

Sexual Selection on Human Faces and Voices

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Humans are highly sexually dimorphic primates, and some of the most conspicuous human sex differences occur in the face and voice. Consequently, this article utilizes research findings on human faces and voices to illustrate how human sex differences may have arisen by sexual selection (i.e., the type of natural selection favoring traits that increase mating opportunities). Evidence suggesting that sexual selection shaped women's faces and voices is reviewed. However, sexual selection likely operated more strongly on men over human evolution. Thus, this research focuses on two types of sexual selection operating on men: female mate choice, which favors traits that attract females, and male contests, which favor traits for excluding competitors from mates by force or threat of force. This article demonstrates how masculine faces and voices advertize critical information about men's mate value and threat potential, and reviews evidence that women's preferences and men's deference to masculine faces and voices reflect this information content. Data suggesting that facial and vocal masculinity influences men's mating opportunities and reproduction are discussed, and the article concludes by highlighting directions for future research.

In some animal species, the two sexes differ so greatly in appearance that they could be mistaken for separate species. Such was the case when Carl Linnaeus, the father of modern taxonomy, misclassified male and female mallard ducks as *Anas boschas* and *Anas platyrhynchos*, respectively (Andersson, 1994). Although men and women may not be as divergent in appearance as male and female mallards, they are not far off. By one subjective assessment, humans are the eighth most visually sexually dimorphic primates (tied with gorillas and white-faced sakis), placing humans in the 90th percentile for visual sexual dimorphism (Dixson, Dixson, & Anderson, 2005). The visual dissimilarity between men and women is partly due to men's greater height and weight, but largely attributable to sex differences in body fat and muscle distribution (Lassek & Gaulin, 2009), along with conspicuous sex differences in body hair and, especially, facial hair. Not only do men and women differ in their soft tissue distribution, but they also differ in skeletal structure (e.g., Enlow & Hans, 1996). Besides the pelvis, probably the most obvious of the many human skeletal sex differences occur in the face. Men tend to have more prominent brow ridges

and a longer lower face, including a larger, more angular mandible and squarer chin.

Men and women also have markedly different vocal characteristics. Voice pitch, measured by mean speaking fundamental frequency, is approximately twice as high in women as in men—a sex difference of approximately 5 *SDs* (Baken, 1987; Puts, Apicella, & Cardenas, 2012). Perhaps less obvious, men speak in a more monotone voice—that is, the standard deviation in fundamental frequency across an utterance is lower in men than in women (Henton, 1995; Puts, Apicella, & Cardenas, 2012). The formant frequencies (frequencies of high energy) of men's voices are also lower and more closely spaced, producing a deeper, fuller vocal timbre in men than in women (Fitch, 1997).

For those interested in understanding the social dynamics of human sexuality, such anatomical and acoustic sexual dimorphisms are particularly relevant. As we will see, these traits affect attractiveness and perceptions of dominance, and predict mate preferences and behaviors related to competition for mates. Thus, clarifying why men and women look and sound different will elucidate how appearance mediates interpersonal relationships, in general, and romantic relationships, in particular. In this review, we focus on sex differences in faces and voices. We consider these aspects of the phenotype because they are highly conspicuous, highly

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sexually dimorphic, and contain abundant information about the individual. Moreover, a greater quantity of pertinent research has been conducted on faces and voices than any other conspicuous aspect of the human phenotype, and these literatures closely parallel one another.

Proximate Causes of Human Facial and Vocal Sex Differences

At proximate and developmental levels, sex differences in faces and voices largely are the consequence of exposure to gonadal sex steroids. For example, peri-pubertal craniofacial development produces pronounced sex differences in the size and shape of the mandible (Srael, 1969), and these changes appear to depend, in part, on elevated testosterone production in males (Verdonck, Gaethofs, Carels, & de Zegher, 1999). Facial sex differences are not simply a consequence of sex differences in overall size, as many facial sexual dimorphisms persist after controlling for allometry (Bastir, Godoy, & Rosas, 2011; Bastir, Rosas, & O'Higgins, 2006; Bulygina, Mitteroecker, & Aiello, 2006; Rosas & Bastir, 2002). Some soft tissue sex differences in the face may be produced and maintained by circulating sex steroids in adults. Men's testosterone levels predicted subjective masculinity ratings of their faces (Penton-Voak & Chen, 2004), and women's estrogen levels predicted subjective femininity ratings of their faces (Law Smith et al., 2006). However, the link between circulating testosterone levels and men's facial masculinity may be complex (e.g., Pound, Penton-Voak, & SurrIDGE, 2009). Testosterone and its metabolite dihydrotestosterone are also responsible for facial hair growth (Farthing, Mattei, Edwards, & Dawson, 1982).

Similarly, at puberty, elevated testosterone levels (Tossi, Postan, & Bianculli, 1976), acting through androgen receptors in the vocal folds (Newman, Butler, Hammond, & Gray, 2000), cause the vocal folds to grow longer and thicker in males than in females (Harries, Hawkins, Hacking, & Hughes, 1998). Men's larger vocal folds (sometimes called "vocal cords") consequently vibrate at approximately one-half the frequency of women's during phonation. Moreover, circulating androgens appear to maintain masculine vocal fold morphology in adults; vocal fundamental frequency negatively correlates with androgen levels in men (Dabbs & Mallinger, 1999; Evans, Neave, Wakelin, & Hamilton, 2008; Puts, Apicella, & Cardenas, 2012) and decreases with androgen treatment (Need, Durbridge, & Nordin, 1993). In addition, males' larynges descend at puberty (Fitch & Giedd, 1999), producing a longer vocal tract and lower, more closely spaced formant frequencies (Fant, 1960). These anatomical and acoustic sex differences are not merely byproducts of the sex difference in body size. Men's vocal tracts and vocal folds are 15% and 60% longer than women's, respectively

(Fant, 1960; Titze, 2000)—several times the 7% to 8% sex difference in stature (Gaulin & Boster, 1985). Moreover, very large sex differences in vocal pitch and timbre persist after the effects of stature are statistically removed (Puts, Apicella, & Cardenas, 2012). Although the proximate causes of the sex difference in voice monotonicity are unclear, the apparent cross-cultural ubiquity of this sex difference (Henton, 1995) suggests that sex hormones may be involved in producing underlying neuropsychological sex differences (Puts, Apicella, & Cardenas, 2012). It is also possible that the processes of gender socialization contribute to (or reduce) the magnitude of facial and vocal sex differences (Fausto-Sterling, 2005).

