

Invited Review

Do men's faces really signal heritable immunocompetence?

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In the literature on human mate choice, masculine facial morphology is often proposed to be an intersexual signal of heritable immunocompetence, and hence an important component of men's attractiveness. This hypothesis has received considerable research attention, and is increasingly treated as plausible and well supported. In this article, we propose that the strength of the evidence for the immunocompetence hypothesis is somewhat overstated, and that a number of difficulties have been under-acknowledged. Such difficulties include (1) the tentative nature of the evidence regarding masculinity and disease in humans, (2) the complex and uncertain picture emerging from the animal literature on sexual ornaments and immunity, (3) the absence of consistent, cross-cultural support for the predictions of the immunocompetence hypothesis regarding preferences for masculinized stimuli, and (4) evidence that facial masculinity contributes very little, if anything, to overall attractiveness in real men. Furthermore, alternative explanations for patterns of preferences, in particular the proposal that masculinity is primarily an intrasexual signal, have been neglected. We suggest that immunocompetence perspectives on masculinity, whilst appealing in many ways, should still be regarded as speculative, and that other perspectives—and other traits—should be the subject of greater attention for researchers studying human mate preferences. *Key words:* attractiveness, competition, faces, female choice, humans, immunocompetence, males, masculinity, mate preferences, testosterone. [*Behav Ecol*]

WHAT DO HUMANS FIND ATTRACTIVE AND WHY?

Physical attractiveness influences numerous life outcomes and social experiences, and has been the subject of extensive research in the human behavioral sciences (e.g., Hamermesh and Biddle 1994; Mazzella and Feingold 1994; Langlois et al. 2000; Andreoni and Petrie 2005). For researchers adopting an evolutionary perspective on human behavior, interest in attractiveness is motivated by a theoretical expectation that attractiveness should be related to mate value and reproductive success (e.g., Symons 1995; Buss 2000; Miller 2001; Rhodes 2006). This expectation has received empirical support in a number of human populations (e.g., Walster et al. 1966; Buss 1989; Langlois et al. 2000; Rhodes et al. 2005; Li and Kenrick 2006; Jokela 2009; also see Pawlowski et al. 2008).

Attractiveness research has concentrated on (1) documenting preferences for various physical traits and (2) attempting to explain the adaptive significance of the preferences. The first part of this endeavor is, in theory, a relatively straightforward research problem: studying preferences in humans, who are adept at both following instructions and interpreting pictorial stimuli, is in many ways easier than studying preferences in other species. The second issue—the nature of the benefits accrued through preferring one potential mate over another—is substantially more difficult to address. Experimental manipulations of human mate choice are difficult for both ethical and practical reasons (Kościński 2009), and when assessing the potential biological benefits of

choosing one potential mate over another, researchers must therefore rely on other methods. These include the observation of naturally occurring correlational data from human partnerships, and the “reverse engineering” of patterns in preferences to infer adaptive “special design” in behavior (e.g., Dawkins 1986; Dennett 1995; Gangestad and Simpson 2000; Andrews et al. 2002). These techniques can provide a useful insight into the likely nature of mate choice adaptations in our own species, yet neither strategy is ideal and evolutionary psychologists have been accused of an over eagerness, in practice, to accept specific adaptationist hypotheses on the basis of this data alone (Gould 1997; Harris 2011).

THE IMMUNOCOMPETENCE HYPOTHESIS OF MALE FACIAL MASCULINITY

Of the various potential benefits proposed to have been associated with attractiveness, health (broadly defined) has received the most research attention, inspired by work in other species (Gangestad and Buss 1993; Barber 1995; Thornhill and Gangestad 1999; Rhodes et al. 2003; Zebrowitz and Rhodes 2004; Weeden and Sabini 2005; Stephen et al. 2009). While a number of components of health may contribute to mate value (Adamo and Spiteri 2009), heritable immunocompetence, or endogenous, genetically-mediated resistance to pathogens, has been the subject of particular interest (Gangestad and Buss 1993; Perrett et al. 1998; Thornhill and Gangestad 1999; Lie et al. 2008). A number of traits, including odor, voice pitch, body size, and various facial traits are hypothesized to signal immunocompetence in humans (Grammer and Thornhill 1994; Perrett et al. 1998; Penton-Voak et al. 1999; Fink and Penton-Voak 2002;

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Rhodes et al. 2003; Feinberg et al. 2005; Grammer et al. 2005; Brown et al. 2008; Stephen et al. 2009).

