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Human Mate Selection Based on Developmental Stability as Signaled Through Physical Attractiveness: An Assessment of the Traits Used to Determine Attractiveness and the Evolutionary Mechanisms for their Development

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What are the criteria used to select a mate? Study of this question on non-human subjects has shown many organisms choose mates based on assessments of health, youthfulness, and fertility, as signaled through certain physical characteristics. Investigations into the mating behaviors of humans, cross-cultural studies of attractiveness, and current medical research link features of attractiveness with health and support the evolutionary perspective that beauty is more than an arbitrary cultural creation. The characteristics which males and females find attractive in the opposite sex are largely the results of the evolution of sexual selection and serve to inform potential mates of the individual's level of developmental stability. This paper investigates which physical traits are used by males and females to determine attractiveness, the correlation between these characteristics and the developmental stability of an individual, and the subsequent effects on mate selection and parental investment.

Introduction

What are the criteria used to select a mate? Study of this question on non-human subjects, including mammals, birds, insects, and plants has shown many organisms choose mates based on assessments of health, youthfulness, and fertility as signaled through certain physical characteristics (Gangestad 1993, Low 1989, Manning 1995, Moller 1990, and Thornhill 1997). Both male and female organisms have been shown to use physical criteria such as symmetrical features, color, size, and unique characteristics as standards in mate selection. The most common examples are the colorful and symmetrical patterns on the wings of a butterfly or the magnificent tail of a peacock. These characteristics are known to attract mates and signal health and high genetic quality (Gangestad 1993, Manning 1995).

In recent years, research on the role of attractive physical features in determining human mate selection have found results consistent with studies of non-human species (Gangestad 1993, Gangestad et al. 1994, Low 1989, Manning 1995, Moller 1990, Moller et al. in press, and Thornhill 1997). But what is attractive? Is it unique to each individual or are there universal standards of beauty? The 'common sense theory' maintains "beauty is in the eye of the beholder" (Etcoff 1994, Johnston 1993). This theory suggests beauty is not objective, but is relative to the personal taste of each individual, as well as, culturally defined. Proponents of this theory contend that consistent patterns in standards of beauty result from education through the mass media, such as television and magazines (Etcoff 1994:186). However, evidence in support of the theory of sexual selection provides consistent results from cross-cultural studies illustrating universal standards of beauty, as well as, mate selection based on the potential partner's perceived quality (Singh 1994:446). As Cosmides et al. wrote regarding the evolutionary forces acting on human behavior (Etcoff 1994:186),

Culture is not causeless and disembodied. It is generated in rich and intricate ways by information-processing mechanisms situated in human minds. These mechanisms are, in turn, the elaborately sculpted product of the evolutionary process. Therefore, to understand the relationship between biology and culture, one must first understand the
Investigations into the mating behaviors of non-human species, cross-cultural studies of human attractiveness, and current medical research link features of attractiveness with health and support the evolutionary perspective that beauty is more than an arbitrary cultural creation (Ettcoff 1994:186). This paper investigates which physical traits are used by males and females to determine attractiveness, the correlation between these characteristics and the developmental stability of an individual, and the subsequent effects on mate selection and parental investment.

What traits constitute beauty is only beginning to be investigated. Morphological variation in the degree of facial symmetry, or fluctuating asymmetry, and body size and shape constitute the physical criteria currently being studied (Singh 1994:446, Thomhill 1997). Symmetry, in reference to bilateral facial features or body structures, is the measure of corresponding left to right traits (Gangestad et al. 1994, Thomhill 1997:1). For example, symmetry is the degree to which both eyes measure from the midline of the face or down from the top of the forehead. Fluctuating asymmetry is the measure of minor deviations from normal bilateral symmetry (Thomhill 1997:1). As with non-human species, physical development is regulated by growth rates, hormone levels, nutrition, pathogen stress, and genetics which correlate to health, fertility, and youthfulness (Gangestad et al. 1994, Johnston et al. 1993, Singh 1994, Thomhill 1997). While fluctuating asymmetry is present to some degree in every individual, the level of the asymmetry serves as a measure of developmental stability, which is an indication of an individual's ability to withstand genetic and environmental stress during growth. According to Thomhill (1997:4),

Fluctuating asymmetry is a sensitive measure of deviation from an ideal state of health at both the population and individual levels, which is theoretically robust, empirically verified across species, and relatively easy to obtain.

