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Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women

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Abstract

We investigated aspects of self-reported health history–the number and duration of respiratory and stomach or intestinal infections and the number of uses of antibiotics over the last 3 years–in relation to measured facial masculinity, developmental instability [facial asymmetry and body fluctuating asymmetry (FA)] and facial attractiveness in a sample of 203 men and 203 women. As predicted from the hypothesis that the degree of facial masculinity is an honest signal of individual quality, men's facial masculinity correlated negatively and women's positively with respiratory disease number and duration. Stomach illness, however, was not associated significantly with facial masculinity and antibiotic use correlated significantly (negatively) only with men's facial masculinity. For both facial asymmetry and body FA, significant, positive associations were seen with the number of respiratory infections. In addition, facial asymmetry was associated positively with the number of days infected and marginally, in the same direction, with antibiotic use. Facial attractiveness showed no significant relationships with any of our health-history measures. This study provides some evidence that facial masculinity in both sexes may signal disease resistance and that developmental stability covaries positively with disease resistance. The validity of our health measures is discussed.

Keywords: Developmental instability; Facial masculinity; Health; Immunocompetence; Physical attractiveness; Sexual selection

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1. Introduction

On average, many of men's and women's facial structures differ. Men have broader and longer chins, deeper and narrower eyes due to brow ridge development, and thinner lips. Sexual dimorphism is facilitated ontogenetically by the ratio of testosterone to estrogen during adolescence (Bardin & Catterall, 1981; Enlow, 1990; see also references in Swaddle & Reierson, 2002). In men, a high ratio influences facial growth until the early 20s (Enlow, 1990). Possibly, estrogen caps the growth of the facial bones, as it does for some other bones, but enhances lip fullness, whereas testosterone, in combination with growth hormones, promotes facial bone growth (for further discussion, see Thornhill & Gangestad, 1993; Thornhill & Grammer, 1999). Sexually dimorphic facial structure hereafter is referred to as "facial masculinity."

Facial masculinity has been a focus of studies of sexual selection in humans. Men with masculine faces may tend to be socially dominant (Mazur & Booth, 1998; Mueller & Mazur, 1997; Swaddle & Reierson, 2002), and hence, men's facial masculinity may play a role in male intrasexual selection. It also affects female choice. The face that normally ovulating women (not using hormone-based contraception) who are at the fertile phase of their ovulatory cycle find most attractive is more masculine than the face found most attractive by women during other phases of the cycle (Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999). One report found this to be especially true when these women are pair-bonded and rating faces for short-term sexual relationships (Penton-Voak et al., 1999). Female preference for men's facial masculinity primarily at peak fertility in the ovulatory cycle, the absence of the preference in women not ovulating due to hormonal contraception, and an enhanced preference in pair-bonded women seeking short-term sexual relationships suggest that the preference is an adaptation that functions to obtain for the offspring a sire of superior genetic quality (Johnston et al., 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999).

That men's facial masculinity may be involved in intrasexual competition and intersexual selection suggests that facial masculinity honestly signals individual phenotypic and related genetic quality (Grammer & Thornhill, 1994; Mueller & Mazur, 1997; Thornhill & Gangestad, 1993). Honest signaling here might work through an immunocompetence handicap mechanism (Folstad & Karter, 1992): Testosterone compromises the immune system's ability to combat disease; hence, only men with superior immune systems can afford high testosterone levels and associated masculinization. Alternatively, high masculinity may signal quality because testosterone allocates energy to functions involved in male–male competition (e.g., muscle growth) that men lacking key competitive abilities do not benefit from to the same extent (McDade, 2005; Thornhill & Gangestad, 1999a, 1999b). In any case, honest signaling through facial masculinization may be partly mediated socially through ongoing male–male competitive testing of quality. (See Roberts, Buchanan, & Evans, 2004, for a review of alternative honest-signal hypotheses and Zahavi & Zahavi, 1997, for further discussion of honest signal evolution).

Fitness is an individual's design for reproductive success, not merely reproductive success (Williams, 1966). Reproductive success arises, in part, through stochastic processes rather

than the design of an individual's traits for solving problems affecting differential reproductive success of individuals. The truth in an individual's honest signal, that is, the phenotypic and genetic quality that the signal depicts, corresponds to the individual's fitness. The evidence reviewed above suggests that men's masculinity contains information about their breeding values for producing sons who will be successful in competition for mates at the fertile phase of their cycle.

