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Chapter

Evolutionary Theory of an Association between Testosterone and Attractiveness Perception in Humans

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Abstract

Literature on psychological function of testosterone in humans has emphasized its association with such traits as aggressiveness and impulsivity. In addition, increasing number of studies have shown the linkage between testosterone level and individual difference in the strength of preference for other's sexually dimorphic traits. According to theorists in the field of evolutionary psychology, the preference pattern for sexual dimorphisms had evolved as an adaptive mechanism to increase the odds of reproductive success. But, so far, there are few systematic syntheses of literatures to validate such evolutionary explanation from the perspective of androgenic function. This chapter aims to give an overview of the existing findings on the association between testosterone and preference pattern in humans and discuss their implications for evolutionary explanation of human attractiveness perception.

Keywords: testosterone, preference, face, voice, evolutionary psychology

1. Introduction

Numerous functions of the central nervous system, perception, motor control, emotion, homeostatic balance, and so on, are discussed in the literature on psychology. The neurophysiological machinery for many of these psychological and cognitive functions has probably evolved as an adaptive mechanism—or at least as a by-product of adaptive mechanisms—to meet the demands of survival in a given environment.

The endocrinological function is tightly intertwined with neural—and hence, psychological—and cognitive functions. For example, in the cascade of fear response, the amygdala initiates a cascade process in the hypothalamic–pituitary–adrenal (HPA) axis, leading to the secretion of glucocorticoids in the adrenal gland, thereby enhancing energy consumption [1, 2]. An important implication of this is that individual differences within the endocrinological function are possibly linked to diversity in psychological traits and responses.

In addition to its physiological actions, testosterone has long been associated with psychological traits such as aggressiveness [3, 4] and impulsivity [5], especially

in males. Empirical studies using a pen-and-pencil questionnaire or well-tested paradigms of behavioral measurement have shown that people with high circulating testosterone levels tend to show more aggressive [3, 4] and dominant behavior [6]. Several earlier studies have identified a positive relationship between testosterone levels and trait impulsivity. At the same time, even when using a similar behavioral paradigm, studies have often reported mixed results as for the association between impulsivity and testosterone level, which indicates intrinsic complexity in androgenic influences on human behavior. For example, our study [7] found sex differences in the association between salivary testosterone levels and impulsivity in financial decision making, which indicates non-linearity in the pattern of influence of testosterone on a few domains of cognitive function (see also [8, 9]).

Attractiveness is among the primary attributes that determine first impressions, and attractive people make good impressions in job interviews [10, 11], receive priority in promotion [12]—possibly through a halo effect ([13, 14] but see [15])— and, importantly, in the context of this chapter, are more likely to have many sexual partners [16, 17].

In contrast to the common sense that beauty and attractiveness are defined by cultural standards, studies in the past three decades have shown the possibility that some physical traits are universally perceived to be attractive and that hormones, including testosterone, play pivotal roles in shaping attractive features and determining the strength of one's preference for them. This chapter aims to give a brief overview of the previous findings on the link between testosterone and human attractiveness perception and discuss the validity of evolutionary explanations for the observed associations.

2. Androgenic regulation of reproductive behavior

Reproduction is, in a sense, the ultimate goal of living organisms—both as individuals and as members of one's own species. In addition to other hormones, testosterone and its metabolites are integrated into the complex web of the neuroendocrine system that controls the reproductive process.

Testosterone plays a pivotal role in the regulation of the male reproductive system; it controls male masculinization in body morphology and physiology [18–20] and sexual behavior [21] in variety of species. The concentration of androgen is much higher in the testes than in the bloodstream, and spermatogenesis is highly dependent on this high level of testicular testosterone [22].

There are a few controversies regarding the role of testosterone in the female reproductive process. However, at least in vitro, several studies have shown that testosterone and its metabolites promote the early stages of ovarian follicular maturation [23] directly as well as via conversion to estrogen through aromatization.

In addition to these physiological effects, several studies have shown that testosterone can modulate the function of the central nervous system, resulting in multiple aspects of reproductive behavior. Circulating testosterone levels are positively associated with male aggression, intra-sex competitiveness, and sexual desire in non-human species [21], which increases the success rate of winning and sexual intercourse with female conspecifics. In accordance with these observations, human studies have also supported the relationship between sexual desire and testosterone levels in both males [24] and females [25].

