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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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Abstract

Masculine traits in human males are expressed in face and shoulder morphology, vocal pitch, and body odour, 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 demonstrates, this range of traits can be directly linked to the activity of neural crest cells (NCC's) at embryonic stages of development. Given this linkage, previously observed sexual selection on masculine traits will inevitably affect embryonic NCC activity across a given population. Since selection for suppressed NCC function is the physiological cause of mammalian domestication syndrome, selection for or against masculine male traits must lead to more or less 'self-domesticated' lineages among human groups. As such, future research into human sexual selection on masculinity will benefit from an appreciation of NCC function and behaviour, and consideration of the evolutionary implications of human self-domestication. This article provides an original integration of two longstanding fields of significant research interest by demonstrating the proximate physiological—and ultimate evolutionary—causes of sexual selection on human masculinity. In doing so, it also explains a peculiar human behaviour, the shaving of facial hair.

1. Masculinity and sexual selection

Recent studies on male and female preferences for beardedness (Dixson & Brooks, 2013; Dixson, Lee, Sherlock, & Talamas, 2017; Dixson, Rantala, Melo, & Brooks, 2017) relate to a broader research program focussed on sexual selection for masculine traits in humans. The goal of these related research themes has been to examine processes of human mate choice and sexual competition, and to understand how these may influence human evolution and behaviour. Masculine morphological traits are associated with particular behavioural predispositions, and both morphology and behaviour have been linked to elevated androgen levels, especially higher testosterone (Book, Starzyk, & Quinsey, 2001; Booth & Dabbs, 1993; Carré, McCormick, & Mondloch, 2009; Kruger, 2006; Lefevre, Lewis, Perrett, & Penke, 2013). In this context, typical masculine behaviour includes competition and dominance behaviour, status striving, and relatively higher reactive aggression, as well as preference

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for multiple partners, and lower inclination to pair bond and provide faithful paternal investment (Booth & Dabbs, 1993; Dibble, Goldey, & Anders, 2017; Goetz et al., 2014; Kruger, 2006; Puts, 2016; Quist et al., 2012; Wilson & Daly, 1985).

Research examining women's preferences for masculine traits has previously demonstrated variation according to menstrual phase and whether long or short-term relationships are sought (DeBruine, Jones, Frederick, et al., 2010; S. W. Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Little et al., 2010; Little, Jones, & Burriss, 2007; I. . Penton-Voak & Perrett, 2000; I. S. Penton-Voak et al., 1999). Related study has also shown that masculinity 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—as well as under conditions of high pathogen presence (DeBruine, Jones, Crawford, Welling, & Little, 2010)—which implies that masculine fathers may provide fitness or survival benefits to offspring. 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 general expectation that women are adaptively predisposed to make context dependant choices between males that offer either 'good genes', or a propensity for faithful pair-bonding and paternal investment (Kruger, 2006; Little, Connely, Feinberg, Jones, & Roberts, 2011; Quist et al., 2012; Trivers, 1972).

2. Selection on masculinity and processes of human self-domestication

Human self-domestication has been a topic of research interest since Darwin (1868) first identified the diverse syndrome of traits that domesticated animals share in common in comparison to their wild relatives or ancestors (e.g. see: Brüne, 2007; Cieri, Churchill, Franciscus, Tan, & Hare, 2014; Fischer, 1914; Groves, 1999; Leach, 2003; Lorenz, 1940). Women's documented preferences for or against morphological cues that correlate with masculine aggression are directly related to human self-domestication because selection against aggressive reactivity is the known driver of this mammalian domestication syndrome (Belyaev, 1979; Trut et al., 2006; Trut, Oskina, & Kharlamova, 2001; Wilkins, Wrangham, & Tecumseh Fitch, 2014), including in our close primate relative, the bonobo (Hare, Wobber, & Wrangham, 2012). Previous work on human self-domestication has identified female mating preferences as a potential driver of this prehistoric (and potentially continuing) 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).

