ANTHROPOLOGIE • L/1 • pp. 33–45 • 2012

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EVOLUTIONARY CONCEPTS OF HUMAN PHYSICAL ATTRACTIVENESS: THE CASE OF MALE PHYSIQUE

ABSTRACT: Perception of certain body traits as attractive or unattractive has a profound effect on our everyday life. Here we employ sexual selection models which aim to explain why perception of specific traits as attractive might have evolved to conceptualize evidence on male body attractiveness. One line of reasoning considers attractive traits to be markers of individual qualities. We specifically focus on two concepts: I) developmental stability and heterozygosity and II) immunocompetence and sexual dimorphism and their link to attractiveness of the human male physique. The available data on preferences for the majority of traits of the human male physique show inverted U curved patterns, which are indicative of a trade-off. Further, we show that several key links between physical appearance and the quality of a mate still need to be established in humans.

KEY WORDS: Attractiveness – Male body – Cue – Health – Fitness – Quality

INTRODUCTION

Charles Darwin (1859) in his classical treatise claimed that male traits, like a colourful plumage, serve as displays of arbitrary beauty for charming females and that these traits bear no signs about the biological quality of a male. He also assumed that humans have no universal measure of attractiveness and that the criteria by which male beauty is assessed are purely arbitrary and often change in time within a single population and markedly differ between populations (Darwin 1871). In contrast, his contemporary, Alfred Russell Wallace (1892), argued that females are more influenced in their choice by qualities affecting the survival of a male, by means of attraction to traits which serve as a cue to the real quality of a male. In the recent decades, the distinction between the Darwinian aesthetical beauty and Wallace's cues of quality has recaptured the attention of evolutionary scientists. At the end of the 1970s, researchers began to interpret perception of physical attractiveness in humans from an evolutionary perspective, that is, as a result of natural and sexual

Received 22 October 2012; accepted 19 March 2013.

selection (e.g., Symons 1979). Subsequent research has shown that it is highly plausible that human criteria of mate selection do not qualitatively differ from those of other species. In other words, they were selected in our evolutionary past and are responsible for our perception of attractiveness and related preferences (Grammer *et al.* 2003). However, it has also turned out that neither the perception of attractiveness nor the traits considered attractive are so strictly defined as implied by Darwin's (1859) or Wallace's (1892) suggestions, especially in humans.

The main aim of this paper is to show that in spite of an enormous body of literature about physical attractiveness published during the past two decades, several theoretical issues remain to be resolved. Here we exclusively focus on evolutionary-informed theories of human physical attractiveness. These are briefly introduced and it is assessed how well-founded they are on empirical findings. Thus, we do not aim to provide a comprehensive review on physical attractiveness, but rather we focus on critical appraisal of the main evolutionary concepts of physical attractiveness. To make the paper concise, we present these concepts using studies on preferences of human male bodily traits. Thus, the extensive body of literature on facial attractiveness is not considered here as it would exceed the limits of this work. For similar reasons, we do not deal here with studies on women's physical attractiveness. These issues have recently been reviewed elsewhere (for a current review of the literature on facial attractiveness see Little *et al.* 2011). Although there is ample evidence that physical attractiveness plays an important role in various social interactions ranging from how well children are treated, job interviews to juridical outcomes, its primary scope lies in romantic relationships. Due to the central role of reproduction in evolutionary theorizing, not surprisingly the majority of evolutionary theories of physical attractiveness revolve around its role in mate attraction. Thus, we too follow this line and deliberately focus mainly on the mate choice context, although we acknowledge the significance of physical appearance in other social contexts as well.

TRAITS CONSIDERED ATTRACTIVE AS CUES OF QUALITY

For the development of any trait acquisition of energy from the environment is needed as proposed by the life-history theory (Roff 1992). The theory assumes that the amount of energy available is limited and each individual must allocate a proportion of the energy to activities which increase his or her chance to survive. This is especially to reach sexual maturity, to reproduce and enhance the chances of survival of offspring, and further factors that generally lead to increased fitness. (Throughout the paper we use the term "fitness" to express a degree to which a given genotype contributes to the gene pool of the next generation, while the term 'physical fitness' is meant to describe parameters of physical performance of an individual such as strength, endurance, etc.). Such a trade-off between the investment into survival, growth, sexual maturity or traits related to attractiveness is thought to be an important drive of the selection of attractive traits and preference for them.

It is assumed that the tendency to be attracted to individuals of the opposite sex exhibiting certain traits provides the individuals so inclined with the advantage of higher reproductive success (Gangestad, Scheyd 2005). Several models have been proposed to explain how such preferences might have arisen.

