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Abstract

Sexual selection has greatly influenced the evolved biology, psychology, and culture of humans and favors individuals who choose healthy and fertile mates. Physical traits that cue quality are generally preferred and perceived as attractive. However, because such traits often involve cost-benefit trade-offs, mate preferences are expected to vary among cultures as a function of local ecology and social environment and among individuals as a function of one's personal experiences and life history. As such, it is essential to understand how ontogenetic and environmental factors influence mate preferences that may be locally adaptive and context specific. Here the authors review a growing body of comparative research, demonstrating predictable patterns in men's and women's preferences for facial averageness, facial symmetry, stature, body mass, and facial and vocal masculinity or femininity both between and within cultures. The authors consider potential factors influencing variation in preferences that include resource availability, disease prevalence, paternal investment, visual experience, and cultural norms.

Keywords

mate preferences, averageness, symmetry, height, body mass index, masculinity

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Introduction

A century and a half ago, Darwin (1859, 1871) published a theory that for the first time recognized that the differences between men and women are largely the result of a process he termed *sexual selection*. Differences in the body, face, and voice of men and women, not unlike sexual dimorphisms found among other primates, he wrote, are the direct result of men's intra-sexual competition over resources and women, and men's and women's intersexual mate preferences. Through the mechanism of inheritance, Darwin realized that mate preferences have played a key role in shaping humankind and species characteristics across the animal kingdom. Sexual selection has indeed greatly influenced the evolved biology and psychology of humans. The origin of numerous traits and behaviors have been linked to this mechanism, including men's hairiness and low voice pitch relative to women's, and women's fat deposits, for example, breasts and buttocks (Barber, 1995; Feinberg, 2008). Some modern theorists suggest that in addition to explaining differences in men's and women's body composition, sexual selection may have played an important role in the evolution of psychological sex differences (such as attitudes toward casual sex or sexual jealousy), art, music, and even language (Buss, 1995; Miller, 2000).

More important, although Darwin (1871) observed that physical beautification was common practice among humans, he also observed that preferences for physical traits (i.e., standards of beauty) varied across different populations. Such cross-cultural and temporal variation in standards of beauty is supported by anthropological accounts of body modification, ranging from historic forms of foot binding to modern-day cosmetic surgery and tattooing (Reischer & Koo, 2004). Thus, though some traits may be preferred in mates across many cultures (see Buss et al., 1990; Shackelford, Schmitt, & Buss, 2005), some are not, and the degree of attractiveness of many physical traits is often influenced by culture.

Cross-cultural variation in standards of beauty, or mate preferences, may result from diverse trajectories of cultural and social evolution where norms, values, or symbolisms differ regionally (Reischer & Koo, 2004). Variation may also arise from differences at an individual level where, for example, repeated visual exposure to certain traits may increase our liking of them (Peskin & Newell, 2004; Principe & Langlois, 2012; Winkler & Rhodes, 2005). In addition, variation in mate preferences may represent behavioral plasticity to locally adaptive strategies (e.g., variation as a function of resource availability; Brown & Konner, 1987; Cohen & Belsky, 2008) or population-level genetic differences (Henrich, Heine, & Norenzayan, 2010; Jennions & Petrie, 1997).

Among others, there are three major motives for studying mate preferences cross-culturally. First, it is unlikely that the preferences of educated, Western undergraduate students who currently make up the vast majority of research participants in psychology and the behavioral sciences (~96%; Arnett, 2008) are representative of all ages, socioeconomic statuses, and cultures (Henrich et al., 2010; Sue, 1999). Second, as is widely accepted in the study of nonhuman animals, different social and ecological environments can have variable impacts on the preference for and the expression and proliferation of fitness-related traits (Andersson, 1994; Emlen & Oring, 1977; Jennions & Petrie, 1997; Partridge, 1987). It is therefore essential to understand how ontogenetic processes influence mate preferences that may be locally adaptive and context specific. Third, culturally dependent social learning may be an integral part of the development of mate preferences. Preferences are relatively plastic and do not evolve in a vacuum but instead coevolve alongside cultural norms, beliefs, and practices that are similarly subject to selective pressures (Boyd & Richerson, 1985; Flinn, 1997; see Hewlett & Cavalli-Sforza, 1986, for evidence of cultural transmission among Aka pygmies).

Cross-Cultural Comparisons of Mate Preferences

Physical characteristics play a large role in mate choice. The morphology of many physical features, such as stature or the shape of the face, is governed by physiological and hormonal developmental trajectories that also largely determine fertility and general health (Feinberg, 2008; Gangestad & Scheyd, 2005). Consequently, physical characteristics can tell us about an individual's genetic quality and so too the quality of his or her offspring. Physical traits can also provide information about mate-relevant economic or social factors, such as income or hunting ability (Escasa, Gray, & Patton, 2010; Harper, 2000). Among a host of contributors to attractiveness judgments, four major classes of physical characteristics have been shown to consistently affect human mate preferences: facial averageness, symmetry, body size, and masculinity. Here, we provide a review of cross-cultural research on mate preferences for these specific dimensions and consider a number of potential explanations for cultural variation. In doing so, we underscore the intimate relationships between evolutionary, ecological, and social influences on variation. While evolutionary theory provides a framework for making predictions about variation in mate preferences, cross-cultural data provide a medium for testing as well as generating new evolutionary predictions and integrating disparate findings. By using an integrative approach to

evolutionary research and theoretical development, we hope to gain better insight into the evolution of the human mating mind.

Averageness

In the late 19th century, Francis Galton, half-cousin of Charles Darwin, observed that superimposed photographs of multiple faces, essentially “average” faces, appeared highly attractive (Galton, 1878). In a first attempt to empirically replicate this observation, Langlois and Roggman (1990) demonstrated that digital composites (i.e., average faces), each made up of 16 or 32 faces of either sex, were judged as more attractive than the individual faces that comprised them. Moreover, the positive relationship between averageness and attractiveness appeared to be linear. Since this time, the *averageness hypothesis* of facial attractiveness has been a contentious one assailed with various methodological and theoretical criticisms (Alley & Cunningham, 1991; DeBruine, Jones, Unger, Little, & Feinberg, 2007; Pollard, Shepherd, & Shepherd, 1999). Many of the methodological concerns, including the notion that average faces are attractive simply due to that fact that averaging faces makes them more symmetrical (see section on Fluctuating Asymmetry), have to date been resolved—providing evidence that averageness and symmetry (among other traits; Perrett, May, & Yoshikawa, 1994) contribute independently to facial attractiveness (Rhodes, Sumich, & Byatt, 1999; Rhodes, Yoshikawa et al., 2001; Valentine, Darling, & Donnelly, 2004).