The proximate physiological mechanism of domestication syndrome is now understood as the suppressed function (probably by limited dispersal) of embryonic neural crest cells (NCC's)—effectively a mild form of neurocristopathy (Wilkins et al., 2014). Current expectations are that selection for lower reactive aggression in mammals (analogous to a suppressed 'fight or flight'

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response) works by promoting a heritable tendency to a smaller and less reactive adrenal system (Sánchez-Villagra, Geiger, & Schneider, 2016; Wilkins et al., 2014)—a trait long recognised among domesticated animal populations (Hemmer, 1990). This causes a diminution of reactivity from the Hypothalamic-Pituitary-Adrenal (HPA) axis and is a result of suppressed embryonic NCC activity (Wilkins et al., 2014). As such, selection for less aggression acts by diminishing normal NCC function and, since NCC's form the basis for a wide range of other derived cell types and biophysical structures (Gilbert, 2010; Schoenwolf, Bleyl, Brauer, & Francis-West, 2008), their diminishment promotes the diverse range of hypoplasic characteristics now recognised as 'domestication syndrome' (Wilkins et al., 2014) (Figure 1).

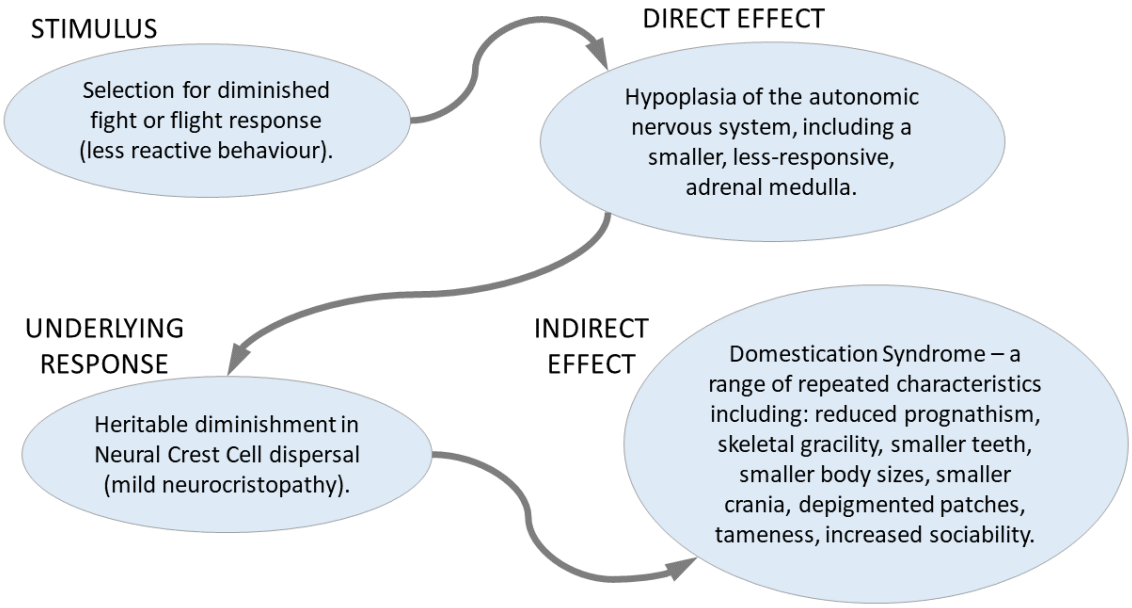

Figure 1: Chain of influence in mammalian domestication from Stimulus (selection for less reactive behaviour) to Indirect Responses (Domestication Syndrome) (based on Trut et al., 2006, 2001; and Wilkins et al., 2014).

3. NCC's and human masculinity

All attributes previously identified as signals of masculinity in human males can be directly associated with the activity of embryonic NCC's (Table 1). These cells are the progenitors of most of the craniofacial region, including the frontal bone, mandible and maxilla, nasal bone and cartilage, and the zygomatic arches, as well as their associated muscle and connective tissue (Cordero et al., 2011; Gilbert, 2010; Knight & Schilling, 2013). As such, they provide the cellular building blocks for all structures currently studied as measurable indicators of human facial masculinity. They also compose the larynx and hyoid (Gilbert, 2010; Schoenwolf et al., 2008; Wilkins et al., 2014), as well as the styloid process (Bhatt, Diaz, & Trainor, 2013)—an attachment site for muscles which control the tongue and larynx—suggesting their diminishment may influence vocal qualities, including voice pitch. Further, they are known to contribute substantially to the development of the shoulder and neck

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(Matsuoka et al., 2005) thereby influencing the size and robusticity of these bodily features. NCC's also form multiple components 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 NCC's 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 reactive (versus 'pro-active') aggression (Weinshenker & Siegel, 2002; Wrangham, 2014). Further, NCC's have very recently been shown to contribute to the development of the anterior pituitary, and each of its various hormone secreting cells (Ueharu et al., 2017). These latter contributions show that embryonic NCC's can influence the function of the HPA axis via their contribution to both the adrenal *and* the pituitary glands.