Ultimate Causes of Human Facial and Vocal Sex Differences

Of central interest in this review are the ultimate causes of sex differences in faces and voices: why these differences evolved. Over human evolution, what reproductive advantages accrued to men with more robust faces and deeper voices or women with more gracile faces and higher voices? Sex differences can evolve via "ordinary" natural selection (e.g., due to niche partitioning; e.g., see Smith, 1993), but sexual selection is the predominant adaptive cause of secondary sex characteristics (Andersson, 1994). Sexual selection is the type of natural selection which favors traits that aid in competition for mates. Facial (Ravosa, 1991; Taylor, 2006; Wood, Li, & Willoughby, 1991) and vocal (Green, 1981; Mitani & Gros-Louis, 1995; Rendall, Kollias, Ney, & Lloyd, 2005) sexual dimorphisms exist across a wide variety of nonhuman primate taxa, and sexual selection is often implicated (Delgado, 2006; Mitani, 1985; Waitt et al., 2003).

Although sexual selection can take other forms, the most studied mechanisms of sexual selection, and those most germane to this review, are mate choice, which favors sexual displays and ornaments for attracting mates, and contest competition, which favors size, strength, aggression, weapons, and dominance displays for excluding competitors by force or threat of force from mates or the resources needed to win them. Ancestral men and women likely competed with their same-sex rivals for mates via both mate choice and contest competition. However, in general, mate choice appears to have been relatively more important than contests in shaping women's traits (Barber, 1995; Buss & Dedden, 1990; Cashdan, 1996, 1998; Low, Alexander, & Noonan, 1987; Schmitt & Buss, 1996), and contests appear to have been more important than mate choice in shaping men's traits (Archer, 2009; Daly & Wilson, 1988, 1990; Puts, 2010). These generalities also seem to apply to faces and voices, as we will see.

Sexual Selection on Women's Traits: Male Mate Choice

Male mate choice for feminine faces and voices may partly account for the evolution of sex differences in these phenotypic characters. Men prefer feminine faces (Cunningham, 1986; Rhodes, 2006; Rhodes, Hickford, & Jeffery, 2000), and facial attractiveness and femininity appear to be particularly important to men when they consider long-term mating contexts (Confer, Perilloux, & Buss, 2010), when men's testosterone levels are high (Welling, Jones, DeBruine, & Smith, et al., 2008), and when the face also appears healthy (Smith, Jones, DeBruine, & Little, 2009). Men with high sex drives also demonstrate stronger preferences for femininity in women's faces than do men with relatively low sex drives (Jones, Little, Watkins, Welling, & DeBruine, 2011). Men also prefer feminine voices (Apicella & Feinberg, 2009; Collins & Missing, 2003; Feinberg, DeBruine, Jones, & Perrett, 2008; Jones, Feinberg, DeBruine, Little, & Vukovic, 2008, 2010; Puts, Barndt, Welling, Dawood, & Burriss, 2011), particularly for short-term, purely sexual relationships (Puts, Barndt, et al., 2011), and when the woman's voice indicates positive social interest (Jones, Feinberg, et al., 2008). The relative importance of women's facial appearances in long-term mating contexts and voices in short-term contexts may reflect these traits' greater associations with long-term reproductive value (Confer et al., 2010) and current fertility (Puts, Barndt, et al., 2011), respectively.

Consistent with the hypothesis that attractive, feminine faces and voices increase women's competitiveness for mates, other women perceive women with attractive faces as more promiscuous (Brewer & Archer, 2007), and those with feminine voices as more attractive to men and more flirtatious (Puts, Barndt, et al., 2011); that is, attractive, feminine women are perceived as greater threats in competition for mates. Feminine faces and voices could not have evolved to help women exclude competitors from mates by force or threat of force, however, because femininity in women's faces and voices decreases the appearance of physical threat (Jones, DeBruine, et al., 2010; Jones, Feinberg, et al., 2010; Main, Jones, DeBruine, & Little, 2009; Perrett et al., 1998), particularly to low-dominance women (Watkins, Quist, Smith, DeBruine, & Jones, 2012). Indeed, women with feminine faces score lower on dominance questionnaires than do women with masculine faces (Quist, Watkins, Smith, DeBruine, & Jones, 2011).

Sexual Selection on Men's Traits

There are several reasons to expect that sexual selection operating on men, rather than on women, played a larger role in the evolution of facial and vocal sexual dimorphisms. First, sexual selection tends to be stronger in the sex that invests less in offspring (Trivers, 1972), is

capable of reproducing at a faster rate (Clutton-Brock & Vincent, 1991), and has a higher variance in reproductive success (Bateman, 1948). In humans, males invest less in offspring than females do (Eibl-Eibesfeldt, 1989; Geary, 2000; Hewlett, 1992), can reproduce at a faster rate (e.g., Chagnon, 1992; Salzano, Neel, & Maybury-Lewis, 1967), and have higher reproductive variance (Chagnon, 1990; Hewlett, 1988; Howell, 1979; Salzano et al., 1967). Thus, sexual selection has almost certainly been stronger in shaping men's traits than women's. Second, sexually selected traits tend to emerge at sexual maturity, and males, more than females, exhibit dramatic pubertal changes in facial appearance and vocal characteristics (Barber, 1995). Finally, as we will see, considerable evidence indicates that masculine faces and voices increase men's success in competition for mates.

Female Mate Choice

Men might have evolved more robust faces, facial hair, and deeper voices partly because women prefer these traits. Indeed, women have been found to prefer faces manipulated to look more masculine than average in some studies (DeBruine et al., 2006; Johnston, Hagel, Franklin, Fink, & Grammer, 2001), although other studies have found women to prefer faces on the feminine side of the male average (DeBruine, Jones, Smith, & Little, 2010; Perrett et al., 1998; Rhodes et al., 2000). Moreover, some studies have found that women prefer facial hair (Pellegrini, 1973; Reed & Blunk, 1990), but other studies have found it to decrease attractiveness to women (Cunningham, Barbee, & Pike, 1990; Muscarella & Cunningham, 1996; Neave & Shields, 2008; Wogalter & Hosie, 1991).