But does men's masculinity honestly signal breeding value for fitness components other than mating success? Relationships between sexually selected traits and fitness components other than mating success are of major theoretical interest. The Darwinian–Fisherian theory of sexual selection's operation proposes that sexual selection favors traits that enhance the mating success of offspring solely through their increased sexual attractiveness. In this case, sexual selection results in increased frequencies of alleles that cause, through the ontogenetic process, the production of offspring that possess enhanced reproductive value, but only in terms of sexual attractiveness and, hence, mating success. Other theories of sexual selection propose that sexual selection favors sexual attractiveness because it is defined by its covariation with other fitness components (Andersson, 1994; Kokko, Brooks, McNamara, & Houston, 2002). In terms of men's masculinity, the question is whether masculinity affects mating success alone or is associated with mating success as well as additional fitness components.

As Kokko et al. (2002) point out, the Darwinian–Fisherian model need not (indeed, should not) imply that, when male sexually selected features covary only with attractiveness, they are not indicators of individual phenotypic and genetic quality. Quality reflects an organism's capacity to generate fitness-enhancing outcomes. Although, under natural conditions, quality should be associated with fitness and generally reproductive success, it need not covary positively with all fitness components, including longevity and health. In some circumstances, selection can favor such extreme investment in sexually selected indicators by high-quality males that they actually have higher rates of mortality and morbidity than do lower quality males (see also Getty, 2002). Empirically, across many species, more ornamented males, compared with less ornamented males, have reduced parasitism and stronger immunity (Møller, Christie, & Lux, 1999) and increased adult survival (Jennions, Møller, & Petrie, 2001), although these patterns are by no means universal across studied species. In a species such as humans, we should probably not expect sexual selection to be sufficiently strong to drive covariation between sexually selected phenotypic indicators of quality and fitness components other than mating success to be negative (although these associations may be weak).

Studies involving multiple approaches have examined the covariation of men's facial masculinity and fitness components other than mating success. One approach examines the associations between rated masculinity of men's facial pictures and rated health of the same faces or actual health history of the men based on medical records. Rhodes, Chan, Zebrowitz, and Simmons (2003) reported that rated masculinity in adolescent male faces correlates positively with rated and actual health (see also Zebrowitz & Rhodes, 2004). Another approach examines health associations using measured facial masculinity based on facial traits showing sexual dimorphism. Gangestad and Thornhill (2003) reported that measured facial masculinity correlates positively with developmental stability, a component of developmental health. Developmental instability was estimated by measuring body (as fluctuating asymmetry, FA)

and facial asymmetry, both of which negatively correlated with men's facial masculinity. Men's facial asymmetry also showed a curvilinear association: Highly feminine and highly masculine male faces were more asymmetric. Gangestad and Thornhill found no evidence that women's facial masculinity linearly relates to body FA but did find a significant curvilinear relationship similar to that found in men. By contrast, Koehler, Simmons, Rhodes, and Peters (2004) found no evidence for associations between body FA or face symmetry and men's measured facial masculinity. In women, they found little evidence that facial asymmetry is associated with masculinity, although body FA positively predicted facial masculinity.

In the current study, we explored further the associations between facial masculinity and health, specifically, associations with incidence of diseases that we assume are parasitic. Ancestrally, individuals' defense against parasitic infections may have been an important fitness component. Through questionnaire, we asked university students to report the number and duration of respiratory and stomach or intestinal influenza infections and antibiotic use over the last 3 years. We examined associations with facial masculinity, measures of developmental instability, and facial attractiveness.

1.1. Facial masculinity

We predicted that men's facial masculinity covaries negatively with these health measures and that women's facial masculinity covaries positively with them. Positive relationships in women are predicted because high masculinity in women corresponds to low estrogen levels. It has been proposed that femininity (facial and bodily estrogenization) signals individual quality in women (Singh, 1993, 1995; Thornhill & Gangestad, 1993; Thornhill & Grammer, 1999).