Developmental stability is also measured by phenodeviants, which are congenital birth defects and minor physical anomalies which occur during development (Thomhill 1997:1). Physical anomalies may occur during the growth of a fetus, as the result of poor maternal nutrition during pregnancy, or may result during childhood growth due to sinus or parasitic infections (Thomhill 1997:33). Once these anomalies occur, subsequent growth is altered which affects development and the phenotypic expression of traits, such as facial bone morphology. Ultimately, various levels of fluctuating asymmetry result.

Individuals with high developmental stability will exhibit a high degree attractive traits which are phenotypic expressions of one's genetic make-up (Thomhill 1997:2). Investigations into the correlation between attractive facial features and an individual's level of developmental stability demonstrates that facial attractiveness is a reflection of developmental stability and that attractiveness is the result of evolutionary forces (Gangestad 1993, Gangestad et al., 1994, and Thomhill 1997:2). Gangestad et al. Wrote (1994:74),

Organisms' genomes specify developmental designs that, if expressed precisely through an epigenetic process, result in adaptive phenotypes.

In other words, the characteristics which males and females find attractive in the opposite sex are largely the results of the evolution of sexual selection and serve to inform potential mates of the individual's level of developmental stability.

Evaluations of developmental stability, through the measure of fluctuating asymmetry, have assessed dental traits; skin texture; and secondary sexual traits, such as the chin, brow ridge, shape of the forehead, area around the eyes, and cheekbones, breasts, and musculature; as well as, non-sexual bilateral traits including,
the ears, wrists, ankles, and feet (Singh 1994:446). These surveys have sought to establish what males and females deem attractive, the normal levels of asymmetry, the conditions under which asymmetries develop, and the mechanisms responsible for their presence. Fluctuating asymmetry has been positively correlated to individual intelligence, mental retardation, mental illnesses, fetal alcohol syndrome, Downe's Syndrome, mating success, ability to fight for resources, and pathogen resistance (Singh 1994:446, Thomhill 1997:5-6, 11, and 14). Furthermore, study of fluctuating asymmetry has confirmed both attractive males and females have greater facial and body symmetry and more sexual partners, regardless of their age, race, marital status, or body size (Singh 1994:446).

Similarities and differences are present between the traits used by males and females in assessing attractiveness. Females show preferences for males with symmetrical and well-developed secondary sex traits, larger body size, and higher musculature development (Gangestad 1993, Low 1989, Manning 1995, and Thomhill 1997, Singh 1994). Whereas, males show preferences for females with high facial symmetry, a small lower face, full lips and a low waist-to-hip ratio (0.7:1) (Gangestad 1993, Low 1989, Manning 1995, and Thomhill 1997, Singh 1994). Randy Thomhill, one of the leading researchers in the area of human mate selection, described this process (1997:36).

Female Choice

Secondary sex traits are those features which develop at puberty. As an individual grows and reaches puberty, hormones are released throughout the body. In males, androgens are released which are self-regulating bio-chemicals responsible for the development of various sex traits (Thomhill 1997:7-8). The primary physical characteristics females find attractive in males are symmetrical facial features, well-developed secondary sex traits such as a strong jaw-line, prominent cheekbones and brow ridge, and large and well developed muscles (Low 1989:332, Gangestad et al. 1994, and Thomhill 1997:7).

Various studies have also illustrated that larger males with more muscular development are preferred over smaller males (Thomhill 1997:35, Manning 1995:150). Thomhill discusses the Ache Indians based on work by Hill and Hurtado in the middle 1980's (Thomhill 1997:35). Ache men who were larger with more muscular development had more offspring than did smaller males (Thomhill 1997:35). Also, Ache women viewed larger and stronger males as more attractive and healthier (Thomhill 1997:35). Other studies discussed by Thomhill showed that American women prefer males with "athletic" builds and that women with larger mates tended to have more orgasms during copulation (Thomhill 1997:35). Furthermore, Thomhill (1997) found males exhibiting high levels of symmetry are more likely to have sex at earlier ages and to have more sex partners than are males with high fluctuating asymmetry.

