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To beard, or not to beard: linking sexual selection on masculinity, embryonic neural crest cells, and human self-domestication.

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Keywords

Sexual Selection, Masculinity, Neural Crest Cells, Human Self-domestication, Immunocompetence, Beardedness.

Abstract

Masculinity in human males is expressed in morphology, vocal pitch, body odour, and testosterone levels, as well as through behavioural predispositions, including competitive status striving, aggressive reactivity, and high reproductive effort at the expense of paternal investment. As this article shows, these masculine secondary sexual traits are linked to the activity of embryonic neural crest cells (NCCs). Since downregulation of NCC function is the physiological cause of mammalian domestication syndrome, it follows that any selection in favour of low masculinity would promote a process of human self-domestication. As such, future research into sexual selection on masculine traits will benefit from an appreciation of embryonic NCC functioning, and consideration of the evolutionary implications of human self-domestication. This article integrates two longstanding fields of scientific interest by revealing the physiological mechanisms of sexual selection on human masculinity, and explaining how these effect evolutionary changes associated with self-domestication. In doing so, it offers a succinct and compelling explanation of the 'good genes' theoretically provided by masculine individuals, and explains a peculiar human behaviour, the shaving of facial hair.

1. Introduction

This article has two principle aims. The first is to demonstrate that all secondary sexual characteristics previously identified as signals of masculinity in human males can be associated with the activity of embryonic neural crest cells (NCCs). The second is to explain how, since domestication (a physiological process characterised by a recognised syndrome of heritable traits) is known to be driven by downregulation of NCCs, differential selection on masculine traits must also cause varying levels of human self-domestication. These

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interactions have important implications which can explain apparent heterochrony in human evolution, theorised selection in favour of 'good genes', and preferences for, or against, beardedness.

1.1. NCCs and the domestication process

NCCs are a transient and pluripotent lineage of embryonic cells involved in the formation of the vertebrate neural tube (Gilbert, 2010; Hall, 2010). Following neural tube formation, NCCs disperse along predetermined pathways within the developing vertebrate embryo and provide cellular progenitors for a variety of different structures and tissue types. These include the bones, muscles and connective tissues of the craniofacial region and shoulder, the bones of the middle ear, the teeth, the hyoid and the larynx, as well as important glands including the adrenal medulla, anterior pituitary, and thymus, plus various nerve structures, and parts of the vertebrate heart (Gilbert, 2010; Hall, 2010; Schoenwolf, Bleyl, Brauer, & Francis-West, 2008; Ueharu et al., 2017). Because of this wide range of contributions, the functional activity of NCCs has a considerable influence upon the morphology, physiology and behaviour of all vertebrate taxa.

Recent scientific research indicates that downregulation of NCCs is the physiological cause of 'domestication syndrome' (Wilkins, Wrangham, & Tecumseh Fitch, 2014), a diverse group of traits that domesticated animal populations share in common when compared to their wild relatives or ancestors. These traits include: less aggression, lower sexual dimorphism, less prognathism, more gracile skeletons, smaller teeth, changes in pigmentation, paedomorphism, and altered reproductive regimes (Hemmer, 1990; Leach, 2003; Trut, 1999; Wilkins et al., 2014). Domestication syndrome was first identified and discussed by Charles Darwin (1868), who collected observations of domesticated animals as part of his evidence for the theory of natural selection. Following Darwin, other authors have noted that modern *Homo sapiens* appear to have been self-domesticated since, when compared to the fossil record of our species, we share a number of the traits seen in domesticated animal populations (Brüne, 2007; Cieri, Churchill, Franciscus, Tan, & Hare, 2014; Fischer, 1914; Groves, 1999; Leach, 2003; Lorenz, 1940). Recent work on human self-domestication has identified female mating preferences as a possible driver of this process which has promoted human sociability and cooperation, thereby dramatically expanding our capacity for knowledge sharing and technological innovation (Cieri et al., 2014; Hare, 2016).

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Selection against aggressive reactivity (analogous to a diminished 'fight or flight' response) is the known cause of mammalian domestication syndrome (Belyaev, 1979; Trut et al., 2006; Trut, Oskina, & Kharlamova, 2001; Wilkins et al., 2014), including in our close primate relative, the bonobo (Hare, Wobber, & Wrangham, 2012). This selection operates by causing a heritable tendency to a smaller and less responsive adrenal system (Sánchez-Villagra, Geiger, & Schneider, 2016; Wilkins et al., 2014), a trait long recognised among domesticated animal populations (Hemmer, 1990). The underlying cause of adrenal size reduction is the suppressed function of embryonic NCCs which form the adrenal medulla and other parts of the autonomic nervous system (Wilkins et al., 2014). This reduction diminishes physiological fight or flight responses, and other forms of autonomic reactivity driven by the Hypothalamic-Pituitary-Adrenal (HPA) axis. As such, selection for less aggression produces a heritable reduction in NCC functioning and, since NCCs provide the basis for a wide range of other derived cell types and biophysical structures (Gilbert, 2010; Hall, 2010), their downregulation promotes the diverse range of relatively benign hypoplasic characteristics associated with domestication (Wilkins et al., 2014) (Figure 1).