1.2. Developmental stability

We predicted the negative associations between health measures and body and facial FA. In many species, including humans, developmental stability appears to be associated positively with health (Møller & Swaddle, 1997; Thornhill & Møller, 1997; Waynforth, 1998). Jones et al. (2001) and Rhodes et al. (2001) found that symmetric faces are rated as healthier than are asymmetric faces, but no consistent relationship between facial symmetry and actual health based on health records.

1.3. Facial attractiveness

We predicted a positive association between health and female facial attractiveness but offered no prediction for men's attractiveness. Although some evidence suggests that facial attractiveness predicts health, results are mixed. Meta-analyses found a positive relationship between facial attractiveness and mental (Feingold, 1992; Langlois et al., 2000) and physical health (Langlois et al., 2000; but see Kalick, Zebrowitz, Langlois, & Johnson, 1998). Robust associations between women's facial attractiveness and facial femininity (e.g., Penton-Voak, Jacobson, & Trivers, 2004) suggest associations between the former and health measures. Men's attractiveness, however, does not consistently covary with masculinity. Penton-Voak

et al. (2004) found a greater female preference for masculinity in men's faces in Jamaica than in the U.K. They argue that male facial attractiveness reflects assessment of paternal investment qualities as well as genetic quality. In societies in which women place particular importance on investment qualities (e.g., U.K.), feminine male faces may be more attractive than masculine ones. Where women find male facial masculinity most attractive, they presumably place greater value on genetic quality.

2. Methods

The data are derived from our larger study of 406 students (203 men and 203 women) at The University of New Mexico on developmental instability and romantic relationships (see Gangestad & Thornhill, 1997, for a fuller description of the sample). Of these, 295 participants provided the results reported by Gangestad and Thornhill (2003).

2.1. Facial masculinity

In the current study, we used the same facial masculinity measures for the participants as in the Gangestad and Thornhill (2003) study. For details, see Gangestad and Thornhill. In short, straight-on facial photographs were used to identify sexually dimorphic facial traits. Five such traits were identified (chin length, jaw width, lip width, eye width, and eye height) and assessed using principal axis factor analysis. These five measures were factor analyzed; two factors, largely reflecting jaw development and brow ridge development, respectively, emerged. A discriminant function analysis using these two factors to discriminate the two sexes yielded a composite that could accurately classify 75% of the faces as male or female. Discriminate function scores were used to measure facial masculinity. To reduce variation due to ethnic variation, we measured facial masculinity only for participants who claimed that their ethnicity was Caucasian or Hispanic (see Gangestad & Thornhill, 2003). Other researchers have used similar approaches for measuring facial masculinity (Koehler et al., 2004; Penton-Voak et al., 2001; Scheib, Gangestad, & Thornhill, 1999).

2.2. Bodily FA and facial asymmetry

Our procedure for measuring bodily FA and facial asymmetry of the participants is described in detail in Gangestad and Thornhill (2003). We use methods of compositing asymmetry within individuals that are supported by a considerable literature indicating that our composites capture individual variation related to the human sexual selection system (e.g., Gangestad & Thornhill, 1997; Thornhill & Gangestad, 1999a, 1999b). In short, for body FA, asymmetry was measured in multiple traits that show developmental instability. Relative FA (absolute asymmetry divided by the average trait size) was summed across the traits to create a composite FA index for each participant. For facial asymmetry, we followed procedures described fully in Scheib et al. (1999) and modified from Grammer and Thornhill (1994) to allow the calculation of both horizontal and vertical components of facial

asymmetry. Horizontal components of asymmetry are differences in the consistency of the midpoint of multiple markers at varying heights of the face (e.g., breadth at the eyes, the bottom of the nose, the lips). Asymmetry exists when the midpoints do not fall on a single vertical line. Vertical components of asymmetry also involve bilateral (left vs. right) asymmetries, but there are differences in the height of features on the right and left sides (e.g., differences in height of the most prominent point of the cheekbones). Both of these components were summed into a composite measure of facial asymmetry. Compositing of traits, both bodily and facial, to estimate developmental instability is important, as individual trait asymmetries covary very weakly with instability (Gangestad & Thornhill, 1999).