One possible mechanism to explain female preference for symmetry and large size may be the immunocompetence handicap principle. This hypothesis postulates that only those individuals who are healthy, meaning an individual without parasites, other infectious pathogens, or developmental defects, will develop robust secondary sex traits because of the high cost of development (Thomhill 1997:7-8). Those males that are weak due to disease

The adult male body is attractive when reflecting testosterone effects and athleticism, which covary with physical and developmental health. The adult female body is attractive when it shows good health, i.e. developmental stability in breasts and high oestrogen levels in low waist-to-hip ratio.

The following sections investigate the particular traits females and males use to assess attractiveness in mate selection and the possible mechanisms responsible for their development.
or genetics, will not be able for afford the energy required for robust and symmetrical development (Thornhill 1997:7-8). There is a relationship between high expressions of sex traits and a high immune system. The highest quality males, exhibiting good sex traits, will also have high quality immune systems (Thornhill 1997:8). Alternatively, low quality males will have low immune systems (Thornhill 1997:7-8).

Attractive adult faces of both sexes reflect secondary sexual traits requiring high titres of sex-specific hormones that may connote immunocompetence, and attractive facial secondary sexual traits may connote greater emotional and psychological health. Also, attractive faces are developmentally healthy as seen in their high developmental stability (Thornhill 1997:36).

The development and symmetry of secondary sex traits and overall size of males indicate their developmental stability, or specifically, their level of health and genetic quality. This is crucial in mate selection since females optimally choose males who are healthy, because they provide high parental investment and produce healthy offspring (Moller et al. In press). Ultimately, the survival and reproductive success of an individual’s offspring are affected by the father’s level of developmental stability because of genetic inheritance and parental investment. Female fitness, based on reproductive success, is limited by paternal investment (Moller et al. In press). Fathers with developmental instability will likely produce offspring with high levels of fluctuating asymmetries or phenodeviations (Thornhill 1997:1-3). Likewise, fathers who are ill cannot provide the same resources and time for raising children, as can fathers who are healthy and strong (Gangestad 1993:80-81).

Male Choice

There are similarities and differences in the traits males and females use to determine attractiveness. Consistent with female choice, males use body size, facial and body symmetry, and secondary sex traits to assess beauty. The particular traits used by males correspond to female hormone levels, fertility, and low pathogen stress. First, standards among American men for female attractiveness were observed (Etcoff 1994, Gangestad et al. 1994, Perrett et al. 1994, Singh 1994, Thornhill 1997). Tendencies among males were shown to focus on particular physical attributes in choosing a mate, including youthfulness, low waist-to-hip ratio, and the development of symmetrical facial features, including a short lower face, full lips, gracile jaw, high cheekbones, and lighter-than-average unblemished skin (Symons in Etcoff 1994:187).

Second, tests to ascertain the role of symmetry in determining attractiveness, as well as, cross-cultural standards of beauty were confirmed (Gangestad et al. 1994, Perrett et al. 1994, Thornhill 1997). In order to test the role of symmetry in judging attractiveness, numerous researchers developed studies with averaged face composites (Langlois and Roggman 1990, Gangestad et al. 1994, Perrett et al. 1994). A composite is a photo of an ideal individual based on the averaging of a series of various photographs together (Perrett et al. 1994:239).

Langlois and Roggman (1990) had subjects rate the original photographs and composites for attractiveness and found that the average faces were the most favored (Gangestad et al. 1994:80). They attributed preference of the average face to additive genetic variance and heterozygosity (Gangestad et al. 1994:80). Facial features have an added genetic variance, which means that if features are extreme in size or shape, they are homozygous, while the middle range expression of features are heterozygous (Gangestad et al. 1994:80). Whether features are homozygous or heterozygous reflects the particular genes acting on the development of these traits (Gangestad et al. 1994:81). The average features, determined the most attractive, are heterozygous and may be associated with fewer genetic mutations resulting in higher
developmental stability (Gangestad et al. 1994:81).