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Table 1: Masculine traits and their relation to the function of NCC's.

Masculine trait	Described by…	Direct influence of NCC's
Facial masculinity	Gangestad & Thornhill (2003); Mitteroecker et al. (2015); Penton-Voak & Perrett (2000).	NCC's 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)	NCC's 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).	NCC's produce the facial dermis and hypodermis including associated hair follicles (Jinno et al., 2010; Krause et al., 2014; Schoenwolf et al., 2008) as well as affecting testosterone levels via HPG axis due to NCC formation of the anterior pituitary gland (Hall, 2010; Schoenwolf et al., 2008).
Low vocal pitch	Feinberg et al. (2008); Puts et al. (2016); Puts et al. (2006).	NCC's 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).
Broad shoulders	(Lee, Brooks, Potter, & Zietsch, 2015)	NCC's provide progenitor cells of neck and shoulder bone (i.e. clavicle and scapula) and associated muscle (Matsuoka et al., 2005).
Competitiveness and aggression	Book et al. (2001)	**Indirect influence of NCC's via Testosterone** NCC contributions to the adrenal gland and anterior pituitary (Ueharu et al., 2017) will influence the activity of both the HPA and HPG axes which stimulate the sympathetic nervous system and influence testosterone and cortisol production 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)	
General bodily hairiness	(Dixson, 2016)	
Male scent	Grammer (1993); Grammer et al. (2005); Thornhill et al. (2013); Thornhill and Gangestad (1999).	

Notes: HPA=Hypothalamic-Pituitary-Adrenal, HPG=Hypothalamic-Pituitary-Gonadal.

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Perhaps most importantly however, NCC contribution to the anterior pituitary also implicates these cells in the functioning of the Hypothalamic-Pituitary-Gonadal (HPG) axis. This is of significant relevance in the context of human masculinity since it provides a proximate link between NCC's 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 NCC's, to date this has not been conclusively demonstrated (Shima & Morohashi, 2017). This interesting potential aside, testosterone production within Leydig cells is known to be triggered by the release of luteinising hormone from the anterior pituitary (Hall, 2010), and, given the anterior pituitary does receive significant input from NCC lineages (Ueharu et al., 2017), this relationship provides a pathway for the activity of embryonic NCC's to influence post-natal levels of testosterone production. Interestingly, a link between NCC's and the HPG axis was previously hypothesised by Wilkins et al. (2014) in their discussion of the shifted timing of reproductive physiology among female domesticated foxes. However, those authors did not consider the effect of suppressed NCC activity upon the HPG axis of *male* foxes, nor does their seminal paper discuss human self-domestication, or sexual selection on the basis of masculine behaviour and morphology. Whilst the majority of current studies concerning masculine human traits assume testosterone level as their ultimate determining mechanism (Apicella et al., 2008; I. Penton-Voak & Perrett, 2000; I. Penton-Voak & Perrett, 2000), NCC-influenced HPG control of testosterone production provides a direct link between the domestication process and every masculine trait previously correlated with testosterone.

A further relevant implication of NCC contribution to the anterior pituitary is that suppressed NCC contributions are likely to cause a reduction in the pituitary's production of growth hormone. A heritable alteration in growth hormone production regimes would be expected to affect the developmental timing of multiple other organs and structures throughout the developing body as has been noted multiple times in evolutionary studies—described as 'heterochronic shift' (Alberch, Gould, Oster, & Wake, 1979; Gould, 1966, 1977). This effect would explain the regular appearance of paedomorphic characteristics in domesticated mammalian populations (Leach, 2003) and may also link to apparent selection for paedomorphic characters in humans (Gould, 1977; Groves, 1989; Perrett et al., 1998). Certainly it could explain observed reductions in sexual dimorphism among human-domesticated mammals, as has been observed across a range of comparable traits, but especially in body size (Zeder, 2008, 2012; Zohary, Tchernov, & Horwitz, 1998).