Maintaining a higher social status leads to an increased likelihood of reproductive success. Testosterone levels have been suggested to modulate the higher-order cognitive process of status seeking behavior. Eisenberger reported that men administered with testosterone make fairer offers in economic bargaining than placebo [26] and are more likely to punish those who make unfair offers [27]; both behaviors are beneficial for elevating one's social status. Likewise, exogenous testosterone administration increases generosity when the audience is observing one's behavior [28], which probably contributes to keeping good reputation.

Recent studies have shown that, in addition to its association with sexual behavior, testosterone levels modulate paternal investment. A longitudinal study [29] showed a reduction in testosterone levels in males after the delivery of their first child, similar to the findings in marmosets. Moreover, the time spent on care-taking was negatively correlated with testosterone levels. In a laboratory study [30], new fathers with low serum testosterone levels showed empathic responses more strongly to the sounds of the infant's cry. These studies indicate a suppressive effect of circulating testosterone on paternal investment.

3. Evolutionary theory of attractiveness

Mainly two types of explanations can be distinguished [31, 32] for certain behaviors or behavioral tendencies observed in animals: proximate and ultimate. The first refers to the description of biological mechanisms underlying animal behavior, such as neural functions and physiological responses. In the case of attractiveness perception, viewing attractive others activates the neural network of the reward system and induces pleasure [33]. This hedonic state is considered to promote the favorable treatment of physically attractive people.

The ultimate explanation of a behavior answers such questions as what kind of adaptive benefit and costs the behavior of interest incurs and how the behavior has evolved. The possession of eye-catching ornaments in certain species, such as the long tail in peacocks, has been a puzzle for evolutionary theorists. Conspicuous tails of peacocks are almost useless in themselves and could jeopardize the survival of a peacock by making it easily detectable by predators. Why did this phenotype evolve in the first place? This question explains the evolutionary roots of sexually dimorphic traits in peacocks.

The costly signaling theory (or good-genes handicap principle) claims that possession of extravagant ornaments functions as an "honest signal" of an individual's health and reproductive prowess [34, 35]. Production and sustainment of the long tail in peacocks is energy consuming and, as mentioned above, has the potential to lower the odds of survival. This indicates that a male with a long tail is healthy and strong enough to survive despite such a large handicap. In this line of reasoning, it follows that it is an adaptive strategy for peahens in bearing offsprings with "good genes" by mating with peacocks with long tails, because a long tail is an honest signal of biological quality. Though controversial, some ethological and experimental studies obtained several pieces of supporting evidence that males with seemingly maladaptive morphological traits achieve higher reproductive success [36–38].

The role of testosterone in the perception of attractiveness is often explained based on its value of signaling. Given the association between androgen and the male reproductive function [18–22, 37, 38], morphological traits linked to high levels of testosterone can serve as a signal of high reproductivity.

Another type of testosterone signaling function has also been suggested, based on the observation that testosterone suppresses the immune response to stressors. Based on this observation, a high level of testosterone can be deemed a handicap in the survival of an organism. Thus, the immunocompetence handicap theory [39, 40] of testosterone claims that morphological traits indicative of high testosterone levels advertise high immunocompetence and higher function of the immunological system because only individuals with strong immunity can survive despite the immunosuppressive effect of testosterone.

These hypotheses claim that masculine morphological traits function as an honest signal of biological quality and fitness of an individual and thus indicate the signaling quality of these traits as an ultimate explanation of why females are attracted to masculine traits in males. Females who are attracted to masculine males mate with a high-quality male, which probably increases the odds of offspring survival. Through sexual selection, traits indicative of high androgen levels have been consolidated in male sexual dimorphism, and the female neural system has evolved to be predisposed to seek males with these traits as mating partners.