In a model first introduced by Fisher (1930), a trait that becomes preferred develops by chance and preference for the most frequent trait is maintained within a population in such a way that offspring of one sex are expected to inherit the trait and offspring of the other sex inherit the preference for a such trait. Thus, the model assumes a genetic linkage between the genes affecting the preference and the genes responsible for the development of the preferred trait (Fisher 1930). However, this does not assume a link between the trait and the quality of the individual who possesses it. For that reason, the model is frequently referred to as the "sexy sons" or, more precisely, "sexy offspring" hypothesis. It should be noted that Fisher's model does not imply any positive relation of fitness and viability of an individual, which in turn could have been possibly reduced by prior investing into "sexy traits".

Another model (or, more correctly, a set of models), explaining how the preferences relate to the fitness of an individual, is frequently referred to as "honest signalling". One potential account of how honest signals have arisen, first introduced by Zahavi (1975), is a model of handicap. According to this model, only individuals of superior quality can afford to develop a trait which reduces their chance of survival and thus can serve as a quality signal. In other words, the trait poses a handicap to its bearer (e.g., deer's antlers). Later it was specified that for such a trait to limit its bearer, its cost must be high, however it must not reduce the fitness of its bearer in such a way that it would be lower than that of individuals without the handicap (Getty 2002). In the other account of honest signals, the quality of an individual is presented by the degree of development of the trait. In other words, a more developed trait shows the higher quality of the given individual, however, this relation is not necessarily linear (Getty 2002). This other account of honest signals focuses on the often-cited relation between attractiveness and the assumed parasite load present in a given individual, as proposed by Hamilton and Zuk (1982).

Although Fisher's runaway selection (Fisher 1930) is frequently presented as an alternative to the models of honest signals, mathematical modelling shows that every trait ultimately becomes costly (Kokko *et al.* 2003). As the cost of maintaining the trait which has evolved through runaway selection rises, the trait becomes an indicator of quality of the particular individual.

The above-reviewed models refer to an organism's quality in general terms. However, preferences might be related to specific qualities such as health, physical fitness etc. Below we focus on a hypothesis proposing such a specific link.

DEVELOPMENTAL STABILITY AND HETEROZYGOSITY

Throughout the evolutionary past of humankind, similarly to other species, infections and parasites have played an important role as they reduce an individual's fitness. It was therefore proposed that individuals will choose mates who show heritable cues of health (Hamilton, Zuk 1982). However, later it was argued that viability and reproductive success might be, to some extent, independent and thus the actual health status of individuals with preferred traits could be higher, the same or even worse than that of individuals lacking such traits (Getty 2002).

In the course of ontogeny, individuals face various adverse environmental effects caused by pathogens, factors affecting the rate of somatic mutation, availability of caloric intake and so on. The ability of an organism to successfully cope with such effects is commonly referred to as developmental stability and its heritability is thought to be relatively high. Developmental stability is assumed to be phenotypically represented by a high degree of bilateral symmetry of an individual's morphology (Møller, Swaddle 1997). A low level of developmental stability is expected to be related to a high level of fluctuating asymmetry (Gangestad *et al.* 1994), i.e., non-directional deviations from perfect symmetry in paired morphological traits (Benderlioglu *et al.* 2004).

Fluctuating asymmetry correlates with the speed of growth, fecundity and survival in many species (Parsons 1990). In humans, it has been previously found that fluctuating asymmetry is associated with the health of an individual, low resting metabolic rate (Manning *et al.* 1997), muscle soreness and shortness of breath (Shackleford, Larsen 1997) or chromosomal abnormalities, including Down's syndrome (Thornhill, Møller 1997). It is therefore expected that males with a lower level of fluctuating asymmetry are more frequently preferred as mates.

The results of previous studies in humans show that low fluctuating asymmetry is positively associated with an overall number of sexual partners in men (Thornhill, Gangestad 1994) and with the age of first sexual intercourse (Thornhill, Gangestad 1994). The level of fluctuating asymmetry thus appears to affect women's preferences and deviations from symmetry significantly change ratings of attractiveness. The effect of fluctuating asymmetry of the male body on ratings of physical attractiveness was tested in a sample of raters from England and Srí Lanka (Dixson *et al.* 2003). The results showed that a silhouette with a natural level of fluctuating asymmetry was rated by women as significantly more attractive than silhouettes manipulated to perfect symmetry in both population settings. Dixson's results are in line with those of studies in which perfectly symmetrical faces and bodies of men were not preferred (Swaddle, Cuthill 1995, Thornhill, Gangestad 1994). On the proximate level, it was suggested that traits which are too symmetric appear "unnatural" to raters and hence less attractive. In contrast, on the ultimate level, traits which are too asymmetric may indicate a poorer quality of the genotype of an individual.

