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ORIGINAL RESEARCH

Estimating the Sex-Specific Effects of Genes on Facial Attractiveness and Sexual Dimorphism

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Abstract Human facial attractiveness and facial sexual dimorphism (masculinity–femininity) are important facets of mate choice and are hypothesized to honestly advertise genetic quality. However, it is unclear whether genes influencing facial attractiveness and masculinity–femininity have similar, opposing, or independent effects across sex, and the heritability of these phenotypes is poorly characterized. To investigate these issues, we assessed facial attractiveness and facial masculinity–femininity in the largest genetically informative sample ($n = 1{,}580$ same- and opposite-sex twin pairs and siblings) to assess these questions to date. The heritability was $\sim$0.50–0.70 for attractiveness and $\sim$0.40–0.50 for facial masculinity–femininity, indicating that, despite ostensible selection on genes influencing these traits, substantial genetic variation persists in both. Importantly, we found evidence for intralocus sexual conflict, whereby alleles that increase masculinity in males have the same effect in females. Additionally, genetic influences on attractiveness were shared across the sexes, suggesting that attractive fathers tend to have attractive daughters and attractive mothers tend to have attractive sons.

Keywords Facial attractiveness · Masculinity–femininity · Mate choice · Sexual selection · Intralocus sexual conflict · Evolutionary genetics · Twin and family studies · Sex limitation

Introduction

Human facial attractiveness is assessed rapidly, automatically, and consistently across ages and cultures (Langlois et al. 2000; Olson and Marshuetz 2005; Slater et al. 1998), and it is correlated with health and reproductive success (Hume and Montgomerie 2001; Prokop and Fedor 2011;

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Rhodes et al. 2001; Weeden and Sabini 2005). These and other observations are consistent with the hypothesis that people prefer facial attractiveness because it is an honest cue of overall genetic fitness (Grammer and Thornhill 1994; Penton-Voak et al. 2001; Penton-Voak and Perrett 2000; Thornhill and Gangestad 1993). Such a link between genetic fitness and attractiveness might occur if fitness-reducing mutations also reduce facial attractiveness, in which case individuals would minimize the number of deleterious mutations in their offspring, and maximize their reproductive fitness, by seeking to mate with physically attractive individuals (Keller 2006).

Research into perceptions of the human face has identified sexual dimorphism as a component of facial attractiveness (Grammer and Thornhill 1994; Penton-Voak et al. 2001; Thornhill and Gangestad 1993). Because sexually dimorphic features develop during puberty under the influence of gonadal hormones (Koehler et al. 2004; Law Smith et al. 2006), the extent to which an individual possesses sex-typical features may indicate his or her ability to produce healthy and attractive offspring and thus serve as an important evolutionary signal of phenotypic or genetic "quality" (Perrett et al. 1998). Thus, sexual selection may favor both increased development of sex-typical features and preferences for sex-typical mates. However, whereas masculine features in women are associated with decreased attractiveness (Welling et al. 2008), results from research into the relationship between attractiveness and male facial masculinity are equivocal. Some studies report benefits to masculine-faced men that may have led to increased reproductive success in ancestral environments, including earlier first intercourse (Mazur et al. 1994) and greater perceived attractiveness, particularly as judged by ovulating women (Little et al. 2008; Penton-Voak et al. 2001; Roney et al. 2011). However, other studies have found female preferences for feminine-faced men (Perrett et al. 1998), and yet others have found that an intermediate level of facial masculinization is preferred (Swaddle and Reierson 2002). Therefore, although it seems reasonable to expect that male facial attractiveness would correlate positively with facial masculinity, the observed relationship between these two qualities is uncertain. One possibility is that masculinity in general, including facial masculinity, may increase overall mate value in males (e.g., via male–male competition), even if it has a low or even negative relationship with facial attractiveness itself.

Nonetheless, from an evolutionary perspective, the possibility that facial masculinity has opposing effects on sexual attractiveness between the sexes creates an evolutionary conundrum. If the alleles that influence the development of sex-typical features in one sex have the same effect in the other sex—that is, if masculine fathers tend to have masculine daughters and feminine mothers tend to have feminine sons—then no single allele at a locus affecting sexual dimorphism will produce optimal fitness in both males and females. To the degree this occurs, opposite-sex relatives (e.g., siblings or parent–offspring pairs) will have negatively correlated reproductive success (Bonduriansky and Chenoweth 2009; Stearns et al. 2012). The result is *intralocus sexual conflict* between alleles that enjoy higher fitness when present in members of one sex (by increasing their sexual attractiveness) but have lower fitness in the opposite sex (by decreasing theirs). With respect to mate choice, intralocus sexual conflict implies a trade-off between choosing mates who can produce either attractive male or attractive female offspring (i.e., "sexy sons" or "sexy daughters"), because attractive mates do not transmit their heritable attractiveness to opposite-sex offspring.

Natural selection might be expected to reduce a positive genetic correlation of masculinity–femininity across sexes (Stearns et al. 2012). If the correlation is initially positive, selection should favor modifier alleles that allow the expression of the trait to differ between the sexes (Rice and Chippindale 2001). Alleles influencing masculinity–femininity would therefore be released from conflict, allowing both males and females to reach their sex-specific fitness peaks (Cox and Calsbeek 2009). The result is termed *sex limitation*, implying a divergence of genetic effects in males and females; sex limitation can range in degree from weak quantitative differences, with genetic effects largely overlapping between sexes, to complete qualitative differences, as when homologous traits in males and females are influenced by entirely separate sets of genes. Large sex differences in the fitness effects of alleles influencing masculinity–femininity will increase selection pressure favoring sex limitation (Rhen 2000; Rice 1984); however, the degree of sex limitation that evolves may be constrained by the amount of time since the sexual conflict developed and by the availability (i.e., introduction through mutation) of modifier alleles allowing sex-dependent expression of the alleles influencing masculinity–femininity (Rhen 2000). The evolution of sex limitation may be enhanced if the relevant alleles (including modifier alleles) exist on the X- or Y-chromosomes (Fairbairn and Roff 2006; Rice 1984).