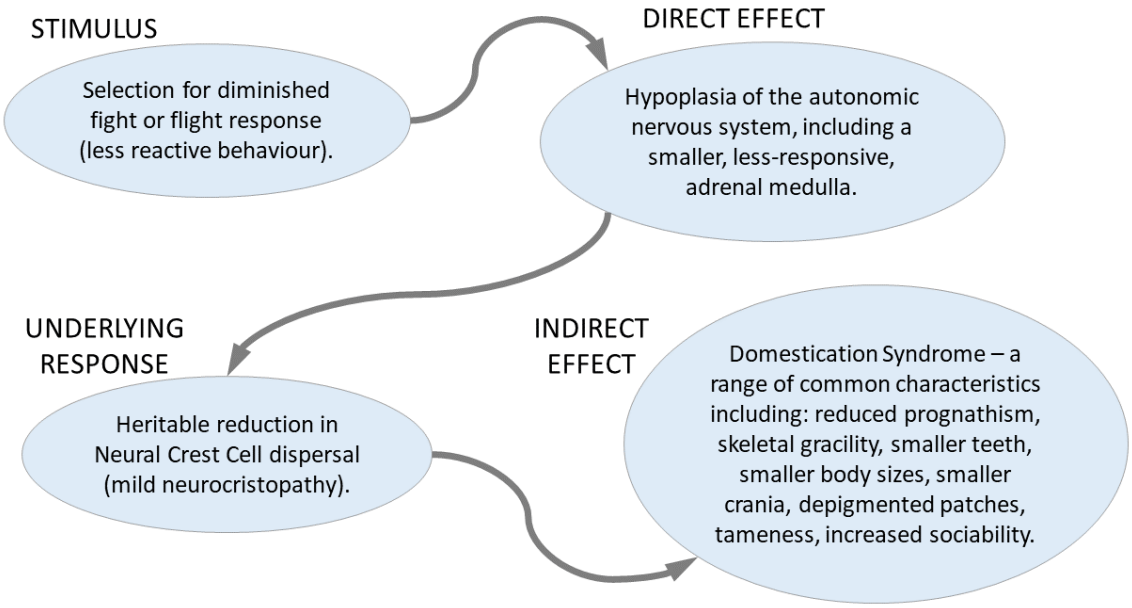

Figure 1: Chain of influence in mammalian domestication from Stimulus (selection for less reactive behaviour) to Indirect Effect (Domestication Syndrome) (based on Trut et al., 2006, 2001; and Wilkins et al., 2014).

1.2. Intersexual selection on human masculinity

The overarching goal of research into sexual selection for masculine traits has been to examine processes of human mate choice and sexual competition, and to understand how these influence human evolution and behaviour. Masculine morphological traits have been

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associated with certain behavioural predispositions, and both morphology and behaviour have previously been linked to elevated androgen levels, especially higher testosterone (Book, Starzyk, & Quinsey, 2001; Booth & Dabbs, 1993; Carré, McCormick, & Mondloch, 2009; de Almeida, Cabral, & Narvaes, 2015; Kruger, 2006; Lefevre, Lewis, Perrett, & Penke, 2013). In this context, masculine behaviours include competition and dominance behaviour, status striving, and relatively higher reactive aggression, as well as preference for multiple partners, and lower inclination to pair bond or provide paternal investment (Booth & Dabbs, 1993; Dibble, Goldey, & Anders, 2017; Goetz et al., 2014; Kruger, 2006; Puts, 2016; Quist et al., 2012; Wilson & Daly, 1985).

Previous research examining women's preferences for masculine traits has demonstrated variation linked to the menstrual cycle and whether long or short-term relationships are sought (DeBruine, Jones, Frederick, et al., 2010; Gangestad & Thornhill, 2008; Little, Saxton, et al., 2010; Little, Jones, & Burriss, 2007; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999; but see Harris, 2013; and Wood, Kressel, Joshi, & Louie, 2014). Related study has suggested masculinity preferences are enhanced under conditions of high pathogen presence (DeBruine, Jones, Crawford, Welling, & Little, 2010; Little, DeBruine, & Jones, 2010), which implies masculine fathers provide some fitness or survival benefit to offspring. Other authors have noted these preferences are higher under conditions of elevated social inequality (Brooks et al., 2010), suggesting women prefer dominant males where low social status could be detrimental to resource access. Further, whilst women's preferences for masculinity are unaffected by depictions of agonistic encounters between males, they are significantly reduced after seeing images of male-on-female aggression (Li et al., 2014). Together, these observations support the expectation that women are adaptively predisposed to make context dependant mating decisions between males with either 'good genes', or those with a higher propensity for pair-bonding and paternal investment (Kruger, 2006; Little, Connely, Feinberg, Jones, & Roberts, 2011; Quist et al., 2012; Trivers, 1972)