However, it is unclear whether the variance in fluctuating asymmetry or resistance to adverse environmental influences reflected by fluctuating asymmetry is heritable (Thornhill, Gangestad 1994). Moreover, the link between developmental stability and parasitism is based on the correlative nature of several studies and the causation thus cannot be easily inferred (Møller 2006).

Fluctuating asymmetry in many species is also related to hetero- and homozygosity (e.g., Mitton 1984). It is thought that heterozygosity allows an individual to easily compensate for negative environmental and genetic influences during development, resulting in a lesser degree of deviation from perfect symmetry. The most up-to-date research on heterozygosity in humans has focused on its relation to the immune system and genes of the Major Histocompatibility Complex (MHC) in particular (Roberts, Little 2008). Products of the MHC genes participate in detection of alien agents in an organism (Hedrick 1994) and heterozygosity within the MHC loci is advantageous because the expression of MHC genes is co-dominant and an individual heterozygous in the MHC loci should potentially have a more efficient immune system. Heterozygosity in MHC loci is partly heritable (Mitton *et al.* 1993), therefore the offspring should have a similar advantage (McClelland *et al.* 2003).

Thus, heterozygosity might present one of the ways by which individuals develop more stable and morphologically more symmetric and average traits (e.g., Mitton 1984). Albeit the evidence for the relation of fluctuating asymmetry and heterozygosity is still inconsistent (Kartavtsev 1990, Livshits, Smouse 1993, Zink *et al.* 1985), fluctuating asymmetry alone appears to be a heritable trait without any necessary linkage to developmental stability or heterozygosity (Thornhill, Gangestad 1994). The patterns of fluctuating asymmetry might underestimate those of developmental stability, for asymmetries only weakly correlate with developmental stability (Gangestad, Thornhill 1999, Van Dongen 1998, Whitlock 1996, 1998). Importantly, fluctuating asymmetry (as a marker of developmental stability) cannot differentiate between environmental and genetic factors contributing to the resulting values of fluctuating asymmetry. Let us consider two individuals who live under the same environmental conditions. Their developmental stability may not be the same because of the differences in the individuals' genotype. In contrast, two individuals with an identical genotype may vary in their fluctuating asymmetry as a result of different environmental conditions they have been living in. It is then questionable what the level of fluctuating asymmetry alone actually says about the quality of an individual, without the knowledge of his hetero- or homozygosity and/or developmental stability, expressed, for example, in terms of his health history.

SEXUAL DIMORPHISM

It has been proposed that the expression or development of sexually dimorphic traits serve as cues to immunocompetence of an individual (Folstad, Karter 1992). The development of many sexually dimorphic traits is responsive to changes in the levels of sex hormones, which are thought to adversely affect the function of the immune system (Thornhill, Gangestad 1993). Therefore it is assumed that only high-quality individuals may afford to develop distinctive sexually dimorphic traits without reducing the function of the immune system below the limits of viability. Testosterone adjusts the use of energy and can allocate it for the development of traits like mate-seeking behaviour or intra-sexual competition (Gangestad *et al.* 2007). Such traits might further include the amount of muscle mass, physical strength or motivation to mate. These traits will not develop without allocating the energy which would otherwise be used to maintain the level of immunocompetence (Gangestad *et al.* 2007). A high level of masculinization in men may thus serve as a cue to a high quality of the immune system and selection may favour the women who prefer these traits. This way they gain advantage in the form of higher reproductive success (Fink, Penton-Voak 2002, Frederick, Haselton 2007, Provost *et al.* 2008). It was recently reported that facial attractiveness positively correlates with the antibody levels after hepatitis B vaccination; a marker of the total of the immune function (Rantala *et al.* 2012). However, similar results regarding the physique are currently not available. Further, it is important to stress that 20 years since the publication of the Immunocompetence handicap theory (Folstad, Karter 1992), convincing evidence about the adverse influence of sexual hormones on immunity is still missing or is not clear for many species, including humans (for review see Roberts *et al.* 2004).

It is well known that mate choice in humans partly relies on morphological traits of the opposite sex (Barber 1995, Hatfield *et al.* 1966) and some of them might be a result of sexual selection (Dixson *et al.* 2007). This may account for certain features of the human male physique, especially the upper body and a greater amount of muscle mass (Lassek, Gaulin 2009), which are sensitive to testosterone (Swami, Tovée 2005).

