronura Brasiliensis*).' *PLoS One* 5 (6): e11385.
- Decety, Jean. 2015. 'The Neural Pathways, Development and Functions of Empathy.' *Current Opinion in Behavioral Sciences* 3 (Supplement C): 1–6.
- Decety, Jean, Inbal Ben-Ami Bartal, Florina Uzefovsky, and Ariel Knafo-Noam. 2016. 'Empathy as a Driver of Prosocial Behaviour: Highly Conserved Neurobehavioural Mechanisms across Species.' *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 371 (1686): 20150077.
- Decety, Jean, Greg J. Norman, Gary G. Berntson, and John T. Cacioppo. 2012. 'A Neurobehavioral Evolutionary Perspective on the Mechanisms Underlying Empathy.' *Progress in Neurobiology* 98 (1): 38–48.
- De Dreu, Carsten K. W., Lindred L. Greer, Gerben A. Van Kleef, Shaul Shalvi, and Michel J. J. Handgraaf. 2011. 'Oxytocin Promotes Human Ethnocentrism.' *Proceedings of the National Academy of Sciences of the United States of America* 108 (4): 1262–66.
- de Waal, Frans. 1998. *Chimpanzee Politics*. Revised Edition. Baltimore, MD: Johns Hopkins Press.
- de Waal, Frans B. M. 2008. 'Putting the Altruism Back into Altruism: The Evolution of Empathy.' *Annual Review of Psychology* 59: 279–300.
- de Waal, Frans B. M., and Stephanie D. Preston. 2017. 'Mammalian Empathy: Behavioural Manifestations and Neural Basis.' *Nature Reviews. Neuroscience* 18 (8): 498–509.
- Dolivo, Vassilissa, Claudia Rutte, and Michael Taborsky. 2016. 'Ultimate and Proximate Mechanisms of Reciprocal Altruism in Rats.' *Learning & Behavior* 44 (3): 223–26.
- DeLouize, Alicia M., Frederick L. Coolidge, and Thomas Wynn. 2017. 'Dopaminergic Systems Expansion and the Advent of Homo Erectus.' *Quaternary International* 427: 245–52.

- Douglas-Hamilton, Iain, Shivani Bhalla, George Wittemyer, and Fritz Vollrath. 2006. 'Behavioural Reactions of Elephants towards a Dying and Deceased Matriarch.' *Applied Animal Behaviour Science* 100 (1): 87–102.
- Dunbar, Robin. I. M. 2003. 'The Social Brain: Mind, Language, and Society in Evolutionary Perspective.' *Annual Review of Anthropology* 32 (October): 163–81.
- Dunfield, Kristen A., and Valerie A. Kuhlmeier. 2010. 'Intention-Mediated Selective Helping in Infancy.' *Psychological Science* 21 (4): 523–27.
- Egas, Martijn, and Arno Riedl. 2008. 'The Economics of Altruistic Punishment and the Maintenance of Cooperation.' *Proceedings of the Royal Society of London B: Biological Sciences* 275 (1637): 871–78.
- Emmons, Robert A., and Michael E. McCullough. 2004. *The Psychology of Gratitude*. Oxford University Press.
- Engelmann, Jan M., Esther Herrmann, and Michael Tomasello. 2015. 'Chimpanzees Trust Conspecifics to Engage in Low-Cost Reciprocity.' *Proceedings. Biological Sciences/The Royal Society* 282 (1801): 20142803.
- Erb, Wendy M., and Leila M. Porter. 2017. 'Mother's Little Helpers: What We Know (and Don't Know) about Cooperative Infant Care in Callitrichines.' *Evolutionary Anthropology* 26 (1): 25–37.
- Eres, Robert, Jean Decety, Winnifred R. Louis, and Pascal Molenberghs. 2015. 'Individual Differences in Local Gray Matter Density Are Associated with Differences in Affective and Cognitive Empathy.' *NeuroImage* 117: 305–10.
- Eriksson, Kimmo, Irina Vartanova, Pontus Strimling, and Brent Simpson. 2018. 'Generosity Pays: Selfish People Have Fewer Children and Earn Less Money.' *Journal of Personality and Social Psychology* 118 (3): 532–44.