In this article, I outline the links between masculinity and NCCs, and explore some of the implications of these biophysical connections with reference to previous research on human sexual selection and self-domestication. I discuss some important ramifications of these observations, especially regarding: ontogenetic processes, including paedomorphism and heterochrony, female selection for 'good genes' and their influence on immunocompetence, and preferences for or against beardedness in human males. I conclude with a discussion of

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the implications of these insights for an expanded understanding of human self-domestication, its role in human evolution, and the construction of our social-niche-based modes of existence.

2. Masculine human traits and NCCs

The role of NCCs in the emergence of domestication syndrome is of singular significance to research regarding intersexual selection on human masculinity because, as this article describes, all previously identified masculine traits result from, or are substantially influenced by, the activity of embryonic NCCs (Table 2). For example, NCCs provide the progenitors of the craniofacial region, including: the frontal bone (and associated brow ridges), the mandible and maxilla, nasal bone and cartilage, and the zygomatic arches, as well as all associated muscle and connective tissues (Cordero et al., 2011; Gilbert, 2010; Knight & Schilling, 2013). As such, they form the cellular foundation for all indicators of facial masculinity discussed by previous authors (e.g. Carré et al., 2009; Cieri et al., 2014; Feinberg, DeBruine, Jones, & Little, 2008; Mitteroecker, Windhager, Müller, & Schaefer, 2015). Further, NCCs compose the larynx and hyoid (Gilbert, 2010; Schoenwolf et al., 2008), as well as the styloid process (Bhatt, Diaz, & Trainor, 2013), an attachment site for muscles which control the tongue and larynx, suggesting their diminished function will influence vocal qualities, including voice pitch, another recognised indicator of relative masculinity (Feinberg et al., 2008; Puts et al., 2016; Puts, Jones, & DeBruine, 2012). With regard to masculine body proportions, especially the shoulder-to-hip ratio (Lee, Brooks, Potter, & Zietsch, 2015; Windhager, Schaefer, & Fink, 2011), NCCs contribute substantially to the development of the neck and shoulder regions (Matsuoka et al., 2005), forming the clavicle and scapula, and thereby influencing the relative size and robusticity of these skeletal components.

Table 1: Masculine traits and their relation to the function of NCCs.

Masculine trait	Previously discussed by…	Direct influence of NCCs
Facial masculinity	Mitteroecker et al. (2015); Carré et al. (2009); Lefevre et al. (2013).	NCCs form all of the facial skeleton, including the frontal bone, mandible, maxilla, zygomatics, and nasal structures, as well as associated cartilage, muscle, and connective tissue (Bhatt et al., 2013; Cordero et al., 2011; Santagati & Rijli, 2003; Schoenwolf et al., 2008).
Large brow ridges	Dixson (2016)	NCCs provide cellular progenitors of the frontal bone, which includes the supra-orbital region of the skull (Mishina & Snider, 2014; Santagati & Rijli, 2003; Schoenwolf et al., 2008).
Facial hair	Dixson and Brooks (2013); Dixson et al. (2017); Dixson et al. (2017).	NCCs produce the facial dermis including associated hair follicles (Jinno et al., 2010; Krause et al., 2014; Schoenwolf et al., 2008) and also affect testosterone levels via the HPG axis due to NCC formation of the anterior pituitary (Hall, 2010; Schoenwolf et al., 2008; Ueharu et al., 2017).
Low vocal pitch	Feinberg et al. (2008); Puts et al. (2016); Puts et al. (2006).	NCCs provide progenitor cells of the hyoid, larynx, and the styloid—the anchor point for tongue and larynx muscles (Bhatt et al., 2013; Mishina & Snider, 2014; Wilkins et al., 2014).
High shoulder to hip ratio	Lee et al. (2015)	NCCs provide progenitor cells of the shoulder bones (i.e. clavicle and scapula) as well as associated muscle (Matsuoka et al., 2005).
		Indirect influence of NCCs via HPG axis and testosterone[1]
Competitiveness and aggression	Book et al. (2001); Almeida (2015)	NCC contributions to the adrenal gland and anterior pituitary (Ueharu et al., 2017) will influence the activity of both the HPA[2] and HPG[3] axes which stimulate the sympathetic nervous system, and influence testosterone and cortisol production respectively, thereby driving a wide range of traits, including: aggression, competitiveness, and status striving behaviours (Casto & Edwards, 2016; Eisenegger, Haushofer, & Fehr, 2011; Montoya, Terburg, Bos, & van Honk, 2012; Salvador, 2012); as well as higher male reproductive effort, in humans (Alvergne, Faurie, & Raymond, 2009; Burnham et al., 2003), and in primates generally (Muller, 2017). Testosterone increases risk-taking behaviour in a range of contexts (Apicella et al., 2008; Wilson & Daly, 1985). It also determines hair thickness, length, and growth rate (Ebling, 1986; Hall, 2010). Its production and subsequent breakdown determines levels of aromatic androstenone and androstenol 'pheromones' produced by apocrine glands (Grammer, Fink, & Neave, 2005; Hall, 2010).
Low pair-bonding and paternal investment.	Booth and Dabbs (1993)	
Risk prone behaviour	Apicella et al. (2008); Wilson and Daly (1985).	
General bodily hairiness	Dixson (2016); Dixson and Rantala (2016).	
Male scent	Grammer (1993); Grammer et al. (2005); Thornhill et al. (2013).	