Similarly, some correlational studies have reported that women prefer a more masculine than average vocal pitch (Collins, 2000; Hodges-Simeon, Gaulin, & Puts, 2010), monotonicity (Hodges-Simeon et al., 2010), and timbre (Hodges-Simeon et al., 2010; but not Collins, 2000). Women also prefer an experimentally masculinized, relative to feminized, mean pitch (Feinberg, DeBruine, Jones, & Little, 2008; Feinberg et al., 2006; Feinberg, Jones, Little, Burt, & Perrett, 2005; Jones, Feinberg, et al., 2010; Riding, Lonsdale, & Brown, 2006; but, see Apicella & Feinberg, 2009). However, Riding et al. (2006) did not find women to prefer men's voices masculinized (increased) in monotonicity, and Feinberg et al. (2005) did not find that masculinizing timbre increased the attractiveness of men's voices. Yet, at least three studies have found that male voices masculinized in both pitch and timbre were simultaneously more attractive to women than the same voices with these acoustic parameters feminized (Feinberg et al., 2006; Feinberg et al., 2005; Puts, 2005).

Much of the variation across studies likely results from differences in the type of study (correlational vs. experimental), manipulation size, rating task (e.g.,

sexual attractiveness vs. attractiveness for a committed relationship), stimulus presentation (e.g., paired masculinized/feminized stimuli vs. no rater hearing the same stimulus twice), and other methodological and sampling details. In general, women appear to prefer faces near the male average (perhaps slightly more feminine) and to prefer voices slightly more masculine than average, particularly in pitch. These results suggest that if female preferences influenced the evolution of masculine faces and voices, then men's voices are now near the optimum under this form of sexual selection. However, a number of variables moderate women's preferences for masculinity. The effects of these moderating variables appear to reflect tradeoffs between the costs and benefits of mating with masculine men, to which we now turn.

Masculinity and mate quality. The expression of androgen-dependent traits, such as facial and vocal masculinity, may signal men's long-term health, or "health proneness" (Folstad & Karter, 1992; Tybur & Gangestad, 2011). One possibility is that androgens are immunosuppressant (Grossman, 1985), and compromising the immune system by producing high androgen levels is feasible only for otherwise healthy individuals (Folstad & Karter, 1992). Some evidence indicates that sex steroids suppress immune function in humans (Bouman, Heineman, & Faas, 2005), although a meta-analysis found that testosterone treatment had little such effect in birds (Roberts, Buchanan, & Evans, 2004). Other evidence suggests that the immunosuppressive effects of testosterone are condition-dependent, with testosterone possibly suppressing immune function to a greater degree in males in poor condition (Moore, Al Dujaili, et al., 2011; Moore, Cornwell, et al., 2011; Roberts & Peters, 2009). If heritable immunocompetence mitigates or eliminates the immunosuppressive costs of high testosterone production, then testosterone-dependent male traits, such as masculine faces and voices, should signal underlying genes that would confer disease resistance to offspring.

Another possibility is that immune system activation suppresses testosterone production. A recent meta-analysis found strong support for this hypothesis across mammals and birds (Boonekamp, Ros, & Verhulst, 2008). If a male's immune system more quickly and efficiently dealt with immune threats, then testosterone production might be suppressed less frequently, less severely, or for shorter durations, and a more masculine phenotype would develop. To the extent that such immune efficiency was heritable, then, ancestral women may have produced healthier offspring by mating with masculine men.

Several studies have reported positive correlations between measures of men's health and their facial masculinity. Masculinity ratings of men's facial photographs have been positively correlated with a health score derived from their medical records (Rhodes, Chan,

Zebrowitz, & Simmons, 2003) and the strength of their immune system response to the hepatitis B vaccine (Krams, Rantala, & Krama, 2010). Thornhill and Gangestad (2006) demonstrated that men with more masculine face shapes reported fewer respiratory illnesses and faster recovery times. Masculine men also reported less frequent use of antibiotics. Using facial metric methods like those of Thornhill and Gangestad, Little, Jones, Waitt, et al. (2008) found that facial masculinity was positively correlated with facial symmetry, another putative index of long-term health, in samples of male undergraduate students in the United Kingdom, African hunter gatherers, and macaques. Although additional studies have reported similar correlations between male facial masculinity and symmetry (e.g., Gangestad & Thornhill, 2003), other studies have not observed this relationship (e.g., Koehler, Simmons, Rhodes, & Peters, 2004). Nonetheless, collectively, these findings make a compelling case that masculine characteristics in men's faces signal important information about long-term health.

Thus, women are likely to value in a romantic partner some characteristics that masculine men appear to possess. However, testosterone is also positively correlated with male infidelity, interest in extra-pair sex, violence, divorce, and low investment in mates and offspring (Booth & Dabbs, 1993; Burnham et al., 2003; Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002; McIntyre et al., 2006). Given that both masculine faces (Penton-Voak & Chen, 2004) and voices (Bruckert, Lienard, Lacroix, Kreutzer, & Leboucher, 2006; Dabbs & Mallinger, 1999; Evans et al., 2008; Puts, Apicella, & Cardenas, 2012) have been associated with elevated testosterone levels, masculine men also likely possess traits that women find unappealing. Indeed, masculine men are also perceived to be more likely to cheat on their romantic partners, more likely to pursue other men's romantic partners, and are ascribed a wide range of personality traits (e.g., emotionally cold or "bad parent"), which suggests they are viewed by women as unsuitable for long-term romantic relationships (Boothroyd, Jones, Burt, & Perrett, 2007; Kruger, 2006; Perrett et al., 1998).

Women's preferences for masculine versus feminine men may reflect this tradeoff between the costs and benefits associated with choosing a masculine partner. The following section discusses evidence for this tradeoff model of women's mate preferences, focusing on four factors thought to affect how women resolve the tradeoff: the temporal context of the relationship sought (short-term versus long-term), women's own physical condition, changes in fertility across the menstrual cycle, puberty and menopause, and local parasite stress and violence.

Temporal context of mating relationships. The potential reproductive benefits of choosing a masculine mate (i.e., offspring inherit disease resistance) can be obtained in both long-term, committed relationships

and short-term, uncommitted relationships. By contrast, the possible costs of choosing a masculine mate (i.e., increased risk of infidelity, low commitment, and low investment) are more pronounced in a long-term relationship. Consequently, many researchers have predicted that preferences for masculinity will be stronger when women judge men's attractiveness for a hypothetical short-term relationship than for a hypothetical long-term relationship (e.g., Gangestad & Simpson, 2000; Little, Jones, Penton-Voak, Burt, & Perrett, 2002; Penton-Voak et al., 2003; Puts, 2005). Consistent with this prediction, several studies have found that women show stronger preferences for masculine characteristics in men's faces (e.g., Little et al., 2002; Penton-Voak et al., 2003) and voices (Puts, 2005) when judging men's attractiveness as short-term partners than when judging men's attractiveness as long-term partners. When mated to masculine men, women also report more frequent and earlier-timed orgasms (Puts, Welling, Burriss, & Dawood, 2012), which may function to selectively recruit sperm of men with good genes (Puts & Dawood, 2006; Thornhill, Gangestad, & Comer, 1995). In addition, women currently in long-term, committed romantic relationships tend to show stronger preferences for masculine men than do unpartnered women (Little et al., 2002). Thus, women in long-term relationships may possess preferences more attuned to recruiting good genes for their offspring than acquiring an investing mate, which they already have.