4. Association between testosterone and attractiveness perception

To evaluate the validity of these evolutionary theories of attractive phenotypes, a good starting point is the examination of existing findings on human attractiveness perception. Over the past three decades, scores of studies have been published on the characteristics of sensory signals that young adult males and females find attractive; many of these studies have dealt with the attractiveness perception of sexual dimorphism in face and voice. These studies generally indicate that certain facial and vocal traits are universally perceived as attractive. Additionally, in line with the proverb "beauty lies in the eyes of the beholder," there is notable intra- and inter-individual differences in the strength of preference depending on the hormonal state. According to several researchers, the pattern of attractiveness perception and findings on the endocrinological basis of individual differences in attractiveness perception.

4.1 Faces

The face is among the most prominent sources of social information, and the human visual system is equipped to extract various kinds of information from others' faces. When female faces are presented side by side, infants as young as two months old spend more time looking at female faces that are evaluated to be more beautiful by adults [41]. Although the ability to capture attention is an inherently different concept from attractiveness, this finding indicates that facial attractiveness may comprise a collection of low-level perceptual features that can be processed by an immature brain.

Studies of young adults have identified facial asymmetry as a strong determinant of perceived facial attractiveness. Fluctuating asymmetry is a random deviation from perfect symmetry in the body and is presumed to reflect an organism's susceptibility to stressors; thus, the lower the fluctuating asymmetry an individual exhibits, the more physically fit he/she is. Previous studies have generally agreed that a low level of fluctuating asymmetry is perceived to be attractive regardless of the face model and evaluator's sex [42, 43] (but see [44]).

Another type of morphological feature that is universally perceived as attractive is the so-called baby schema ("Kindchenschema" [45]). Infants of many species share a collection of similar morphological traits such as large eyes, round contours, and small noses. Baby schema is asserted to function as a releaser of caretaking behaviors of adult conspecifics [46]. Glocker et al. [47] showed that a computer-synthesized infant face with its "baby schema" exaggerated activates the reward region more vigorously than the original image. Attractiveness perception in baby schema is seemingly influenced by the endocrinological function. Hahn et al. [48] revealed that intra-individual fluctuation in rewarding value one finds in a baby's face is dependent on testosterone levels. Testosterone works in concert with oxytocin to modulate the responses of infants' faces. A behavioral study [49] revealed that nulliparous women with high testosterone levels are slower in detecting infant face was accelerated by exogenous administration of oxytocin, most prominently in women with high testosterone levels.

Certain adults strongly exhibit baby schemas on their faces. Studies in the field of social psychology have revealed that people implicitly project infant-like traits such as innocence and incompetence [50, 51]. In our study [52], which investigated neural substrates linked to this over-generalization of baby schema to adult faces, part of the ventral striatum was more strongly activated to babyish than the mature version of an identical face. Part of the inter-individual variance in this activation was explained by the oxytocin level; however, in contrast to the case of infant face, testosterone was not identified as a determinant of reward system activation to faces of baby-faced adults.

In contrast to the case of low fluctuating asymmetry and baby schema that are almost universally perceived to be attractive [42, 43, 46, 52], the attractiveness perception of sexual dimorphisms in the human face is dependent on both the model's and the rater's sex. Sexual dimorphism refers to morphological features exaggerated in one sex. In the case of the human face, sexual dimorphisms in prototypical male faces include masculine features, such as large jawbones, protruded eyebrows, angular facial contours, and thinner lips, whereas feminine features are characterized by morphological features exaggerated in the opposite direction.

As can be intuitively understood, females with more feminine faces are perceived as more attractive than masculine ones [53] (but see [54]). If feminine features in female faces are exploited as signals of fecundity, it follows that preference for feminine faces is particularly prominent in male viewers compared to female viewers. This conjecture is supported in many studies [53, 55, 56], but some argue that there is considerable variation among males in the strength of preference for feminine female faces depending on self-perceived attractiveness and mating strategy [57, 58].

Another line of study found a positive association between circulating testosterone levels and the degree of male preference for femininity in female faces [59]. The results of correlational studies are further bolstered by the finding of a causal relationship between testosterone levels and perceived attractiveness in feminine morphological features. Welling et al. showed that winning in competition enhances male preference for female faces' femininity [60]. Although they did not directly measure testosterone concentration, this finding hints at the possibility that testosterone level is causally linked to the attractiveness perception of female sexual dimorphism in males because winning in competition is known to result in phasic testosterone increase [61]. More direct evidence for causal linkage comes from testosterone administration studies that the administration of a testosterone patch increases preference for feminine faces [62]. At the same time, another administration study reported a contradictory result that exogenous administration of testosterone decreases preference for femininity in female faces in a long-term relationship context [63].