Here, we review the immunocompetence hypothesis with respect to masculine facial morphology in men, as face shape has received a large amount of research attention (Kościński 2009). In this literature, high masculinity is generally defined as exaggerated sex-typical features (i.e., men with traits at the extreme of the distribution of a sexually dimorphic trait are considered more masculine than men with average trait size). Masculine face-shape traits include wide cheekbones, mandibles and chins, prominent brow ridges, long lower faces, and thin lips (Hunter and Garn 1972; Tanner 1990). While a number of nonshape cues (color, hairiness, and movement; Frost 1994; Morrison et al. 2007; Stephen et al. 2009) may also vary between the sexes, shape cues have been the focus of the majority of research regarding masculinity and immunocompetence, and these latter traits are widely proposed to be associated with each other (e.g., Barber 1995; Perrett et al. 1998; Penton-Voak et al. 1999, 2001, 2003, 2004; Johnston et al. 2001; Little et al. 2002, 2008a; Swaddle and Reiersen 2002; Koehler et al. 2003; Rhodes et al. 2003; Cornwell et al. 2004; Scarbrough and Johnston 2005; Waynforth et al. 2005; DeBruine et al. 2006; Kruger et al. 2006; Rhodes 2006; Saxton et al. 2006; Thornhill and Gangestad 2006; Rhodes et al. 2007; Scott et al. 2008; Boothroyd et al. 2009; Moore et al. 2009; Smith et al. 2009; Vukovic et al. 2009). While a general link between phenotypic health and attractiveness seems likely (perhaps particularly in ancestral environments), the central role of heritable immunocompetence signaling properties of masculinity have increasingly been treated as established, rather than hypothetical. Research papers and textbooks on evolutionary psychology present the immunocompetence hypothesis of masculinity preferences as plausible, well established, or even as factual despite the absence of direct tests (Rossano 2003; Bressan and Stranieri 2008; Cartwright 2008; Little et al. 2010; DeBruine et al. 2010a, 2010b).

The key assumptions of the immunocompetence hypothesis in this context are that testosterone is associated with (1) facial masculinity and (2) genetically heritable immunocompetence. These assumptions lead to clear predictions regarding female preferences for masculinity. What, however, is the evidence for these assumptions, and does empirical data support the predictions of the immunocompetence hypothesis?

DOES TESTOSTERONE INFLUENCE FACIAL MASCULINITY?

There is a direct relationship between testosterone and male traits in many species (see Roberts et al. 2004; Hau 2007; McGlothlin et al. 2008), and similarly, a causal relationship between testosterone and masculinity in men has received reasonable support. Sex differences in the production of testosterone are almost certainly causal in the development of many sexually dimorphic traits in humans (Bardin and Catterall 1981; Tanner 1990; Enlow and Hans 1996; Bulygina et al. 2006). For men, both facial masculinity and circulating testosterone increase with maturity in adolescence (Enlow and Hans 1996) and the exogenous administration of testosterone during this time may influence the growth of certain dimorphic traits, such as mandible length and face height (Verdonck et al. 1999).

In addition, a number of authors have reported evidence of a relationship between facial masculinity and direct measures of circulating testosterone in adulthood (Penton-Voak and Chen 2004; Roney et al. 2006; Pound et al. 2009). While results are not entirely consistent (Neave et al. 2003;

Honekopp et al. 2007; Peters et al. 2008), the one study to have employed an objective measure of masculinity (i.e., quantifying physical differences in face shape) as opposed to subjective masculinity “scores” (i.e., derived from participant ratings) did report a positive relationship with testosterone (Pound et al. 2009). In light of these findings, the assumption that masculinity is a correlate of exposure to testosterone appears to be reasonable.

IS TESTOSTERONE RELATED TO HERITABLE IMMUNOCOMPETENCE?