NCC's also contribute to the development of the thymus, and so play a role in T-cell production and the functioning of the immune system; at least until puberty when the thymus and its influence begins to diminish (Gilbert, 2010; Hall, 2010). This would suggest that relatively masculine individuals should have a better functioning immune system in childhood, and that sexual selection in favour of

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masculine traits would, therefore, provide offspring with relatively elevated childhood immunity; a particular benefit for sons given their consistently higher mortality curve (Klein, 2000). Elevated immunity from foetal stages through to puberty could also explain the higher body and facial symmetry observed in more masculine males since asymmetry is thought to be caused by pathogenic influences during early development (Møller & Swaddle, 1997; Thornhill & Gangestad, 1999). Elevated immunity in offspring would also provide an entirely sufficient explanation of the 'good genes' that are offered by masculine individuals and preferentially selected by females in fertile phases in lieu of male propensity for paternal investment.

However, the above supposition is counter to currently popular theory related to 'the handicap principle' (Zahavi, 1975; Zahavi & Zahavi, 1999) which has been used to suggest that relatively high testosterone males are more attractive to females because of testosterone's immunocompetence suppression effect (Folstad & Karter, 1992). According to this perspective, masculine traits indicate a relative handicap and, therefore (via a somewhat convoluted logic), imply 'good genes' that are capable of survival despite compromised immunity levels. By contrast, if masculine traits are an indication of relatively elevated NCC dispersal and function, they should correlate with a larger thymus and a consequently better-functioning childhood immune system, rather than a handicapped one. Further empirical research into the relation between NCC's, the masculine thymus, and human immune system function is required and may prove illuminating in regard to these apparent theoretical discrepancies.

4. NCC's and male beardedness

In regard to investigations of men's and women's preferences for beardedness (Dixson & Brooks, 2013; Dixson, Lee, et al., 2017; Dixson, Rantala, et al., 2017), it is interesting to note two significant ways in which NCC's influence men's capacity for the growth of facial hair. The first is via the NCC's indirect influence upon testosterone production (described above) since it has long been known that testosterone affects the length, thickness, timing, and rate of growth of bodily hair (Ebling, 1986; Hall, 2010). However, the second mode is a far more direct relationship: along with their role in the formation of the facial skeleton, cranial NCC's have been shown to form all of the vertebrate facial dermis and epidermis, including associated hair follicles (Jinno et al., 2010; Krause et al., 2014; Schoenwolf et al., 2008). Because of this, the volume and density of a man's natural coverage of facial hair are likely to provide others with a direct indication of his relative levels of embryonic NCC function and, therefore, his overall physiological masculinity.

For potential female partners, this would help to indicate a male's likelihood of competitive success and relative status outcomes (Dixson, 2016; Puts, 2016), as well as his predisposition to a given reproductive strategy—especially willingness to faithfully invest parental resources, or not (Booth & Dabbs, 1993; Kruger, 2006). Of equal importance however, male facial hair would provide a signal to

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other males indicating relative propensity for competitiveness and dominance behaviour, or its complement, a capacity for sociable and cooperative interaction. Perhaps unsurprisingly, this is what previous study of male and female responses to bearded faces would suggest. For example, empirical investigation by Dixson (2010) showed women preferred non-bearded male faces and that men's perceptions of aggression were enhanced by the presence of beards. Further, men and women both perceived bearded male faces as indicating relatively higher status (Dixson, 2010).

Of substantial interest for current research into human male beards is the question of why men would ever shave this highly visible indicator of their sex. This apparent emasculation behaviour appears unique to humans and seems logically counterproductive from the perspective of reproduction and evolutionary fitness (Dixson, Rantala, et al., 2017). However, male desires to remove facial hair can be neatly explained with reference to its signalling of embryonic NCC function and associated physiological masculinity. In this case, shaving a beard would act to influence sexual and social outcomes for a given male by modifying the perceptions and expectations of individuals with whom they interact. In regard to female mating preferences, by decreasing perceptions of masculinity, shaving a beard should lessen any expectation of unfaithfulness or sexually aggressive behaviour. This would be an advantage to males seeking a pair-bonded relationship and wanting to emphasise capacity for faithful paternal investment. Alternately, from the perspective of male-male social interaction, a thick beard should signal tendencies toward aggressive dominance and competitive behaviour and may, therefore, elevate the perceived threat posed by the bearded individual to other men. It follows that regularly shaving facial hair should help to smooth threat perception in others and hence might increase levels of trust enjoyed by a given male. This should be especially beneficial within high density social environments which require regular and complex interaction with distant acquaintances and relative strangers.

