

Part 2

Tolerance, Sensitivity and Emotional Vulnerability

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

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

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

CHAPTER 4

The Evolutionary Basis for Human Tolerance – Physiological Responses

Abstract

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

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

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

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

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



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

Introduction

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

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

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

Intergroup tolerance in the human evolutionary past

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



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

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

Evidence from movements of raw materials, the sizes of archaeological sites, inbreeding deformities and genetics, argue that early human social groups were surprisingly constrained in size and insular in scope, with

interactions beyond the local group relatively rare. In reality, evidence for intercommunity interactions does not become widespread until much later in human evolution, and at least after 300,000 years ago.

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

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

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

It seems unlikely that there was *no* interaction between communities in early humans. Distributions of similar artefacts suggest that something



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

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

It is only after 300,000 years ago, beginning in Africa, that a novel openness to new relationships, and the capacities and needs to connect to an extended social group, appear to have emerged (Dunbar, Gamble, and Gowlett 2014). From bounded groups with constrained mobility and limited contacts between each other we see the emergence of fluid

connections across large social landscapes. In these new social contexts, supportive alliances provided a social buffer for resource shortfalls and people maintained connections with a wide number of allies (Coward and Gamble 2008; d'Errico and Stringer 2011; Foley and Gamble 2009; Spikins et al. 2021). Raw materials and finished artefacts that might previously have only come within a predicted home range were now drawn from well outside this range, sometimes even over thousands of kilometres, suggesting both higher levels of mobility and a degree of intergroup exchange (Féblot-Augustins 2009; Layton, O'Hara, and Bilsborough 2012; Marwick 2003).

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

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

The evolutionary background to human physiological reactions to unfamiliar people

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

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



the same skin tone as ourselves (Sapolsky 2017). Our immediate intuitive emotional reactions can be at odds with our principles.

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



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

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

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

Overcoming these reactions, and being able to effectively collaborate with other communities in a sustained way that goes beyond the occasional tolerance seen in bonobos, will have been a major challenge for human societies. The formation of new collaborative social alliances will have depended, firstly, on individuals being friendly enough to enable encounters, rather than being fearful or aggressive, and, secondly, on their being



open to treating less-familiar individuals a lot like family members, even though their habits, behaviour or ideas may have seemed foreign (Wiessner 2002: 22). Whilst we typically explain changes in the archaeological record involving new patterns of mobility, new alliances and greater cultural connectivity after 300,000 years ago in terms of changes in cognitive capacities or cultural change, changes in emotional motivations may be far more significant than we have imagined (Spikins et al. 2021).

What might have happened, and why?

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

Neurobiology, emotional responses and social behaviour

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

Social behaviour in mammals in general is mediated through hormonal and, in turn, physiological responses to particular social situations. As a result, one of the main ways in which social behaviour changes between species is through genetic changes influencing hormone pathways – that is, how the neurobiology of our brains influences us physiologically in any particular social situation or our ‘gut feelings’ (Narvaez 2014; Narvaez et al. 2013; Zink and Meyer-Lindenberg 2012). Certain social situations may make us anxious or afraid, others make us excited, and yet others make us feel calm, connected and secure. Changes over time in the selective advantages and disadvantages of different social behaviours, including behaviours towards

individuals who are rarely seen or unfamiliar, are strongly influenced by 'gut feelings' under the control of hormonal responses. Of course, how we behave is about far more than simple biological responses. As discussed in Chapter 1, our perceptions of a social situation influence our hormonal responses and, in turn, our physiological reactions, after which we also have a top-down control over what we think and how we behave. However, how *we feel* can have significant effects on our behaviour towards other people.