The immunocompetence hypothesis proposes that masculinity is a reliable signal of disease resistance, and is derived from a handicap model of sexual signaling (Zahavi 1975; Hamilton and Zuk 1982). Research suggests that steroids such as testosterone may be immune stressors (Grossman 1985; Angele et al. 2000; Messingham et al. 2001; cf. Roberts et al. 2004). Such findings have led to the hypothesis that only immunocompetent males should be able to “afford” high levels of testosterone, and hence that exaggerated sex-typical traits (which are proposed to be mediated by testosterone) should be an honest signal of heritable immunity to local pathogens (see Folstad and Karter 1992; Muehlenbein and Bribiescas 2005), and hence a “good genes” indicator.

The direct evidence for a link between facial masculinity and phenotypic health in humans is tentative. Rhodes et al. (2003) found evidence of a weak association between apparent masculinity and adolescent health, but used subjective ratings of masculinity, which are not equivalent to anatomical measures (a point we will return to later). Thornhill and Gangestad (2006) found a negative correlation between masculinity and self-reported past respiratory disease, but no relationship between masculinity and intestinal illness. They did use objective measures of masculinity, but their findings were based on self-reported health, which may be confounded with personality and social status variables, and is of questionable validity (Newell et al. 1999; Oshio and Kobayashi 2010). For example, evidence suggests that men are less likely to admit to illness than women (Young et al. 2010)—an intra-sexual analog would suggest that highly masculine men may be less likely to report illness than less masculine men.

Moreover, the proposal of a general, positive association between masculinity and good health is somewhat difficult to reconcile with the evidence regarding human immunity and testosterone. This evidence is mixed and often indicates a null or negative association between the two (see Muehlenbein and Bribiescas 2005; van Anders 2010).

Researchers interested in good genes sexual selection in humans rely heavily on the animal literature for empirical support and theoretical inspiration. However, there is an increasingly complex and uncertain picture emerging from research into immunity in nonhuman species with a growing interest in viewing immunity as a compound trait, consisting of multiple, often unrelated (or even negatively correlated) subcomponents (Adamo 2004; Loker et al. 2004; Lee 2006; Matson et al. 2006; Lawniczak et al. 2007). The nature of the relationship and the direction of causality between immune response and testosterone production is a subject of ongoing debate (Braude et al. 1999; Boonekamp et al. 2008) as is the issue of what types of evidence (i.e., negative, positive, or null relationships between health and trait expression) actually constitute support for good genes models of sexual ornamentation (Getty 2002). Consistent with this complexity, recent reviews from animal literature report that the evidence regarding testosterone and immunity is ambiguous and difficult to interpret (Roberts et al. 2004), varying considerably with the type of immune response measured

(Hau 2007) and with the species (or even the population) investigated (Muehlenbein and Bribiescas 2005; Hau 2007). At present, there is no clear evidence of a general, cross-species link between testosterone, genetically mediated immunity, phenotypic health and trait size, from which patterns among humans can straightforwardly be inferred.

DO WOMEN PREFER MASCULINITY?

In light of the equivocal support for a health-masculinity link, the plausibility of the immunocompetence hypothesis rests largely on the evidence regarding preferences. A straightforward prediction of the immunocompetence hypothesis is that masculinity should increase attractiveness. This prediction can be tested by assessing natural variation in masculinity among male faces and its association with rated attractiveness. A common alternative method is computer graphic morphing, in which facial photographs are manipulated to produce masculinized and feminized versions of a given face (Perrett et al. 1998). These images are presented to observers, often in forced-choice experiments, to examine preferences for masculinity.