The observed pattern of attractiveness perception of masculine facial features was somewhat complicated. In contrast to feminine female faces, which are judged to be attractive by both males and females alike [53], masculine male faces are not unequivocally perceived to be more attractive than less-masculine faces [64, 65]. One plausible reason for this observation is that masculine features are coupled with the impressions of dominance and untrustworthiness [53].

Sex hormones engender variations in females' perceptions of attractiveness in masculine male faces at both inter- and intra-individual levels. One correlational study has reported that females with high estradiol level show stronger preference for male faces with high testosterone [66]. A seminal study by Penton-Voak et al. [67] revealed cyclic fluctuations in the preference for masculine and feminine versions of a male face across the menstrual cycle. More specifically, during late follicular and ovulatory phase with high conception risk, females preferred masculine over feminine versions of identical male faces for partner of short-term relationship more than during the luteal phase with low conception risk. Several later studies successfully replicated this "ovulatory shift" pattern in females' perceptions of attractiveness in masculine facial features [66, 68, 69]. One interpretation of the ovulatory shift is that fluctuations in facial preference across the menstrual cycle are dependent on the mating strategy [66]. During the late follicular to ovulatory phase, females seek to find sexual partner with "good genes" to bear offspring with the greatest chance of survival, which makes them prefer masculine features. Testosterone levels are often linked to poor parental investment in fathers [29, 30]. Thus, it is a good strategy for females to mate with males with feminine morphology, from whom they can expect greater effort in parenting during the luteal phase. Partial support for the association between mating strategy and masculinity preference in females is obtained in several studies. For example, Roney et al. [70] reported that females rated male faces with high interest in children and those with high masculinity more attractive as long- and short-term partners, respectively (see also [71]). Menstrual cycle is accompanied by cyclic change in levels of multiple hormones. Consistently, several studies found a relationship between facial masculinity preference and estradiol [66] and progesterone [69] (but see [72, 73]). Testosterone level also fluctuates during menstrual cycle [74, 75]. This observation raises the possibility that facial masculinity preferences is also linked to testosterone level in females, but previous studies reported mixed findings as for this conjecture [71, 76, 77].

It should be noted that the phenomenon of cyclic shift in facial masculinity preference and its "mating strategy" interpretation are far from established in its current state. Many methodological problems have been pointed out in the studies on cyclic shift in face preference [78]. Several empirical studies reported no difference in masculinity preference between high and low conception risk phases during menstrual cycle [73] or lack of association between hormonal status and masculinity preference [72] (see [78] for a brief review). One study even reported that females preferred faces of males with relatively low level of serum testosterone during the fertile phase of menstrual cycle [79] in direct contradiction to the widespread interpretation.

4.2 Voices

Prominent sexual dimorphisms in human voices become clearly observable after puberty, during which the morphology of the vocal tract undergoes maturational

changes [80] under hormonal influences [81]. Sexual dimorphism in voice expresses itself through two main aspects: fundamental frequency and formant dispersion [82, 83]. The fundamental frequency of a voice is the frequency at which the vocal fold vibrates, and its perceptual correlation is the pitch. Formant refers to the local zenith in the frequency in power distribution, where the power within specific frequency ranges is amplified by resonance in the vocal tract. The combination of formant frequencies determines the perceived vowel category.