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

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

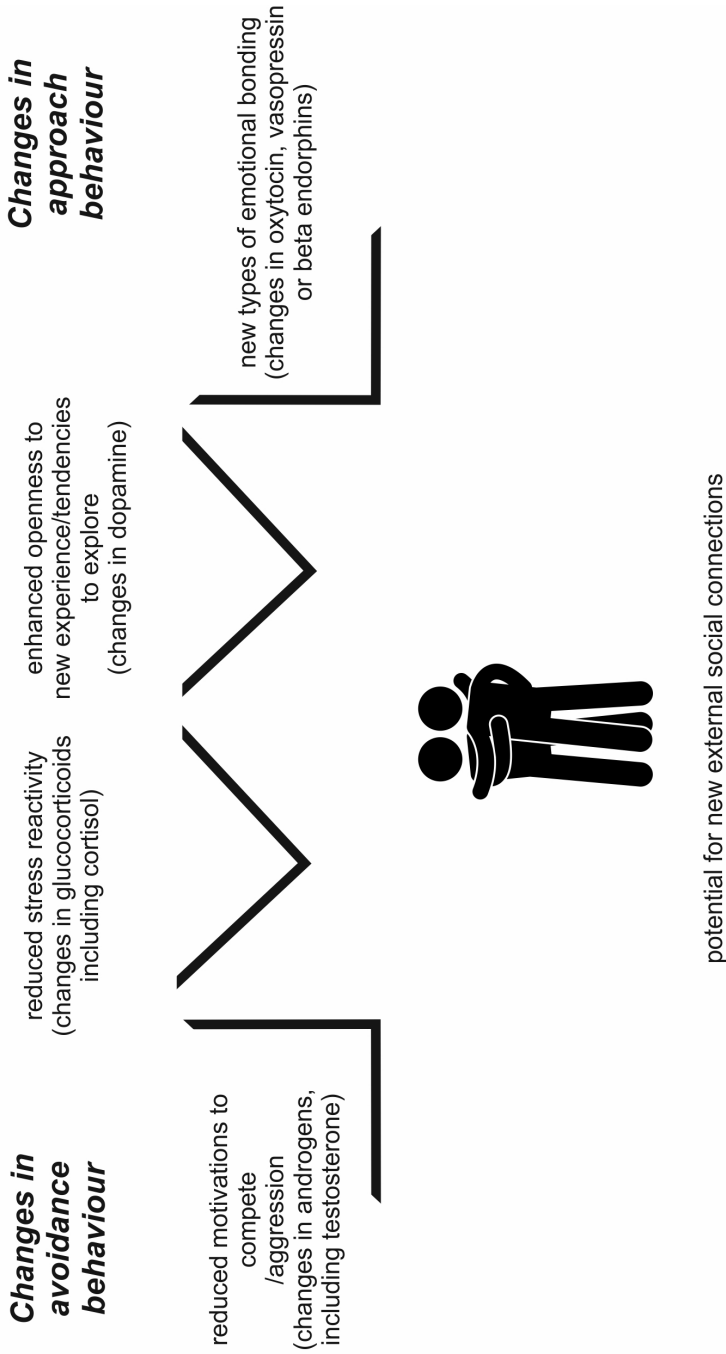


Figure 4.3: Changes in emotional dispositions involved in moving from constrained social groupings to large-scale social alliances. Penny Spikins, CC BY-NC 4.0.

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

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

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

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

Competition and aggression – the role of androgens

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

We know that variations in testosterone influence human social behaviour, so it only makes sense to conclude that changes in testosterone pathways over time would also change social behaviours on a larger scale. Tendencies in humans to collaborate or compete with strangers in economic games



show a relationship with individual variations in testosterone levels, for example. Those who tend to be most collaborative tend to have lower levels of testosterone than those who are more likely to adopt a selfish strategy (Eisenegger et al. 2017; Mehta et al. 2017). This is important, as long-term collaborations tend to depend on individuals being prepared to be generous rather than immediately selfish. Those with typically tolerant and collaborative personalities are also associated with lower levels of testosterone than individuals who display traits of narcissism such as extreme selfishness and self-centredness (Pfafftheicher 2016). Moreover, in an evolutionary context, reduced levels of testosterone are associated with increased levels of paternal care in species such as social carnivores (de Bruin, Ganswindt, and Roux 2016). We might reasonably expect selection pressures on testosterone to have been significant in changes in the balance of competition or collaboration in human evolution.