Averageness may be attractive as a consequence of a perceptual bias, wherein average faces appear prototypical and thus are easier to process (Halberstadt & Rhodes, 2000; Winkielman, Halberstadt, Fazendeiro, & Catty, 2006). Others have posited that averageness is a cue to health via a heritable resistance to disease (Koeslag, 1990; Symons, 1979; Thornhill & Gangestad, 1999). For instance, Lie, Rhodes, and Simmons (2008) found that women preferred the faces of men with genetic diversity associated with enhanced pathogen immunity and that this preference was in fact mediated by facial averageness. There is also evidence that people with average faces look healthier than those with distinctive faces (Rhodes, Zebrowitz et al., 2001). These explanations are not necessarily mutually exclusive, as a perceptual bias for prototypicality may have evolved as a mechanism to detect facial cues to health. In any case, selection may favor individuals who prefer average-faced mates.

Preferences for facial averageness have been well documented in a number of Western populations (reviewed in Rhodes, 2006, and Thornhill & Gangestad, 1999). Jones and Hill (1993) were among the first to examine preferences for averageness cross-culturally, testing whether faces that

measured closest to their population average were rated as more attractive than those that deviated from it. Preferences for averageness within and between the five cultural groups (United States, Russia, Brazil, Paraguay, and Venezuela) were weak but in the anticipated direction. The Ache Indians of Paraguay showed, by far, the strongest preference for facial averageness within a culture. In fact, even individuals from the other four populations preferred averageness most among the Ache Indians than among their own or other populations.

We can consider several potential explanations for the comparatively strong averageness preference found among the Ache. As Jones and Hill suggest, deviations from averageness correlated strongest with age in the Ache sample (Jones & Hill, 1993). Thus, averageness could be an especially salient cue to youthfulness in this population (or at least in this study sample) where youth of course signals fecundity in women and facial cues to youth are attractive to men (Jones, 1995; Maroulis, 1995). Alternatively, the Ache may be more vulnerable to parasites and disease relative to the other populations, potentially increasing the relative importance of cues to pathogen resistance (e.g., facial averageness) in mate choice and other social decisions (Low, 1990). Methodological limitations of this preliminary study, however, likely contributed to the variation in attractiveness ratings as suggested by a failure to replicate the established relationship between averageness and attractiveness in American faces (though the trends were in the predicted direction).

More recently, using modern computer-graphic face-morphing techniques to test people's preferences for average face composites, average faces have been shown to be preferred within cultures by Chinese and Japanese participants (Rhodes, Yoshikawa et al., 2001) and by another group of hunter-gatherers, the Hadza of Northern Tanzania (Apicella, Little, & Marlowe, 2007). Hadza preferred a 20-face Hadza composite over a less average, 5-face Hadza composite, $64 \pm 26\%$ of the time. Likewise, Europeans preferred a 20-face European composite $60 \pm 25\%$ of the time. Thus, both cultures showed a preference for facial averageness within their own culture, though the researchers did not test whether the stronger preference for averageness among Hadza than among Europeans was statistically significant. Interestingly, whereas European raters preferred averageness in all faces (European: 60%; Hadza: 58%), the Hadza, who have limited experience with White faces, showed a preference only within their own culture (Hadza: 64%; European: 51%; Apicella et al., 2007). This suggests that a preference for averageness may be reinforced through visual experience, as exposure to a number of unique individuals is required to form a population-specific concept of prototypically or averageness (Apicella et al., 2007).

These studies provide several testable predictions for future investigation of the causes of variation in preferences for facial averageness.

Fluctuating Asymmetry

The body plan for many paired features of the face and body is perfect symmetry. Morphological fluctuations from bilateral symmetry that have no directionality (i.e., fluctuating asymmetry) typically result from genomic stress, such as homozygosity of major genes and genetic mutations, and environmental stress, such as malnutrition and pollution, or an interaction of the two (Özener & Fink, 2010; Parsons, 1990, 1992). The degree to which an individual is capable of withstanding the effects of such stressors during development and, in turn, maintain a high degree of bilateral symmetry, is in part genetically heritable (Mather, 1953; Parsons, 1990).

In many species, fluctuating asymmetry is especially apparent in male secondary sexual characteristics (Manning & Chamberlain, 1993; Møller & Pomiankowski, 1993). Because it is conspicuous and linked to a hereditary resistance to stress, symmetry, not unlike facial averageness, may act as a cue to developmental stability or heritable health (Parsons, 1990, 1992; Thornhill & Gangestad, 1999, 2006; Thornhill & Møller, 1997) and may play a role in mate choice across species, including humans (Little, DeBruine, & Jones, 2011; Waynforth, 1998).

Preferences for symmetrical faces have been documented in humans, though largely within North America and Europe (Fink, Neave, Manning, & Grammer, 2006; Grammer & Thornhill, 1994; Perrett et al., 1999). Results from early studies testing preferences for facial symmetry in other regions such as Brazil and Japan (Jones & Hill, 1993; Kowner, 1996) were difficult to interpret due to measurement error and stimulus abnormalities (Palmer & Strobeck, 1986; Perrett et al., 1999; Rhodes, Roberts, & Simmons, 1999). More recent experimental work has documented a general mate preference for symmetry among Japanese undergraduates (Rhodes, Yoshikawa et al., 2001). Moreover, studies of slash-and-burn agriculturists in rural Belize indicate that symmetrical men in these villages have relatively more sex partners and more offspring than do asymmetrical men. Although such data are correlational, they suggest that symmetry may confer on Belizian men an intersexual and/or intrasexual mating advantage (Waynforth, 1998).