At the opposite extreme from intralocus sexual conflict is a scenario in which modifiers have evolved that reverse the effects of the genes influencing masculinity–femininity between the sexes. For example, if the expression of sexually dimorphic traits depends on underlying heritable quality or condition (e.g., mutational load), then 'high quality' masculine males will tend to father 'high quality' feminine daughters and vice versa. Although the sex reversal, intralocus sexual conflict, and sex-limited models all are consistent with "good genes" models of mate

choice, which posit that sexually attractive traits are cues to "good genes" (i.e., genes with few fitness-reducing mutations and/or genes better adapted to current challenges, such as pathogens), the sex reversal scenario allows for the possibility that the same alleles can increase sexual dimorphism in both sexes.

All of these models presuppose that facial attractiveness and facial masculinity–femininity are heritable. Previous research has provided suggestive but incomplete evidence that this is the case. McGovern et al. (1996) reported correlations in physical attractiveness from a large sample of female identical twins ($r = 0.65$, $n = 334$) and fraternal twins ($r = 0.33$, $n = 216$), suggesting a heritability of 64 % with a very small contribution from the shared environment. Two other studies have shown that identical twins possess correlated levels of facial attractiveness ($r = 0.74$, $n = 34$; Mealey et al. 1999) or overall physical attractiveness ($r = 0.54$, $n = 25$; Rowe et al. 1987). Fraternal twins were not included in either of these studies, making it impossible to differentiate genetic from environmental causes of twin similarity, although these correlations provide an approximate upper limit on the heritability of attractiveness. Cornwell and Perrett (2008) showed that parental attractiveness predicts offspring attractiveness for daughters but not for sons; this study's design also led to confounds between genetic and environmental influences, though it suggests that genetic factors may contribute up to 60–70 % of the variance in women's facial attractiveness (twice the reported correlations: $r = 0.31$, $n = 104$, between daughters and their mothers; $r = 0.36$, $n = 95$, between daughters and their fathers). The same study also found correlations between parents' and same-sex offspring's facial femininity or masculinity, suggesting heritabilities around 60 %, assuming no contribution from the shared environment to parent–offspring resemblance ($r = 0.32$, $n = 104$, between mothers and daughters; $r = 0.31$, $n = 62$, between fathers and sons). Correlations for opposite-sex pairs were low, pointing to some degree of sex limitation in the transmission of sexually dimorphic facial features.

The purpose of the present study is twofold. First, we used ratings of photographs to quantify the degree to which masculinity–femininity and attractiveness are heritable in the largest sample to investigate this question to date [$n = 1{,}580$ monozygotic (MZ) and dizygotic (DZ) twins and their siblings]. Same-sex pairs allowed estimation of overall differences between the sexes in genetic and environmental influences, while opposite-sex pairs allowed estimation of cross-sex genetic correlations (Eaves 1977; Jinks and Fulker 1970). The second purpose of this study is to introduce a framework for testing the three competing evolutionary genetic models of sexual dimorphism, and to apply this framework to our own data. Although we lacked power to make strong conclusions in our own data, omnibus tests allowed for some differentiability between the models.

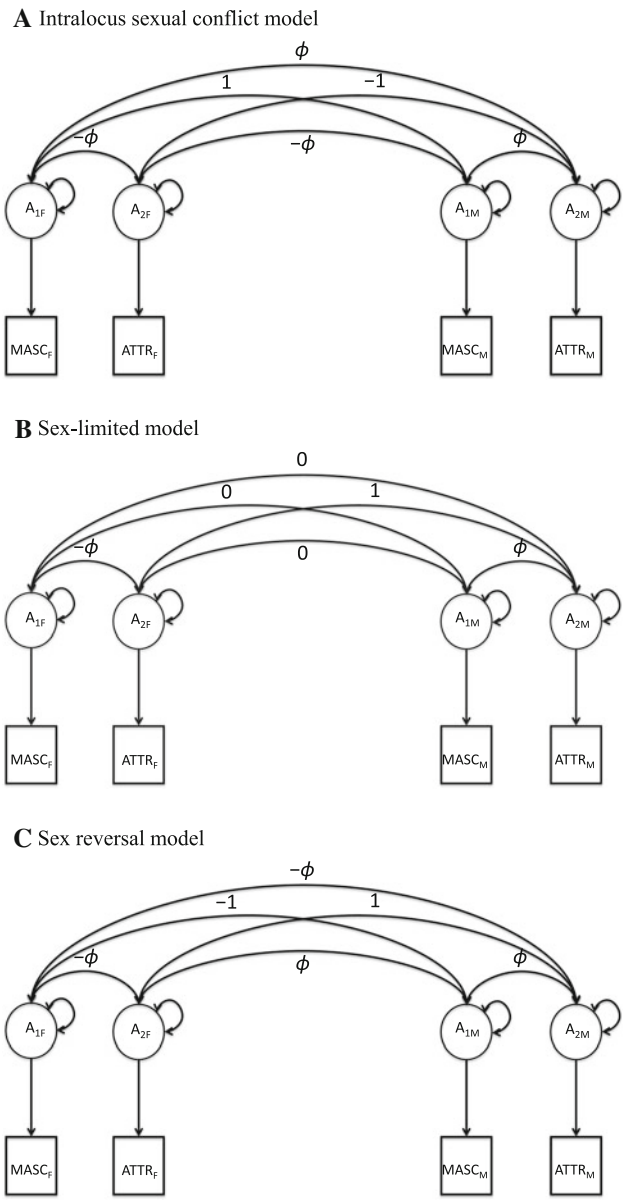

Fig. 1 Competing evolutionary models of cross-sex genetic correlations in *Attractiveness* and *Masculinity–femininity*. **a** *Intralocus sexual conflict model*: signs (+/−) of genetic correlations indicate that genes increasing sexual attractiveness in one sex decrease it in the other. **b** *Sex-limited model*: only the genetic effects on *Attractiveness* are shared between the sexes; all other genetic correlations are 0. **c** *Sex reversal model*: signs of all cross-sex genetic correlations indicate that genes increasing sexual attractiveness in one sex also increase it in the other. Subscript *F* indicates female phenotypes and additive genetic factors, subscript *M* those for males