[1]NCC influence upon the HPG axis is described in more detail within the main text. [2]HPA=Hypothalamic-Pituitary-Adrenal. [3]HPG=Hypothalamic-Pituitary-Gonadal.

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NCCs also form multiple aspects of the peripheral nervous system, including all sympathetic and parasympathetic ganglia, and the adrenal medulla (Gilbert, 2010; Wilkins et al., 2014). As such, suppressed activity of embryonic NCCs will moderate propensity for autonomic reactivity effected by the Hypothalamic-Pituitary-Adrenal (HPA) axis (Wilkins et al., 2014), especially the so-called 'fight or flight' response, associated with levels of reactive (versus 'pro-active') aggression (Weinshenker & Siegel, 2002; Wrangham, 2014). Furthermore, NCCs have been shown to contribute to the development of the anterior pituitary, and its various hormone-secreting cells (Ueharu et al., 2017). This latter, recently identified, contribution strongly suggests that NCC function influences levels of HPA axis reactivity via contributions to both the adrenal *and* the pituitary glands.

Perhaps most importantly however, NCC contributions to the anterior pituitary also implicate these cells in the functioning of the Hypothalamic-Pituitary-Gonadal (HPG) axis. This is highly significant in the context of human masculinity since it provides a proximate link between NCCs and the production of testosterone in men. Aside from small quantities produced by the NCC-derived adrenal medulla, most male testosterone is produced within the Leydig cells of the testes (Hall, 2010). Whilst it has been recently hypothesised that Leydig cells are themselves derived from NCCs, to date this has not been conclusively demonstrated (Shima & Morohashi, 2017). This interesting potential aside however, testosterone production within Leydig cells is known to be triggered by the release of luteinising hormone from the anterior pituitary (Hall, 2010). Therefore, the fact that this important gland does receive significant input from NCC lineages suggests a functional link between the downregulation of embryonic NCCs, lower production of luteinising hormone as part of the HPG axis, and lower levels of testosterone in males.

A connection between downregulation of NCCs, domestication syndrome, and the HPG axis was previously hypothesised by Wilkins et al. (2014) in their discussion of the shifted timing of reproductive physiology among domesticated female foxes. However, those authors did not consider the effect of suppressed NCC activity upon the HPG axis of *male* foxes, nor upon the production of testosterone. Given that testosterone production influences a wide array of male secondary sexual traits across vertebrate taxa, increased understanding of this NCC connection is likely to prove insightful across a range of biological research areas. Most studies concerning masculine human male traits have assumed relative levels of testosterone as their ultimate determining cause (e.g. Apicella et al., 2008; Feinberg, Jones, Little, Burt, &

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Perrett, 2005; Peters, Simmons, & Rhodes, 2008; Scott, Clark, Boothroyd, & Penton-Voak, 2013). However, NCC-influence upon HPG axis regulation of testosterone provides a clear physiological link between variation in NCC function and all male traits previously correlated with this influential hormone. Interestingly, the nature of this link suggests testosterone levels will show only correlation (in contrast to causation) with many male secondary traits. This distinction may explain inconsistencies in previous research findings on the connections between testosterone and masculine human morphology, as well as between testosterone and immunocompetence (Peters et al., 2008; Scott et al., 2013)—discussed further below.