2.3. Health measures

Research participants completed a questionnaire about the socioeconomic status (SES) of their home of upbringing, sexual history, a brief health history, and other personal information. The brief medical report asked: How many times and days in the past 3 years have you had a respiratory infection (colds, flu) or stomach or intestinal flu? They were asked to indicate the number of episodes of each type of illness and the total duration of each type of illness in the past 3 years. In addition, they reported the total number of infections for which they took antibiotics in the past 3 years. We assume that the health measures used assess individual differences in immunocompetence, that is, the ability to defend against parasitic infections. To eliminate extreme outliers, the number of infections within each category was truncated to 10 (affecting the values for three males and four females for respiratory infections, and one male for stomach infections). The number of days ill for each of the infections was truncated to 100 days (affecting three males and four females for respiratory infections and one male for stomach infections). The number of times that antibiotics were used was truncated to 10 (affecting four males and three females). In total, 1% of all observations were affected by truncation. To reduce extreme skewness, days ill were log-transformed.

2.4. Attractiveness ratings

Head-on photographs of faces were rated for physical attractiveness on a scale of 1–10 (1=*very unattractive*, 10=*very attractive*). Ratings of each picture were summed across 8 or 10 male and female raters. Rater number varied across the first and second halves of data collection. Cronbach alphas were .84 for both phases. For a fuller discussion of our procedures for assessing participants' attractiveness, see Gangestad and Thornhill (1997).

3. Results

Analyses were performed using GLM (SPSS-PC 12.0). The results for associations between developmental instability and masculinity in the men and women are reported in Gangestad and Thornhill (2003). The current paper focuses on facial masculinity and developmental stability in relation to the health measures.

Table 1
Descriptive statistics of health measures (pertaining to the last 3 years) by sex of research participant

	Men		Women	
Variable	Mean	S.D.	Mean	S.D.
Respiratory infections				
Number	1.80	2.41	2.60	2.93
Days infected	8.33	16.96	10.52	15.71
Stomach and intestinal infections				
Number	1.11	1.92	1.30	1.50
Days infected	3.68	9.97	3.57	5.30
Number of times antibiotics used	1.68	2.31	2.59	2.59

n=198–202 men and 196–199 women.

For each predictor–facial masculinity, body FA, facial FA, and physical attractiveness–three sets of initial GLM analyses were performed. First, we performed analyses on number of infections. Respiratory infections and stomach/intestinal infections were treated as two levels of a repeated factor (infection type). Overall effects of predictors reflect their ability to predict the sum of respiratory and stomach infections, but we were also able to assess whether predictors differentially relate to these two types of illness. Second, we performed analyses on logged number of days with infection, again treating respiratory and stomach/intestinal infections as two levels of a repeated factor. Third, we ran analyses on times that antibiotics were used. Follow-up analyses examined the effects on each of the health measures alone, as well as within-sex correlations between predictors and health measures.

Within each of these sets, we performed two different analyses. First, we simply examined each health measure as a function of the predictor, sex, and the interaction between the predictor and sex. Second, we controlled for a number of potential confounding variables that are discussed widely in the literature as covariates of health: age, height, weight, and SES. For a priori predictions, we used directed tests (Rice & Gaines, 1994), where we allocated .04 of the overall alpha to a predicted tail and .01 to tail contrary to prediction. Specifically, we used directed tests to assess the interaction between facial masculinity and sex, and the main effects of body FA, facial FA, and physical attractiveness.[1]

Table 1 provides descriptive data for all health measures. On average, participants reported two to three respiratory infections and one to two stomach or intestinal infections, accounting for approximately 9–10 and 3–4 days sick, respectively. Whereas men took antibiotics

[1] The personality trait of negative affectivity has been found to correlate positively with reported illness, but not actual illness; hence, it acts as a nuisance factor in health research (Watson & Pennebaker, 1989). Our questionnaire included measures that allowed an assessment of negative affectivity. Approximately one half of the sample rated themselves on three traits used to tap the dimension of stress reaction on the multidimensional personality questionnaire (MPQ; Tellegen, 1982). The remaining participants rated themselves and their relationship partners (members of the opposite sex in the sample) on 100 traits of the California Adult Q-Set (CAQ; Block, 1961). Factor analysis of the CAQ reveals a set of items that tap negative affectivity (Lanning, 1994). For this portion of the sample, we averaged the self-rating and partner-rated subscales for this trait. In fact, negative affectivity did not correlate with any of the features that we examined (facial masculinity, body FA, facial FA, and facial attractiveness) within either sex (all r<.07, ns). Because our sample did not complete the same measure of negative affectivity and because negative affectivity is not confounded with the features of interest, we did not control for it in our analyses.