A Framework for Testing Competing Evolutionary Genetic Models of Sexual Dimorphism

The predictions made by the three competing evolutionary models of sexual dimorphism are quantified in Fig. 1. These models quantify what types of within-sex and cross-sex genetic correlations might be expected between two traits, one that is under sexual selection in opposite directions between the sexes (e.g., masculinity–femininity), and one that is under selection in the same direction in both sexes (e.g., attractiveness). Although we do not expect the genetic correlations between any two such sexually selected traits to ever fit exactly the extreme predictions laid out in Fig. 1, the expectations provide some leverage in understanding which sets of estimated genetic correlations are most consistent with which model.

In all models, we assume that ϕ is the positive genetic correlation between facial masculinity–femininity and facial attractiveness in males, and that $-\phi$ is the genetic correlation between facial masculinity–femininity and facial attractiveness in females—i.e., increased facial masculinity is associated with increased attractiveness in males and decreased attractiveness in females. According to a strong version of the intralocus sexual conflict model (Fig. 1a), the genetic effects acting upon facial masculinity–femininity are expected to be identical between the sexes. This might occur if the genetic factors are autosomal and there is no selection for sex-limited genetic effects or if constraints block the evolution of sex limitation/reversal. If so, the expected genetic correlation between male and female facial masculinity–femininity would be ~ 1 (alleles making males masculine also make females masculine). Given this, the intralocus sexual conflict model would predict that genes influencing male attractiveness are negatively correlated with female attractiveness, and under a strong version of this model, the genetic correlation between male and female facial attractiveness would therefore be -1. Genetic correlations of 1 and -1 between the sexes imply that each trait is influenced by identical sets of genes in males and females; therefore, the degree to which these two sets of genes correlate must also be identical in magnitude, both within each sex and between sexes. Given these four correlations, the final two genetic cross-trait cross-sex correlations must necessarily be equal to $-\phi$ (between male masculinity–femininity and female attractiveness) and ϕ (between male attractiveness and female masculinity–femininity) to maintain internal consistency between all the correlations.

According to a sex-limited model (Fig. 1b) hypothesizing that the genetic effects acting upon facial masculinity–femininity are not shared between the sexes, the genetic correlation between opposite-sex relatives' levels of masculinity–femininity is expected to be zero. This might occur if modifier alleles (e.g., that exist on sex chromosomes) have evolved to express or silence masculinity–femininity alleles depending on sex. Furthermore, given that there are no trade-offs in attractiveness between the sexes under this model, we might assume that the genetic correlation between female and male attractiveness is ~ 1. Although there is no clear algebraic expectation for what the cross-trait cross-sex genetic correlations should be in this scenario, it is reasonable to predict that both cross-sex genetic correlations between facial masculinity–femininity and facial attractiveness will also be zero. Similarly, the internal consistency of this model does not require that the within-sex cross-trait genetic correlations (ϕ and $-\phi$) be equal in magnitude; but, for comparability with the other models, we will assume that they are.

Finally, according to the sex reversal model (Fig. 1c), the genetic influences on facial masculinity–femininity act oppositely in the two sexes, and therefore the genetic correlation between male facial masculinity–femininity and female facial masculinity–femininity is expected to be -1. Likewise, the cross-sex cross-trait genetic correlations between male facial masculinity–femininity and female facial attractiveness is expected to equal ϕ (e.g., 'good' genes that increase masculinity in fathers also increase attractiveness in daughters), and that between female facial masculinity–femininity and male facial attractiveness is expected to equal $-\phi$ (e.g., 'good' genes that decrease masculinity in mothers increase attractiveness in sons).

Materials and Methods

Sample

Our sample consisted of 1,580 individuals, including 150 female monozygotic (MZ) twin pairs, 108 male MZ pairs, 140 female dizygotic (DZ) twin pairs, 114 male DZ pairs, 174 opposite-sex DZ twin pairs, and 106 non-twin siblings of twins (57 female, 49 male). We retained 102 individuals whose co-twins' data were unavailable, to increase accuracy of mean and variance estimates. 242 participants (15.3 %) were from the Longitudinal Twin Study (LTS, located in CO, USA; Rhea et al. 2012) and 1,338 participants (84.7 %) were from the Brisbane Adolescent Twin Study (BATS, located in QLD, Australia; Wright and Martin 2004). All non-twin siblings ($n = 106$) and all DZOS twins ($n = 365$) were from the BATS sample. BATS participants were, on average, younger (15–22 years, median = 16) than LTS participants (21–24 years, median = 22). All participants gave informed written consent, and approval to code and analyze these data was obtained from Institutional Review Boards at the University of Colorado and the Queensland Institute of Medical Research.

Photographic Materials

Photographs of LTS participants were taken between 2009 and 2010. Participants were asked to adopt a neutral facial expression while four digital photographs were taken. Photographs of BATS participants were taken between 1996 and 2010. Because BATS photographs were not intended for facial assessment, they exhibited more variation than LTS photographs in characteristics that could potentially impact attractiveness assessments. For instance, participants were not instructed to adopt a neutral facial expression or to face the camera directly.

JPG color image files from both cohorts typically had resolution of 300 × 400–400 × 600 pixels. We cropped images so faces occupied 70–80 % of total image area. For display to judges (see below), the four images of each LTS participant were arranged in a 2 × 2 collage with a total area of 17.2 × 22.8 cm^2; BATS participants' single images were also sized to 17.2 × 22.8 cm^2; all images were displayed against a black background.