Despite some evidence of a consistent preference for symmetry across cultures, Little, Apicella, and Marlowe (2007) speculated that the *degree* to which symmetry is preferred might vary between affluent societies and those with a lower socioeconomic status. If preferences for symmetrical mates can be costly, then the costs and benefits associated with such a preference may

depend on certain ecological factors. Because high-quality (e.g., symmetrical) males may be less likely to invest time and resources into their mates and offspring than lower-quality males (Gangestad, 1993; but see Waynforth, 1999), a preference for symmetry may constitute a trade-off between heritable pathogen resistance and parental investment.

Given the above, Little et al. hypothesized that facial symmetry may be preferred less in regions where parental investment is most important (i.e., a key factor in accounting for the variation in quality of offspring) and more in regions where disease prevalence or pathogen load is high and the disease resistance of offspring is paramount (e.g., East Africa; Low, 1990). Indeed, whereas both U.K. and Tanzanian populations preferred symmetrical to asymmetrical opposite-sex faces in this study, preferences for symmetry were strongest among the Tanzanian Hadza hunter-gatherers (Little et al., 2007). Interestingly, despite their lack of preference for averageness in White faces (Apicella et al., 2007), the Hadza preferred symmetry in both White and Hadza faces. This suggests that preferences for symmetry are not likely to be a byproduct of preferences for averageness (see section on Averageness).

The number of studies investigating preferences for symmetry cross-culturally to date is limited. Nevertheless, these studies provide support for the influence of environmental context on preferences and offer clues as to which factors might influence variation. Future work may benefit from more cross-cultural research on the relative and/or additive roles of visual experience, pathogen prevalence, and other ecologically relevant factors, in the formation of preferences for facial averageness and symmetry.

Stature

Cross-culturally, men are on average taller than women (Holden & Mace, 1999). However, the degree of sexual dimorphism in stature (male height/female height) varies regionally. Among nonindustrial societies, such variation has been linked to phylogenetic as well as cultural factors such as divisions in labor; for example, cross-cultural variation in sexual dimorphism in stature appears to be negatively related to women's contributions to communal sustenance (Holden & Mace, 1999). Mate choice and intrasexual competition have also greatly contributed to sexual dimorphism among humans and a number of other species. Here we briefly introduce factors that contribute to variation in stature but focus our discussion on how and why preferences for stature (or for sexual dimorphism in stature) might vary cross-culturally.

In most mammalian species, large males have an advantage over small males both intra- and inter-sexually. Larger males are more dominant than

smaller males. Larger males are more likely to win physical competitions with other males and so to gain access to territory and resources (reviewed in Lindenfors, Gittleman, & Jones, 2007). Perhaps consequently, females in a number of diverse species have demonstrated a preference for mating with larger males in the population (Bisazza & Marconato, 1988; Cooper & Vitt, 1993). Similarly, men living in North America and Europe can benefit from a large body size. Taller men living in these regions are healthier than shorter men as measured by cardiorespiratory disease, stroke, and overall mortality rates (La Batide-Alanore et al., 2003; Peck & Vågerö, 1987; Smith et al., 2000); although, given inherent trade-offs in energy allocation during development (see below), the direction of causality between stature and health is unclear. In the United States, Great Britain, Sweden, Germany, Poland, and Denmark, taller men have on average a higher level of education, higher socioeconomic and professional status, and/or higher income compared to shorter men (Judge & Cable, 2004; Peck & Vågerö, 1987; Szklarska, Koziel, Bielicki, & Malina, 2007; Teasdale, Owen, & Sørensen, 1991). Finally, taller American and European men have been shown to have higher reproductive success than shorter men (Feingold, 1982; Mueller & Mazur, 2001; Murray, 2000; Nettle, 2002a; Pawlowski, Dunbar, & Lipowicz, 2000).

Although being tall can be beneficial to men, at least in North America and Europe, a large body size comes at a cost that not all populations of people may be equally equipped to bear (Blanckenhorn, 2000). An individual's finite energy reserves must be allocated not only to physical growth but also to somatic maintenance and reproduction—essentially as a trade-off (see Roff, 1992, for a review of life history theory). Trade-offs in energy allocation toward growth versus reproduction are known to vary regionally (Onland-Moret et al., 2005; Teriokhin, Thomas, Budilova, & Guegan, 2003; Walker et al., 2006). In addition to growth–reproduction trade-offs, maintaining a large body size can be especially costly in regions where food availability is at times scarce. Large body size may also impede hunting as men with smaller frames may be more inconspicuous to their prey; indeed, there is some evidence that body size correlates negatively with food returns in an African population of hunter-gatherers, the *!Kung San* (Lee, 1979).

Considering these costs, evolutionary and life-history theories suggest that the recognized positive correlations among stature, health, fitness, and socioeconomic factors documented in American and European men may not apply to men in regions with comparatively limited resources. As such, we may predict that women's preferences for men's stature will vary cross-culturally, wherein women living in North America and Europe will prefer taller men compared to women living in regions with fewer resources. Indeed, North

American and European women do generally prefer taller men to men of shorter or average stature (Swami et al., 2008) and prefer men to be taller than their female partner (higher sexual dimorphism in stature; Fink, Neave, Brewer, & Pawlowski, 2007; Kurzban & Weeden, 2005; Pawlowski, 2003; Pawlowski & Koziel, 2002; Pierce, 1996; Shepperd & Strathman, 1989). The tendency for a male to be taller than his female partner is typically referred to as the “male-taller norm” (Gillis & Avis, 1980). When presented with pairs of six male-female silhouettes that varied in relative stature, women from Germany, Austria, and Britain agreed that pairs in which the male was taller were most appropriate (Fink et al., 2007).

