

CHAPTER 5

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

Abstract

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

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

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

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



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

Introduction

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

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

interact with humans. This experiment remains the most remarkable example of rapid domestication of a wild animal yet recorded.

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

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

Though no experiments have ever quite matched those with silver foxes, there are other cases of similar changes under pressures for tameness, reduced aggression or tolerance in other animals. Rats selected for tameness show similar changes in face shape, for example (Singh et al. 2017). Even less forcefully directed selection pressures can create similar changes. A long-term study for over 14 years of free-living wild house mice in Switzerland exposed to human handling as pups also demonstrated changes associated with domestication, including a reduction in snout length and

change in pigmentation (Geiger, Sánchez-Villagra, and Lindholm 2018). What was particularly interesting about this latter study is that, in this case, mice were not being actively selected for aggression, simply being passively exposed to greater interaction with humans. They were always able to come and go as they wished, through holes in the barn used for the experiment. In a sense, then, perhaps these mice had ‘self-domesticated’ in response to a new adaptive niche in which food and freedom from predators was readily available as long as they could tolerate handling from humans. The same types of changes in snout length and braincase size, and in levels of sexual dimorphism, are even seen between rural and urban red foxes (*Vulpes vulpes*) in the UK, which match the changes occurring under ‘domestication syndrome’ (Parsons et al. 2020).

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

Human self-domestication?

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

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

increasing friendliness or tameness with anatomical changes, particularly to the shape of the face (Singh et al. 2017).

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

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

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

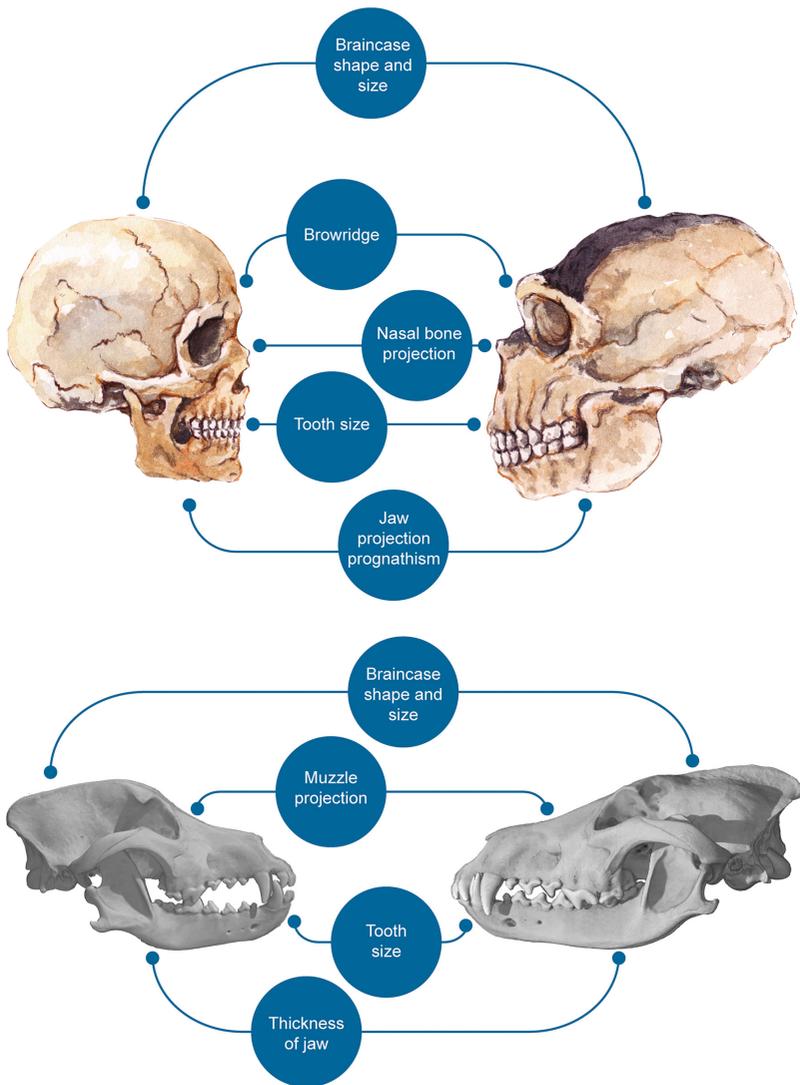


Figure 5.2: Salient craniofacial differences between modern humans (top left) and Neanderthals (top right), and between dogs (bottom left) and wolves (bottom right). The pattern of recent cranio-facial changes in modern humans (above) shows a remarkable similarity to that of domesticated animals such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