Table 2
Results of GLM analyses with sexes combined: facial masculinity and developmental stability in relation to health in the last 3 years

	Facial masculinity	Facial Masculinity×Sex	Facial Masculinity× Infection Type	Facial Masculinity× Sex×Infection Type
Total infections	−.03	**−.13** (.010)	−.05	**−.18** (.002)
Days infected	−.03	**−.12** (.025)	−.04	**−.15** (.010)
Antibiotic use	−.08	−.07	–	–
	Body FA	Body FA×Sex	Body FA× Infection type	Body FA×sex× infection type
Total infections	**.10** (.025)	.04	.04	.00
Days infected	.00	.00	.00	.07
Antibiotic use	.00	.03	–	–
	Facial FA	Facial FA×Sex	Facial FA× Infection Type	Facial FA×Sex× Infection Type
Total infections	.07	.00	**.12** (.038)	.00
Days infected	*.09* (.073)	.05	**.13** (.025)	.05
Antibiotic use	*.10* (.057)	.00	–	–
	Facial attractiveness	Facial Attractiveness×Sex	Facial Attractiveness× Infection Type	Facial Attractiveness× Sex×Infection Type
Total infections	.03	.03	.00	.07
Days infected	.03	.03	.03	.03
Antibiotic use	−.03	.00	–	–

Values reported are effect sizes (β). Effect sizes controlled for age, height, weight, and SES are very similar to the reported values. Bold values are significant at $p<.05$. Italicized values are significant at $p<.10$. p values are in parentheses for all effects, with $p<.10$.
SES, socioeconomic status of upbringing. FA, developmental instability or fluctuating asymmetry.
A negative Trait×Sex effect indicates that the trait has a more negative effect for males, and vice versa. A negative Trait×Sex×Infection Type interaction indicates that the Trait×Sex interaction is more negative for respiratory infections, and vice versa. A positive Trait×Infection Type interaction indicates that the trait has a more positive effect for respiratory infections, and vice versa.

1.68 times, on average, women took them 2.59 times. Overall, these data suggest that women are sicker than men are. We assume that health reports are not biased within each sex in a manner that would confound our interpretations.

Tables 2 and 3 summarize the results of the GLM analyses. Table 4 reports within-sex correlations.

3.1. Facial masculinity

As predicted, facial masculinity interacted with sex to predict number of infections and days with infection [$F(1,290)=4.62$, $p<.02$, and $F(1,282)=4.26$, $p<.03$, respectively]. Unexpectedly, however, these two way interactions were moderated by the kind of infection

Table 3
Results of GLM analyses with sexes combined: individual infections in the last 3 years in relation to facial masculinity, body and facial asymmetry, and facial attractiveness

	Effect			
Health measure	Facial Masculinity×Sex	Body FA	Facial FA	Facial attractiveness
Respiratory infections				
Number	**−.19** (.001)	**.09** (.044)	**.11** (.034)	.00
Days infected	**−.17** (.002)	.00	**.14** (.011)	.00
Stomach and intestinal infections				
Number	.04	.07	−.04	.03
Days infected	.02	−.03	−.03	.04

Values reported are effect sizes (β). A negative Facial Masculinity×Sex effect indicates that the association with facial masculinity is more negative for males than for females. Bold values are significant at $p<.05$. p values are in parentheses for all significant effects. All significant values here were also significant when age, height, weight, and SES were controlled, with the exception of the effect of facial FA on number of respiratory infections, where $p=.051$.