To date, neither of these approaches has provided clear support for the prediction that masculinity is attractive to women (see Rhodes 2006 for meta-analytic review). While some correlational studies have documented small positive preferences for masculinity (Penton-Voak et al. 2001; Neave et al. 2003; Rhodes 2006; Rhodes et al. 2007), other similar studies have produced null or inconclusive results (Cunningham et al. 1990; Koehler et al. 2004; Thornhill and Gangestad 2006; Komori et al. 2009; Scott et al. 2010; Puts et al. 2011). In addition, much of the correlational research (Cunningham et al. 1990; Koehler et al. 2003; Rhodes et al. 2003, 2007) has been based on subjective ratings of masculinity, which may be attributed to faces on the basis of dimorphic nonshape cues such as color and hair growth, or possibly on the basis of attractiveness itself (Eagly et al. 1991; Scott et al. 2010; Komori et al. 2011; see DeBruine et al. 2010b for discussion). Experimental data should provide more accurate insight into the direction of preferences (DeBruine et al. 2010b), but when tested using digital morphing techniques, preferences remain highly inconsistent between experiments, and if anything appear to favor facial femininity (Perrett et al. 1998; Rhodes 2006; Rennels et al. 2008). This failure to find preferences for masculinity is not attributable to the use of novel stimuli such as composite photographs—indeed, using more ecologically valid stimuli seems to reduce, rather than increase, reported preferences for masculinity (Scott and Penton-Voak 2011). One serious concern is the reliance on two alternative forced-choice experiments with stimuli that vary in one dimension only. Such experiments produce non-random responses, but may force participants to discriminate between faces on the basis of traits that might otherwise be ignored, and cannot therefore be used to assess their importance (Peters et al. 2009; Penton-Voak 2011).

THE TRADE-OFF PROPOSAL: IMMUNOCOMPETENCE AT THE EXPENSE OF PATERNAL INVESTMENT?

To reconcile these findings with the immunocompetence hypothesis, it has been suggested that preferences reflect strategic pluralism, with females adjusting their mate preferences in accordance with their individual and environmental circumstances (Penton-Voak et al. 1999, 2004; Gangestad and Simpson 2000; Little et al. 2001, 2008a, 2010; Thornhill and Gangestad 2006; DeBruine et al. 2010a, 2010c). Strategic pluralism proposes that heritable quality may be traded off against exclusive investment; a proposal supported by

evidence of an association between attractiveness and “riskiness” (i.e., probability of low investment in one’s partner) among humans (Bogaert and Fisher 1995; Gangestad and Simpson 2000; Jankowiak and Ramsey 2000; Waynforth 2001; Hill and Reeve 2004; Singh 2004; Weeden and Sabini 2007). Integrating this principle into immunocompetence perspectives has generated the proposal that masculinity preferences reflect a trade-off between heritable disease resistance (signaled by masculine face shape), and paternal investment (signaled by femininity).

There are two ways by which this reciprocal association may manifest itself. In the first, men adjust their mating and paternal efforts facultatively, investing less when their masculine charm rewards mating effort handsomely (cf. Burley 1986). This proposal runs into immediate difficulty as there is no clear preference for masculinity, as discussed above. To date, attempts to model a quality-investment trade-off in human mate choice (e.g., Hill and Reeve 2004) treat the sexual attractiveness of high-quality males as a premise. While such models can accommodate some “constraint” on preferences for high-quality men, this constraint is not anticipated in contexts of low investment, and is not predicted to actually reverse preferences (produce an overall preference for low-quality men). Indeed, the rationale for expecting that high-quality men offer less investment than low-quality men is precisely that they are sexually attractive: if they are not attractive, then it is no longer viable for them to follow a low paternal investment strategy.

A second manifestation of the masculinity/investment association proposes a more obligatory link between the two, so that investing in masculine ornamentation has a pleiotropic effect on parental effort. Males advertise immunocompetence via masculinity, but advertise substandard paternal investment at the same time. Implicitly, it is this version of the trade-off proposal that is widely treated as capable of explaining facial preferences (Penton-Voak et al. 1999, 2004; Little et al. 2001, 2008a, 2010; Gangestad and Scheyd 2005; Thornhill and Gangestad 2006; DeBruine et al. 2010a, 2010b). General preferences for femininity, for example, are proposed to be the result of the prioritizing paternal investment over genetic quality (Perrett et al. 1998; Fink and Penton-Voak 2002; Little et al. 2002; Penton-Voak et al. 2004).