The largest differences in body constitution between men and women arise during puberty and early reproductive age, stimulated by levels of sex hormones regulating lipid tissue distribution (Vague 1956). Steroid hormones form either android (high testosterone level) or gynoid (high level of oestrogen) fat distribution, which can be assessed by measuring the waist-hip ratio index (WHR). WHR thus appears a cue to the action of steroidal hormones, sexual maturity and risk of cardiovascular or metabolic disorder (Björntorp 2009, Deridder *et al.* 1990, Evans *et al.* 1983). Previous studies have found that men's silhouettes with male-typical WHR (from 0.90 to 0.95) are rated by women as the most attractive (Singh 1995), with a positive correlation between attractiveness ratings of men's WHR and perceived health (Furnham *et al.* 1997). On the other hand, silhouettes out of the male-typical WHR range are rated as more likely to be older, with poorer health and shorter life span (Han *et al.* 1999).

Several studies examined preferences for male body shape in a cross-cultural perspective, assuming greater preference for endomorphic (i.e., stout) body builds in countries with poorer socio-economic conditions. Such a body build might be a marker of higher mate quality, which could be especially valuable in adverse environment. To test this hypothesis, Furnham and Nordling (1998) recruited raters from Denmark and Portugal, two European populations varying in net income. However, they did not find any convincing differences in body shape preferences between the two populations. Female raters from both settings rated the "V" body shape as the most attractive. This is characterised by large and broad shoulders, medium-sized waist and a small gluteo-femoral area. Perhaps the two populations the participants were recruited from in this study did not show enough variation in terms of economy (Furnham, Nordling 1998).

Moreover, other studies which employed the Waist-to-Chest Ratio (WCR) confirmed that a "V"-shaped upper body positively correlates with ratings of attractiveness. Nevertheless, the WCR (where WCR < 1 results in a "V"-shaped body) was the primary determinant of attractiveness only in western and urban samples of raters. Raters of rural origin (e.g., in Malaysia) preferred bodies with a more tubular body shape (WCR ≅ 1) (Swami, Tovée 2005). The best predictor of attractiveness in this sample was the BMI, explaining about 50% of variability (Swami, Tovée 2005).

The effect of overall variability of the male physique on female-rated attractiveness of the male body in several different countries (England, Srí Lanka, Cameroon, China, USA, and New Zeeland) was tested by Dixson and colleagues. They found that the mesomorphic physique (muscular body type) was rated as the most attractive in all the populations except China, where the average male somatotype was rated as the most attractive (Dixson *et al.* 2007), while the endomorphic physique (stout body type) was rated as the most unattractive in all the tested populations (Dixson *et al.* 2003, 2007a, 2007b, 2010). However, the somatotypes not only allow us to classify body constitution variability but they can also be used for physical fitness (e.g., strength, endurance) and health assessments as well (Carter, Heath 1990). Physical performance and health in the endomorphic somatotype are on average lower with a higher risk of cardiovascular disorders (Bolonchuk *et al.* 2000, Katzmarzyk *et al.* 1998). In contrast, the mesomorphic somatotype on average excels in physical performance tests and exhibits cardiovascular health up to a certain level (Carter, Heath 1990).

The above-reviewed female preferences have been shown to have their implications for real-life behaviour as men with the preferred physique and a high level of physical fitness indicate a younger age of first sexual intercourse and a higher number of sexual partners (Faurie *et al.* 2002, Frederick, Haselton 2007, Gallup *et al.* 2007, Hughes, Gallup 2003). In the light of the results on women's preferences for the male physique and sexual behaviour of men with such a physique, the level of physical fitness could be seen as a more reliable marker of attractiveness (Hönekopp *et al.* 2007) than cues of immunocompetence (Folstad, Karter 1992).

Besides body build, another sexually dimorphic trait that is assumed to explain most of the variance in ratings of physical attractiveness of the human male physique is body height (Pawłowski, Kozieł 2002). The life history theory considers differences in adult body height to be a result of different strategies of allocation of available energy during the development (Sear 2010). Every organism optimizes allocation of the available energy into growth and the immune system or reproduction and the pattern of this allocation is reflected in the adult height (Sear 2010). One key moment of the individual's ontogeny is that of the timing of the termination of growth and the start of reproduction since humans, like many other species, separate the period of growth from that of reproduction, both of which are costly (Sear 2010). Individuals developing in adverse or unpredictable environmental conditions are expected to finish growth and start reproduction earlier, which results in a smaller body size, compared to that of individuals who develop in more favourable and predictable environmental conditions, who can thus afford to allocate energy to a prolonged period of growth and postpone reproduction; a strategy which results in a bigger body size.