[respiratory vs. stomach/intestinal; $F(1,290)=10.20$, $p<.005$, and $F(1,282)=6.70$, $p<.01$, respectively]. Follow-up analyses revealed sex by facial masculinity effects for respiratory infections only (see Table 3). These relations held significant in subsequent analyses, controlling for potential confounding variables. As seen in Table 4, male facial masculinity significantly and negatively predicted the number of respiratory infections, days with respiratory infection, and antibiotic use. Female facial masculinity significantly and positively predicted the number of respiratory infections and days with respiratory infection.

3.2. Body FA

As predicted, body FA significantly and positively predicted the number of infections [$F(1,387)=4.25$, $p<.03$]. No effect was observed, however, on days of infection

Table 4
Correlations by sex of each health measure (pertaining to last 3 years) with facial masculinity, body and facial asymmetry, and facial attractiveness

	Facial masculinity		Body FA		Facial FA		Facial attractiveness	
Health measure	M	F	M	F	M	F	M	F
Respiratory infections								
Number	**−.19**	**.18**	.07	*.11*	**.16**	.08	.08	−.05
Days infected	**−.16**	**.19**	.06	−.04	*.15*	*.13*	.06	−.05
Stomach and intestinal infections								
Number	.03	−.05	.01	**.14**	−.03	−.05	.01	.07
Days infected	.02	−.03	−.02	.09	−.14	.06	.05	.04
Antibiotic use	**−.21**	.00	.05	−.01	*.13*	.08	.00	−.05

Correlations in bold are significant at $p<.05$; for correlations in italics, $p<.10$. All tests are directed tests (Rice & Gaines, 1994).

[$F(1,377)=0.12$, ns]. Unlike the associations with facial masculinity, the association between FA and number of infections was not moderated by the type of infection [$F(1,387)=0.76$, ns]. The association with the number of infections held when potential confounding variables were controlled [$F(1,376)=4.29$, $p<.03$].

3.3. Facial FA

Facial FA did not significantly predict the total number of infections [$F(1,295)=1.50$, $p=.139$] and predicted total days infected at only a marginal level of significance [$F(1,286)=2.47$, $p=.073$]. As with facial masculinity, however, the effect of facial FA was significantly moderated by the type of infection [$F(1,295)=4.35$, $p<.04$, and $F(1,286)=5.09$, $p<.03$, for infections and days infected, respectively]. Follow-up analyses yielded significant associations of facial FA with respiratory infections but not stomach/intestinal infections. Facial FA also predicted, at a marginal level of significance, number of times antibiotics were used [$F(1,295)=2.85$, $p=.057$]. The association between facial FA and days infected with respiratory infections held when potential confounding variables were controlled, although the association with the number of respiratory infections was marginally significant when these variables were controlled.[2]

3.4. Facial attractiveness

We found no associations between facial attractiveness and any of the health measures: for total infections, $F(1,337)=0.69$, ns; for days infected, $F(1,330)=0.82$, ns; for antibiotic use, $F(1,368)=0.25$, ns.

3.5. Other effects

Relative to men, women reported a greater number of infections [$F(1,376)=5.25$, $p<.03$], a greater number of days infected, [$F(1,366)=5.66$, $p<.02$], and greater antibiotic use [$F(1,376)=6.62$, $p<.02$]. SES interacted with the type of infection to predict days infected [$F(1,366)=6.91$, $p<.01$]. Participants from homes of higher SES reported more days of respiratory infections [$t(366)=2.49$, $p<.01$] but not more stomach/intestinal infections [$t(366)=-.89$, ns]. No other control variables had consistent effects across analyses.

[2] We also performed separate analyses on horizontal and vertical components of facial FA (see Methods). The effects of the total measure are driven by variation in horizontal components. In fact, horizontal components alone have stronger effects than the total measure does; they significantly predict total infections, days infected, and antibiotic use. FA×Infection Type interaction effects are also significant with horizontal components. Vertical components did not significantly predict any infection. The variation across individuals is much greater in horizontal components than in vertical components, perhaps leading to these differences. Full results are available from the authors.

3.6. Predictors of facial attractiveness

In this sample, male facial attractiveness did not significantly covary with facial masculinity (r=−.09), body FA (r=.00), or facial FA (r=−.05). Female facial attractiveness was significantly and negatively predicted by facial masculinity (r=−.30, p<.001) and facial FA (r=−.19, p<.02), but not body FA (r=−.03). (These null results for facial attractiveness and body FA were previously reported by Gangestad & Thornhill, 1997).