Rating Procedure

Photographs were rated on two core traits (*Attractiveness* and *Masculinity–femininity*) and three covariates (*Acne*, *Smiling*, and *Grooming*) by undergraduate research assistants (19–30 years, median = 22) from the University of Colorado Boulder. To encourage judges to use the entire range of trait rating scales, they viewed a slideshow consisting of 50 randomly selected target faces (all male or all female) displayed for 2 s each prior to assigning ratings. Immediately following the slideshow, the same 50 faces were rated in randomized order, to minimize order effects. Ratings tasks were untimed; entering a rating prompted the appearance of the next face. This procedure continued, alternating between sets of male and female targets, until all faces were rated.

Over the course of one semester, four female and four male judges rated all faces on *Attractiveness* and subsequently rated all faces on *Masculinity–femininity*. They were instructed to rate each face relative to other faces in the same 50-image set and to distribute their scores approximately uniformly to minimize inter-rater differences in variability and maximize information (variability) in individual ratings. Both traits were rated on 1–7 scales (*Attractiveness*: 1 = low, 7 = high; *Masculinity–femininity*: 1 = very feminine, 7 = very masculine). No special instructions were given to judges before rating *Attractiveness*, because reliability and validity of facial attractiveness ratings are supported in the literature (Langlois et al. 2000). Prior to rating *Masculinity–femininity*, judges received a lesson on typical sexual dimorphism in human facial and cranial dimensions—for example, that female faces tend to feature a more tapering jaw line and that male faces tend to be longer below eye level. Given that intercorrelations among specific sexually dimorphic facial features are reportedly low (Penton-Voak et al. 2001), it is possible that facial masculinity and femininity are separate dimensions, as appears to also be the case with psychological masculinity and femininity (Bem 1974; Constantinople 1973). However, in the present study the construct is necessarily one-dimensional because judges rated masculinity/femininity on a single dimension; this is consistent with previous investigations of facial and bodily sexual dimorphism (e.g., Lee et al. 2013; Little et al. 2007; Penton-Voak et al. 2001; Perrett et al. 1998; Welling et al. 2007), which have generally treated the construct as one-dimensional.

Across all eight judges, inter-rater reliability was higher for *Attractiveness* (Cronbach's $\alpha = 0.87$) than for *Masculinity–femininity* ($\alpha = 0.66$). Given that mate choice and reproductive success are issues central to this study, it could be argued that ratings assigned by judges of opposite sex to the target face have higher ecological validity than do ratings given by judges of the same sex as the target face. Indeed, male judges rated female targets' *Attractiveness* more reliably ($\alpha = 0.82$, 95 % CI [0.80, 0.084]) than did female judges ($\alpha = 0.74$, 95 % CI [0.72, 0.77]), and female judges rated male targets' *Masculinity–femininity* more reliably ($\alpha = 0.55$, 95 % CI [0.50, 0.60]) than did male judges ($\alpha = 0.28$, 95 % CI [0.18, 0.36]). However, as discussed below, the twin correlations and results from structural equation models did not differ depending on whether or not we restricted analyses to ratings by judges of the opposite-sex to the target face, so all results presented below utilize ratings by both male and female judges.

The following semester, a different set of seven female and four male judges rated faces on three additional covariates of facial attractiveness. Ten of them (6 female, 4 male) rated the amount of *Acne* in faces (1 = no acne, 7 = heavy acne). Ten (7 female, 3 male) rated *Smiling* (1 = no smile, 2 = partial smile, 3 = full smile). Nine (7 female, 2 male) rated *Grooming* (defined as the apparent time and effort the target had spent managing his or her appearance; 1 = little time or effort, 7 = much time or effort). Inter-rater reliability was high for all covariates (*Acne*: $\alpha = 0.94$; *Smiling*: $\alpha = 0.98$; *Grooming*: $\alpha = 0.88$). We averaged the scores for each target face to create composite scores for *Acne*, *Smiling*, and *Grooming*.

Data Analysis

We fit a bivariate biometrical model decomposing phenotypic variances of *Attractiveness* and *Masculinity–femininity* into components attributable to additive genetic effects (i.e., heritability) and non-shared environmental

effects (idiosyncratic non-genetic effects, including measurement error), controlling for effects of age, age squared, sex, cohort (USA or Australia), and year the photo was taken. Behavioral genetic studies of twins often also estimate either non-additive genetic (due to dominance or interactions across multiple loci) or shared environmental (e.g., features of the rearing environment) variance. We omitted non-additive genetic and shared environmental variance components from the analyses presented here, because there was little evidence for either in full models in which we estimated them. However, full models including estimates of non-additive or shared environmental effects are shown in Supplementary Table I. Genetic correlations between opposite-sex twins were modeled to estimate the extent to which genetic effects are similar or different between females and males. We used the structural equation modeling package OpenMx (version 1.3.0; Boker et al. 2011) for R (version 2.15.3; R Core Team 2013) for these analyses. There was no significant reduction in model fit when means, variances, and covariances for non-twin siblings were constrained to equal those for DZ twins; hence, in all analyses, these two groups were combined. The ability to do so increased both the precision of our parameter estimates and our confidence that the data we obtained from the twin sample is representative of the non-twin population (Eaves 2009).

In follow-up analyses, in addition to the control variables described above, we also controlled for the effects of *Smiling*, *Grooming*, *Acne*, and BMI on ratings of *Attractiveness* and *Masculinity–femininity*. Decisions about whether to smile, differences between participants in instructions on grooming (some participants were asked not to wash their hair for an unrelated aspect of the study), acne as a young adult (which probably has only transient effects on attractiveness) and body mass index (which ostensibly showed less variation in environments in which the genes we are interested in evolved) could all be considered nuisance variables with respect to the evolutionary genetic hypotheses being tested here. However, in controlling for these variables, we removed $\sim$40 % of the variation in *Attractiveness* and $\sim$20 % of the variation in *Masculinity–Femininity*, reducing the precision of estimates of heritability and genetic correlations. (See Supplementary Table II for genetic analyses of all five rated facial traits together.)