Another major implication of NCC contributions to the anterior pituitary is that their downregulation should logically affect the pituitary's production of growth hormones. As a result, diminished embryonic NCC functioning should moderate the size and developmental timing of multiple organs and bodily structures. It follows that variation in NCC activity could explain the altered ontological development previously observed in multiple evolutionary studies and commonly described as a process of 'heterochrony' (Alberch, Gould, Oster, & Wake, 1979; Gould, 1966, 1977; Hanken, 2015). This effect is likely to account for the common occurrence of paedomorphism among domesticated mammalian populations (Leach, 2003) where NCC downregulation is known to occur (Wilkins et al., 2014), and may also explain apparent paedomorphism in humans (Gould, 1977; Groves, 1989; Perrett et al., 1998; Shea, 1989; Zollikofer, 2012). Furthermore, disproportionate downregulation of male growth hormone would account for lower size sexual dimorphism commonly seen among animal domesticates (Helmer, Goucherin, Monchot, Peters, & Sana Segui, 2002; Zeder, 2008, 2012; Zohary, Tchernov, & Horwitz, 1998). Notably, NCC influence upon growth hormone levels, when coupled with their direct cellular contribution to various structures throughout the body, implies that their downregulation would simultaneously influence both heterochrony *and* heterotopy, the two fundamental aspects of evolutionary change discussed by evo-devo scholars since Haeckel's description of these terms in the mid-nineteenth century (Hanken, 2015; Zelditch, Sheets, & Fink, 2000).

3. Masculinity, good genes, and selection on immunocompetence

Embryonic NCCs are also known to provide the cellular progenitors for the vertebrate thymus, a glandular organ which matures and releases T-cells involved in bodily immune response (Gilbert, 2010; Hall, 2010). As such, varying levels of NCC activity should directly moderate capacity for T-cell production, with significant implications for the functioning of

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the immune system; at least until puberty, when the thymus and its influence begins to decline. This implies that relatively masculine individuals will have better functioning childhood immune systems, and that intersexual selection in favour of masculinity would confer this relatively elevated immunity upon offspring—a particular benefit for sons given their consistently higher mortality curves (Klein, 2000). Elevated immunity up until puberty could also explain higher body and facial symmetry observed in masculine males since asymmetry is thought to be caused by pathogenic influences during early development (Little et al., 2008; Møller & Swaddle, 1997; Thornhill & Gangestad, 1999). Improved childhood immunity would provide an entirely sufficient explanation of the 'good genes' theoretically offered by masculine individuals and sometimes preferred by females in lieu of propensity for paternal investment. It would also be consistent with women's elevated preference for masculinity under high pathogen load (DeBruine, Jones, Crawford, et al., 2010; Little, DeBruine, et al., 2010) and high social inequality (Brooks et al., 2010); the latter perhaps due to high infant mortality where resource access, hence childhood nutrition, is poor.

However, this explanation of selection for good genes contrasts somewhat with a suite of existing theories associated with 'the handicap principle' (Zahavi, 1975; Zahavi & Zahavi, 1999). According to these related perspectives, masculine traits should provide a 'costly signal' in the form of a relative survival handicap, and thereby imply superior genes capable of survival despite this handicap. That is, according to these theories, cryptic and unspecified 'good genes' are advertised by overt display of traits that are inherently bad—for instance, signals of compromised immunity; in self, and in offspring. These perspectives have been widely applied in studies across multiple taxa. For instance, previous biological research suggests that bright and sexually attractive colours in male birds must be an indication of a handicap, with testosterone-related immunity suppression, and high parasite load, both having been suggested as underlying mechanisms (Folstad & Karter, 1992; Hamilton & Zuk, 1982). Research and debate continues regarding associations between immunocompetence and male secondary sexual traits (e.g. bright feathers, or human masculinity) with the publication of many contradictory results (see reviews by: Foo, Nakagawa, Rhodes, & Simmons, 2017; Roberts, Buchanan, & Evans, 2004; Scott et al., 2013).

In support of the alternative hypothesis suggested here, it seems pertinent to note that many male secondary sexual characteristics, including colour producing melanocytes in vertebrate feathers, skin, and pelage, are directly derived from embryonic NCCs. As such, whilst more

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brightly coloured feathers may correlate with testosterone level (see the NCC-HPG axis connection discussed in Section 2), they also provide a direct indication of elevated embryonic NCC function, and should, therefore, associate with a larger thymus, higher T-cell production, and relatively elevated juvenile immunocompetence. As mentioned, this effect would provide a succinct and sufficient explanation for any female preference for NCC-associated male secondary traits; including cues of masculinity in humans. As such, similar mechanisms may motivate female preferences across most, if not all, vertebrate taxa. Further empirical research into associations between NCCs, the vertebrate thymus, and juvenile immune system function may prove illuminating regarding any theoretical discrepancies between this succinct hypothesis and the wide range of others currently associated with the handicap principle.