Individual variation in preferences may also be explicable in these terms; a trade-off between indirect benefits and direct costs could explain, for example, why women have stronger preferences for masculinity when conception is likely (during the follicular phase of the menstrual cycle, and when they are of reproductive age), in the context of a short- rather than long-term relationship, and when they already have partners (see Penton-Voak et al. 1999; Penton-Voak and Perrett 2000; Johnston et al. 2001; Jones et al. 2005; Welling et al. 2007; Little et al. 2008b; Gangestad and Thornhill 2008; Little et al. 2010, or Jones 1998 for a review of positive findings; see Scarbrough and Johnston 2005; Saxton et al. 2006; Yu et al. 2007; Peters et al. 2009; Vukovic et al. 2009; Harris 2011; Moore et al. 2011 for failures to replicate). These shifts in preference are consistent with the prediction that masculine men should be more attractive in contexts in which the benefits of heritable immunocompetence are important and can be realized, and less attractive when paternal investment is a priority. Further support for this proposal is derived from evidence that women appear to have stronger preferences for masculinity in countries where national health is poorer (and hence, presumably, where immunocompetence is more important) (Penton-Voak et al. 2004; DeBruine et al. 2010a), after being primed with pathogen-relevant images (Little et al. 2011) and when they report high levels of pathogen disgust (DeBruine et al. 2010c).

IS MASCULINITY ASSOCIATED WITH REDUCED DIRECT BENEFITS?

In order for the immunocompetence trade-off hypothesis to be tenable, masculinity must be associated with reduced parental investment, and consequently with reduced direct benefits in humans. In many species, endogenous and experimentally increased testosterone is linked to increased mating effort and a concomitant decrease in parental effort (Muller et al. 2009). This pattern is also evident in humans, although most data is, understandably, correlational: testosterone is lower in fathers and men in committed relationships cross culturally (van Anders and Watson 2006; Alvergne et al. 2009; Muller et al. 2009), while high testosterone is associated with more sexual partners (Bogaert and Fisher 1995; van Anders et al. 2007; Peters et al. 2008), troubled interpersonal relationships, infidelity, violence, and divorce (Booth and Dabbs 1993). Evidence that masculinity itself is associated with a mating/parenting trade-off is preliminary, but indicates that desire for, and history of, more short-term sexual partners, may be associated with rated facial masculinity (Rhodes et al. 2005; Boothroyd et al. 2008, 2011).

The further assumption, however, that exclusive paternal investment straightforwardly implies net direct benefits for females, is substantially more difficult to justify. There is little reason to assume, a priori, that monogamous partnerships are universally equivalent to increased direct benefits. When male resource holding capability is unequal and linked to mating success, polygyny may pay off for females (see Orians 1969; Borgheroff Mulder 1990; Gibson and Mace 2007). While women in some populations seem to suffer negative health and fertility consequences from polygamous marriages, this evidence is not straightforward or consistent, and even in relatively equal societies, wives in polygamous marriages may sometimes have equal or greater resource access than women in monogamous marriages (Hames 1996; Gibson and Mace 2007). Cross-cultural variability is also observed in the evidence regarding masculinity and resources: while participants from Western industrial populations tend to regard masculinity as a cue of poor parenting (Perrett et al. 1998; Kruger 2006; Boothroyd et al. 2007), the Matsigenka of Peru appear to regard it as a cue of provisioning ability (Yu et al. 2007). At present, therefore, there is little evidence for a universal pattern of association between direct benefits and exclusive investment, or between provisioning and facial morphology.

DO WOMEN'S PREFERENCES SUPPORT THE TRADE-OFF PROPOSAL?

As noted, the evidence regarding variation in women's preferences for masculinity is often described as providing support for the immunocompetence trade-off hypothesis of male facial morphology (e.g., Gangestad and Thornhill 2008). Certainly, there is a good deal of evidence that is consistent with such a hypothesis; as described above, multiple authors have found that, in Western/postindustrial populations, women are more likely to select masculinized facial stimuli as attractive when they are fertile, and when considering short-term versus long-term relationships. What is less clear, however, is whether such findings warrant the stronger claim: that women preferentially mate with masculine men in short-term/high-fertility contexts, and that this is explicable in terms of heritable immunocompetence.