In contrast, women in regions with comparatively fewer resources do not show the same preference for male tallness as do women in regions with relatively higher resource availability. When presented with the same six male-female silhouettes of variable sexual dimorphism in stature, women of the Himba, a nomadic pastoral tribe of northern Namibia, preferred figures in which the male and female silhouettes were of equal height compared to figures in which the male was taller than the female (Sorokowski, Sorokowska, Fink, & Mberira, 2012). Similarly, among the Hadza tribe living in Tanzania, only 2% of women surveyed listed large body size as an attractive mate characteristic (Marlowe, 2004). Hadza marriages in which the wife was taller than the husband were common compared to Britain and in fact as frequent as would be expected by chance alone (Sear & Marlowe, 2009). Although these cross-cultural comparisons must be interpreted with caution (Sear, 2010), they highlight the likelihood that absolute or relative male tallness is in fact not a universally attractive mate preference owing to cultural and ecological variation across human populations.

The costs and benefits associated with taller stature vary regionally for women as well. In the United States and Great Britain, taller women have higher incomes than do shorter women (Judge & Cable, 2004) but are not necessarily healthier or more reproductively fit. Like taller men, taller women are less susceptible to heart disease, stroke, and respiratory disease (Peck & Vågerö, 1987; Smith et al., 2000) but, at the same time, show much higher rates of reproductive cancers and related mortality than do shorter women (Hilakivi-Clarke et al., 2001; Tretli, 1989). In fact, research indicates that in Norway and Britain both taller and shorter women have lower fitness than average-sized women, suggestive of an inverted-U-shaped relationship between stature, health, and fitness among European women (Engeland, Bjorge, Selmer, & Tverdal, 2003; Nettle, 2002b), though once again causality is unclear.

In regions where poverty and child mortality rates are comparatively higher than in Europe or North America (e.g., Guatemala and the Gambia),

the correlation between women's height and fitness appears positively linear rather than U shaped (Pollet & Nettle, 2008; Sear, Allal, & Mace, 2004). This is an especially interesting finding because taller women are known to have later first births due to the aforementioned trade-off between growth and reproduction. Despite this disadvantage, taller women in stressed environments have higher total fitness than shorter women because their stature also appears to decrease the probability that their offspring will die prematurely. In a recent cross-cultural comparison of 42 developing countries, maternal height correlated negatively with child mortality (Monden & Smits, 2008).

Considering the appreciable cross-cultural variation in the relationship between fitness and stature among women, we might predict that men living in North America or Europe may prefer short or average-sized women compared to tall women whereas men living in environmentally stressed regions with high child mortality rates might prefer tall compared to short or average-sized women. Indeed, research suggests that European and American men prefer women of short to average stature compared to tall stature and show a bias toward the male-taller norm by also preferring women shorter than themselves (Cameron, Oskamp, & Sparks, 1977; Pawlowski & Koziel, 2002; Salska et al., 2008; Shepperd & Strathman, 1989; Swami et al., 2008). Although there is some evidence that the male-taller norm is absent among the Hadza, signifying that short women are not necessarily preferred over tall women by Hadza men as mates (Sear & Marlowe, 2009), additional controlled experiments have not yet been conducted and are required to discern whether men in high child mortality environments prefer taller compared to shorter women.

Body Mass Index

Weight, often measured relative to height via a body mass index (BMI), is predictive of general health in both sexes. Individuals who are either underweight or extremely overweight ($BMI < 18.5$ or $> 30 \text{ kg/m}^2$) can experience a multitude of chronic health problems such as heart disease, cancer, and diabetes (Chan, Rimm, Colditz, Stampfer, & Willett, 1994; Kopelman, 2000; Seidenfeld & Rickert, 2001). In addition to general health effects, women's weight can affect reproduction and fertility. Women of reproductive age typically require some minimum amount of body fat, or weight given height, to remain fecund (Frisch & McArthur, 1974). Those who are either underweight or extremely overweight are at a higher risk of becoming infertile as a consequence of amenorrhoea (Seidenfeld & Rickert, 2001; Zaadstra et al., 1993).

Despite the benefits associated with an average body weight in women, men in North America and Europe generally prefer thin compared to average or overweight women (Fallon & Rozin, 1985; Kurzban & Weeden, 2005). A similar and in fact more extreme preference for thinness has been documented in Japan (Swami, Caprario, Tovée, & Furnham, 2006). It appears, however, that men in most other cultures show a preference for comparatively heavier women (for review see Brown & Konner, 1987). For instance, among the Matsigenka agriculturalists of Peru and the Hadza hunter-gatherers of Tanzania, drawings representing the heaviest category of women were rated as most attractive, healthiest, and most preferred as a wife (Westman & Marlowe, 1999; Yu & Shepard, 1998). Similarly, in cross-cultural comparisons of British or Greek and Ugandan men, only the African men preferred drawings of heavy female figures compared to thin female figures (Furnham & Baguma, 1994; Furnham, Moutafi, & Baguma, 2002). South African Zulu men also show a stable preference for women with BMIs ranging from 23 kg/m² (normal) to 38 kg/m² (very obese; Tovée, Swami, Furnham, & Mangalapsad, 2006), in contrast to British men, most of whom prefer a BMI of 20.5 kg/m² (low-normal; Tovée et al., 2006).

What factors might contribute to cross-cultural variation in men's preferences for women's weight? For most of human history, larger women were favored (Brown & Konner, 1987). During periodic food shortages, for instance, women with adequate fat stores were among the few women still able to reproduce and lactate. Population-level food shortages are, of course, rare in many industrialized parts of the world today, including North America, Europe, and some parts of Asia, where there is an ease of availability and overabundance of food. As such, *ideal* body mass may vary across different environments as a function of resource availability, where heavy rather than thin women may be preferred in comparatively low-resource regions. Evidence for this prediction is mixed. Anderson and colleagues (Anderson, Crawford, Nadeau, & Lindberg, 1992) reported a positive relationship between regional food scarcity and men's preferences for female body mass. However, Ember and colleagues (Ember, Ember, Korotayev, & de Munck, 2005) reported a negative or no relationship between resource scarcity and body mass preferences among two distinct samples of preindustrial societies, and further, provided evidence that the relationship between scarcity and body mass preferences may in fact be modulated by food storage.