In sum, the temporal context of the imagined relationship affects women's masculinity preferences in ways consistent with tradeoff theories of women's mate preferences. However, the relationship between women's masculinity preferences and interest in short-term, uncommitted relationships is less clear. For example, some researchers have found that women who report being more open to short-term relationships showed stronger preferences for masculine male faces (Smith, Jones, Little, et al., 2009; Waynforth, Delwadia, & Camm, 2005), whereas other researchers have not (Glassenberg, Feinberg, Jones, Little, & DeBruine, 2010; Provost, Kormos, Kosakoski, & Quinsey, 2006). Other studies have revealed correlations between women's reported openness to short-term relationships and their preferences for masculine characteristics in men's voices, body shapes, and gaits (Jones, Boothroyd, Feinberg, & DeBruine, 2010; Provost et al., 2006; Provost, Troje, & Quinsey, 2008). These mixed findings may reflect factors confounded with mating strategy, such as women's physical attractiveness (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008) or the tendency to assess sexual strategy as a relatively stable trait, rather than as a changeable state.

Women's own attractiveness. Several studies have shown that women's preferences for masculine men's faces and voices are positively correlated with their

own attractiveness and beliefs about their own attractiveness (Little & Mannion, 2006; Smith, Jones, Welling, et al., 2009; Vukovic et al., 2008; Vukovic et al., 2010). Perhaps women higher in mate value are able to recruit investment from more masculine men than can women lower in mate value. Consistent with this hypothesis, these associations are more pronounced for judgments of men's attractiveness as a long-term partner (Little et al., 2002; Penton-Voak et al., 2003). Consequently, studies exploring the relationship between women's openness to short-term relationships and their preferences for masculine men may need to control for women's own attractiveness.

Changes across the menstrual cycle, puberty, and menopause. Further evidence for adaptive, facultative responses to male masculinity comes from studies suggesting that women's masculinity preferences are stronger around ovulation (the point in the menstrual cycle where fertility is highest) than during other cycle phases (Gangestad & Thornhill, 2008; Jones, DeBruine, et al., 2008). For example, many studies have found that women show stronger preferences for masculine male facial traits during the late follicular (fertile) phase of the menstrual cycle (Johnston et al., 2001; Jones, Little, et al., 2005; Little, Jones, & DeBruine, 2008; Vaughn, Bradley, Byrd-Craven, & Kennison, 2010). Similar results have been observed for women's preferences for men's voices (Feinberg et al., 2006; Puts, 2005; see also Puts, 2006), body shapes (Little, Jones, & Burriss, 2007), body odors (Havlicek, Roberts, & Flegr, 2005), behavioral displays (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004), personality descriptions (Lukaszewski & Roney, 2009), and gaits (Provost et al., 2008). Many studies of hormonal mediation of behavioral and neurobiological responses to male faces complement these findings (Johnston, Arden, Macrae, & Grace, 2003; Lacreuse, Martin-Malivel, Lange, & Herndon, 2007; Macrae, Alnwick, Milne, & Schloerscheidt, 2002; Roney & Simmons, 2008; Roney, Simmons, & Gray, 2011; Rupp et al., 2009; Welling et al., 2007), as do differences in preferences for masculine men among circum-pubertal girls (Little et al., 2010; Saxton, DeBruine, Jones, Little, & Roberts, 2009), circum-menopausal women (Jones, Vukovic, Little, Roberts, & DeBruine, 2011; Saxton et al., 2009; Vukovic et al., 2009), and women using oral contraceptives versus women with natural menstrual cycles (Feinberg, DeBruine, Jones, & Little, 2008; Little et al., 2002; Puts, 2006).

Recent work on the hormonal correlates of individual differences in women's masculinity preferences has produced mixed results. Early work, using estimated hormone levels, emphasized the possible effects of progesterone (Jones, Little, et al., 2005; Puts, 2006). Subsequent work, using within-subjects designs and

measured hormone levels, has shown different and somewhat inconsistent results. For example, Welling et al. (2007) found that masculine faces were preferred more when women's testosterone levels were relatively high, observed no equivalent association with estrogen, and found some evidence for a complex relationship between progesterone and trait estrogen levels. By contrast, Roney et al. (2011) observed a relationship between women's estrogen levels and preferences for the faces of men with high testosterone, and reported a weak relationship between women's testosterone levels and masculinity preferences. Work on the cognitive processes that contribute to cyclic shifts in women's masculinity preferences is unclear, with researchers variously emphasizing ease of access to sex-stereotyped information (Macrae et al., 2002) and the effects of sexual desire (Welling, Jones, & DeBruine, 2008), among other possibilities.

Although the hormonal and psychological mechanisms that underpin correlations between masculinity preferences and female fertility remain poorly understood, greater inroads have been made in unraveling the possible ultimate functions of increased preferences for masculine men when women are more likely to conceive. Increased attraction to masculine men during the late follicular phase of the menstrual cycle may function, at least partly, to increase the likelihood that women have healthy offspring while maintaining a relationship with a committed and investing long-term partner. This explanation emphasizes the importance of extra-pair sex for the evolution of fertility-contingent masculinity preferences and is, understandably, controversial (e.g., see Harris, 2011). Nonetheless, it has received empirical support from a variety of sources. For example, several studies have found that the effects of the menstrual cycle phase on women's preferences for masculine men are greater when women assess men's attractiveness as potential short-term partners than when they assess men's attractiveness as potential long-term partners (Little, Cohen, Jones, & Belsky, 2007; Penton-Voak et al., 1999; Puts, 2005) or when women already have a romantic partner (Penton-Voak et al., 1999).