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

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

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

Implications

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

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

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

Complex social emotions are one particular example of our tendency to assume adaptedness. Complex social emotions, created through an interplay of both affective and cognitive empathy (discussed in Chapter 1), are important motivators of our behaviour. We feel social emotions, such as guilt or gratitude, because of our understanding of what other people think or feel about us, and our understanding of what is expected of us or them. These social emotions tend to motivate us to behave in prosocial ways that help others. We can make a plausible argument for why gratitude may have been selected for, starting with reciprocal relationships, which we see in

non-human primates, and becoming a basis for strong alliances based on give and take (Allen 2018). Certainly, gratitude plays an important function in our positive social relationships, encouraging support and mutual collaboration (Smith et al. 2017; Wood et al. 2010). Certain genes even predispose people to a greater likelihood of experiencing gratitude (vanOyen Witvliet et al. 2018). However, despite the advantages and link to particular genes, gratitude might equally simply be a side effect of changes in affective and cognitive empathy occurring for other reasons. Other complex social emotions, such as shame, do not even seem to serve even a useful function, with feelings of shame strongly associated with depression and motivating an unhelpful withdrawal from relationships (Gilbert 2000).

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

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

The advantages of increasing tolerance

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

Increasing tolerance has been argued to be associated with important developments such as reduced aggression and greater egalitarianism through levelling mechanisms (Wrangham 2019), increased collaboration (Hare 2017), more sophisticated language and communication (Thomas and Kirby 2018), enhanced self-awareness and creativity (Zwir et al. 2021), enhanced emotional expressivity in faces (Godinho et al. 2018), and even changes in body cognition, allowing more sophisticated tool use (Bruner and Gleeson 2019). Certainly, a new tolerance and capacity for external

social focus to human communities would have allowed connections to form between living groups and kin groups. At the same time, a reduction in stress reactivity accompanied by increased novelty seeking will have motivated the maintenance of distant social connections, reduced inbreeding, and created regional connected communities. Such connected communities, in turn, reduce the risks imposed by local resource shortfalls (Pisor and Surbeck 2019; Spikins et al. 2021). Forming external allies provides the possibility of creating large-scale resilient networks that buffer effects of ecological changes and, moreover, allow knowledge and culture to spread. Moreover, a certain playfulness, or attraction to novelty, may also at least partly explain extensive dispersions, and attraction towards new ways of doing things (discussed in Chapter 4).

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

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

A combination of increasingly challenging and increasingly fragmented environments seems to have driven particular selection pressures on both physical and social characteristics. In this period, we also see material evidence for increased mobility in certain regions of Africa in the form of raw materials travelling further away from the source until their eventual discard. These extended distances of raw material transport may reflect more

external-focusing social behaviours in human populations, and a greater ease with which longer-distance movements across many territories could take place. At around 300,000 years ago in the Olorgesailie basin in South Kenya, at a time of increasingly variable environments and periods of resource stress (Potts et al. 2018), we see raw material being procured from a wider area. From typically local raw material distance transfers of around five kilometres, we see new movements of obsidian of around 25 to 50 kilometres, and up to 95 kilometres in certain cases, implying interactions with neighbouring groups (Brooks et al. 2018). The distances over which materials are transported also increase in other regions. Middle Stone Age populations in the Kalahari imported preferred silcrete raw material from up to 295 kilometres, particularly during drier periods (Nash et al. 2013; Nash et al. 2016). Certain populations seem to be more mobile, and better able to negotiate moving through areas usually occupied by particular groups, or even exchanges with them.

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

Increasingly harsh environments, environmental unpredictability and landscape diversity may have been significant factors in changing the selective advantages and disadvantages of dispositions towards unfamiliar individuals. Unpredictable environments will have led to an increased frequency of shortfalls in resources. Diverse and fragmented landscapes reduce the synchronicity of shortfalls, however, as different groups would not all have experienced shortfalls at the same time (Campenni, Cronk, and Aktipis 2017). Moreover, optimum conditions for peaceful interaction between



groups occur in the most fragmented landscapes, as these are the contexts in which populations can control their interaction and maintain their own integrity (Rutherford et al. 2014). For human societies, pressures to share will have been exacerbated by a reliance on a far greater variety of resources – not only food and water but also flint raw materials for making tools, other resources such as salt (Pisor and Surbeck 2017) or even medicines (Spikins et al. 2021). Initially, changes in disposition towards unfamiliar individuals may simply have meant that interactions at the boundaries between living groups become more friendly and collaborative in nature, encouraging shared resource exploitation in these particular locations. Through time, the nature of intergroup collaboration could have become more sophisticated and, in turn, more effective in reducing the impact of unpredictable resources and frequent shortfalls (discussed in Spikins et al. 2021).