Sustenance factors cannot in any case explain differences that have been reported between, for example, Japanese and British men's preferences (Swami et al., 2006) or the preferences of Zulu migrants and British natives

both residing in Europe (Tovée et al., 2006). Rather, cultural variation in social norms, ideologies, and lifestyle may account for some of the additional variation in men's preferences for women's weight (e.g., Cachelin, Rebeck, Chung, & Pelayo, 2002; Yu & Shepard, 1998). These social factors include ideologies associated with material wealth and consumerism and with stigmas associated with obesity (see Brown & Konner, 1987, for detailed discussion). Moreover, continuous visual exposure to thin bodies has been shown to increase preferences for thinness (Winkler & Rhodes, 2005). Thus, culturally specific social experience and media exposure to underweight women is likely to contribute to men's preferences for thinness in America, Europe, and in Eastern regions that have been heavily exposed to Western media. In Japan, for instance, women report feeling pressure to be thin from media sources as well as from friends and family (Kowner, 2002).

Waist-to-Hip Ratio

The amount of fat on the body (e.g., BMI) is relatively independent of the distribution of fat on different parts of the body, such as the hips and buttocks (Marlowe & Westman, 2001), though the two measures correlate to some degree (Singh & Singh, 2006). This distribution of fat, often measured as the width of one's waist relative to one's hips (waist-to-hip ratio), is largely determined by sex hormones. Among women, waist-to-hip ratio is a probable cue to age and fertility (Singh, 1993, 1994a, 1994b; Zaadstra et al., 1993). Over the past two decades, researchers have contested the relative contribution of BMI and waist-to-hip ratio to women's attractiveness (Singh, 1994a, 1994b; Singh & Singh, 2006; Swami & Tovée, 2007; Tovée et al., 1999). The debate remains unresolved—owing largely to the difficulty of methodologically divorcing size and shape (see Swami & Tovée, 2007, for discussion) and due to interactions between the two measures on perceptions of women's attractiveness (Singh, 1994a). Nevertheless, there is some evidence that size and shape each contribute independently to the overall variance in preferences for women's bodies (Singh, 1994a; Swami & Tovée, 2007).

Singh (1993) stated that the optimally attractive waist-to-hip ratio in women is 0.7 and provided evidence to suggest that this is stable across cultures (Singh, Dixon, Jessop, Morgan, & Dixon, 2010; Singh & Luis, 1995). Recent cross-cultural research, however, suggests that the preferences of American and European men, who generally do rate a female waist-to-hip ratio of 0.7 as most attractive (Singh, 1993, 1994b; Westman & Marlowe, 1999), may not be universal to men in all other cultures (Furnham et al., 2002; Marlowe & Westman, 2001; Yu & Shepard, 1998). Some have postulated that

potential population differences in men's preferences for body shape reflect locally adaptive strategies (Manning, Trivers, Singh, & Thornhill, 1999) or differences in visual exposure to Western bodies (Yu & Shepard, 1998). However, due to the vast differences in the stimuli used across studies (see Gray, Heaney, & Fairhall, 2003, p. 255)—some of which have yielded various results even within the same society (e.g., the Hadza: Marlowe, Apicella, & Reed, 2005; Marlowe & Westman, 2001; Westman & Marlowe, 1999)—in addition to evidence that stimuli used to measure waist-to-hip ratio preferences have been confounded by cues to weight (Furnham et al., 2002; Sugiyama, 2004; Swami & Tovée, 2007), it is not yet possible to say with confidence whether and how preferences for waist-to-hip ratio vary culturally or which factors may contribute to such variation. Additional, standardized research is greatly needed in this domain.

Facial Masculinity

On average, men have wider cheekbones and jaws, a more prominent brow, and less fat on their cheeks and lips than do women (Thornhill & Gangestad, 1999). The formation of these masculine facial features in men is driven by the production of testosterone, wherein higher testosterone-to-estrogen ratios are related to more masculine features (Bardin & Catterall, 1981; Bruckert, Liénard, Lacrois, Kreutzer, & Leboucher, 2006; Dabbs & Mallinger, 1999; Penton-Voak & Chen, 2004). Testosterone, in addition to masculinizing the face and body, is positively correlated with men's social status and dominance (Booth, Granger, Mazur, & Kivlighan, 2006; Mazur & Booth, 1998). Testosterone has been shown to lower immune responsiveness and increase susceptibility to disease in a number of vertebrate taxa (Folstad & Karter, 1992). As such, testosterone-dependent traits (e.g., secondary sexual characteristics and masculine male features) are thought to act as signals to male health and fitness because only high-quality individuals are able to develop and/or maintain these costly markers (Zahavi, 1975). Although similar mechanisms are likely to operate among primates, empirical evidence for a testosterone-mediated handicap among humans is to date still growing (see Muehlenbein & Bribiescas, 2005, for review; see also Rantala et al., 2012).

Despite the potential immunological benefits afforded to offspring and increased dominance associated with masculinity, preferring masculinity in a mate also carries costs (see Gangestad, 1993). Masculine men (i.e., men with high levels of testosterone) are less likely to invest time and resources into caring for their offspring and mates (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002; Muller,

Marlowe, Bugumba, & Ellison, 2009; Waynforth, 1999). Masculine men are more likely to cheat on their partners, get divorced (Booth & Dabbs, 1993), exhibit antisocial behaviors (e.g., aggression; Booth et al., 2006), and are often perceived by women as less caring and honest than are men with more feminine features (Perrett et al., 1998). Given this trade-off between increased dominance/health but decreased paternal/resource investment from masculine compared to feminine men, we expect women's preferences for facial masculinity to vary cross-culturally (and indeed, even within cultures) depending on local or individual conditions and the relative importance of developmental health versus parental and resource investment.

In the United States and Europe, several studies have found that women generally prefer facial masculinity among men (DeBruine et al., 2006; Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak et al., 2001), but others have found that women generally prefer facial femininity (Perrett et al., 1998; Rhodes, Chan, Zebrowitz, & Simmons, 2003). As predicted, these individual differences appear to be moderated by evolutionarily relevant factors such that masculine faces (cueing dominance and/or immunological competence) are preferred over feminine faces (cueing parental and resource investment) by women in the fertile phase of their menstrual cycle (Johnston et al., 2001; Little, Jones, & DeBruine, 2008; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999) or life cycle (Little et al., 2010) and by women seeking a short-term as opposed to a long-term relationship, especially as a potential extra-pair relationship (Little, Jones, Penton-Voak, Burt, & Perrett, 2002).