Other studies have presented converging evidence that women's interest in extra-pair mating is greater around ovulation than during other phases of the menstrual cycle. Women report more frequent sexual fantasies about men other than their primary partner near ovulation than at other times (Gangestad, Thornhill, & Garver, 2002; see also Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006), and a similar pattern of results has been observed for women's reported commitment to their romantic partner (Jones, Little, et al., 2005). In addition, women are more receptive to men's courtship invitations (Guéguen, 2009a, 2009b), more likely to dress attractively and express interest in revealing clothing (Durante, Griskevicius, Hill, Perilloux, & Li, 2011; Durante, Li, & Haselton, 2008; Grammer,

Renninger, & Fischer, 2004; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007), more likely to attend social gatherings where they might meet men (Haselton & Gangestad, 2006), and report both greater extra-pair flirtation and mate-guarding by their primary partner (Gangestad et al., 2002; Haselton & Gangestad, 2006) during the late follicular phase of the menstrual cycle. More important, recent studies have found that women with more masculine romantic partners show smaller changes in their sexual interests during the menstrual cycle (Gangestad, Thornhill, & Garver-Apgar, 2010).

While the extra-pair mating account of cyclic preference shifts predominates in the literature, a different, but not mutually exclusive, explanation focuses on the potential benefits of increased commitment and attraction to relatively feminine men when raised progesterone prepares the body for pregnancy (Jones, DeBruine, et al., 2008; Puts, 2006). As mentioned earlier, women report greater commitment to their primary romantic partner during the luteal phase of the menstrual cycle when the body prepares for pregnancy (Jones, Little, et al., 2005). Analyses of other aspects of women's behaviors, such as their dress, sexual fantasy about extra-pair men, and extra-pair flirtation, also suggest that women's bonds with their partners are strengthened during the luteal phase of the cycle (Durante et al., 2008; Gangestad et al., 2002; Haselton & Gangestad, 2006). This strengthened bond, together with increased preferences for men displaying cues of prosociality and commitment when progesterone levels are raised (DeBruine, Jones, & Perrett, 2005; Jones, Little, et al., 2005), may reflect adaptations designed to increase the amount of care and support available to women during pregnancy. Indeed, such an account might also explain why some studies have found that women's preferences for masculine versus feminine versions of women's faces also change across the menstrual cycle (Jones, Perrett, et al., 2005; Welling et al., 2007). More important, both the extra-pair mating and "care-during-pregnancy" accounts of cyclic shifts in women's mate preferences may reflect the two sides of the tradeoff between the costs and benefits of mating with masculine men.

Parasite stress and violence. The preceding paragraphs have focused on the utility of tradeoff theory for generating predictions about how women's sexual strategy and fertility might influence their preferences for masculine men within a given culture. By contrast, other research has explored factors that predict variation across cultures in women's preferences for masculine men. For example, the potential heritable health benefits of choosing a masculine male partner may be greater in geographic regions with high pathogen loads, where disease risk is greater. DeBruine, Jones, Crawford, Welling, and Little (2010) investigated this possibility by measuring face preferences in a large

sample of women from 30 countries. DeBruine, Jones, Crawford, et al. (2010) observed a significant correlation between the average preference for masculine men in each country and a composite health index derived from various World Health Organization health measures (e.g., average mortality rate, life expectancy, and years of life typically lost to communicable disease).¹ Moreover, this tendency for women in healthier countries to show weaker preferences for masculine men remained significant after controlling for national wealth and average sociosexuality. Subsequent analyses of these data showed that this relationship between a nation's health and masculinity preferences was also not due to population density, female empowerment, or fertility rates (Brooks et al., 2011). This link between health factors and women's masculinity preferences complemented prior work showing that, within a culture, women who experienced greater pathogen disgust exhibited stronger preferences for masculine faces (DeBruine, Jones, Tybur, Lieberman, & Giskevicius, 2010).

Because most of the populations considered in these studies demonstrated preferences for feminized over masculinized versions of faces (e.g., see also Perrett et al., 1998), Penton-Voak (2011) suggested that the observed relationships with health variables reflected women in regions with poor health being less discriminating about facial masculinity, rather than preferring it more. However, in both samples, health factors were better predictors of women's masculinity preferences than they were of a discrimination score (the unsigned difference between each population's masculinity preference score and what would be expected by chance), suggesting that this is not the case (DeBruine, Jones, Crawford, et al., 2010). Indeed, this discrimination score was entirely uncorrelated with the health factor score in the analysis of U.S. states, and controlling for it in analyses did not alter the pattern of results.

Brooks et al. (2011) questioned the importance of health factors, suggesting that women may show stronger preferences for masculine (i.e., dominant and physically strong) men in more violent regions. Evidence that incidence of violence is better than health factors at predicting regional variation in masculinity preferences is mixed and complicated by high correlations between health and violence measures. Brooks et al. found that homicide rates were positively correlated with masculinity preferences and better predicted variation in countries' masculinity preferences than did DeBruine, Jones, Little, Crawford, and Welling's (2011) health factor. However, DeBruine et al. (2011) found that simply adding wealth (which DeBruine, Jones, Crawford, et al., 2010, demonstrated was highly correlated with masculinity preferences) to Brooks et al.'s regression

model altered the results so that the health factor became the better predictor. In addition, DeBruine et al. (2011) demonstrated that differences in health factors among U.S. states predicted regional variation in U.S. women's preferences for masculine men, whereas measures of regional variation in violence did not.

Whereas these correlational studies paint a confusing picture of whether violence- or health-related factors are more important for predicting regional variation in women's masculinity preferences, two recent experiments suggest that both factors independently shape women's masculinity preferences. In one of these experiments, Little, DeBruine, and Jones (2011b) found that priming women with pictures depicting pathogen-related cues increased women's preferences for masculine male faces. In the second experiment, Little, DeBruine, and Jones (2011a) found that priming women with pictures depicting male-male violence also increased women's preferences for masculine male faces. Collectively, these two findings suggest that concerns about health and violence independently affect how women resolve the tradeoff between the costs and benefits of choosing a masculine mate.

In sum, tradeoff theory has been a fruitful source of predictions about patterns of women's preferences for male masculinity. As predicted, women show greater preferences for masculinity in a short-term mating context than in a long-term mating context. In addition, women's masculinity preferences change in relation to their own fertility in ways consistent with the idea that the genetic benefits of mating with a masculine man are greater during high fertility. Finally, individual differences in masculinity preferences in relation to women's physical condition, and regional variation in average masculinity preferences in relation to parasite stress and violence, further illustrate the utility of tradeoff theory. Although women do not show the consistent, strong preferences for masculine traits evident in many other species (Andersson, 1994), masculinity appears to play a role in women's mate preferences.