Of note regarding selection on masculine human immune systems, Boothroyd et al. (2017) recently found a significant non-linear correlation between facial masculinity and offspring survival in two traditional human societies. In this study, moderately masculine fathers were found to have lower offspring mortality than those with both relatively low, or relatively high, masculinity (Boothroyd et al., 2017). This appears to demonstrate the limits to offspring survival from either theoretical extreme on the continuum between men with 'low masculinity, low immune function, but higher inclination to paternal investment', and those with 'high masculinity, high immune function, but low paternal investment'. Further, it suggests a centralised optimum of masculinity with regard to offspring survival, as well as a degree of stabilising selection, with implications for the adaptiveness of any female masculinity preference (Boothroyd et al., 2017).

This apparent trade-off in the relative fitness of highly masculine males is pertinent to discussions around good genes and immunocompetence because most permutations of the handicap principle suggest secondary sexual traits (such as masculinity in humans) will inflict a specific cost upon individuals that possess them (Folstad & Karter, 1992; Hamilton & Zuk, 1982; Zahavi, 1975; Zahavi & Zahavi, 1999). However, where an alternative reproductive strategy is forgone, 'good genes' need only inflict an opportunity cost rather than imposing a direct handicap upon the individual male. In humans, this would occur if, as is expected, high masculinity meant a trade off against capacity for paternal investment. In this case, highly masculine males incur an opportunity cost by foregoing potential fitness benefits from increased investment. Essentially, the existence of two mutually exclusive strategies removes

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any logical requirement for *costly* signalling of good genes, instead requiring only a signal of relative propensity for one strategy or the other. A further implication of this perspective is that the 'goodness' of masculine genes will be context dependant; that is, the relative benefits of masculinity will vary in accord with the specific advantages of the 'masculine non-investment' strategy under a given set of environmental, or social, conditions.

4. NCCs, masculinity, and male beardedness

Regarding recent investigation into men's and women's preferences for beardedness (Dixson & Brooks, 2013; Dixson, Lee, et al., 2017; Dixson, Rantala, et al., 2017; Neave & Shields, 2008), it is interesting to note two significant ways in which NCC function affects men's capacity for the growth of facial hair. The first is via indirect NCC influence upon the pituitary and its regulation of testicular testosterone production (Section 2) since it has been established that testosterone affects the length, thickness, and rate of hair growth (Ebling, 1986; Hall, 2010). The second provides a far more direct relationship since, along with their role in the formation of the facial skeleton, cranial NCCs have been shown to form the vertebrate facial dermis, including its associated hair follicles (Jinno et al., 2010; Krause et al., 2014; Schoenwolf et al., 2008). Because of this, the various qualities of a man's natural coverage of facial hair (Figure 2) provide an indication of his relative level of embryonic NCC function, and, therefore, should correlate with his overall physiological masculinity.

Figure 2: Two full-grown beards. Left: Che Guevara, aged 31. Right: Karl Marx, aged 43. Wikimedia Commons (2017).

It follows that for potential female partners, the natural coverage and density of a man's beard may help to indicate his likelihood of competitive success and his relative status, as well as his predisposition to a given reproductive strategy; especially willingness to invest paternal resources, or not. Logically, the qualities of a man's facial hair will also provide a signal to other males indicating relative propensity for competitiveness and dominance behaviours; or, conversely, capacity for sociable and cooperative interaction. In accord with these

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expectations, previous studies of male and female responses to bearded faces have found perceptions of aggression, competitiveness, and elevated social status were all enhanced by the presence of beards (Dixson, Lee, et al., 2017; Dixson & Vasey, 2012; Neave & Shields, 2008). Contrastingly however, research into female attraction to bearded faces has shown inconsistent results, with higher female preferences observed for every stage of beard growth, including: clean shaven (Dixson & Vasey, 2012), bearded (Pellegrini, 1973; Reed & Blunk, 1990), and intermediate stubble (Dixson & Brooks, 2013; Neave & Shields, 2008).

Given multiple techniques used to assess these preferences, it seems likely any discrepancies result from methodological or theoretical inconsistencies. For instance, if capacity for beard growth is an indication of embryonic NCC function (and, hence, overall physiological masculinity), then test materials showing heavily bearded individuals at various stages of growth are unlikely to reveal processes of adaptive selection. Since capacity to grow a thick beard should correlate with other masculine facial features, utilising a particularly masculine face to determine levels of female attraction to beards is more likely to show only personal or cultural preferences for beardedness, rather than adaptive decision rules based on differences in physiological masculinity. Similarly, studies that generate facial composites of varying masculinity and artificially add thick stubble or full beards are also likely to prove inadequate. Low masculinity, low NCC, males should show a relatively slight or patchy coverage of facial hair even with a fully-grown beard (Figure 2), whilst highly masculine individuals should show capacity for a thick masculine beard at almost any stage of growth.