Studies comparing women's preferences for facial masculinity across cultures also find that facial masculinity preferences may relate to relative parasite load and/or expectancies of parental investment. Perrett et al. (1998) did not find population-level differences in facial masculinity preferences between Scottish and Japanese women (in both cultures, women preferred feminized to average or masculinized male faces), but Japan, like Scotland, maintains low disease and mortality rates and high rates of paternal investment. Women in both of these regions may therefore benefit most by choosing men who are likely to share time and resources over disease resistance. In contrast, we would predict that in regions where disease is more prevalent, the dominance and immunocompetence of a mate (and resultant offspring) may be relatively more important compared to regions with lower rates of disease (Low, 1990). We might further predict that in societies in which most sexual relationships are short term, masculinity preferences might also be comparatively stronger than in societies in which long-term relationships are the norm. Indeed, cross-cultural research provides support for these predictions. Penton-Voak, Jacobson, and Trivers (2004) compared preferences for male facial masculinity in British

women with those of women living in rural Jamaica where health care is relatively more limited and pathogens are more common. In addition, long-term relationships and paternal investment are very rare in Jamaica compared to Britain and, as such, most children are born to unwed mothers. As predicted, Jamaican women preferred masculine rather than feminine male faces more than did British women (Penton-Voak et al., 2004).

DeBruine and colleagues (DeBruine, Jones, Crawford, Welling, & Little, 2010) compared facial masculinity preferences of thousands of women from 30 different countries as a function of those regions' National Health Indexes as given by the World Health Organization (e.g., mortality rates, life expectancy, and impact of communicable disease). As expected, the lower the health of the nation, the higher the likelihood that women in that region preferred facial masculinity. Although national income inequality and homicide rates (potential indices of male-male competition) often covary with a nation's health and also predict regional variation in women's facial masculinity preferences (Brooks et al., 2011), the National Health Index can account for variation in women's preferences over and above that explained by these other factors (DeBruine, Jones, Little, Crawford, & Welling, 2011).

Vocal Masculinity and Femininity

Voice pitch is a sexually dimorphic, hormone-dependent physical trait in humans. Pitch, the perceptual correlate of fundamental frequency and/or corresponding harmonics, is produced by vibration of the vocal folds (Titze, 1994). Men receive a large surge of testosterone at puberty that interacts with growth hormones to develop larger, longer, and thicker vocal folds. As a consequence, men speak with a voice pitch that is on average an octave (i.e., one half) lower than that of women (Titze, 1989).

Vocal masculinity is, in effect, very similar to facial masculinity. Both vocal and facial masculinity vary within and between sexes and can thus provide reliable information about an individual's sex-hormone levels (Dabbs & Mallinger, 1999; Feinberg, 2008, for review). High testosterone is associated with increased dominance and potentially disease resistance but decreased resource investment among men (see section on Facial Masculinity). Thus, akin to preferences for masculinity in the face, it can be expected that women prefer masculine voices most when the benefits of preferring masculinity outweigh the costs.

In North America and Europe, women show strong consensus in their preference for masculine (i.e., low-pitched) male voices compared to average or feminine (i.e., high-pitched) male voices (Collins, 2000; Feinberg, Jones,

Little, Burt, & Perrett, 2005; Jones, Boothroyd, Feinberg, & DeBruine, 2010; Pisanski & Rendall, 2011; Vukovic et al., 2008, 2010). Nevertheless, there is predictable variance in the degree to which different individuals in these regions prefer vocal masculinity. For instance, vocal masculinity preferences correlate negatively with age of first menses (Jones et al., 2010) and are strongest during the fertile phase of a woman's menstrual cycle (Feinberg et al., 2006; Puts, 2005) and among naturally cycling women as opposed to women taking oral contraceptives (Feinberg, DeBruine, Jones, & Perrett, 2008). Women's vocal masculinity preferences are also stronger when rating stimuli in the context of a short-term as opposed to a long-term relationship (Feinberg et al., 2012; Puts, 2005). This effect of relationship context is furthermore influenced by the degree to which a woman attributes negative traits, such as low trustworthiness or high dominance, to masculine men (Vukovic et al., 2011).

Finally, women are also more likely to prefer vocal masculinity if they perceive themselves to be attractive (Feinberg et al., 2012; Vukovic et al., 2008) or have an attractive (high-pitched) voice (Vukovic et al., 2010), perhaps because attractive women are better able to obtain and retain attractive men as mates. By contrast, women who perceive themselves to be relatively healthy prefer masculine men less, particularly in the context of short-term relationships (Feinberg et al., 2012). This is similar to findings by DeBruine et al. (2010, 2011), and Little et al. (2011), who showed that women in pathogen-sensitive situations tend to prefer facial masculinity relatively more. Such work suggests that not only are individual differences in preferences quite complex but also appear to be consistent across modalities.

To date, because study of the human voice as a factor in mate-choice is fairly recent, very few researchers have examined correlates of and preferences for voice pitch outside of the Western hemisphere or between cultures. Some preliminary research has been conducted in Tanzania among the Hadza. In a recent comparative study of vocal cues to threat potential, Hadza men's voice pitch correlated negatively with indices of physical strength (Puts, Apicella, & Cárdenas, 2012). In two earlier studies, Hadza men with low-pitched voices had higher reproductive success than men with high-pitched voices (Apicella, Feinberg, & Marlowe, 2007) and were perceived by Hadza women as better hunters (Apicella & Feinberg, 2009). Intriguingly, only women who were not breastfeeding (about half of the sample) preferred low-pitched men as potential marriage partners relative to breastfeeding women, who preferred high-pitched men (Apicella & Feinberg, 2009). High-pitched (i.e., feminine) men are more likely to invest in their mates and offspring than are masculine men (Gangestad, 1993); perhaps this can explain why lactating women, whose energy and food

reserves are depleted and who are in any case unable to conceive, preferred relatively feminine men (Apicella & Feinberg, 2009).