Fundamental frequency is lower in males than in females [82]. Similarly, formant dispersion, which is the frequency distance between neighboring formants, is narrower in males [84], and spacing between formants is related to body size in macaques [85] though the relationship is relatively weak in humans [86]. Based on these observations, many experimental studies have focused on the association between these vocal features and voice impressions. As in the case of facial masculinity, voices with muscular features, low fundamental frequency, and narrow formant dispersion give an impression of dominance [87]. A male's voice with a low fundamental and formant frequency is evaluated as more attractive by females than that with a high frequency [88, 89]. Likewise, males prefer female voices with high fundamental frequency and wide formant dispersion [90]. One explanation for such pattern of preference is that acoustic characteristics of voice reflect body size and physical function of speakers; females prefer males with voice indicative of a large body size [91, 92] and physical strength [93]. A recent study [83] has identified a curvilinear relationship between perceived attractiveness and fundamental/formant frequency: overall, male voices with low fundamental frequency tended to be rated higher in attractiveness. Interestingly, this effect was particularly pronounced when female raters evaluated voice attractiveness in a short-term rather than in a long-term context, closely replicating the pattern observed in face attractiveness studies [94]. Outside of the laboratory, it has been shown that males—but not females—with a low-pitched voice succeed in bearing a greater number of children [95].

Relatively less research has been conducted on whether hormonal status modulates the attractiveness perception of sexually dimorphic traits in voices, and we are yet to obtain a coherent picture regarding this issue. A few studies found cyclic variation in masculine traits in male's voice across menstrual cycle [84, 96], especially in females with low trait estradiol level [84]. Pisanski et al. [97] have linked intra-individual fluctuation in females' preference for masculine traits in men's voice to female's salivary level of estradiol rather than progesterone or testosterone. In males, Kandrik et al. [98] failed to find any association between attractiveness perception in feminine voices and testosterone levels.

5. Signal value of sexual dimorphisms

Although still equivocal, previous research has found some pieces of evidence supporting evolutionary theory of attractiveness perception. Another important aspect to be considered in validating the signaling hypothesis is whether attractive traits actually signal qualities advantageous for reproduction and offspring survival. Although this number is disproportionally small compared to purely psychological and observational studies that address the pattern and mechanism of attractiveness perception, researchers have made progress in empirically validating the signal value of attractive features. The activational effect of androgens has been shown to contribute to cranial growth [99] and vocal apparatus maturation [80]. Consistently, previous studies have revealed an association between the expression of masculine traits and testosterone levels in facial morphology [100] and acoustic features of voice [83, 101]. However, linking muscular features and reproductive processes in males is not straightforward. Few studies have empirically investigated the relationship between reproductive function and masculine traits. A pioneering study by Soler et al. [102] reported a positive association between facial attractiveness and semen quality, as assessed by sperm motility and morphology. However, later studies failed to replicate the predicted association between semen quality, attractiveness, and masculinity in the face [103] and voice [104].

The immunocompetence handicap theory of testosterone asserts that men with high testosterone levels possess strong immune functions and thus physical health [39, 40]. Studies have tested this conjecture by investigating the association between face evaluations and actual health records [42, 105, 106]. Several pieces of supporting evidence were obtained from these studies. For example, facial masculinity and asymmetry have been linked to actual health status, indexed by antibiotic use and a history of respiratory disease [42]. However, the association between ratings of masculinity and attractiveness and actual health status was modest or absent [105]. Thus, it is possible that sexual dimorphism reflects actual health status, but people are not good at exploiting this information to its full extent, which indicates limited signaling value of sexual dimorphisms. Kalick et al. [106] observed that perceived facial attractiveness mitigated the association between perceived and actual health. More specifically, participants were good at predicting health status based on facial information for moderately attractive faces but not for extremely attractive or unattractive faces. This finding indicates that the signal value of sexual dimorphism was degraded by the halo effect of perceived attractiveness.

Another line of research has directly investigated the association between masculine traits and the strength of the immune response. A comprehensive study [107] on multiple aspects of the immune response, including both humoral and cell-mediated immunity and serum levels of free testosterone, dihydrotestosterone (DHT), and dehydroepiandrosterone, identified a positive association between the strength of the immune response to influenza vaccination and free testosterone and DHT; however, many of the pairwise correlations were null. Another study [40] investigated the association between facial attractiveness, testosterone levels, and immune response to hepatitis B vaccination. The results revealed that males with high testosterone levels showed stronger immune responses, and males with stronger immune responses were rated more attractive by females than those with weak immune responses, giving strong support to the immunocompetence handicap theory. These associations were particularly prominent in males with low glucocorticoid levels. Thus, existing studies provide some support for the immunocompetence handicap theory [39, 40] but at the same time reveal the need for further modification of this theory by integrating multiple measures of immune response and hormonal status.