Male Contest Competition

Sex differences in faces and voices may also have evolved through male contest competition. Hypertrophic growth of male vocal folds and the descent of the larynx at puberty produce deep, resonant vocalizations that exaggerate apparent size (Fitch, 1997). Men's facial hair may have similarly evolved to increase the apparent size of the jaw and brow (Guthrie, 1970; Muscarella & Cunningham, 1996; Neave & Shields, 2008). Studies investigating the role of male contests have explored relationships between facial or vocal masculinity and dominance (social influence through force or threat of force; Henrich & Gil-White, 2001). Although dominance may be less relevant to men's mating success in modern life than it was over human evolution (Puts,

¹A similar pattern of results was observed when DeBruine, Little, and Jones (in press) reanalyzed these data using more direct measures of parasite stress created by Fincher and Thornhill (in press).

2010), the underlying logic of these studies is that past contest competition would have favored signals of threat potential and deference to these signals. Indeed, men's voices masculinized in pitch or timbre are perceived as emanating from men who are more dominant than are the feminized versions (Feinberg et al., 2006; Feinberg et al., 2005; Jones, Feinberg, et al., 2010; Puts, Gaulin, & Verdolini, 2006; Puts, Hodges, Cardenas, & Gaulin, 2007; Watkins, Fraccaro, et al., 2010; Wolff & Puts, 2010). Correlational studies have also found that more masculine (lower) within-utterance pitch variation (greater monotonicity) predicts dominance perceptions (Aronovich, 1976; Hodges-Simeon et al., 2010; but, see Tusing & Dillard, 2000). Likewise, male faces with beards are rated as more dominant than clean-shaven faces (Addison, 1989; Muscarella & Cunningham, 1996; Neave & Shields, 2008; Pellegrini, 1973; Reed & Blunk, 1990).

Experimental manipulations that increase the facial masculinity of male photographs also strongly increase the appearance of dominance (Boothroyd et al., 2007; DeBruine et al., 2006; Jones, DeBruine, et al., 2010; Perrett et al., 1998; Watkins, Fraccaro, et al., 2010; Watkins, Jones, & DeBruine, 2010). However, whereas deep voices and beards seem to have mainly signaling functions, some structural features of men's faces may enhance fighting success more directly. Modern assailants preferentially target the face (Guthrie, 1970; Shepherd, Gayford, Leslie, & Scully, 1988), and higher levels of male-male than female-female violence (Archer, 2004; Daly & Wilson, 1988, 1990; Ellis et al., 2008) likely contribute to more facial (Shepherd et al., 1988), and especially mandibular (reviewed in Puts, 2010), fractures in men than in women. Over human evolution, such conditions may have helped to produce the greater robusticity of men's skulls. Female assault victims suffer a higher proportion of facial fractures than do male assault victims (Shepherd et al., 1988), suggesting that men's skulls are indeed more resilient against violent assault.

Masculinity predicts dominance. Masculine traits, thus, convey the impression of dominance, but deference to masculine faces and voices would not be maintained by selection unless masculinity was a reliable signal of formidability. In fact, masculinity seems to indicate aggressive potential. For example, Fink, Neave, and Seydel (2007) found that ratings of men's facial masculinity were positively correlated with their handgrip strength—a good predictor of general upper body strength. Sell et al. (2009) found that participants could accurately assess men's physical strength and fighting ability from face images alone in samples ranging from U.S. college students to Bolivian horticulturalists and Andean pastoralists. Other studies have reported correlations between putative masculine facial cues and measures of aggression. Carré and McCormick (2008) found that men with face shapes characterized by a relatively

high width:height ratio, which the authors suggest is sexually dimorphic, were more likely to engage in aggressive behavior in a laboratory task. Similarly, professional and college hockey players with higher facial width:height ratios spent longer in the penalty box and committed more fouls (Carré & McCormick, 2008). Whereas some researchers have suggested that this aspect of face shape may not be sexually dimorphic when measured from face images (Pound et al., 2010), Carré and McCormick's findings present converging evidence for a correlation between men's physical masculinity and both their ability and willingness to fight.

Consistent with the idea that men use facial masculinity to assess other men's abilities to compete for resources, Watkins and colleagues (Watkins, Fraccaro, et al., 2010; Watkins, Jones, & DeBruine, 2010) observed that low-dominance men were particularly sensitive to dominance cues in men's faces and voices. However, these findings should be treated cautiously, as other studies have observed no similar relationships between men's own dominance and their sensitivity to dominance cues in other men's voices (Wolff & Puts, 2010). Exploring individual differences in men's dominance sensitivity may, nonetheless, provide important insights into the role of masculine cues in communicating dominance to potential rivals.

People also accurately assess men's fighting ability and physical strength from their voices (Sell et al., 2010), but it is not presently clear which acoustic variables communicate this information. Although some studies have found relationships between vocal pitch and men's height (Graddol & Swann, 1983) and weight (Evans, Neave, & Wakelin, 2006), most have not (Bruckert et al., 2006; Collins, 2000; Kunzel, 1989; Lass & Brown, 1978; Rendall et al., 2005; Sell et al., 2010; van Dommelen & Moxness, 1995). Similarly, some studies have found relationships between vocal timbre and men's height (Evans et al., 2006; Greisbach, 1999; Rendall et al., 2005; Sell et al., 2010), but others have not (Collins, 2000; Gonzalez, 2004). Some researchers have found relationships between vocal timbre and weight (Evans et al., 2006; Gonzalez, 2004), but most have not (Bruckert et al., 2006; Collins, 2000; Rendall et al., 2005; Sell et al., 2010).

Puts, Apicella, and Cardenas (2012) presented evidence that mean standardized formant frequency ("formant position") is a superior measure of masculinity in vocal timbre to mean spacing between consecutive formant frequencies ("formant dispersion")—the measure used by most previous studies. In this study, formant position was more sexually dimorphic than formant dispersion in both a U.S. sample and a sample of Tanzanian foragers. Puts, Apicella, and Cardenas (2012) found that masculine formant position was related to handgrip strength and height, but formant dispersion was related to neither. Masculine pitch (measured by mean fundamental frequency) was related to

height and testosterone levels, and masculine vocal dynamics (measured by monotonicity, or low within-utterance variation in fundamental frequency) was related to physical aggression. In another study, men who perceived themselves to be better fighters than their competitors lowered their voice pitch when addressing them, whereas men who believed they were less dominant raised their pitch (Puts et al., 2006).