These methodological issues were addressed by Dixson and Rantala (2016) and Dixson et al. (2016) who separated men into four categories based on their capacity for facial hair coverage (‘very light’, ‘light’, ‘medium’ and ‘heavy’) after a given period without shaving. These predetermined levels of beard growth capacity were then ranked by survey participants in order of attractiveness: from light (most attractive), to medium, to heavy, and then very light (least attractive). Despite methodological differences, this order of preference is broadly consistent with earlier studies that found degrees of stubble were more attractive than either clean shaven, or full-bearded faces (Dixson & Brooks, 2013; Neave & Shields, 2008). Taken together, these observations conform to a preference for intermediate facial masculinity (at least as signalled by facial hair). Such a centralised distribution in women’s preferences would seem evolutionarily adaptive given the non-linear relationship between childhood

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mortality and masculinity found by Boothroyd et al. (2017) (Section 3), and adds further support for a level of stabilising selection on masculinity, and underlying NCC function.

5. Why do men sometimes shave?

Of interest for current research into human male beards is the question of why men would ever shave this highly visible indicator of their sex (Dixson, Rantala, et al., 2017). This emasculating behaviour appears unique to humans and seems logically counterproductive from the perspective of reproduction and evolutionary fitness. However, male facial hair removal can be explained with reference to signalling of embryonic NCC function and associated physiological masculinity. From this perspective, shaving a beard should act to modify sexual and social outcomes for a given male by influencing the perceptions of individuals with whom they interact. In relation to female mating preference, by reducing the overt display of a highly visible masculine trait, shaving a thick beard should moderate expectations of promiscuity or sexually aggressive behaviour. This would provide a relative advantage to males seeking a pair-bonded relationship and wanting to emphasise capacity for paternal investment (as suggested by Barber, 2001). Alternatively, among less-masculine individuals, removal of very sparse facial hair might lessen perceptions of immaturity or low social status. Regarding male-male social interaction and competition, a relatively thick beard would signal a predisposition to competitive status striving and reactive aggression and could, therefore, elevate the perceived threat posed by the bearded individual. It follows that regular shaving of thick facial hair would help to smooth threat perceptions in other males and so increase levels of trust and cooperation enjoyed by a relatively masculine man. Alternatively, the shaving of facial hair by less masculine males may lessen unwanted perceptions of immaturity or low social status in dealings with other men. Both these possible justifications for shaving should be especially beneficial within densely-populated environments which require regular interaction with distant acquaintances and strangers.

Despite this expectation however, empirical assessment of beard frequency in urban situations suggests beardedness is actually more common under densely populated conditions (Dixson, Rantala, et al., 2017). Notably however, this study did not differentiate between men's natural capacity for heavy or light facial hair growth. Instead, population ratios of beardedness (drawn from Facebook profile pictures) were assessed based on three categories: clean-shaven, bearded, and non-beard facial hair (Dixson, Rantala, et al., 2017). As such, an elevated presence of beardedness in large population centres, cannot be assumed to show that

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urban men are more physiologically masculine, but rather that facial hair is more fashionable in large cities. It could be that large populations offer expanded and diverse social niches (an individual can belong to multiple professional and social groups) and so may provide more opportunities for masculine males to engage in competition or sexual display. Alternatively, if dense populations offered benefits to cooperative and sociable individuals, then an appearance of low masculinity would be an advantage, and so, lightly bearded males may be more likely to grow and display scant facial hair. Fashions for beardedness have been shown to fluctuate (Barber, 2001; Robinson, 1976), and researchers have identified a certain novelty value in the attractiveness of both beards and cleanshaven-ness, leading to reproductive benefits for facial hair non-conformists (Janif, Brooks, & Dixson, 2014).

6. Implications for human self-domestication research

Based on male adaptations for combat and aggression, recent authors have promoted the idea of male-male competition as the paramount driver of human evolution (Hill, Bailey, & Puts, 2017), or at least of *male* human evolution (Scott et al., 2013). In contrast with this suggestion however, whilst it is clear that the average man is more physically robust and behaviourally aggressive relative to the average women, ongoing male competition cannot succinctly explain several observed trajectories in human evolutionary change. Evidence that recent evolution has involved significant reduction in male competition and mean masculinity levels includes: decreased sexual dimorphism, smaller body size, and less skeletal robusticity (Frayer & Wolpoff, 1985; Hill et al., 2017; Lindenfors & Tullberg, 2011; Ruff, 2002; Ryan & Shaw, 2015); diminished craniofacial masculinity and prognathism (Cieri et al., 2014); and increased capacity for cooperation and social tolerance (Burkart et al., 2014; Hare, 2016; Hawkes, 2013; Hrdy, 2011; Sterelny, 2011). Rather than supporting a hypothesis of continuing evolutionary influence from male contest competition, these trends are consistent with reductions in biophysical adaptation for male-male competition, and a corresponding drop in physiological masculinity, which this article has linked to downregulation of embryonic NCC functioning and a process of human self-domestication.