- Fashing, Peter J., and Nga Nguyen. 2011. 'Behavior toward the Dying, Diseased, or Disabled among Animals and Its Relevance to Paleopathology.' *International Journal of Paleopathology* 1 (3–4): 128–29.
- Fashing, Peter J., Nga Nguyen, Tyler S. Barry, C. Barret Goodale, Ryan J. Burke, Sorrel C. Z. Jones, Jeffrey T. Kerby, Laura M. Lee, Niina O. Nurmi, and Vivek V. Venkataraman. 2011. 'Death among Geladas (*Theropithecus gelada*): A Broader Perspective on Mummified Infants and Primate Thanatology.' *American Journal of Primatology* 73 (5): 405–9.
- Fehr, Ernst, and Simon Gächter. 2002. 'Altruistic Punishment in Humans.' *Nature* 415 (6868): 137–40.
- Feldman, Ruth. 2017. 'The Neurobiology of Human Attachments.' *Trends in Cognitive Sciences* 21 (2): 80–99.

- Frank, Erik T., and K. Eduard Linsenmair. 2017. 'Saving the Injured: Evolution and Mechanisms.' *Communicative & Integrative Biology* 10 (5–6): e1356516.
- Fraser, Orlaith N., Daniel Stahl, and Filippo Aureli. 2008. 'Stress Reduction through Consolation in Chimpanzees.' *Proceedings of the National Academy of Sciences of the United States of America* 105 (25): 8557–62.
- Gfrerer, Nastassja, and Michael Taborsky. 2017. 'Working Dogs Cooperate among One Another by Generalised Reciprocity.' *Scientific Reports* 7 (March): 43867.
- Gilbert, Paul. 2015. 'The Evolution and Social Dynamics of Compassion.' *Social and Personality Psychology Compass* 9 (6): 239–54.
- Goetz, Jennifer L., Dacher Keltner, and Emiliana Simon-Thomas. 2010. 'Compassion: An Evolutionary Analysis and Empirical Review.' *Psychological Bulletin* 136 (3): 351–74.
- Gonçalves, André, and Dora Biro. 2018. 'Comparative Thanatology, an Integrative Approach: Exploring Sensory/Cognitive Aspects of Death Recognition in Vertebrates and Invertebrates.' *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 373 (1754). DOI: <https://doi.org/10.1098/rstb.2017.0263>.
- Gouin, Jean-Philippe, C. Sue Carter, Hossein Pournajafi-Nazarloo, Ronald Glaser, William B. Malarkey, Timothy J. Loving, Jeffrey Stowell, and Janice K. Kiecolt-Glaser. 2010. 'Marital Behavior, Oxytocin, Vasopressin, and Wound Healing.' *Psychoneuroendocrinology* 35 (7): 1082–90.
- Grossmann, Tobias, Manuela Missana, and Kathleen M. Krol. 2018. 'The Neurodevelopmental Precursors of Altruistic Behavior in Infancy.' *PLoS Biology* 16 (9): e2005281.
- Hart, Benjamin L. 2011. 'Behavioural Defences in Animals against Pathogens and Parasites: Parallels with the Pillars of Medicine in Humans.' *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 366 (1583): 3406–17.
- Hart, Donna, and Robert W. Sussman. 2011. 'The Influence of Predation on Primate and Early Human Evolution: Impetus for Cooperation.' In: Robert W. Sussman and C. Robert Cloninger (eds.) *Origins of Altruism and Cooperation*: 19–40. New York: Springer.
- Heyes, Cecilia. 2020. 'Culture.' *Current Biology: CB* 30 (20): R1246–50.
- Horowitz, Alexandra. 2011. 'Theory of Mind in Dogs? Examining Method and Concept.' *Learning & Behavior* 39: 314–17.

- House, Bailey, Joseph Henrich, Barbara Sarnecka, and Joan B. Silk. 2013. 'The Development of Contingent Reciprocity in Children.' *Evolution and Human Behavior: Official Journal of the Human Behavior and Evolution Society* 34 (2): 86–93.
- Hrdy, Sarah B. 2011. *Mothers and Others*. Harvard University Press.