To evaluate the support for each of the competing evolutionary genetic models in Fig. 1, we refit our base model such that the cross-sex genetic correlations were constrained to equal the values predicted under each of the competing models (Fig. 1). Differences between -2 times the log-likelihoods ($-2LL$) of base and nested (constrained) models are distributed as χ^2 statistics with degrees of freedom equal to the number of parameters omitted from the constrained model; thus, we used χ^2 tests to compare each constrained model's fit relative to the base model. Because the three competing models are not nested one within another, we compared their goodness of fit using Akaike Information Criterion values ($AIC = -2LL + 2k$, where k is the number of parameters the model estimates; thus, lower values indicate better fit to the data).

Results

Phenotypic Correlations

Table 1 presents the within-person correlation matrices for *Attractiveness*, *Masculinity–femininity*, *Grooming*, *Acne*, and *Smiling*, separately for female and male participants. Table 2 shows the maximum-likelihood estimates of correlations of residualized *Attractiveness* and *Masculinity–femininity* between related individuals, as a function of zygosity and sex.

Table 1 Phenotypic intercorrelations, by sex of participant

Variable	1	2	3	4	5
1. Attractiveness		−0.05	**0.43**	**−0.34**	0.07
		[−0.12, 0.03]	[0.36, 0.48]	[−0.40, −0.27]	[−0.00, 0.14]
2. Masculinity–femininity	**−0.74**		−0.04	**0.18**	0.02
	[-0.77, −0.71]		[−0.11, 0.04]	[0.11, 0.25]	[−0.05, 0.09]
3. Grooming	**0.57**	**−0.45**		**−0.16**	**0.09**
	[0.52, 0.61]	[−0.50, −0.40]		−0.23, −0.09]	[0.02, 0.16]
4. Acne	**−0.44**	**0.30**	**−0.36**		0.02
	[−0.50, −0.39]	[0.24, 0.36]	[−0.41, −0.30]		[−0.06, 0.09]
5. Smiling	**0.10**	**−0.11**	**0.09**	−0.01	
	[0.04, 0.17]	[−0.18, −0.04]	[0.02, 0.15]	[−0.08, 0.06]	

Correlations [95 % confidence intervals] for males ($n = 708$) are above the main diagonal, those for females ($n = 848$) below. Statistically significant correlations ($p < 0.05$) are in bold print

Table 2 Residualized *Attractiveness* and *Masculinity–femininity* correlations, by sex and zygosity group

Between twins	MZFF ($n = 150$)	MZMM ($n = 107$)	DZFF ($n = 161$)	DZMM ($n = 130$)	DZOS ($n = 219$)
Attractiveness and *Masculinity–femininity* not controlled for *Acne*, *Grooming*, *Smiling*, or BMI					
Attractiveness	**0.62**	**0.63**	**0.43**	**0.29**	**0.21**
	[0.52, 0.70]	[0.50, 0.72]	[0.29, 0.53]	[0.11, 0.44]	[0.10, 0.31]
Masc-fem	**0.50**	**0.51**	**0.21**	0.10	**0.15**
	[0.38, 0.59]	[0.36, 0.63]	[0.06, 0.35]	[−0.08, 0.28]	[0.03, 0.26]
Attractiveness—Masc-fem	**−0.50**	−0.01	**−0.27**	−0.01	**−0.20**[a]
	[−0.58, −0.41]	[−0.12, 0.10]	[−0.38, −0.14]	[−0.13, 0.12]	[−0.30, −0.10]
					−0.14[b]
					[−0.25, −0.02]
Within person	Females ($n = 848$)	Males ($n = 708$)			
Attractiveness—Masc-fem	**−0.74**	−0.06			
	[−0.77, −0.70]	[−0.14, 0.02]			
Attractiveness and *Masculinity–femininity* controlled for *Acne*, *Grooming*, *Smiling*, and BMI					
Attractiveness	**0.48**	**0.51**	**0.28**	0.11	**0.15**
	[0.36, 0.58]	[0.37, 0.63]	[0.14, 0.41]	[−0.09, 0.29]	[0.03, 0.26]
Masc-fem	**0.38**	**0.48**	**0.17**	0.14	0.10
	[0.25, 0.50]	[0.31, 0.60]	[0.02, 0.32]	[−0.04, 0.30]	[−0.02, 0.21]
Attractiveness—Masc-fem	**−0.35**	0.08	**−0.15**	0.01	**−0.12**[a]
	[−0.43, −0.24]	[−0.03, 0.20]	[−0.27, −0.03]	[−0.12, 0.14]	[−0.22, −0.01]
					−0.10[b]
					[−0.21, 0.02]
Within person	Females ($n = 848$)	Males ($n = 708$)			
Attractiveness—Masc-fem	**−0.60**	0.06			
	[−0.64, −0.55]	[−0.02, 0.14]			

Between- and within-person correlations [95 % confidence intervals] are presented. Statistically significant correlations ($p < 0.05$) are in bold print. Sample sizes for "dizygotic" pairs (DZFF, DZMM, DZOS) are larger than those reported in the text, due to the inclusion of non-twin siblings in the groups used to estimate these correlations

[a] Correlation between male *Attractiveness* and female *Masculinity–femininity*

[b] Correlation between female *Attractiveness* and male *Masculinity–femininity*

Bivariate Analysis of Attractiveness and Masculinity–Femininity

Figure 2a shows results of the bivariate model of *Attractiveness* and *Masculinity–femininity* not controlled for *Grooming*, *Acne*, *Smiling*, or BMI. Both traits demonstrate substantial heritability in females ($h^2_{Attr} = 0.64$, $h^2_{Masc} = 0.49$) and in males ($h^2_{Attr} = 0.70$, $h^2_{Masc} = 0.50$). Decreased *Masculinity–femininity* is associated with increased *Attractiveness* both genetically ($r_A = -0.86$, 95 % CI [−1.0, −0.70], $p < 0.001$) and environmentally ($r_E = -0.40$, 95 % CI [−0.45, −0.19], $p < 0.001$) in females. In males, the additive genetic effects that increase *Masculinity–femininity* are modestly, but not significantly, associated with reduced *Attractiveness* ($r_A = -0.12$, 95 % CI [−0.32, 0.08], $p < 0.12$), implying very little overlap in the heritable factors influencing both traits. The non-genetic effects that increase *Masculinity–femininity* are also associated with modest reductions in *Attractiveness* ($r_E = -0.19$, 95 % CI [−0.42, 0.02], $p = 0.04$).