Given these apparent trends among *Homo sapiens*, it is plausible that similar reductions in NCC-driven masculinity have occurred during earlier hominin evolution. For example, based on craniofacial morphology, Clark and Hennenberg (2015, 2017) have recently suggested *Ardipithecus ramidus* shows signs of self-domestication relative to the last common ancestor with chimpanzees and bonobos. An effect which these authors ascribe to reductions in male-

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male competition and related change in reproductive and social behaviour. Given the connection between NCCs and masculinity outlined in this article, such socio-sexual changes could explain several aspects of hominin evolution. For example, since all vertebrate tooth primordia are derived from NCCs (Gilbert, 2010; Hall, 2010) and are known to be smaller under domestication (Wilkins et al., 2014) self-domestication via downregulation of NCCs may explain the relatively diminished canines of early hominins (see Delezene, 2015), as well as size reductions in post-canine teeth among more recent humans (Brace, Rosenberg, & Hunt, 1987). The occurrence and later disappearance of sagittal cresting in hominin evolution may also reflect NCC activity since this bony ridge emerges above the interparietal region, an area of the skull also formed from NCC progenitors (Jiang, Iseki, Maxson, Sucov, & Morriss-Kay, 2002). Interestingly, it has recently been suggested that sagittal crests play a role in sexual selection and social signalling among several extant hominoid primates (Balolia, Soligo, & Wood, 2017).

Accepting there has been an evolutionary trend toward downregulation of NCCs among ancestral humans (mirroring a process of self-domestication, and with a consequent reduction in masculinity), it remains to consider what evolutionary pressures could have promoted this longstanding trend. Whilst stabilising intersexual selection in favour of moderate masculinity may persist (Boothroyd et al., 2017), improvements in the relative reproductive fitness of low-masculinity males would eventually lead to lower average levels of NCC function across a given population. Factors with the potential to promote these trends include any socioecological condition or change that would benefit the fitness of more sociable (hence, less masculine) males, or decrease the fitness of high masculinity individuals.

One aspect of our evolution that must have significantly benefited lower levels of masculinity, is the increased altriciality of human infants. This well-recognised trend (van Schaik, 2016; Zollikofer & Ponce de León, 2010) would inevitably increase the relative reproductive fitness of capable parental investors, particularly among females, and, to some extent, among males as well (Hrdy, 2011). Coincident increases in social interaction and communication complexity may also have enhanced the fitness of sociable paternal investors via group sanctions against some particularly masculine reproductive behaviours, including: repeated extra-pair copulation, and violent sexual coercion and mate guarding. Varying levels of female social status would also affect the efficacy of the latter two male mating strategies; limiting their relative fitness in groups where women exercised effective sexual autonomy.

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Self-domestication among *Homo sapiens* has been characterised as a necessary process in our evolution towards a more cooperative and sociable form; allowing for the development of human culture, knowledge sharing, and dramatic technological advance (Cieri et al., 2014; Hare, 2016). Reductions in masculine aggression that occurred as part of this process were a beneficial evolutionary development, essential to the emergence of our complex 'social-niche'-based modes of existence (see Odling-Smee, Laland, & Feldman, 2003; Sterelny, 2011). Interestingly, given its association with the recent rise and increased technological complexity of human civilisations, the strongest effects of this process appear to have emerged only relatively very recently in our evolution. This may imply that human self-domestication is a continuing (and possibly also accelerating) process. Increased social cohesion, evidenced by higher density living and higher interactive complexity, may add positive feedback for such a process; including via group or state sanctions against violent behaviour and the segregation of antisocial individuals (Pinker, 2011; Wrangham, 2014).

Given the benefits of enhanced cooperation and social interaction that follow from the process of self-domestication, as well as the inherently socio-sexual selective mechanisms which promote it, increased scientific understanding of this topic should provide further support for some existing social and political programs. These include those aimed at increasing the economic and political empowerment of women, as well as at cooperative global efforts to reduce pathogenic influences, improve social equality, and eliminate destructive hostility and violence. To expand capacity for empirical investigation of human self-domestication, further research into the activity of NCCs and the genetic switches that control their function and dispersal are likely to prove insightful. Scientific understanding may initially progress via non-human studies since selection on male secondary traits is likely to influence the function of embryonic NCCs across vertebrate taxa. Given the associations shown here, future research into sexual selection on masculine traits should proceed with an enhanced paradigmatic foundation via reference to embryonic NCC function, and a broader understanding of its effects on human biology and behaviour, as individuals, and as a society.

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investigation of sexual selection and associated theory. This research was supported by an Australian Government Research Training Program Scholarship.

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