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

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

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

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

Chimpanzees are renowned for their tendencies to get into aggressive conflict with other groups, in contrast to more common patterns of avoidance in primates as a whole. Testosterone levels rise from infancy onwards, and



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

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

The apparent similarities may be superficial, however. Cases of human feuding tend to be skewed towards adolescent and young adult males, who are

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

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

Perhaps the most remarkable influence of social context is that testosterone has even been linked to increased generosity in humans, where a reputation for generosity is considered a mark of status and thus something worth competing for (Diekhof, Wittmer, and Reimers 2014). Moreover,



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

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

Differences between androgen responses in chimpanzees and bonobos undoubtedly help explain the capacities for intergroup collaboration in bonobos, as described at the introduction to this chapter. In contrast with common chimpanzees, intergroup encounters at the borders of bonobo groups are far less aggressive. Fruth and Hohmann (2018) estimated that intergroup encounters occur around one to three times a year amongst groups at LuiKotale, DRC, and sometimes involve threat displays, although actual aggression or violence is very rare. However, importantly, neighbouring groups sometimes forage together. Groups come into contact more

often when fruit trees at their shared boundaries are ripe, for example, with both groups exploiting the same fruit trees (Sakamaki et al. 2018). Most remarkable of all is the recorded instance of bonobos sharing food at the borders between groups, described in the introduction to this chapter. These individuals were clearly comfortable sharing with those from other communities, something that Fruth and Hohmann commented would be 'unthinkable' in chimpanzees (Fruth and Hohmann 2018: 99). It seems likely that differences in androgen levels between chimpanzees and bonobos had a major influence in the distinctions in intergroup behaviour between the two species. These might help us understand, therefore, how reduced tendencies towards aggression may also have played a part in changes in sociability in recent human evolution (Wrangham 2014; Wrangham 2018).

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

Fear, stress reactivity and cortisol

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

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



limits of where your group lives, such as by vocalisations or threat displays, and minimise interactions with other groups and warn unfamiliar individuals not to approach. Howler monkeys (genus *Alouatta* of the subfamily Alouattinae), for example, demarcate their territory through sound in an attempt to avoid other groups as much as possible.

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

Evolutionary reductions in stress reactivity can constrain fearful reactions and so promote approach behaviour. Reduced stress reactivity may be more important in changes in tolerance in domestic dogs than any changes in androgens, for example (Miklosi 2014). Cortisol levels are a key element to tameness in domesticated species, and cortisol levels are three to five times lower in ‘tame’ domesticated foxes than in wild ones (Trut, Oskina, and Kharlamova 2009), discussed in Chapter 5. Reductions in cortisol are also key to tolerance in humans. Studies show that human aggression has no simple relationship to testosterone but also appears to be mediated by stress reactivity through cortisol (Montoya et al. 2012). Increased tolerance in humans is thus likely to be a much more complex issue than simply reductions in androgens. The type of increased friendliness that promotes close

interactions with unfamiliar individuals seems to involve not just reductions in aggression but also reduced fear through reduced stress reactivity.

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

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

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



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

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

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

Goal seeking exploration and novelty – the influence of dopamine

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

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

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

Dopamine can play an important role in directing different behaviour between males and females. It is changes in dopamine and reward-seeking behaviour that allow individuals to overcome their reluctance to associate with members of other groups in the context of mating. At sub-adulthood, males or females (depending which sex moves, usually only one) experience novelty and risk as pleasurable, largely through changes in dopamine and actively seek out members of other groups. We can see this process in male



baboons. As a male baboon matures, their feel-good dopamine reward through novelty reduces, and they begin to seek higher and higher levels of novelty to feel any kind of thrill. When neighbouring groups meet, the males will threaten each other and then the groups will retreat, but the adolescent males may linger far longer, appreciating the novelty of the other group. Slowly, the individual will spend more time with the other group, until eventually they transfer groups (Sapolsky 2017: 162). Changing hormones at adolescence have changed how males *feel* about other groups.