5. Implications for future research into human self-domestication

Several recent authors have promoted the idea of male-male competition as the major driver in human evolution due to apparent male adaptations for combat, aggression, and violence (Hill, Bailey, & Puts, 2017; Puts, 2010). However, whilst it is true that, relative to women, men are more physically robust and behaviourally aggressive, the suggestion that present sexual dimorphisms are sufficient evidence to infer the predominance of male competition in human evolution is undermined by recent reductions in human skeletal size and robusticity (Frayer, 1980; Frayer & Wolpoff, 1985; Hill et al., 2017; Ruff, 2002; Ryan & Shaw, 2015), as well as diminished craniofacial masculinity and prognathism (Cieri et al., 2014), and increases in cooperative capacity and social tolerance (Hare, 2016; Sterelny, 2011). Each of these trends is consistent with a reduction in male-male competition and a corresponding drop in mean aggression as expected as part of the self-domestication process. Intersexual selection via the exercise of female preferences for relatively less-masculine males is the only form of sexual selection

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likely to explain the observed downward trends in masculine characteristics which this paper has linked to NCC activity and human self-domestication. Given this expectation it is reasonable to suggest that there should be higher selective pressure for domestication, and against masculine traits, in cultural situations where women more freely exercise their own mate preferences, and under conditions of relative social equality or low pathogen threat (Brooks et al., 2010; DeBruine, Jones, Crawford, et al., 2010; Gleeson and Kushnick, in prep.).

These observations could also provide increased insight into earlier hominin evolution. For instance, Clark and Hennenberg (2015, 2017) have recently suggested that *Ardipithecus ramidus* shows signs of possible self-domestication relative to the last common ancestor with chimpanzees and bonobos. Although fossil evidence for extinct hominin species remains relatively scant, it has been conclusively shown that intersexual selection will influence typically male-associated (hence, 'masculine') traits in non-hominin primates. The apparent self-domestication of bonobos (Hare et al., 2012), observable as behavioural sociability, low aggression, paedomorphism, and relatively lower sexual dimorphism, when compared to chimpanzees, appears to result from elevated female social status and a consequent capacity for female mate choice (Tokuyama & Furuichi, 2016; White, Waller, & Boose, 2013; Wrangham, 1986). A contrasting example of sexual selection in favour of masculine primate traits is provided by the gorilla, where an exaggerated sagittal crest has recently been shown to perform a role in sexual selection processes in this highly sexually dimorphic species (Balolia, Soligo, & Wood, 2017). The sagittal crest may be a particularly revealing indication of relative masculinity and high NCC presence and activity, since it consists of a late-maturing ridge of cranial bone located directly over the inter-parietal region, an area that, like the frontal and facial skeleton, is composed entirely from NNC's (Jiang, Iseki, Maxson, Sucov, & Morriss-Kay, 2002). This observation may provide further insight into the early loss of sagittal crests within *Homo* and an indication of ancient selective pressures for diminished NCC activity and reduced masculinity.

Self-domestication among *Homo sapiens* has been characterised as a necessary process in the evolution of humans 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). Implied reductions in masculine aggression would have provided a positive evolutionary influence in the construction of our social-niche based modes of existence (discussed by Odling-Smee, Laland, & Feldman, 2003; Sterelny, 2011). Perhaps most interestingly, given its association with the rise of human civilisations, it appears the strongest effects of the self-domestication process have occurred only relatively recently in our evolution; this may well imply that self-domestication is an ongoing—and possibly accelerating—process in our species. Given the implication of increasingly enhanced cooperation and social interaction that follow from this process, as well as the inherently socio-sexual selective mechanisms which drive it, improved scientific understandings of human self-

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domestication may provide support for a number of existing social and political programs; in particular, the increased economic and political empowerment of women, as well as more cooperative global efforts towards human betterment and reductions in destructive hostility and violence.

In order to expand capacity for empirical investigation of human self-domestication via sexual selection on masculine traits, further study of the genetic switches that control NCC function and dispersal are likely to prove extremely useful. Increased understanding of these factors could enhance medical and psychological understandings of various pathologies and anti-social human behaviour. Future research into human male masculinity and sexual selection should now proceed with an enhanced paradigmatic foundation via reference to mechanisms of underlying selection on embryonic NCC function, and an understanding of its varied and multiple effects on human biology and behaviour, as individuals, and as a society.

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