Female Choice Versus Male Contests

Given evidence that facial and vocal masculinity in men have been shaped both by female choice and by male contests, it is reasonable to ask which mode of sexual selection played a larger role in the evolution of these traits. Do masculine faces and voices appear to be sexual ornaments or threat displays? As discussed earlier, male traits, such as facial masculinity, are closer to the optimum under female choice than under male contests. Thus, on the one hand, female choice may appear more influential if it won out against male contests in moving the mean closer to the optimum under female choice.

On the other hand, many additional factors might move masculine traits nearer the optimum under mate choice, including ecological costs and benefits of producing and maintaining masculine traits and, more important, the costs of advertising more dominance than one can back up (Rowher, 1977; Rowher & Ewald, 1981). Moreover, this reasoning based on the optimum trait value under mate choice assumes that modern female preferences are comparable to those that shaped men's faces and voices over human evolution. Making a similar assumption, one can ask about the effect of masculinity on attractiveness to mates compared to the effect on perceptions of dominance. In other words, how well does masculinity serve the alternative (but not mutually exclusive) putative functions of mate attraction versus dominance signaling? The answer is that, across studies, masculine traits are more effective at signaling dominance. Experiments that have compared masculinized to feminized male facial photographs have found larger, positive effects on the appearance of dominance than on attractiveness (DeBruine et al., 2006; Perrett et al., 1998). The same is true for studies that have compared masculinized to feminized male voices (Feinberg et al., 2006; Feinberg et al., 2005; Puts et al., 2006) and for studies that have compared men with and without facial hair (Muscarella & Cunningham, 1996; Neave & Shields, 2008; Pellegrini, 1973; Reed & Blunk, 1990).

However, the effect of masculinity on dominance may be more linear near the male average, and the effect on attractiveness may be more curvilinear. If so, then it might be misleading to compare effects on attractiveness versus dominance using only two levels of masculinization/feminization because such a linear

comparison would adequately describe the effect of masculinity/femininity on dominance, but not the curvilinear effect on attractiveness. Figure 1 illustrates how the effect of masculinity on attractiveness might be underestimated by a comparison of only masculinized and feminized stimuli (data from Puts, 2005; Puts et al., 2006). In this case, it is more appropriate to compare the feminized and masculinized versions of the male trait to the unmanipulated condition. Again, however, the result is that over the normal range of male trait values (in this case, male voices), masculinity has larger effects on dominance than it does on attractiveness. Therefore, although additional research is needed, traits such as masculine facial structure, beards, and

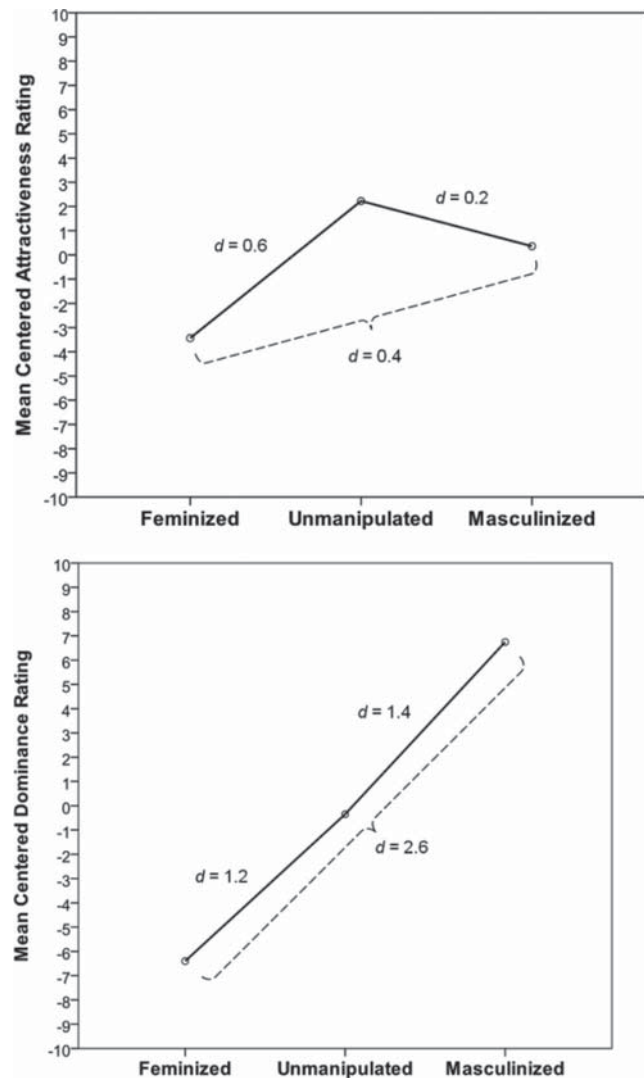


Figure 1. Effects of vocal masculinity on men's attractiveness and apparent dominance. *Note.* Vocal masculinity has larger effects (measured in standard deviations, Cohen's d) on perceptions of dominance than on attractiveness. Voices were rated by women in the fertile phase of their cycle for attractiveness in a short-term, purely sexual relationship and by men for physical dominance (e.g., fighting ability). For additional methodological details, see Puts (2005) and Puts, Gaulin, and Verdolini (2006).

deep voices appear better designed by selection for winning male contests than for attracting mates.

Evidence That Faces and Voices Affect Male Mating and Reproductive Success

If sexual selection shaped men's faces and voices, then facial and vocal masculinity must have contributed to male mating and reproductive success over human evolution. Evidence that masculine faces and voices contribute to mating opportunities in modern samples would support the possibility that these conditions held ancestrally. In fact, several studies have demonstrated that men with masculine faces and voices report more sexual partners, and more short-term and extra-pair sexual relationships in particular, than their relatively feminine peers report (Hodges-Simeon, Gaulin, & Puts, 2011; Hughes, Dispenza, & Gallup, 2004; Puts, 2005; Rhodes, Simmons, & Peters, 2005). Complementing these findings, Apicella, Feinberg, and Marlowe (2007) observed a positive correlation between men's vocal masculinity and their reported reproductive success in a natural fertility sample of African hunter-gatherers; controlling for age, men with lower-pitched voices reported more children born to them and a greater number of currently living children than men with relatively higher-pitched voices. As men's voice pitch was unrelated to the mortality rate of their children, this correlation may reflect a positive effect of masculine voice pitch on men's mating opportunities. Moreover, other studies have found that men with more masculine faces tend to score higher on the Sociosexual Orientation Inventory (Simpson & Gangestad, 1991), a questionnaire that assesses interest in pursuing short-term, uncommitted romantic relationships and numbers of sexual partners and one-night stands the respondent has had in the past (Boothroyd, Cross, Gray, Coombes, & Gregson-Curtis, 2011; Boothroyd et al., 2008). Collectively, these findings suggest that masculine faces and voices evolved because they elevated reproductive success through increasing mating opportunities.