Studies conducted so far have focused on how sexual dimorphism in stature (SDS), i.e., differences in height between partners, affects mate preferences. The results indicate that women prefer men who are relatively taller than themselves (Pawłowski 2003, Salska *et al.* 2008, Swami *et al.* 2008). These preferences are influenced by women's own height (Pawłowski 2003); short women prefer a greater difference in the SDS whereas tall women prefer a smaller difference in the SDS (Pawłowski 2003). This adjustment can increase the pool of potential partners with regard to the distribution of height within the given population in contrast to preference for partners with a certain height, which would lead to a reduction of the pool of potential partners (Pawłowski 2003). Further, the variability in height is related to the risk of chronic health problems (Park *et al.* 2003) and disorders such as pituitary gigantism or Marfan's syndrome (Salska *et al.* 2008). Since height is a heritable trait (Silventoinen *et al.* 2001) it may be a cue to one's fitness and to the efficiency of the individual's immune system (Judge, Cable 2004, Sorokowski, Pawłowski 2008).

Importantly, recent studies in Himba (Namibia) (Sorokowski *et al.* 2011) and Datoga (Tanzania) (Sorkowski, Butovskaya 2012) people show that the pattern commonly found in the Western populations cannot be considered universal, as in the Himba sample, the preferred body height of a partner was similar to height of the rater and in the Datoga sample, women preferred much taller or much shorter partners. While preferences in the mentioned populations basically follow the one reported in the Western samples, nevertheless the "male-taller norm" is less pronounced here. Up to date, it is not clear what influences the preferences for a potential partner's body height, as body height is affected not only by genetic differences but also by environmental influences. It can be suggested that body height preferences may be influenced by cultural/stereotypical, environmental, and/or ecological conditions which need to be further investigated, e.g., by comparing height preferences and gender roles in the selected populations or testing ecological demands on body height dimorphism.

The size and height of an individual are commonly seen as characteristics that play a significant role in terms of reproductive success (Pawłowski *et al.* 2000), socio-economic status (Silventoinen *et al.* 1999), intra-sexual competition (Carrier 2011), and hence fitness. Pawłowski *et al.* (2000) have shown that taller men have higher reproductive success and it has been assumed that shorter men are disadvantaged in mate choice (Nettle 2002, Pawłowski *et al.* 2000), probably due to inter-sexual competition as taller men are perceived as healthier (Silventoinen *et al.* 1999) and more attractive (Pawłowski 2003), or due to the intra-sexual competition as taller men have the advantage of greater striking force (Carrier 2011) and perceived dominance (Watkins *et al.* 2010). However, a positive correlation of height and reproductive success cannot be considered universal, as results follows a rather curvilinear association between height and a number of children, with men of average height attaining the highest reproductive success (Stulp *et al.* 2012).

INDIVIDUAL DIFFERENCES IN PREFERENCES

The majority of the above-reviewed studies focused on a general pattern of preferences for specific features of the male body. However, the life-history theory posits that the outcome of trade-offs between growth and reproduction, for instance, varies across individuals depending on their current condition. As a consequence of such a variation, we may also expect inter-individual variation in mate preferences. In other words, preferences are expected to be relatively flexible in a condition-dependent manner. Unfortunately, the literature on the inter-individual variability in preferences for the male physique is rather limited.

One's own mate value appears to be an influential factor in mate preferences. More specifically, there is a robust body of evidence that physical attractiveness is an important determinant of the female mate value (Weeden, Sabini 2005). Thus, predictors of women's body attractiveness such as WHR, BMI (Furnham *et al.* 2002, Swami *et al.* 2006) and body height (Pawłowski, Koziel 2002) may modulate female preferences for the male physique (Björntorp 1997, Tovée *et al.* 2012, Weeden, Sabini 2005).

Nonetheless, only few studies considered the influence of a rater's own attractiveness on perception of body attractiveness of others. It has been shown that women who perceive themselves as attractive prefer a more masculine male body build (Little *et al.* 2007) and women with a BMI within a range that is considered attractive perceive the mesomorphic body build as more attractive (Třebický 2012). However, more studies are definitely needed as individual variation in traits related to fertility and fecundity might play a significant role in women's preferences. These would include the effect of fecundity markers such as age, breast symmetry, average levels of oestrogen hormones and so on.