4. Discussion

The current research asked young men and women to self-report their respiratory and intestinal/stomach infections, total duration of each type of infection, and antibiotic use over the last 3 years. Based on theory and data concerning the evolution of sexually selected traits, we predicted that men's reports would negatively covary with facial masculinity, and women's reports would show positive relationships. Overall, the results supported the prediction: There was a significant interaction between sex and facial masculinity in predicting both overall number of infections and number of days infected. This overall effect, however, was moderated by the type of infection. Stomach ailments and days ill from such ailments showed no significant relationship with facial masculinity. By contrast, our predictions were supported with respect to respiratory infections. These findings are not due to the confounding effects of age, height, weight, or SES. Antibiotic use covaried significantly (and negatively) with male but not female facial masculinity.

Thus, the research we report in this paper provides evidence that male masculinity is a marker of resistance to infection, although, more specifically in this population, respiratory diseases. Similarly, women's facial femininity may signal honestly resistance to respiratory pathogens. We assume that our health measures target individual differences in immunocompetence. It is reasonable to suggest that immunocompetence is related positively to fitness.

Our results also provide additional, albeit weak, evidence that developmental stability predicts infection susceptibility. The total number of infections related negatively to body FA, and the number of and days infected with respiratory infections were associated with facial FA. The overall pattern, despite its mixed quality, suggests associations between developmental stability and resistance to infection. Additional research is needed.

We found no evidence that facial attractiveness in either sex predicts our health-history measures. Overall, studies of the relationship between facial attractiveness and health have generated a mixture of positive and negative results (see Introduction). We predicted a positive relationship between attractiveness and health for women, but no prediction was made for men, as men's facial attractiveness varies across societies and raters within a society, depending upon various circumstances (see Penton-Voak et al., 2004, and the Introduction).

We chose to study respiratory and stomach infections because they are common and, hence, would occur across many individuals in our sample of participants. In contrast, some other diseases that are relevant to examining immunocompetence are uncommon and, thus, would require very large samples for study. Stomach ailments may not be as valid as respiratory

infections in assessing immunocompetence, as they may commonly stem from causes other than infectious agents (e.g., dietary change, travel, and other lifestyle events). The same issue, however, can be raised with respiratory illnesses. If participants confuse respiratory infections with allergies, their reports may not address immunocompetence. We reasoned, too, that antibiotic use would be memorable and, hence, allow the assessment of bacterial disease resistance. The validity of recall of our health measures, however, is unknown.

Understanding the relationship, if any, between masculinity or developmental stability and health might be advanced most effectively by direct assessment of immune system activation such as circulating levels of leucocytes and immunoglobulins. Such studies could be informed by recent research on nonhuman animals that has examined the relationship between sexually selected male signals and immunocompetence. For example, in certain birds, males with relatively large signals (e.g., larger tails) show lower levels of leucocytes and immunoglobulins than do less decorated males. This pattern indicates that males with exaggerated signals generally invest in defense against parasites less so than those with less exaggerated signals (Møller et al., 1999). A study design that sampled people who were not suffering currently from an infectious disease would be useful. Male masculinity would be expected to relate negatively, and female masculinity relate positively, to the two immune system parameters. Developmental stability should correlate negatively with both measures in both sexes. The strongest tests of these predictions for humans would presumably involve a study of people living in a setting with limited modern health care. Along these lines, Hurtado, Hurtado, Hill, and Gangestad (2004) found a strong, negative association between immunoglobulin E and developmental stability in the Ache, a Paraguayan Amerindian group heavily exposed to macroparasites (notably, ascarid worms).

Associations between health and facial features in adolescence and young adulthood need not imply similar associations at other life stages. Individuals of differing condition may have different life history trajectories. Men in better condition may trade future health for current mating effort. (Indeed, testosterone has detrimental effects on longevity, as revealed by the relatively long lifespan of castrated men; e.g., Daly & Wilson, 1983). Future research may also investigate how sexually selected features covary with immune activation across the life course.

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