Conclusions and Directions for Future Research

The aforementioned evidence indicates that sexual selection has shaped men's and women's faces and voices, and that male contests, female mate choice, and male mate choice all played roles in the evolution of human facial and vocal sexual dimorphisms. Indeed, a range of contest-relevant traits (e.g., physical strength) can be accurately assessed from men's facial and vocal masculinity. Moreover, the patterns of men's perceptions of other men's dominance are consistent with male-male contests having shaped men's faces and voices. Similarly, the patterns of women's preferences for male masculinity, especially the link between

women's fertility and masculinity preferences, and men's preferences for female femininity are consistent with mate choice having shaped men's and women's faces and voices. Although the utility of considering these two types of sexual selection for understanding male facial and vocal masculinity is clear, there are a number of important and unresolved questions for future research.

An important next step is to clarify what benefits faces and voices signal to potential mates. For example, although correlational studies have implicated both indexes of male-male competition and pathogen prevalence in women's preferences for male facial masculinity (Brooks et al., 2011; DeBruine, Jones, Crawford, et al., 2010), these factors are often confounded, and relationships differ between samples (DeBruine et al., 2011). Experimental studies, such as those that examine changes in preferences after viewing cues of environmental pathogens (e.g., Little, DeBruine, & Jones, 2011b), are needed to determine the contexts in which each of these effects is most pronounced. For example, masculinity may be more important as a dominance cue when resources are scarce, and competitiveness for these resources is critical, whereas masculinity may be more important as a cue of heritable health when resources are abundant, and women can consider qualities beyond resource-holding potential in possible mates.

It will be particularly important to continue investigating how putative sexually selected traits, such as the facial features and vocal characteristics discussed earlier, affect mating and reproductive success. For example, do masculine faces and voices increase men's sexual opportunities, as some research suggests? If so, to what extent are these mating advantages due to increased dominance among men, and to what extent are they due to greater attractiveness to women? Because the mating environments of many modern societies are likely to differ in important ways from those in which human mating adaptations evolved, it will be essential to examine these questions cross-culturally, especially in traditional societies.

Future research should also determine how face and voice preferences and dominance perceptions relate to actual mate choices and contest outcomes. Thus far, work on these issues is sparse, but encouraging. For example, facial appearance is correlated with the number of penalty minutes in male ice hockey players and with aggressive behaviors among undergraduate men in laboratory tasks (Carré & McCormick, 2008). In addition, dominance ratings of military cadets' faces predict the rank they ultimately achieve in the military (Mueller & Mazur, 1996), and women's preferences for masculine face shapes predict their ratings of their actual and ideal partners' masculinity (DeBruine et al., 2006). Although these findings present encouraging signs that perceptual characteristics of faces are relevant to real-world contests and mate choices, more work of this

type is needed to bridge the gaps between lab-based research and real-world behavior.

Another unanswered question is how people integrate information from cues in different domains (e.g., face and voice masculinity) with information about attitudes and intentions (e.g., emotional content and movement). Preliminary research suggests that such interactions are important; for example, gaze direction interacts with facial masculinity, such that masculine face shapes increase perceptions of dominance in faces with direct gazes more than in faces with averted gazes (Main et al., 2009). Similarly, cues of social interest in faces and voices modulate preferences for physical characteristics, such as attractive color and texture cues (Jones, DeBruine, Little, Conway, & Feinberg, 2006) and voice pitches (Jones, Feinberg, et al., 2008). More experimental work is needed to elucidate the integrative processes that underpin appraisals of potential mates and competitors. Our understanding of social perception would be enriched by further work exploring how familiarity with and explicit social knowledge about potential mates and competitors (e.g., past performance in competitive encounters with rivals or previous behavior in romantic relationships) figure in contest- and mating-related perceptions.

Although the research described here provides evidence for the ultimate functions of perceptions of men's facial and vocal masculinity, the proximate mechanisms for individual differences in these perceptions remain unclear. Steroid hormones, such as progesterone, estradiol, and testosterone (Jones, Perrett, et al., 2005; Puts, 2006; Roney & Simmons, 2008; Roney et al., 2011; Welling et al., 2007), are likely to mediate shifts in women's masculinity preferences over the ovulatory cycle and across life stages, but more work is needed. Studies of visual adaptation and social learning suggest that experience produces individual variation in face and voice preferences. Such studies have generally focused on mate choice (reviewed in Little, Jones, DeBruine, & Caldwell, 2011), but social learning can also influence perceptions of men's dominance (Jones, DeBruine, Little, Watkins, & Feinberg, 2011). In addition, experience with faces and voices can recalibrate judgments of masculinity and associated attributions (Buckingham et al., 2006), and conditioning and associative learning can contribute to preferences and perceptions (e.g., Jones, DeBruine, Little, & Feinberg, 2007). Establishing how such relatively simple socio-cognitive processes interact to provide rich and colorful preferences and perceptions is essential to more fully understand social perception, mate preferences, and perceptions of rivals.

The research described here focuses on men's faces and voices partly because research on women's faces and voices is more limited, which may owe in part to the widely held view that sexual selection operated more strongly on men. Nevertheless, sexual selection has probably been heavily influential in shaping women's

traits (Hrdy, 1981; Puts, 2010); thus, future research should continue to investigate the roles of faces and voices in women's status, dominance, and attractiveness. Preliminary work suggests that facial masculinity is a valid cue to women's physical dominance (Quist et al., 2011). Other studies suggest that women's attractiveness moderates women's social dominance and plays a key role in the threat they pose to rivals for mates (e.g., Cashdan, 1998; Maner et al., 2003; Puts, Barndt, et al., 2011). Yet, other research indicates that there is considerably more variation in men's preferences for feminine women than many researchers initially suspected (e.g., see Burriss, Welling, & Puts, 2011; Welling, Jones, DeBruine, Smith, et al., 2008). It will be important to assess how women's traits and their dominance and attractiveness affect mating outcomes, especially the investment that they obtain from mates. Further work on these issues will inform the ultimate functions of women's facial appearance and vocal characteristics, and address this imbalance in the literature on human sexual selection.

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