Another factor which shows individual variation in preferences is fluctuation across the menstrual cycle (i.e., fluctuations of actual fertility). During the follicular phase of the cycle, when probability of conception is highest, women in general prefer more masculine faces (Jones *et al.* 2008, Little *et al.* 2007, Peters *et al.* 2009). In a similar fashion, they prefer greater development of other sexually dimorphic traits such as body height (Pawlowski, Jasienska 2005), masculine body shapes (Little *et al.* 2007) and the mesomorphic component of the somatotype (Třebický 2012). An alternative explanation stresses increased preferences for less masculine facial traits during the non-fertile phase (Jones *et al.* 2005). This preference might help find a mate exhibiting a greater tendency towards nursing behaviour and less prone to infidelity (Jones *et al.* 2005). It is thought that due to their association with a higher testosterone level, individuals with masculine traits may potentially tend more towards aggressive behaviour (Benderlioglu *et al.* 2004) and partnership instability (Burnham *et al.* 2003).

Thus, variation in preferences across the menstrual cycle might reflect variation in preferences for direct and indirect benefits and might ultimately lead to maximization of potential benefits from mating (Penton-Voak *et al.* 1999).

DISCREPANCY BETWEEN PREFERENCES AND ACTUAL MATE CHOICE

Throughout this paper we have almost exclusively focused on preferences. Aside from a scarce evidence from speed dating sessions (Stulp *et al.* 2012) and silhouette preferences (Třebický 2012), it seems that preferences are hardly ever actually explored in mate choice and should not be equated with actual mate choice. In contrast to preferences, mate choice is limited for several reasons. Firstly, a mate with the preferred trait may not be available, interested or could be subject to intense competition. Secondly, mate selection is a complex process and multiple traits are considered. A single individual rarely, if ever, possesses the exact combination of the most desired traits. Consequently, other traits may outweigh the most desired trait under consideration. For these reasons, we may frequently observe a discrepancy between the most preferred trait and quality of the trait in the actual partner.

For example, and as shown above, male height is related to mate choice in Western societies. However, recent studies indicate that mating with taller men is not cross-culturally universal and, as recent results from the Hadza people (Tanzania) show, there is no evidence for a general male-taller norm. In contrast to Western societies, mating appears not to be affected by men's height in the Hadza sample (Sear, Marlowe 2009).

One may ask about the rationale of the research on preferences when its findings may not reflect the actual mate choice. The primary significance of the research on preferences is that it allows us to explore perception irrespective of the actual real-life settings. Such studies may give us significant insights into the evolved psychological mechanisms and test evolutionary-inspired hypotheses. Further, studying the discrepancy between preferences and the actual mate choice allows us to test the relative significance of individual traits. The traits which are crucial in mate selection will be reluctantly compromised and vice versa.

IMPLICATIONS

As has been shown above, women exhibit consistency in their preferences for men's physique, which may present a cue to a higher level of muscularity or sexual dimorphism, physical fitness and health. A moderate degree of development of muscularity and height appears to be the most attractive. Previous studies on attractiveness have often considered only linear effects. In contrast, the inverted-U hypothesis suggests that preferences for an extreme degree of trait development might be limited and follow a more curvilinear pattern, i.e., ratings increase up to a certain point but the traits which exceed a certain limit are rated as less attractive (Frederick, Haselton 2007). Such inverted U patterns of ratings can be seen in the ratings of height (Pawłowski 2003), muscle development (Frederick, Haselton 2007, Lynch, Zellner 1999), fluctuating asymmetry (Dixson *et al.* 2003) or the composition of a somatotype (Třebický 2012). Although the mesomorphic component of a somatotype positively affects attractiveness ratings, its effect is neither absolute nor linear (Třebický 2012).

A great degree of development of masculine traits is related to high levels of testosterone (Bhasin 2003), which is assumed to reduce the immunity of an individual (Folstad, Karter 1992, Thornhill, Gangestad 1993). In contrast to the expected linear relationship of the development of a trait and its attractiveness, in the immunocompetence handicap theory (Folstad, Karter 1992) heterozygous individuals are expected to exhibit better immunocompetence and because heterozygosity is manifested in phenotypic averageness, one might assume that the traits exhibiting a degree of development that falls within the range of the population norm should be rated as the most attractive (Thornhill, Gangestad 1993, Watson, Thornhill 1994). It is then advantageous for individuals of the opposite sex to prefer masculine traits in mates which are developed slightly more than is the population average (as described by the inverted U pattern), and achieve the most beneficial trade-off between the ability of a man to hunt, fight or defend and the weakest adverse effect of testosterone on the immune system possible (Barber 1995). Individuals should avoid mating with others who are out of the population norm in terms of trait development; accordingly, such a degree of development may serve as a cue to a disadvantageous genotype. However, the adverse effect of the sexual hormone on the function of the immune system in humans is yet to be fully established.