The two within-trait and two cross-trait additive genetic correlations provide four separate estimates of the genetic overlap between the sexes. The cross-sex genetic correlation in *Attractiveness* ($R_{22} = 0.85$, 95 % CI [0.48, 1.0], $p < 0.001$) suggests extensive overlap between males and females in the genetic influences on facial attractiveness. The positive genetic correlation between female *Masculinity–femininity* and male *Masculinity–femininity* ($R_{11} = 1.0$, 95 % CI [0.00, 1.0], $p = 0.02$), implying that genes influencing facial masculinity–femininity behave identically in the two sexes, supports the intralocus sexual conflict model,

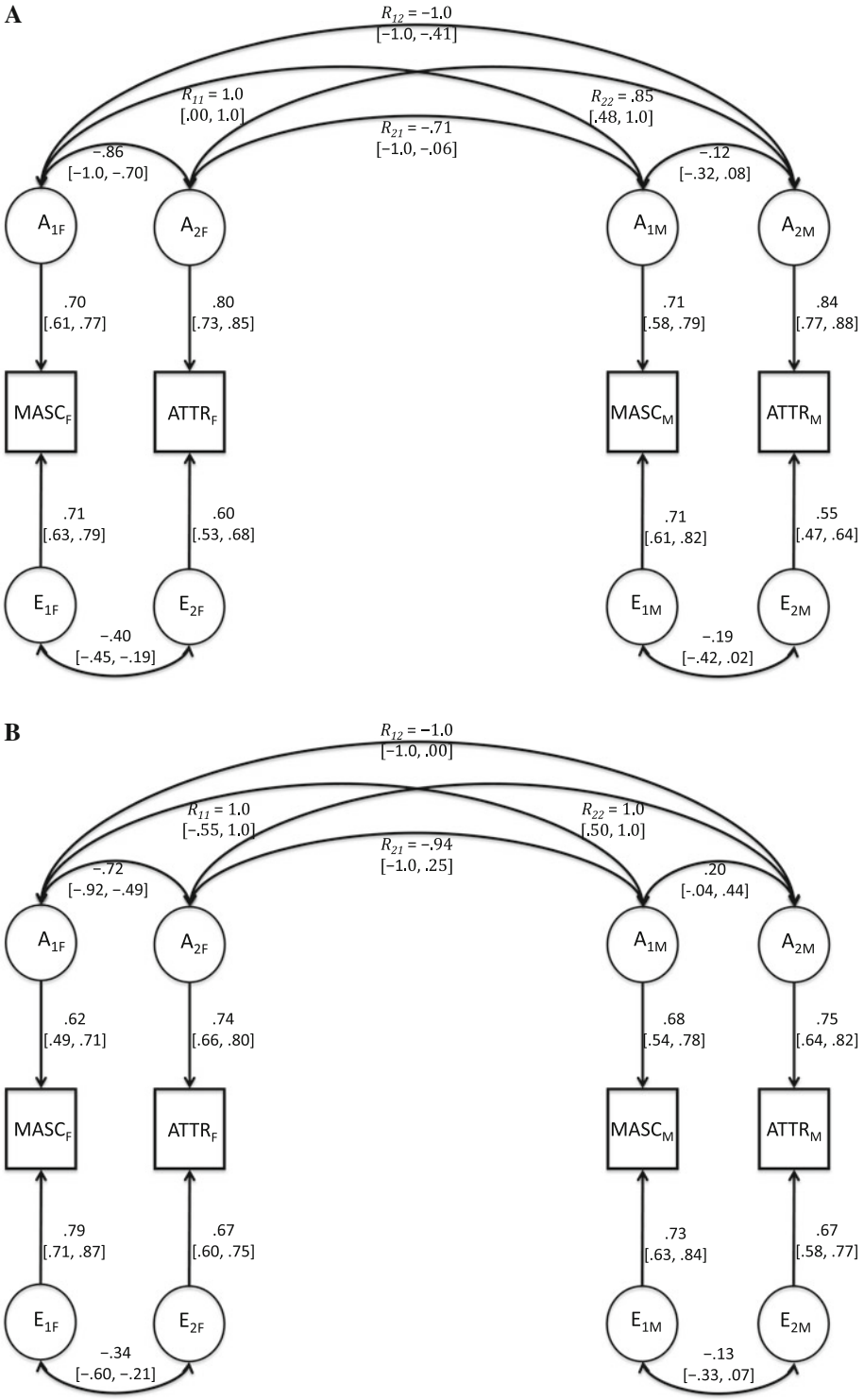

Fig. 2 Results of the bivariate model of *Attractiveness* and *Masculinity–femininity*. A_1 and A_2 are additive genetic factors of *Masculinity–femininity* and *Attractiveness*, respectively; E_1 and E_2 are non-shared environmental factors. Path coefficients on the straight arrows are the factor loadings [95 % CI] and are equivalent to the square root of the additive genetic variances (heritabilities) and environmental variances reported in the text. Genetic and environmental correlations [95 % CI] are on the curved arrows connecting two different *A* or *E* factors. *Note:* Cross-sex genetic correlations (labeled *R*) do not include adjustment for 50 % genetic identity by descent between DZOS twins. **a** Results using *Attractiveness* and *Masculinity–femininity* ratings not controlled for *Grooming*, *Acne*, *Smiling*, or BMI. **b** Results using *Attractiveness* and *Masculinity–femininity* ratings controlled for *Grooming*, *Acne*, *Smiling*, and BMI