- Jouventin, Pierre, Yves Christen, and F. Stephen Dobson. 2016. 'Altruism in Wolves Explains the Coevolution of Dogs and Humans.' *Ideas in Ecology and Evolution* 9 (1). DOI: <https://doi.org/10.4033/iee.2016.9.2.n>.
- Kokko, Hanna, Rufus A. Johnstone, and J. Wright. 2002. 'The Evolution of Parental and Alloparental Effort in Cooperatively Breeding Groups: When Should Helpers Pay to Stay?' *Behavioral Ecology: Official Journal of the International Society for Behavioral Ecology* 13 (3): 291–300.
- Kosfeld, Michael, Markus Heinrichs, Paul J. Zak, Urs Fischbacher, and Ernst Fehr. 2005. 'Oxytocin Increases Trust in Humans.' *Nature* 435 (7042): 673–76.
- Lonsdorf, Elizabeth V., Michael L. Wilson, Emily Boehm, Josephine Delaney-Soesman, Tessa Grebey, Carson Murray, Kaitlin Wellens, and Anne E. Pusey. 2020. 'Why Chimpanzees Carry Dead Infants: An Empirical Assessment of Existing Hypotheses.' *Royal Society Open Science* 7 (7): 200931.
- Madden, Joah R., and Tim H. Clutton-Brock. 2011. 'Experimental Peripheral Administration of Oxytocin Elevates a Suite of Cooperative Behaviours in a Wild Social Mammal.' *Proceedings. Biological Sciences/The Royal Society* 278 (1709): 1189–94.
- Maddin, Hillary C., Arjan Mann, and Brian Hebert. 2019. 'Varanopid from the Carboniferous of Nova Scotia Reveals Evidence of Parental Care in Amniotes.' *Nature Ecology & Evolution* 4 (1): 50–56.
- Marsh, Abigail A. 2019. 'The Caring Continuum: Evolved Hormonal and Proximal Mechanisms Explain Prosocial and Antisocial Extremes.' *Annual Review of Psychology* 70 (January): 347–71.
- Martin, Alia, and Kristina R. Olson. 2013. 'When Kids Know Better: Paternalistic Helping in 3-Year-Old Children.' *Developmental Psychology* 49 (11): 2071–81.
- Melis, Alicia P., and Michael Tomasello. 2013. 'Chimpanzees' (Pan Troglodytes) Strategic Helping in a Collaborative Task.' *Biology Letters* 9 (2): 20130009.
- Mendonça, Sara Etz, Elisa A. Merçon-Vargas, Ayse Payir, and Jonathan R. H. Tudge. 2018. 'The Development of Gratitude in Seven Societies: Cross-Cultural Highlights.' *Cross-Cultural Research: Official Journal of the Society for Cross-Cultural Research* 52 (1): 135–50.

- Mondanaro, Alessandro, Marina Melchionna, Mirko Di Febbraro, Silvia Castiglione, Philip B. Holden, Neil R. Edwards, Francesco Carotenuto, et al. 2020. 'A Major Change in Rate of Climate Niche Envelope Evolution during Hominid History.' *iScience* 23 (11): 101693.
- Nagasawa, Miho, Shouhei Mitsui, Shiori En, Nobuyo Ohtani, Mitsuaki Ohta, Yasuo Sakuma, Tatsushi Onaka, Kazutaka Mogi, and Takefumi Kikusui. 2015. 'Social Evolution. Oxytocin-Gaze Positive Loop and the Coevolution of Human-Dog Bonds.' *Science* 348 (6232): 333–36.
- Ne'eman, R., N. Perach-Barzilay, M. Fischer-Shofty, A. Atias, and S. G. Shamay-Tsoory. 2016. 'Intranasal Administration of Oxytocin Increases Human Aggressive Behavior.' *Hormones and Behavior* 80 (April): 125–31.
- Nesse, Randolph M. 2009. 'Runaway Social Selection for Displays of Partner Value and Altruism.' In: Jan Verplaetse, Jelle de Schrijver, Sven Vanneste, and Johan Braeckman (eds.) *The Moral Brain*: 211–31. Springer.
- Palagi, Elisabetta, and Giada Cordoni. 2009. 'Postconflict Third-Party Affiliation in *Canis Lupus*: Do Wolves Share Similarities with the Great Apes?' *Animal Behaviour* 78 (4): 979–86.