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

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

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

appears from a male one. Females may stay within their own group most of the time, but at least sometimes venturing to associate with other groups is more appealing than scary.

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

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



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

Increases in the presence of particular dopamine variants may even be implicated in human dispersals after 100,000 years ago. One particular dopamine receptor variant, the 7R (seven repeats or the long allele version) form of dopamine DRD4, is particularly interesting. The 7R variant is associated with relative unresponsiveness to dopamine (i.e. greater thrills are needed for the same response) and is associated with a host of behaviours, including extraversion, exploratory behaviour, novelty seeking, promiscuity, less sensitive parenting, impulsivity and susceptibility to ADHD (Bakermans-Kranenburg and van Ijzendoorn 2006; Chen et al. 1999; Garcia et al. 2010). Polymorphisms in DRD4 predate the dispersal of modern humans out of Africa after 60,000 years ago (Chang et al. 1996; Chen et al. 1999; Ding et al. 2002; Kidd, Pakstis, and Yun 2014). Modern populations that undertake long migrations tend to have greater proportions than more sedentary populations of individuals with long alleles of the DRD4 gene, associated with novelty seeking and hyperactivity (Chen et al. 1999). Moreover, populations farthest from the African origin have the highest rates of the 7R variant associated with impulsivity and novelty seeking. The Ticuna, Surul and Karitiana, occupying the Amazon Basin, have a roughly 70% incidence of 7R variant; the Gujibha and Quechua of northern South America have an incidence of around 55%; and the Maya in Central America have an incidence of around 40%, with lower incidences in more northern populations of the Americas, for example (Ding et al. 2002; Matthews and Butler 2011; Sapolsky 2017). Individuals more prone to novelty seeking may be more likely to find the prospect of new regions alluring, and the familiar as boring, as well as being less prone to stress in novel situations. How they behave will, of course, be

influenced by culture, and what is novelty seeking and risk-taking in one society might seem tame in another. Equally, as with many subtle hormonal distinctions, differences bring both advantages and disadvantages. There will be contexts in which it may be beneficial to be more prone to novelty seeking, and in others where it is less so. Risk-taking, and a desire for novelty, might be beneficial overall in yielding rewards in terms of accessing new resources, or might be a disadvantage due to an increased mortality risk.

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

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

Bonding hormones

As we have seen in Chapter 1, bonding hormones play an important role in social bonding, motivating generosity, care for the vulnerable and altruism within close-knit social groups. Selection on neuroendocrine pathways, including oxytocin and serotonin, are associated with differences in social behaviour between chimpanzees and bonobos, for example (Kovalaskas,



Rilling, and Lindo 2020). Changes in oxytocin and beta endorphins are likely to have played a role in the expansion of compassion towards a broader set of group members that we saw occurring between 2 and 1.5 million years ago (Feldman 2017; Gordon et al. 2010). Oxytocin, in particular, is involved in social touch, grooming, and behaviours that facilitate strong emotional bonds, motivate generosity and altruism, and reduce stress (Snowdon 2011).

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

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

et al. 2015). Differing empathy between individuals mirrors, in some ways, the effects that increasing prosociality and tolerance have had on increasingly social sensitive humans in the later stages of human evolution.