although the confidence interval is somewhat wide (0–1.0). Likewise, the negative genetic correlation between male *Masculinity–femininity* and female *Attractiveness* ($R_{21} = -0.71$, 95 % CI [−1.0, −0.06], $p = 0.01$) is consistent with intralocus sexual conflict. The negative genetic correlation between female *Masculinity–femininity* and male *Attractiveness* ($R_{12} = -1.0$, 95 % CI [−1.0, −0.41], $p < 0.001$) matches the prediction of the sex reversal model, suggesting that the same genes that increase men's facial attractiveness decrease women's facial masculinity. Repeating this analysis using only ratings assigned by judges of opposite sex to the target faces did not produce

substantially different results—except that estimates of genetic variance were lower and estimates of environmental variance higher, due to the relative increase in measurement error resulting from using fewer judges' ratings.

We also fit the bivariate genetic model of *Attractiveness* and *Masculinity–femininity* after controlling for *Smiling*, *Grooming*, *Acne*, and BMI (Fig. 2b). Both traits showed somewhat higher heritabilities in males ($h^2_{Attr} = 0.56$, $h^2_{Masc} = 0.46$) than in females ($h^2_{Attr} = 0.55$, $h^2_{Masc} = 0.38$). Additive genetic effects that decrease *Masculinity–femininity* in females are associated with greater *Attractiveness* ($r_A = -0.72$, 95 % CI [−0.92, −0.49], $p < 0.001$). Similarly, environmental factors influencing *Masculinity–femininity* in females correlate negatively with those influencing *Attractiveness* ($r_E = -0.34$, 95 % CI [−0.60, −0.21], $p < 0.001$). In males, the additive genetic correlation between *Masculinity–femininity* and *Attractiveness* is positive but non-significant ($r_A = 0.20$, 95 % CI [−0.04, 0.44], $p = 0.06$), whereas the environmental correlation is negative but non-significant ($r_E = -0.13$, 95 % CI [−0.33, 0.07], $p = 0.1$).

The genetic correlation between male and female *Attractiveness* ($R_{22} = 1.0$, 95 % CI [0.50, 1.0], $p < 0.001$) indicates that the genes affecting facial attractiveness are completely shared between the sexes and is consistent with the prediction of the sex-limited and sex reversal models models. The negative correlation between male *Attractiveness* and female *Masculinity–femininity* ($R_{12} = -1.0$, 95 % CI [−1.0, 0.00], $p = 0.003$) is most consistent with the sex reversal model, and suggests that men's facial attractiveness is increased by the same genes that increase women's facial femininity. The other two cross-sex correlations are non-significant and have wide confidence intervals, limiting our ability to interpret their point estimates. As before, fitting the model to opposite-sex ratings yielded results very similar to those shown here.

Comparison of Competing Evolutionary Genetic Models

As a whole, the model using *Attractiveness* and *Masculinity–femininity* ratings not controlled for *Grooming*, *Acne*, *Smiling*, or BMI was most consistent with the sex-limited model ($AIC = 1{,}636.54$), followed by the intralocus sexual conflict model ($AIC = 1{,}670.46$, $\Delta AIC = 33.92$) and the sex reversal model ($AIC = 1{,}932.96$, $\Delta AIC = 296.42$). The sex-limited model ($\chi^2(5) = 46.18$, $p < 0.001$), sexual conflict model ($\chi^2(5) = 80.1$, $p < 0.001$), and sex reversal model ($\chi^2(5) = 342.61$, $p < 0.001$) all fit significantly worse than the full, unconstrained model.

Using *Attractiveness* and *Masculinity–femininity* ratings controlled for *Grooming*, *Acne*, *Smiling*, and BMI, the sex-limited model ($AIC = 947.64$) again fit better than the intralocus sexual conflict model ($AIC = 963.24$, $\Delta AIC = 15.61$) and slightly better than the sex reversal model ($AIC = 948.36$, $\Delta AIC = 0.72$). Again, all three constrained models fit significantly worse than the full, unconstrained model (sex-limited model $\chi^2(5) = 15.34$, $p = 0.009$; sex reversal: $\chi^2(5) = 16.06$, $p = 0.007$; sexual conflict model $\chi^2(5) = 30.95$, $p < 0.001$).

Discussion

We have attempted to describe the genetic architecture of facial features contributing to variation in facial attractiveness and dimorphism. According to a common interpretation of Fisher's fundamental theorem (Fisher 1930), traits related to fitness, such as sexually selected traits, should show little additive genetic variation. However, we found substantial heritability in two traits likely to be under sexual selection in humans, facial attractiveness and facial masculinity–femininity. There are several potential explanations for this; one is that there is a trade-off between the sexes in alleles that increase sexual attractiveness in males vs. those that do so in females (the intralocus conflict model). Such a trade-off can lead to standing genetic variation in sexually attractive traits because the causal alleles appear in males and females with equal probability. If such an allele's benefit to one sex is roughly balanced by its cost to the other sex, the allele may be nearly neutral with respect to fitness and may drift to appreciable frequencies, leading to standing sexually antagonistic genetic variation across multiple loci influencing the trait (Rhen 2000; Rice 1984; Rice and Chippindale 2001; but, see Turelli and Barton 2004). Our results give limited support to this model. Specifically, the positive genetic correlation between male and female masculinity–femininity and the negative genetic correlation between female attractiveness and male masculinity–femininity may lead to intralocus conflict between the sexes, which may in turn contribute to the maintenance of genetic variation in both traits.