- Panksepp, Jaak, and Jules B. Panksepp. 2013. 'Toward a Cross-Species Understanding of Empathy.' *Trends in Neurosciences* 36 (8): 489–96.
- Pearce, Eiluned, Rafael Wlodarski, Anna Machin, and Robin I. M. Dunbar. 2017. 'Variation in the β -Endorphin, Oxytocin, and Dopamine Receptor Genes Is Associated with Different Dimensions of Human Sociality.' *Proceedings of the National Academy of Sciences of the United States of America* 114 (20): 5300–305.
- Pérez-Manrique, Ana, and Antoni Gomila. 2017. 'The Comparative Study of Empathy: Sympathetic Concern and Empathic Perspective-Taking in Non-Human Animals.' *Biological Reviews of the Cambridge Philosophical Society* 93 (1): 248–69.
- Plotnik, Joshua M., and Frans B. M. De Waal. 2014. 'Asian Elephants (*Elephas Maximus*) Reassure Others in Distress.' *PeerJ* 2 (February): e278.
- Pruetz, Jill Daphne. 2011. 'Targeted Helping by a Wild Adolescent Male Chimpanzee (*Pan Troglodytes Verus*): Evidence for Empathy?' *Journal of Ethology* 29 (2): 365–68.
- Rajhans, Purva, Nicole Altvater-Mackensen, Amrisha Vaish, and Tobias Grossmann. 2016. 'Children's Altruistic Behavior in Context: The Role of Emotional Responsiveness and Culture.' *Scientific Reports* 6 (May): 24089.
- Rapaport, Lisa G. 2011. 'Progressive Parenting Behavior in Wild Golden Lion Tamarins.' *Behavioral Ecology: Official Journal of the International Society for Behavioral Ecology* 22 (4): 745–54.

- Rasa, O. Anne E. 1983. 'A Case of Invalid Care in Wild Dwarf Mongooses.' *Zeitschrift Für Tierpsychologie* 62 (3): 235–40.
- Reggente, Melissa A. L., Filipe Alves, Cátia Nicolau, Luís Freitas, Daniele Cagnazzi, Robin W. Baird, and Paolo Galli. 2016. 'Nurturant Behavior toward Dead Conspecifics in Free-Ranging Mammals: New Records for Odonotocetes and a General Review.' *Journal of Mammalogy* 97 (5): 1428–34.
- Richards, Evelleen. 2017. *Darwin and the Making of Sexual Selection*. University of Chicago Press.
- Rilling, James K. 2011. 'The Neurobiology of Cooperation and Altruism.' In: Robert W. Sussman and C. Robert Cloninger (eds.) *Origins of Altruism and Cooperation*: 295–306. New York: Springer.
- Romero, Teresa, and Filippo Aureli. 2008. 'Reciprocity of Support in Coatis (Nasua Nasua).' *Journal of Comparative Psychology* 122 (1): 19–25.
- Romero, Teresa, Miguel A. Castellanos, and Frans B. M. De Waal. 2010. 'Conso-lation as Possible Expression of Sympathetic Concern among Chimpanzees.' *Proceedings of the National Academy of Sciences of the United States of America* 107 (27): 12110–15.
- Romero, Teresa, Marie Ito, Atsuko Saito, and Toshikazu Hasegawa. 2014. 'Social Modulation of Contagious Yawning in Wolves.' *PLoS One* 9 (8): e105963.
- Romero, Teresa, Miho Nagasawa, Kazutaka Mogi, Toshikazu Hasegawa, and Takefumi Kikusui. 2015. 'Intranasal Administration of Oxytocin Promotes Social Play in Domestic Dogs.' *Communicative & Integrative Biology* 8 (3): e1017157.
- Romero, Teresa, Kenji Onishi, and Toshikazu Hasegawa. 2016. 'The Role of Oxytocin on Peaceful Associations and Sociality in Mammals.' *Behaviour* 153 (9–11): 1053–71.
- Rooker, Kelly, and Sergey Gavrilets. 2016. 'Evolution of Long-Term Pair-Bonding in Humans.' In: Todd K. Shackelford and Viviana A. Weekes-Shackelford (eds.) *Encyclopedia of Evolutionary Psychological Science*: 1–14. Cham: Springer International Publishing.