Perrett also tested the theory of averageness by comparing attractiveness in composites with similar face shapes (Perrett et al. 1994:239). This study was based on the premise that an average face composite derived from moderately attractive faces, should not differ in attractiveness from an average face composite built from beautiful faces (Perrett et al. 1994:240). He further postulated that any exaggerations away from the average features should be considered less attractive (Perrett et al. 1994:240). In addition, to test the cross-cultural attitudes of attractiveness, Perrett used both Caucasian and Japanese students as participants in evaluating multi-ethnic female photographs (Perrett et al. 1994:241).

Perrett confirmed cross-cultural standards of beauty by illustrating both Caucasian and Japanese students rated Caucasian and Japanese faces the same. Students of both ethnicities choose the same cross-ethnic photographs as the most attractive (Perrett et al. 1994:241). Furthermore, he concluded the most attractive faces for males and females were not the most average faces and that some preferences for extreme features were present (Perrett et al. 1994:241).

Additional investigations of particular facial features, studied independent of the whole face, reveal similar results (Gangestad et al. 1994). Some traits are preferred in sizes larger or smaller than the average size and morphology traits. For example, the average size nose is considered more attractive, while, prominence in the areas around the eyes and high cheekbones are preferred over the averages (Gangestad et al. 1994:81). Furthermore, extreme male features considered the most attractive include a prominent brow ridge and cheekbones and a larger than average chin width and length (Gangestad et al. 1994:81). Photographs of individuals exhibiting prominence in these areas were determined to be more attractive than the averaged composites.

The mechanism for preference of prominent secondary sex traits may be related to the increased production of testosterone needed to develop these traits during puberty (Gangestad et al. 1994:81). Development of these traits are costly and occur at some suppression of the immune system. Therefore, the presence of prominent secondary sex traits may be associated with higher levels of disease resistance as was discussed earlier as the immunocompetence handicap principle (Gangestad et al. 1994:81).

Males have been shown to prefer larger than average female lip size (Johnston et al. 1993:197). The average lip size in the Caucasian population is 16.8 mm. However, the most desirable size, determined through Johnston et al. Investigations, is 19.4 mm (1993:197). Moreover, the size of a female's lips change throughout adolescence and are determined by the amount of fat deposits (Johnston et al. 1993:197). Fat deposits are controlled by estrogen levels which are significant for female development and fertility (Johnston et al. 1993:197).

The 'high fertility hypothesis', according to the research of Buss, predicts males prefer females with the most reproductive value. Therefore, characteristics indicating high reproductive value are more highly regarded (Johnston et al. 1993:196). The 'high fertility hypothesis' may explain why certain female traits are deemed attractive by males. Abundant medical research has established the roles of various hormones in developmental stability, fertility, and pathogen resistance (Etcoff 1994:187). Female traits most valued as attractive by males, such as a small lower face, full lips and a low waist-to-hip ratio, are associated with the highest levels estrogen (Singh 1994, Thomhill 1997:32). Estrogen is responsible for developing a strong immune system and lower levels of testosterone, which are important to female long term developmental stability and health (Thomhill 1997:32). For example, females have significantly lower risks of developing heart
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more attractive, healthier, and more preferred for short and long-term relationships (1994:445, 470). Furthermore, Singh found females with lower waist-to-hip ratios were ranked as 22-24 years of age, while higher waist-to-hip ratios were judged as 25-27 years old, which supports youthfulness as an important criteria in mate selection (1994:470).

Research by Manning (1995:150) showed that female body symmetry is also an important component to attractiveness. According to Manning (1995), the diet industry in Western societies is extensive because beauty is determined by thinness, while in many traditional societies, obesity is considered attractive and is associated with higher economic and social status. Low (1979) also found that in Western societies, men of high social and economic status were more often married to thinner women than were males of low economic-social status (Manning 1995:151). Furthermore, Thornhill and Gangestad (1993) found that asymmetry is more common among heavy females than light females (Manning 1995:150).