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

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

diversity, resilience to resource shortfalls and the cultural transmission of innovations (Spikins 2021).

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

The constraints and disadvantages of increasing tolerance

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

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

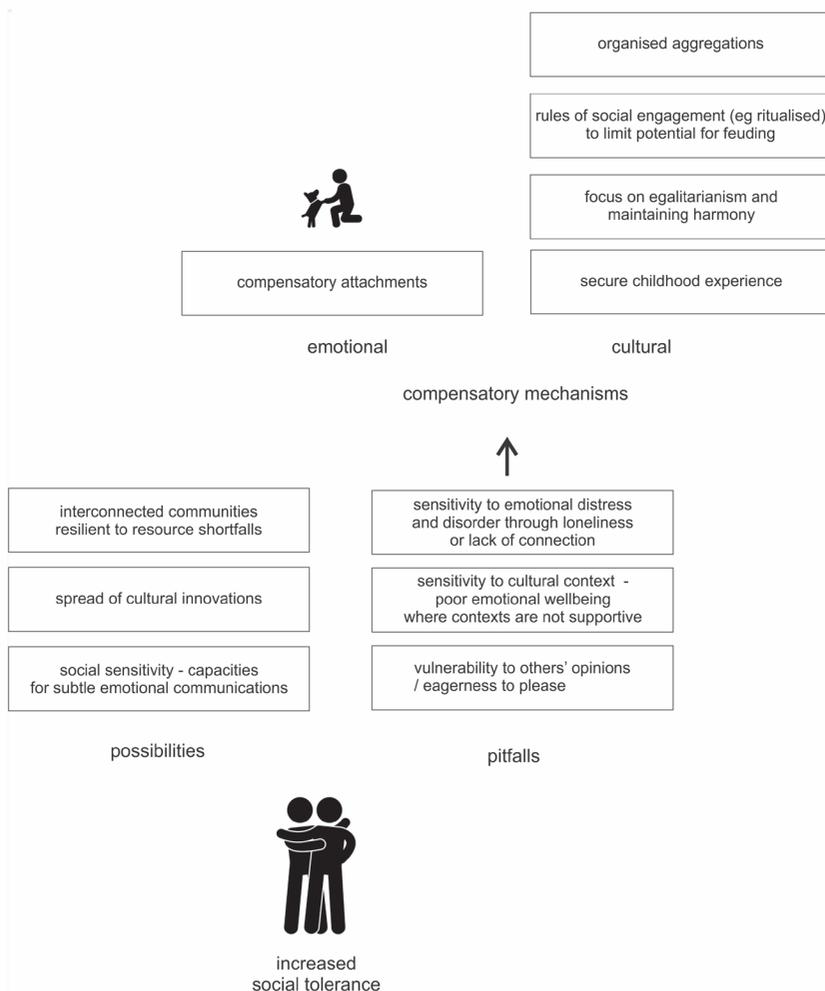


Figure 5.3: Representation of new styles of community connection developing in recent human evolution through neuroendocrine changes, leading to greater external tolerance and approachability. Penny Spikins, CC BY-NC 4.0.

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

Most obviously, direct effects of recent genetic changes influence human vulnerability to specific emotional and cognitive disorders. Recent changes

in neurological plasticity are associated with the emergence of a greater number of deleterious alleles, bringing heightened susceptibility to the appearance of abnormalities, particularly those affecting cognition (Castellano et al. 2014; Cruz, Vilà, and Webster 2008; Theofanopoulou et al. 2017).

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

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

Because of recent changes in human evolution, we are all remarkably sensitive to the effects of loneliness, which has an even more pronounced effect on health than obvious physical onslaughts such as smoking (Holt-Lunstad