Results of the above-reviewed studies which employed attractiveness ratings also indicate that women prefer traits of the male physique which might provide a cue to physical fitness (e.g., the mesomorphic somatotype and tallness) (Thomis *et al.* 1998). Women should be attracted to such traits whereas their offspring may profit not only from the indirect benefits but also from the direct ones.

A common denominator of all cues of quality mentioned above is health (Weeden, Sabini 2005) which is usually related to immunocompetence, heterozygosity, developmental stability and fitness in many species (Møller, Swaddle 1997). The concept of health encompasses not only the actual absence of disease, but also effectiveness of the immune system, lower incidence of pathogen-induced diseases, better ability to allocate the available energy during development, and may be a cue to health during growth and maturity. Health does not necessarily imply a longer life span of an individual or higher physical fitness, though. Traits related to the reproduction potential of an individual are expressed in the concept of health disproportionally (Weeden, Sabini 2005). Getty (2002) and Kokko and Johnstone (2002) emphasize that health or survival only have an important place in the modern theory of evolution as long as they contribute to an increase in the reproductive success. Hence there is no evidence of a direct and linear relation between health and physical fitness. Healthy individuals are not necessarily more physically fit, but physically fitter individuals are supposed to be healthier. A greater mesomorphic component is related not only to higher physical fitness but also to lower prevalence of cardiovascular disorders (Carter, Heath 1990, Katzmarzyk *et al.* 1998, Malina *et al.* 1997). The relation between physical attractiveness and health is likely to be subtle, especially in the Western, Educated, Industrialized, Rich and Democratic (WEIRD) individuals who participate in most of behavioural studies (Henrich *et al.* 2010) in which the evidence is often mixed or missing (Geary 2005, see also review by Weeden, Sabini 2005). It is likely that the relation between traits of attractiveness and sexual hormones or the efficiency of the immune system is not fully expressed and thus not easily detected in populations that are not under environmental stress (Geary 2005). Traits assumed to be indicators of environmental stress (e.g., fluctuating asymmetry) are likely to be more distinct indicators of physical attractiveness and health in populations which are more at risk of parasite infection or poorer caloric intake (Grammer *et al.* 2005). Therefore, attempts to explain evolutionary processes which are based solely on results from the Western samples should be treated with caution as reproductive strategies may differ depending on the specific environmental conditions.

It is generally assumed that the above-discussed sexually dimorphic traits are products of inter-sexual selection. This might seem self-evident due to the fact that men and women in the Western societies are virtually free to choose mates on the basis of beauty and physical fitness. These criteria and conditions are so pervasive today that it is tempting to think of them as being characteristic of the human evolution. But are these preferences really the primary force? It was recently argued by Puts (2010) that inter-sexual selection has been the primary mechanism of sexual selection in men, which contradicts the mainstream theoretical predictions. In particular, male intra-sexual selection might override other mechanisms of sexual selection (e.g., mate choice, sperm competition) by excluding rivals by force from opportunities to mate and it is thought to be the main form of mating competition in men.

Men are larger, stronger, faster, and more physically aggressive than women (see Puts 2010 for a review). Men report engaging in and inclinations to engage in, more physical aggression than women (Buss, Perry 1992) and perpetrate more offensive physical aggression in all societies studied (Ellis *et al.* 2008). Relatively greater male upper-body muscle mass and strength suggest an evolutionary history of fighting in men (Sell *et al.* 2009). Thus men's anatomy and behaviour predicts male intra-sexual competition to be the primary mechanism shaping the human male phenotype. Further, several masculine traits are perceived as attractive (e.g., muscular physique), however a higher degree of development of these traits increases perceptions of dominance more substantially than it increases ratings of attractiveness and masculinity. This has been found to produce smaller positive effects on attractiveness to women than on dominance judged by men (Puts *et al.* 2006). Thus, masculine traits appear to be probably designed for intra-sexual competition rather than for attraction of potential mates. Body size, strength and aggression are probably helping modern-day men to win mating opportunities in much the same way they helped their ancestors, rather than to increase their attractiveness for the opposite sex. Therefore, preferences for the physique with cues to a high level of physical fitness could be adaptive for women as men with such a physique might be successful in intimidating potential rivals in the intra-sexual competition (Barber 1995, Gangestad *et al.* 2007) and men with a higher level of physical fitness are perceived as better fighters (Sell *et al.* 2009). In sum, this suggests that neither intra-nor inter-sexual selection have been the single selection pressure, but they have interacted in shaping the human male phenotype.