Men's preferences for women's voices have also been examined cross-culturally, though to date only among a small number of cultures. Women with feminine (i.e., high-pitched) voices have higher levels of estrogen than women with more masculine voices (Abitol, Abitol, & Abitol, 1999). Thus, vocal femininity may cue female fertility (Bryant & Haselton, 2009), and facial and vocal femininity are likely to be correlated (Collins & Missing, 2003). In the United Kingdom and Canada, men show high consensus in their preference for high-pitched female voices compared to average or low-pitched female voices (Collins & Missing, 2003; Feinberg et al., 2008; Pisanski & Rendall, 2011) and thus appear to prefer femininity in multiple female features (Collins & Missing, 2003; Feinberg, 2008). Although voice pitch was not found to predict reproductive success among female Hadza gatherers (Apicella et al., 2007), Hadza men did prefer women with high-pitched voices as potential wives compared to women with low-pitched voices (Apicella & Feinberg, 2009). This was true despite the fact that Hadza men perceived high-pitched women as being less successful gatherers of food, lending credence to the notion that female fecundity is highly important in this population (Marlowe, 2004).

Conclusion

Research on human mate preferences has been largely restricted to North American and European university populations, greatly limiting our realization and understanding of factors contributing to variation in preferences. In this article, we have demonstrated how a small but growing archive of comparative research has begun to illuminate predictable cultural differences in preferences for facial averageness, symmetry, and sexually dimorphic traits including stature, BMI, waist-to-hip ratio, and facial and vocal masculinity or femininity (see Table 1 for summary). In addition to cross-cultural variation, a number of studies have also demonstrated individual differences in men's and women's mate preferences within cultures, highlighting the importance of examining variation at both an individual and population level.

Where possible, we have highlighted specific areas of research that would profit most from future cross-cultural work. In reviewing the literature, it becomes evident that men's preferences for women's traits are underrepresented in cross-cultural research, indeed in research in general, relative to women's preferences for men's traits. Specific tests of men's preferences for women's stature in environments with high child mortality rates (where we

Table 1. Preferences for Six Physical Traits Compared Across a Sample of Mono- and Cross-Cultural Studies

Study ^a	Sample(s)	Stimulus sex	Preference ^b	Description of preference
Preferences of Both sexes				
Facial averageness				
Langlois & Roggman, 1990	United States (students)	M, F	✓	16- and 32-face composites preferred over individual faces
Jones & Hill, 1993	United States, Brazil (students); Russia (community); Paraguay (Ache); Venezuela (Hiwi)	M, F	✓	Trend toward a general preference for average individual faces but strongest for Paraguayan sample
Rhodes, Yoshikawa et al., 2001a	Japan (students); Chinese (students living in Australia < 6 months)	M, F	✓	Composite own-race faces preferred over individual faces
Apicella, Little, & Marlowe, 2007	Europe (online); Tanzania (Hadza)	M, F	✓	20-face composites preferred to 5-face composites within and between cultures (Europe) or within culture (Hadza)
Lie, Rhodes, & Simmons, 2008	Australia (students)	M	✓	Averageness ratings and attractiveness ratings correlated
Facial symmetry				
Jones & Hill, 1993	United States, Brazil (students); Russia (community); Paraguay (Ache); Venezuela (Hiwi)	M, F	✗	Symmetry and attractiveness ratings did not correlate except for photos of Russian women (see section Fluctuating Asymmetry)
Grammer & Thornhill, 1994	Germany (students)	M, F	✓	Natural symmetry correlated with attractiveness
Kowner, 1996	Japan (students)	M, F	✗	Symmetry and attractiveness ratings correlated positively only for old individuals (see section Fluctuating Asymmetry)
Perrett et al., 1999	Scotland (not specified)	M, F, M, F	✓	Perfect symmetry preferred over original asymmetry
Rhodes, Yoshikawa et al., 2001a	Japan (students)	M, F	✓	Perfect symmetry preferred over original asymmetry
Fink, Neave, Manning, & Grammer, 2006	Austria (students)	F	✓	High natural symmetry preferred over low symmetry
Little, Apicella, & Marlowe, 2007	Britain (students); Tanzania (Hadza)	M, F	✓	Symmetry preferred above chance within and between both cultures, but strongest among Hadza

(continued)

Table 1. (continued)

Study ^a	Sample(s)	Stimulus sex	Preference ^c	Description of preference
Women's preferences for men's traits				
Tall stature (absolute or relative)				
Pawlowski, 2003	Poland (students)	M, F pairs	✓	Females preferred figure drawings of pairs in which male was taller than female, and this interacted with own height
Fink, Neave, Brewer, & Pawlowski, 2007	Germany, Austria, U.K. (students)	M, F pairs	✓	Females preferred figure drawings of pairs in which male was taller than female, and this interacted with own height
Swami et al., 2008	Britain (community)	N/A	✓	Females reported ideal height of males greater than average height
Sorokowski, Sorokowska, Fink, & Mberira, 2012	Namibia (Himba)	M, F pairs	✗	Females preferred figure drawings of pairs in which male was of equal height to female
Perrett et al., 1998	Scotland, Japan (not specified)	M	✗	females preferred feminized over average or masculinized faces within and between cultures
Johnston, Hagele, Franklin, Fink, & Grammer, 2001	United States, Austria ^d (students)	M	✓	Females preferred masculinized over average faces, especially in the fertile phase of their menstrual cycles
Rhodes, Chan, Zebrowitz, & Simmons, 2003	Australia (students)	M	✗	No significant correlation between female's ratings of male facial masculinity and attractiveness
DeBruine et al., 2006	United Kingdom (not specified)	M	✓	Females preferred masculinized over feminized faces
Penton-Voak, Jacobson, & Trivers, 2004	United Kingdom (students), Jamaica (Parish communities)	M	✗	Jamaican females preferred masculinized male faces within and between cultures but British females did not
DeBruine, Jones, Crawford, Welling, & Little, 2010	30 countries (online)	M	✓	Females' masculinity preferences correlated with the health of the nation in which they resided

(continued)

Table 1. (continued)