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

Other related hormone changes are also significant, and attention has also particularly been drawn to changes in serotonin pathways. Serotonin is another hormone influencing our mood and social behaviour that is likely to have been subject to selection pressures in human evolution. It plays a role in influencing attachment styles (Gillath 2008) and propensities to obey or challenge social rules (Gelfand 2011; Mrazek et al. 2013). A particular polymorphism of serotonin influences social sensitivity and, with it, susceptibility to supportive or unsupportive environments within modern populations. Alleles within the 5-HTT linked polymorphic region confer greater plasticity to the effects of childhood mistreatment. One form is associated with greater empathetic perspective-taking in supportive environments but also brings disadvantage in terms of a higher risk of traits such as



depression or impulsivity in unsupportive or traumatic childhood environments (Flasbeck et al. 2019). As a result, those of us inheriting a tendency to be more socially sensitive, under the influence of genetic differences influencing the hormone serotonin, are both more severely affected by negative social experiences and more buoyed up by positive ones (Assary et al. 2020). The former have even been dubbed ‘orchids’ – so empathetic and highly tuned to the emotional and social tone of their environment that they are more deeply affected than others by cruelty, neglect or isolation, particularly in childhood, whilst the latter dubbed ‘dandelions’ are more resilient and better able to thrive regardless of their environment (Boyce 2016). Orchids do particularly well in supportive social environments, understanding others more fully and forming close social relationships, and particularly benefiting from the confidence and emotional wellbeing that such environments foster. However, they are more likely to do badly where such support is lacking. There seems to be an evolutionary balance between these alternative strategies – one (orchids) that is particularly successful in supportive environments and another (dandelions) more resilient to harsh social context. This polymorphism even influences our propensity to be prone to feeling nostalgic (Luo 2019) and, so, our tendencies to derive comfort from past (rather than present) experiences. Variations in serotonin pathways within populations provide a good example of how increasing social sensitivity is not simply an advantage but also sometimes a disadvantage depending on context.

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

As more genetic studies are undertaken, we are likely to have an even better understanding of the influence of these genetic changes on neurochemical responses. However, it is always wise to be somewhat cautious not to over-interpret genetic evidence. On the level of differences within populations we need to be particularly careful. There *are* differences *within* populations that are strongly influenced by inherited genetics, such as autism or dyslexia, that should not be ignored and which challenge us to be better at

understanding *different but equal* perceptions of the world (discussed in Chapter 3). However, we should not imagine that people with particular serotonin polymorphisms or particular oxytocin receptor genes or any other genetic difference affecting hormonal mechanisms could or should be identified as different. Such influences are only felt at population level and not at the individual, and are far less significant than culture, background or individual choice in how people behave. To begin to separate people according to these subtle genetic differences would be folly.

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

Selective pressures on human tolerance

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

Social influences on tolerance inevitably played some role in human evolutionary changes. However, there are other explanations. Amongst non-human apes and other primates, the ecological context plays a key role



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

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

Conclusions

We would be wrong to see the suspicion of unfamiliar individuals, which is so typical of most 'wild' animals, as equally natural to humans. Life in highly collaborative societies, discussed in Part 1, is likely to have set in place pressures for humans to simply be less aggressive than their distant ancestors. However, the changes in emotional dispositions that paved the way for the formation of recognisably human tolerance to unfamiliar individuals seem to have occurred relatively late in our evolutionary history. These changes were probably more complex than simply related to reduced aggression, and seem to have involved different hormonal pathways influencing

aggression, fear, excitement and anticipation and bonding. Though internal social processes may have played a part in these transformations, ecological factors may also have had an important role.

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

Key points

- Most animals tend to avoid unfamiliar individuals belonging to other kin groups, or are even aggressive towards them.
- Neuroendocrine responses influence systems of hormones that govern avoidance or approach behaviours, such as through feelings of safety and security, feelings of threat or desires to explore.
- Evolved physiological changes, such as reduced stress responses towards unfamiliar individuals, can be advantageous in situations where intergroup collaboration may be an advantage.
- Evolutionary changes affecting reductions in avoidance behaviours (such as through changes in androgens or stress reactivity) and enhancements of approach behaviours (such as changes in dopamine or bonding hormones) are implicated in changes in tolerance in recent human evolution.
- An increasing external tolerance or approachability in human responses towards unfamiliar individuals brings both advantages and disadvantages, including not only the possibilities of formation of large-scale social networks but also social sensitivities and emotional vulnerabilities.



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