Finally, we would like to point out several methodological issues which might have affected the outcome of some of the above-reviewed studies. The major is the inconsistency and the form of the stimuli employed for studying physical attractiveness. The stimuli frequently capture the variability of the human male physique insufficiently (e.g., Dixson *et al.* 2003) or unnaturally. They often take on the form of line drawings originally based on real male body variability, but with unnatural manipulations (e.g., Dixson *et al.* 2003) or the form of line drawings based solely on draughtsmen's interpretations resulting in low validity forms (Lynch, Zellner 1999). Another common form of the stimuli employed are digitally morphed images or composite images produced by overlapping several individual photographs. Even here the resulting validity might be limited. The resulting morphs or composites based on the correlative nature of studies may be outside the range of possible morphological variability. For example, in a study by Little *et al.* (2007) masculine and feminine morphs of bodies were created. However, the feminine body morphs were not based on the shapes of male bodies rated as feminine, but rather they were based on ratings of female body shapes, and thus could not capture the variability of the male physique.

CONCLUSION

Research on physical attractiveness has been one of the central topics in current human ethology, behavioural ecology and evolutionary psychology as it might have significant impact on one's reproductive success. It is expected that the perception of attractiveness is sensitive to traits linked with biological or other qualities of the given individual. However, in spite of an enormous body of literature on physical attractiveness, core evolutionary inspired theoretical concepts are rather vaguely phrased and several theoretical issues still remain to be resolved.

The aim of the paper was to briefly demonstrate these theoretical concepts and review empirical findings of the studies on preferences of selected human male body traits. In particular, we discussed theories of developmental stability, its relation to fluctuating asymmetry and heterozygosity. A modest level of symmetry appears to be perceived as the most attractive, individuals showing a lower level of fluctuating asymmetry are rated as more attractive similarly as heterozygote individuals. Although body symmetry appears to be related to developmental stability, and might be a marker of heterozygosity, these three concepts cannot be freely interchanged as they refer to distinctive qualities. Subsequently, we discussed theories on immunocompetence and sexual dimorphism and its expression in overall body build and body height. In general, only slightly more athletic and taller men higher development of body build and body height are perceived as the most attractive. Further, individuals of greater physical fitness show higher level of body build and/or height development. These associations suggest that body attractiveness might cue to physical fitness rather than supporting immunocompetence theory which still lacks robust empirical evidence in humans. Finally, a vast majority of human male body features shows that a moderate development appears to be the most attractive and that preferences for these traits seem to follow a curvilinear pattern.

Due to the central role of reproduction in evolutionary theorizing, a majority of the evolutionary theories of physical appearance focus on its role in mate attraction. However, some of the human male body features might have arisen as a result of intra-sexual competition. As men are on average stronger, more physically aggressive, and more frequently engage in physical contests than women in all societies studied so far, it suggests a relatively high level of male intra-sexual competition in human evolutionary history. Further, more developed male-typical traits increases perception of dominance more substantially than it increases ratings of attractiveness. It could be assumed that men's anatomy and behaviour predicts male intra-sexual competition to be the highly influential mechanism shaping the human male phenotype. Thus, both inter- and intra-sexual selection should be considered in the context of human male body build.

Most of the studies so far explored a general pattern of the preferences; however, life-history theory proposes that one may expect individual variations in preferences related to the actual conditions of the given individual. On similar note, we currently need more studies based on raters from non-Western countries as cultural and environmental variables may contribute to the variations in preferences. Thus, both individual- and society-level differences should be explored in future studies. Finally, one should note that preferences cannot be equated with actual mate choice as the mate choice in contrast to the preferences might be restricted by various factors such as availability of the preferred partner, importance of the preferred trait and so on.

In conclusion, we hope that the paper will contribute to unravelling the blurred theoretical issues and help future researches on physical attractiveness to follow new avenues for further research.

ACKNOWLEDGEMENTS

We would like to thank Lenka Nováková for numerous valuable advices and language corrections and two anonymous reviewers for valuable comments on the earlier versions of the manuscript. VT was supported by Charles University Grant Agency grant GAUK 695512 and SVV-2012-265 703 grant by the Czech Ministry of Education, Youth and Sports. KK was supported by Czech Grant Agency grant GACR P407/11/1464, and JH was supported by Charles University Research Centre UNCE 204004.

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