6. Potential explanations for failure to find signal value of sexually dimorphic features

Many attractiveness perception studies in humans rely on the assumption that attractive features function as signals of, and advertise, the biological quality of an individual to the opposite sex. This assumption has garnered some support from

behavioral studies on the human attractiveness perception of faces [46, 66–70] and voices [88–90, 93, 95]. Several of these studies show that people prefer sexually dimorphic traits indicative of high reproductivity [62, 66–70] and immunocompetence [108] and a low level of fluctuating asymmetry that reflects robustness against biological harm [42, 43]. However, it is currently difficult to assume that evolutionary theory of attractive perception has been unanimously supported by empirical studies.

There are several pieces of evidence indicating the association between sexually dimorphic traits, such as low-pitched voice, facial masculinity, and testosterone level [83, 100, 101]. However, there are few studies on the link between these masculine features, actual health records, reproductive prowess indexed by semen quality, and immunocompetence.

The reason for the lack of clear evidence for the signal value of sexual dimorphism is yet to be clarified. One reason, of course, is that the attractiveness of sexual dimorphism, including sexual dimorphism and the neural machinery to perceive sexual dimorphism as attractive, has evolved for reasons other than its signal value. The Fisherian runaway hypothesis [109] proposes that sexually dimorphic features, such as the grandiose ornament of the peacock's tail, can evolve even when they do not signal biological fitness. First, certain features emerge in one sex either as a signal of biological quality or as a result of perceptual bias. If the feature sexually attracts the opposite sex, individuals with this feature achieve greater reproductive success. Thus, this is an adaptive strategy for the other sex to mate with individuals with this feature. Through generations, the development of this feature and preference for it in individuals of the opposite sex reinforce each other in a positive feedback loop with no regard to the actual signal value. In this case, there is only loose or no association between the sexually selected feature and biological quality.

Another reason is that most existing studies have focused on the attractiveness perception of features that reflect biological fitness at the trait level, and a relatively small number of studies have dealt with the attractiveness perception of features that fluctuate within an individual depending on one's physical state [108]. The probability of bearing offspring with "good gene" depends on the mating partner's current health status as well as the baseline level of reproductivity and biological quality. Sexual dimorphism in the face and voice is a stable marker of trait-level biological quality, and current health status is more sensitively reflected in features such as skin texture [110], adiposity [108, 111], and subtle timbral features of jitter and simmer in voice [112]. Several studies have raised the possibility that these state markers are more tightly linked to health status and exert stronger influences on attractiveness perception [108, 110, 111] and mating strategy than features reflecting unchanging trait-level biological fitness. Scott et al. [110] reported that skin coloration is prioritized over facial masculinity in the evaluation of health status and attractiveness from facial information. Likewise, Rantala et al. [108] revealed a stronger association between circulating testosterone and adiposity than between circulating testosterone and masculinity in the face and body. Furthermore, the link between facial attractiveness and the strength of the immune response to hepatitis B vaccination is mediated by adiposity and not by masculinity.

7. Conclusion

Several behavioral studies have found supporting evidence for the assertion that attractive features have been sexually selected; however, this pattern is not necessarily

unequivocal. Furthermore, there is limited evidence for a link between sexually dimorphic traits and biological traits, such as immunocompetence and reproductivity. In its current state, existing studies mainly focus on attractiveness perception of phenotypes that are supposed to reflect trait-level fitness and health status. Furthermore, a few studies have incorporated the measurement of multiple hormones, failing to appreciate a potential interaction between sex steroids and other endocrinological factors influencing attractiveness perception. Moreover, as most studies have adopted a correlational design, their ability to identify the causality of the observed associations is limited. More comprehensive studies on the perception of attractiveness, incorporating experimental manipulation of sex-steroid administration, would enrich the knowledge in this field of research and provide a more solid basis to discuss the validity of the evolutionary roots of human attractiveness perception.

Conflict of interest

The author declares no conflict of interest.

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