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

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

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

<p>PHYSIOLOGICAL</p> <p>Attachment insecurity leads to:</p> <ul style="list-style-type: none"> – increased distress at stressful events (Mikulincer and Florian 1998) – greater physiological reaction to betrayal (Lawler-Row et al. 2006) – increased cortisol levels (Jaremka et al. 2013) – increased feelings of pain (Davies et al. 2009) – impairments in immune system function (Gouin and MacNeil 2019; Jaremka et al. 2013)
<p>COGNITIVE/EMOTIONAL</p> <p>Attachment insecurity leads to:</p> <ul style="list-style-type: none"> – reduced abilities to regulate emotions (Mikulincer and Shaver 2018) – reduced ability to suppress negative thoughts (Gillath et al. 2005) – greater propensity to depression and anxiety (Bejinaru 2017) – reduced confidence to explore new situations and new relationships (Feeney and Van Vleet 2010) – reduced creative problem-solving (Mikulincer, Shaver, and Rom 2011) – increased reaction of amygdala to threats (Norman et al. 2015) – impaired prefrontal cortex development (Insel and Winslow 2011; Strathearn 2018)
<p>SOCIAL DYNAMICS</p> <p>Attachment insecurity leads to:</p> <ul style="list-style-type: none"> – reduced compassionate helping (Gillath, Shaver, and Mikulincer 2005; Mikulincer et al. 2005) – a negative (vs positive) slant on others motivations (Mikulincer and Shaver 2005) – increased negative orientation towards out-groups (Mikulincer and Shaver 2001; Saleem et al. 2015) – greater conflict and violence in romantic relationships (Mikulincer and Shaver 2005) – reduced tendencies to forgive offences or betrayal (Lawler-Row et al. 2006)

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

caring) social actors in their imagined worlds during their degree. Marwell and Ames (1981), Frank et al. (1993), and more recently Bauman and Rose (2011), explored these effects in now-famous studies. They found that,

as they progressed through their degree, undergraduates in economics became less able to share and develop relationships based on trust, and less willing to contribute to the public good. Effectively, they changed their internal emotional schema towards social relationships, arguably becoming better prepared to survive in their perception of a self-oriented social environment around them. Despite thinking of ourselves to be individual independent beings, resilient to the opinions or attitudes of others around us, we are surprisingly vulnerable to the emotional tone of the social context we have experienced in the past and the one we live in today.

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

Compensatory mechanisms

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

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

We may think of our emotional vulnerabilities, and the risks they bring of pain and suffering, as weaknesses, but they exist through being essential to a shared communal strength and resilience against hard times. Connected communities would probably not have been possible without emotional vulnerabilities driving a need to connect to others and to belong to a larger community, the desires to feel valued, or concerns about reputation. As we explore in Chapters 8 and 9, other pathways with equally viable, albeit less connected, ways of living also existed. However, modern human ancestors built on motivations to care for others (discussed in Chapters 1 and 2) with recent changes in tolerance, adding further drives for new types of emotional connection. Because we need to belong and make wide social connections, we seek out others beyond our local group when, without such needs, we might be content with our local kin. Because we are driven to explore, we like to meet new and different peoples. Because we are sensitive to others' judgements, we seek to fulfil social roles and be accepted

and respected. Because we are prone to loneliness, we seek extensive networks of friends and allies. Even expressions of vulnerability themselves promote trust and social connection (Evans and Krueger 2009; Strohkorb Sebo, Traeger, and Jung 2018). Furthermore, changes in human face shapes over the last 100,000 years allow much greater expression of emotions that make us vulnerable, such as insecurity or sympathy (Godinho, Spikins and O'Higgins 2018).

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

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

same way to bolster confidence and wellbeing at times of insecurity. These compensatory attachments are extraordinarily rare, if even ever recorded, in other animals.

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

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

Conclusions

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

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

Transformations in tolerance and friendliness appear to have been key to enabling connected communities to emerge, providing resilience to resource shortfalls through sharing beyond local groups. In turn, connected communities allow for innovations to spread rapidly, enabling quick technological responses to environmental changes. However, increasing social tolerance also brings disadvantages. Social sensitivity during development leaves individuals vulnerable to unsupportive contexts, with insecure

attachments having widespread effects in many different realms of social life and even physical health. Compensatory cultural mechanisms to facilitate social connections such as aggregations may have partly mitigated these vulnerabilities. Equally, compensatory attachments to non-human beings may also have provided emotional comfort at times of stress.

Key points

- Human emotional capacities and tendencies towards increased tolerance in recent human evolution (after 300,000 years ago) seem to have followed similar paths to those seen in domesticated and self-domesticated species, with similar changes seen in anatomical and genetic evidence.
- The reasons for human 'self-domestication', as well as precisely what this means, remain debated.
- At the scale of human communities, increases in social tolerance provide the basis for the emergence of large-scale interconnected societies, which are resilient to resource shortfalls and are technologically responsive to ecological changes.
- At the scale of individuals, increased tolerance brings remarkable emotional sensitivities, but also vulnerabilities to the effects of insecure or unsupportive development.
- Compensatory attachments beyond those to other people may have emerged to provide additional emotional support at times of stress.

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