	Study ^a	Sample(s)	Stimulus sex	Preference ^c	Description of preference
Vocal masculinity	Collins, 2000	Netherlands (not specified)	M	✓	Females preferred naturally low over high voice pitch
	Feinberg, Jones, Little, Burt, & Perrett, 2005	Scotland (students)	M	✓	Females preferred lowered over raised voice pitch
	Apicella & Feinberg, 2009	Tanzania (Hadza)	M	✗	Breastfeeding females preferred high pitch more than did non-breastfeeding females within and between cultures
	Pisanski & Rendall, 2011	Canada (students)	M	✓	Females preferred low to high pitch in natural voices
Men's preferences for women's traits					
Short to average stature (absolute or relative)	Pawlowski, 2003	Poland (students)	M, F pairs	✓	Males preferred figure drawings of pairs in which male was taller than female, and this interacted with own height
	Salska et al., 2008	United States (community)	N/A	✓	Personal ads revealed male preferences for women of the same height or shorter than themselves
	Swami et al., 2008	Britain (community)	N/A	✓	Males reported ideal height of females equal to sample average
Low body mass index (BMI)	Fallon & Rozin, 1985	United States (students)	F	✓	Males preferred below-average weight figures
	Yu & Shepard, 1998	United States (students); Peru (Matsigenka, Shipetari, Alto Madre)	F	✗	U.S. and Alto Madre males preferred figures of normal weight; Matsigenka and Shipetari preferred overweight
	Westman & Marlowe, 1999	United States (students); Tanzania (Hadza)	F	✗	U.S. males preferred underweight or normal-weight figures; Hadza males preferred overweight figures
	Furnham, Moutafi & Baguma, 2002	Britain, Greece, Uganda (students)	F	✗	British and Greek males preferred lightweight figures; Ugandan males preferred heavyweight figures
	Swami, Caprario, Tovée, & Furnham, 2006	Britain (not specified); Japan (community)	F	✓	All males preferred photos of women with lower-than-average BMIs, but lowest BMIs preferred among Japanese

(continued)

Table 1. (continued)

Study ^a	Sample(s)	Stimulus sex	Preference ^c	Description of preference
Tovée Swami, Furnham, & Mangalapsad, 2006	Britain (Caucasian natives; African natives, African migrants for < 18 months); South Africa (Zulu natives)	F	✗	Caucasian and African British natives preferred photos of women with low-normal BMIs; Zulu migrants preferred slightly higher BMIs than British natives; Zulu natives preferred photos of women with high BMIs
Collins & Missing, 2003	Britain (not specified)	F	✓	Males preferred voices of women with naturally high pitch
Apicella & Feinberg, 2009	United Kingdom (sample used only for voice stimuli); Tanzania (Hadza)	F	✓	Males chose raised over lowered U.K. voices as potential wives (preference neared significance for Hadza voices)
Feinberg, DeBruine, Jones, & Perrett, 2008	Scotland (students & online)	F	✓	Males preferred naturally high (Study 1) and raised (Study 2) over average or low voice pitch
Pisanski & Rendall, 2011	Canada (students)	F	✓	Males preferred high to low pitch in natural voices

^aThe list of studies included here on mate preferences in Western cultures is nonexhaustive.

^bSex of reported stimulus used to assess participants' preferences: M = male, F = female.

^cIndicated preference: ✓ = found among all samples in the study; ✗ = not found among one or more samples in the study.

^dOnly two Austrian students participated in the study.

predict that taller rather than shorter women will be preferred) could provide further evidence for the context specificity of body size preferences in humans. Likewise, standardized and unconfounded stimuli must be used to accurately assess men's preferences for women's waist-to-hip ratios cross-culturally. Additional cross-cultural research on men's preferences for facial and vocal femininity is also required to establish whether and under which circumstances men's preferences for femininity might vary.

Additional comparisons of preferences for facial averageness and symmetry across variable socioeconomic environments and across different visual repertoires will help to clarify the relative contribution of visual adaptation and/or cues to health in forming preferences for average and symmetrical mates. Of course, future research should also investigate how preferences for other evolutionarily relevant physical traits that were beyond the scope of this review, such as neoteny, skin texture, or breast size, vary cross-culturally, as well as how physical traits relate to one another (perhaps dynamically) in their relative contributions to assessments of attractiveness or in mate choice (e.g., Currie & Little, 2009). It may also prove fruitful to utilize more exploratory methods of investigation for the reason that other, perhaps culturally specific, mate preferences may be emergent from the data.

Finally, although data on the practices and preferences of nomadic people such as the Hadza have begun to accumulate, many groups or subcultures of people are currently underrepresented in cross-cultural research on mate preferences. We review some recent work on the mating traditions and preferences of rural agriculturalists (e.g., Penton-Voak et al., 2004; Pollet & Nettle, 2008; Waynforth, 1998, 1999; Yu & Shepard, 1998), but it is minimal considering that approximately 36% of the world's labor force works in the agriculture sector (Central Intelligence Agency, 2012). A second, perhaps less obvious, group of people to consider for future research are the urban poor. The number of urban poor in the world is also high, with anywhere from 7% (China) to 37% (Colombia) of poor people living in urban areas during the 1980s and 1990s (Haddad, Ruel, & Gerrett, 1999). Although these individuals live in industrialized environments, they differ from urban people of higher socioeconomic status in many potentially relevant ways (e.g., health risks; resources for parental care) and therefore offer a more accessible and affordable means of testing specific evolutionary predictions about factors that contribute to variation in mate choice.

As a growing body of comparative research reveals, mate preferences can only be understood by combining evolutionary, life history, and social approaches. Earlier cross-cultural work in biological anthropology attempted to marry genetic and geographic factors with phenotypic variation but largely

ignored the influential role of the social and ecological environment (Cartmill, 1998). In contrast, evolutionary psychology provides a strong interdisciplinary framework from which to make context- and cost-dependent predictions about mating decisions. Cross-cultural research provides an ideal opportunity to test and construct evolutionary predictions about mating behavior across a number of highly heterogeneous contexts, wherein variation in geography, economy, communication, health, and family systems may prove essential to a comprehensive understanding of human mate preferences.

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