- Schaller, George B. 2009. *The Serengeti Lion: A Study of Predator-Prey Relations*. University of Chicago Press.
- Schaller, George B., and Gordon R. Lowther. 1969. 'The Relevance of Carnivore Behavior to the Study of Early Hominids.' *Southwestern Journal of Anthropology* 25 (4): 307–41.
- Scheele, Dirk, Andrea Wille, Keith M. Kendrick, Birgit Stoffel-Wagner, Benjamin Becker, Onur Güntürkün, Wolfgang Maier, and René Hurlmann. 2013. 'Oxytocin Enhances Brain Reward System Responses in Men V

- iewing the Face of Their Female Partner.' *Proceedings of the National Academy of Sciences of the United States of America* 110 (50): 20308–13.
- Schino, Gabriele, and Filippo Aureli. 2010. 'Primate Reciprocity and Its Cognitive Requirements.' *Evolutionary Anthropology* 19 (4): 130–35.
- Smaldino, Paul E., Lesley Newson, Jeffrey C. Schank, and Peter J. Richerson. 2013. 'Simulating the Evolution of the Human Family: Cooperative Breeding Increases in Harsh Environments.' *PLoS One* 8 (11): e80753.
- Smith, Adam S., Anders Agmo, Andrew K. Birnie, and Jeffrey A. French. 2010. 'Manipulation of the Oxytocin System Alters Social Behavior and Attraction in Pair-Bonding Primates, *Callithrix Penicillata*.' *Hormones and Behavior* 57 (2): 255–62.
- Smith, Jennifer E., Eli M. Swanson, Daphna Reed, and Kay E. Holekamp. 2012. 'Evolution of Cooperation among Mammalian Carnivores and Its Relevance to Hominin Evolution.' *Current Anthropology* 53 (S6): S436–52.
- Snowdon, Charles T. 2011. 'Behavioral and Neuroendocrine Interactions in Affiliation.' In: Robert W. Sussman and C. Robert Cloninger (eds.) *Origins of Altruism and Cooperation*: 307–31. New York: Springer.
- Stietz, Julia, Emanuel Jauk, Sören Krach, and Philipp Kanske. 2019. 'Dissociating Empathy from Perspective-Taking: Evidence from Intra- and Inter-Individual Differences Research.' *Frontiers in Psychiatry* 10: 126.
- Suvilehto, Juulia T., Lauri Nummenmaa, Tokiko Harada, Robin I. M. Dunbar, Riitta Hari, Robert Turner, Norihiro Sadato, and Ryo Kitada. 2019. 'Cross-Cultural Similarity in Relationship-Specific Social Touching.' *Proceedings. Biological Sciences/The Royal Society* 286 (1901): 20190467.
- Taborsky, Michael, Joachim G. Frommen, and Christina Riehl. 2016. 'Correlated Pay-Offs Are Key to Cooperation.' *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 371 (1687): 20150084.
- Taylor, S. E., L. C. Klein, B. P. Lewis, T. L. Gruenewald, R. A. Gurung, and J. A. Updegraff. 2000. 'Biobehavioral Responses to Stress in Females: Tend-and-Befriend, Not Fight-or-Flight.' *Psychological Review* 107 (3): 411–29.
- Ten Velden, Femke S., Katie Daughters, and Carsten K. W. De Dreu. 2017. 'Oxytocin Promotes Intuitive rather than Deliberated Cooperation with the in-Group.' *Hormones and Behavior* 92 (June): 164–71.
- Thompson, Philip R. 1975. 'A Cross-Species Analysis of Carnivore, Primate, and Hominid Behaviour.' *Journal of Human Evolution* 4 (2): 113–24.
- Tomasello, Michael. 2014. 'The Ultra-Social Animal.' *European Journal of Social Psychology* 44 (3): 187–94.

- Tousignant, Béatrice, Fanny Eugène, and Philip L. Jackson. 2017. 'A Developmental Perspective on the Neural Bases of Human Empathy.' *Infant Behavior & Development* 48 (Pt A): 5–12.