The best explication for differential body weight preferences is the 'food security' hypothesis which maintains female body fat is adaptive in environments with fluctuating food availability (Manning 1995:150). It is, therefore, logical that males in regions with food shortages would prefer females exhibiting access to nutritional resources and thus, prefer heavier females. However, a paradox exists between the adaptive function of increased fat deposits for survival in environments with food scarcity and the correlation between obesity and lower developmental stability. Obesity is linked to variety of serious health conditions including heart disease and parasitic infection (Manning 1995:151). Perhaps obesity is considered attractive in regions with low food resources, in spite of its association with high fluctuating asymmetry, because the immediate risk of nutritional stress outweighs risks associated with fluctuating asymmetry.

Theory of Sexual Selection

All societies have expressive art forms which use the human body, whether it is through clothing, ornaments, cosmetics, tattooing, or body painting (Ember et al. 1990:455). The reasons for such decorations may be aesthetic, artistic, religious, sexual, or political and they vary among each culture. According to Ember et al. (1990:445),

The body may have been one of the first objects of art - that is, an object of nature that people transformed into an object of culture by the addition of symbols.

One function of body decoration may be beauty, as these symbols attract the attention of the opposite sex and may serve to inform potential mates of socio-economic status. Ember et al. (1990:456) points out the function of eroticism in body decoration and cites examples of females painting their lips in order to attract attention to that area or wearing jewelry around the neck or ankle, again to attract male attention to those areas of the body. The mechanisms for cultural differences between types of body adornment, as well as, the differences between male and female adornment are not well investigated.

To understand male and female preferences for attractive physical features, and the subsequent effects on mate selection and parental investment, the theory of sexual selection and two alternative theories are examined: the 'common sense' theory and the theory of natural selection. The role of attractiveness in mate selection is best explained by the theory of sexual selection which states (Thornhill 1997:5),

...the individual variation in offspring production that is the consequence of individual differences in traits that affect access to mates.

Three possible mechanisms may explain the theory of sexual selection: the good parent hypothesis, the parasite avoidance hypothesis, and the good genes hypothesis.
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Three possible mechanisms may explain the theory of sexual selection: the good parent hypothesis, the parasite avoidance of hypothesis, and the good genes hypothesis
evidence includes societies without Western mass media and suggests that something other than learned attitudes are responsible for determinations of what is attractive. Alley and Cunningham's 1993 study of thirty-seven societies found male preferences for females at an average age of 24.8 years (Johnston 1993:196). Also, Singh (1994) found that Caucasian and Japanese students ranked the same female Caucasian and Japanese faces as the most attractive.

The second alternative theory to mate selection is natural selection. Langlois and Roggman (1990) hypothesized that natural selection is the mechanism operating behind the development of attractiveness in evolution. Johnston et al. (1993:194) wrote:

As a result of natural selection, genes which contribute to an individual's survival will be passed on to the next generation and the frequencies of these genes will continue to increase with each new generation.

The theory of natural selection maintains three points. First, attractive features will become average over generations, because extreme features are not the most adaptive and will be selected against (Johnston et al. 1993:194). Second, individuals should be attracted to average features, because it is in their best reproductive interest to mate with those who have high levels of fitness (Johnston et al. 1993:194). Third, attractive features are adaptive to each particular environment. Therefore, different environments should have different standards for beauty (Johnston et al. 1993:194). For example, people living in particular environments such as tropical forests have adapted the most beneficial physical characteristics given the limits on their environment, for example, nose morphology or body stature. Johnston et al. Wrote (1993:194),

Wide, flat noses are best for the hot, steamy climate of the tropics, where the nose need only contribute a small proportion of the required moisture and warming, whereas a much larger nose is required for conditioning the air in a cold, arid climate.