On the other hand, the positive genetic correlation between male and female attractiveness and the negative genetic correlation between male facial attractiveness and female facial masculinity–femininity suggest that alleles influencing variation in these traits are consistently beneficial—or maladaptive—regardless of sex. One mechanism for maintaining genetic variation in the face of such directional selection is mutation-selection balance: although some of the alleles affecting these traits are conducive to both sexes' reproductive success, a constant influx of deleterious mutations is introduced each generation that maintains a degree of maladaptive variation in the population (Houle 1992).

Additionally, an important question in theories of mate choice is whether preferences are driven by the "indirect benefits" a mate may provide (i.e., the transmission of high-quality genes to offspring, in which case fitness-related traits must exhibit additive genetic variation), or by "direct benefits" (investments of resources, protection, etc., that a mate provides to oneself and one's offspring, in which case heritable variation in fitness-related traits is not required). Although our finding of substantial heritability in both phenotypes ($h^2 = 0.40$–0.61) suggests that mate choice for genetic quality might be a viable explanation for preferences for attractive and sexually dimorphic mates, there are caveats associated with this interpretation, in light of both the lack of a correlation between men's facial masculinity and their own attractiveness and the detrimental relationship between men's facial masculinity and their female relatives' facial attractiveness. Lee et al. (2013) note that male facial masculinity might benefit from being correlated with other physical (Little et al. 2007) or behavioral (Gangestad et al. 2004) markers of masculinity which are themselves the targets of female choice; or, that facial masculinity might be associated with positive outcomes in intrasexual competition (Puts 2010; Sell et al. 2009), perhaps thereby enhancing men's ability to provide directs benefits to mates and offspring.

Limitations

The primary limitation in our results is evident from Fig. 2: the cross-sex genetic correlation estimates have wide confidence intervals, limiting our ability to distinguish among the evolutionary models we were interested in testing. The wide confidence intervals are caused by the small sample of opposite-sex DZ twins or siblings in the sample, upon which these estimates are based. A twin sample supplemented with a larger number of opposite-sex siblings or twins would be helpful for testing the evolutionary models we have outlined here.

A further limitation of the present study is its use of a twin-only design, which produces parameter estimates that are biased in predictable directions (Eaves et al. 1978; Keller and Coventry, 2005). Even though estimates of shared environmental and non-additive genetic influences could be omitted from our full model without significantly reducing its fit to the data (see Supplementary Materials), these effects can cancel each other out in twin-only designs, appearing as additive genetic variation. Nevertheless, estimates of additive genetic variation in twin-only designs tend to be good estimates of overall (additive+non-additive) genetic variation (Keller et al. 2010). Estimates of additive genetic variation presented here should therefore be interpreted as estimates of overall genetic variation. However, the estimates of the genetic correlations provided here are based only on opposite-sex DZ twins because opposite-sex MZ twins do not exist, and therefore may be due entirely or in part to shared environmental influences.

Another limitation is our use of only one photograph for most participants, which must reduce the validity of our measures. A series of photographs from multiple angles, or observations made in person, would provide judges with information about three-dimensional contours of the face and reduce the stochastic effects of facial expressions captured at a single instant, thereby improving the validity of judges' ratings of facial attractiveness and dimorphism. In addition, some participants in our sample (the majority of whom were approximately 16 years of age) presumably had yet to develop their adult levels of facial masculinity or femininity. Although we controlled for chronological age, we could not control for variation in age of pubertal onset or rate of pubertal development, which are not perfectly correlated with age. The unmodeled residual variation might substantially affect the genetic architecture of facial masculinity–femininity as estimated from any given sample and could, given the large genetic component of variation in pubertal timing (Eaves et al. 2004), account for our finding some mild evidence for genetic non-additivity in male masculinity–femininity (Eaves and Silberg 2003). An older sample (18 +) might better reveal the relationship between masculinity and facial attractiveness.

Finally, we note that our target faces were rated by same- and opposite-sex judges, and we made no attempt to measure or control for possible hormonal effects on female judges' assessments. Therefore, ratings of the men in our sample do not reflect the potential increase in perceived attractiveness of highly masculine men due to women's ovulatory shift toward a greater preference for masculinity in men's faces (Roney et al. 2011). This limitation might attenuate both the within-male genetic and environmental correlations between facial attractiveness and masculinity and their genetic correlations with the same traits in females. Analyses using only ratings given by opposite-sex judges yielded very similar results to those reported here. A similar pattern of correlations was reported by Lee et al. (2013), who applied an objective, shape-based measure of facial sexual dimorphism in the BATS portion of the sample reported on here. For example, women's facial attractiveness was negatively correlated with both their own and their male co-twins' facial masculinity ($r = -0.17$ and -0.13, respectively), whereas men's facial attractiveness was not related to their level of facial masculinity ($r = 0.01$). The objective masculinity measure reflects only differences in face shape, as captured in front-facing photographs, that discriminate between male and female faces; it is unaffected by cues such as facial hair and skin tone and texture, which presumably influenced judges' subjective ratings. The fact that both measures of facial masculinity bear similar relationships to facial attractiveness suggests that,

averaging across the ovulatory cycle, women and men perceive masculinity similarly to shape-based measures; however, it is unclear how the ovulatory shift in preferences, by affecting the way attractiveness is perceived, would impact the results of the hypothesis tests we present.

Conclusion

We have introduced a modeling framework for testing three models for the evolution of sexually selected traits that might have antagonistic genetic effects between the sexes. Although we lacked power to make definitive statements about the merit of these three models when applied to our sample, our results do suggest that the genetic influences on both facial attractiveness and facial masculinity–femininity appear to be the same, and in the same direction, in males and in females. Moreover, this study provides among the first estimates of the amount of genetic variance present in facial attractiveness and sexual dimorphism in contemporary populations. Substantial heritability is found in both facial attractiveness (~ 60 %) and in facial masculinity–femininity (~ 50 %), a prerequisite for "sexy sons" and "sexy daughters" good genes hypotheses.

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