- Trumble, Benjamin C., Adrian V. Jaeggi, and Michael Gurven. 2015. 'Evolving the Neuroendocrine Physiology of Human and Primate Cooperation and Collective Action.' *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 370 (1683): 20150014.
- Vaidyanathan, Gayathri. 2011. 'Apes in Africa: The Cultured Chimpanzees.' *Nature* 476 (7360): 266–69.
- Vaish, Amrisha, Malinda Carpenter, and Michael Tomasello. 2009. 'Sympathy through Affective Perspective Taking and Its Relation to Prosocial Behavior in Toddlers.' *Developmental Psychology* 45 (2): 534–43.
- Vaish, Amrisha, Malinda Carpenter, and Michael Tomasello. 2010. 'Young Children Selectively Avoid Helping People with Harmful Intentions.' *Child Development* 81 (6): 1661–69.
- vanOyen Witvliet, Charlotte, Lindsey Root Luna, Jill V. VanderStoep, Robert D. Vlisides-Henry, Trechaun Gonzalez, and Gerald D. Griffin. 2018. 'OXTR rs53576 Genotype and Gender Predict Trait Gratitude.' *The Journal of Positive Psychology* 14 (4) 417–26.
- Warneken, Felix. 2016. 'Insights into the Biological Foundation of Human Altruistic Sentiments.' *Current Opinion in Psychology* 7 (Supplement C): 51–56.
- Warneken, Felix. 2018. 'How Children Solve the Two Challenges of Cooperation.' *Annual Review of Psychology* 69: 205–29. Available at: <http://www.annualreviews.org/doi/abs/10.1146/annurev-psych-122216-011813>.
- Warneken, Felix, Brian Hare, Alicia P. Melis, Daniel Hanus, and Michael Tomasello. 2007. 'Spontaneous Altruism by Chimpanzees and Young Children.' *PLoS Biology* 5 (7): e184.
- Warneken, Felix, and Michael Tomasello. 2007. 'Helping and Cooperation at 14 Months of Age.' *Infancy: The Official Journal of the International Society on Infant Studies* 11 (3): 271–94.
- Watanabe, Takamitsu, Masanori Takezawa, Yo Nakawake, Akira Kunimatsu, Hidenori Yamasue, Mitsuhiro Nakamura, Yasushi Miyashita, and Naoki Masuda. 2014. 'Two Distinct Neural Mechanisms Underlying Indirect Reciprocity.' *Proceedings of the National Academy of Sciences of the United States of America* 111 (11): 3990–95.
- Whiten, A., J. Goodall, W. C. McGrew, T. Nishida, V. Reynolds, Y. Sugiyama, C. E. Tutin, R. W. Wrangham, and C. Boesch. 1999. 'Cultures in Chimpanzees.' *Nature* 399 (6737): 682–85.

- Wittig, Roman M., Catherine Crockford, Tobias Deschner, Kevin E. Langergraber, Toni E. Ziegler, and Klaus Zuberbühler. 2014. 'Food Sharing Is Linked to Urinary Oxytocin Levels and Bonding in Related and Unrelated Wild Chimpanzees.' *Proceedings. Biological Sciences/The Royal Society* 281 (1778): 20133096.
- Yamamoto, Shinya, Tatyana Humle, and Masayuki Tanaka. 2012. 'Chimpanzees' Flexible Targeted Helping Based on an Understanding of Conspecifics' Goals.' *Proceedings of the National Academy of Sciences of the United States of America* 109 (9): 3588–92.
- Yasue, Miyuki, Akiko Nakagami, Keiko Nakagaki, Noritaka Ichinohe, and Nobuyuki Kawai. 2018. 'Inequity Aversion Is Observed in Common Marmosets but Not in Marmoset Models of Autism Induced by Prenatal Exposure to Valproic Acid.' *Behavioural Brain Research* 343 (May): 36–40.
- Zak, Paul J., Angela A. Stanton, and Sheila Ahmadi. 2007. 'Oxytocin Increases Generosity in Humans.' *PLoS One* 2 (11): e1128.
- Zhang, Yan, Fanchang Kong, Yanli Zhong, and Hui Kou. 2014. 'Personality Manipulations: Do They Modulate Facial Attractiveness Ratings?' *Personality and Individual Differences* 70 (November): 80–84.