As discussed earlier, recent research in the area of average facial features and beauty suggests the most average features are not always determined to be the most attractive, which addresses the second point of theory of natural selection (Johnston et al 1993:194, Etcoff 1994, Perrett et al. 1994). Again, Alley and Cunningham, as well as Johnston et al. (1993:197), concluded the average faces were mostly regarded as beautiful, however, individual faces with particular extreme characteristics were scored as the most beautiful. Preferences for exaggerated traits away from the averages, such as females with larger than average lip size and males with more prominent brow ridges and jaw lines were preferred over the composites or averages (Johnston 1993, Singh 1994). These studies illustrate that preferences for individuals with high indications of fertility, such as estrogen, or high levels of developmental stability are favored. Yet, as evidence for the 'good genes' hypothesis has shown, genetic inheritance is also important in developmental stability and mate selection. Johnston et al. (1993:197) may best resolve this discussion.

The population average face is best considered as a compromise between the influences of natural and sexual selection. It reflects the most adaptive characteristics for survival in a local environment, modified by sexual selection in the direction that the opposite sex finds to be most beautiful.

Summary

Whether we look at scientific studies or popular Western culture, physical attractiveness is an important determination in life-long mating partners. The fashion, cosmetics, diet, and entertainment industries in American society are centered around concepts of beauty and the role of beauty in determining human behavior. Cross-culturally, people adorn their bodies through a variety of creative expressions.
Investigations into the mating behaviors of a host of non-human species have concluded that mammals, birds, and insects choose partners who are healthy, fertile, and youthful based on assessments of physical criteria. Studies using human subjects have also explored mating behavior, the use of physical attractiveness in mate selection, and the evolutionary mechanisms behind beauty. Their results have been consistent with studies of non-human subjects.

The particular physical criteria used by females include, symmetrical and prominent secondary sex traits, large body size, and well developed musculature. Physical traits important in female assessments of attractiveness are determined by high levels of testosterone and other androgens which signifies stable growth and a healthy immune system. The absence of parasites, congenital defects, and other pathogens are important to females who are seeking a partner to invest in a relationship, as well as, children.

Likewise, the particular physical criteria used by males include, symmetrical and gracile secondary sex traits, exaggerated lip size, small body size, youthfulness, and a low waist-to-hip ratio. Additionally, the female traits shown to be important to males in determining attractiveness and choosing a mate are also linked to hormones such as estrogen and low levels of androgens. Moreover, high levels of estrogen are crucial to female health and fertility.

Finally, attractive physical traits were shown to be consistent with a high level of developmental stability which signifies the appropriate levels of specific hormones and low levels of fluctuating asymmetry, pathogen stress, and congenital defects. Moreover, several possible mechanisms were discussed as possible explanations for the use of attractiveness in human mating selection, parental investment, and male and female reproductive success; including the 'good parent' hypothesis, the 'good genes' hypothesis and the parasite avoidance hypothesis.

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### Table I. Measures of Developmental Stability

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<tr>
<td>Ears</td>
<td></td>
</tr>
<tr>
<td>Wrist</td>
<td></td>
</tr>
<tr>
<td>Ankle</td>
<td></td>
</tr>
<tr>
<td>Feet</td>
<td></td>
</tr>
</tbody>
</table>

### Table II. Health Risks Associated with High Waist-to-hip Ratios (>8.5)

<table>
<thead>
<tr>
<th>Late Menarche</th>
<th>Type II diabetes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gallbladder Disease</td>
</tr>
<tr>
<td></td>
<td>Carcinomas of the endometrium, ovary, and breast</td>
</tr>
<tr>
<td></td>
<td>Heart Disease</td>
</tr>
<tr>
<td></td>
<td>Stroke</td>
</tr>
<tr>
<td></td>
<td>Mortality</td>
</tr>
</tbody>
</table>

### Table III. Female Preferences

| Symmetrical and Well Developed Secondary Sex Traits
| Symmetrical facial features
| Symmetrical facial features |
|----|------------------|
| Larger body size          | Short lower face |
| Developed musculature     | Gracile jaw     |
| Strong jaw line           | High cheekbones |
| Prominent cheekbones and brow ridge | Full lips |
| Low waist-to-hip ratio (<8.5) |                  |
| Youthfulness              |                  |
| Lighter-than-average,     |                  |
| Unblemished skin          |                  |