There are reasons to be cautious about such a claim. First, the effects observed often fail to replicate: although early publications were largely supportive of the immunocompetence perspective (e.g., Penton-Voak et al. 1999; see Gangestad 2008), the effects reported were small (see Figure 1 for an illustration of the mean differences between stimuli preferred

at high- and low-fertility phases of the menstrual cycle), and several more recent results have been negative (e.g., Scarbrough and Johnston 2005; Saxton et al. 2006; Yu et al. 2007; Peters et al. 2009; Rupp et al. 2009; Vukovic et al. 2009; Harris 2011; Vaughn 2010).

Second, the evidence relating to context effects is drawn largely from populations in developed/industrial countries, who share similar ("Western") culture and media, and may have greater cyclical variation in hormonal profile than other women, particularly those in natural fertility populations (Ellison 1994; Vitzthum et al. 2002). Few authors have tested preferences in less developed environments and/or societies with low exposure to Western culture, but among those who have, attempts to replicate menstrual cycle effects and relationship-context effects have been inconsistent (Yu et al. 2007; Penton-Voak and Scott 2010; also see Scott et al. 2008).

Third, the context-dependent, preference-shift data themselves are often not consistent with the immunocompetence hypothesis: when only good genes benefits are offered (e.g., in short-term relationships, where paternal noninvestment is implied, particularly in the case of extra-pair copulations), the expectation is for unambiguous preferences for masculinity, as poor parenting (the major associated cost of indirect benefits) is irrelevant. In several studies often cited as supportive of the immunocompetence hypothesis, however, women do not appear to favor masculinity in any context, with a shift in preferences toward, but not beyond, average masculinity for short-term relationships (e.g., Penton-Voak et al. 1999; Little et al. 2001, 2002). There have been concerns that this pattern of preferences may reflect methodological issues in stimuli preparation, but these objections do not appear well founded (Scott and Penton-Voak 2011). As such, it is hard to conclude that female choice is the selection pressure leading to the observed facial sexual dimorphism in humans.

Perhaps most significantly, when assessed using comprehensive, objective measures (rather than subjective ratings or a reliance on forced-choice experiments in which only one variable is manipulated), natural variation in masculinity appears to be unrelated to male attractiveness (Thornhill and Gangestad 2006; Scott et al. 2010; Puts et al. 2011), even among populations exposed to high pathogenic stress (Stephen et al. 2012). Tests for a curvilinear relationship have likewise found no association (Scott et al. 2010), and there is no evidence to suggest that these null findings result from individual variation in preferences (Scott et al. 2010). The proposal that masculinity is unrelated to attractiveness is consistent with results suggesting that testosterone and attractiveness are likewise not associated (Neave et al. 2003; Peters et al. 2008; Moore et al. 2011). Together, these findings suggest that even if masculine facial morphology is a correlate of immunocompetence, females choose to use other cues to judge attractiveness (e.g., color, body build, posture, movement) when they are available.

This view is consistent with a model of mate choice in which females prioritize cues of current condition over cues of immunity. Due to the existence of pathogenic fluctuation and complexity, current condition may be a better predictor of future disease resistance than past immunity. If choosiness imposes a cost on females, they may therefore attend primarily to cues of current condition, potentially deriving little further benefit from simultaneously attending to cues of past immunity (Adamo and Spiteri 2005). The emphasis on current condition (versus immunity) is expected to be greater when pathogen fluctuation is fast relative to host generation length, which, a priori, should occur more often in species with slow life histories (such as humans). Consistent with this theoretical expectation, attractive male traits (e.g.,



Figure 1
Visual illustration of the size of menstrual cycle shifts in preferences documented in [Penton-Voak et al. 1999](#). Photos show mean masculinity preferred at high fertility (L) and low fertility (R).

muscularity) are often cues of good condition, unattractive male traits (e.g., central adiposity, baldness) are cues of poor current health, and masculine facial morphology, which is unlikely to vary greatly with current condition post adolescence (due to being a stable trait), appears to be largely irrelevant to attractiveness.

A counterargument to the claims of [Scott et al. 2010](#) is that reported variation in masculinity preferences in other, non-face traits such as voice pitch and body shape provide convergent evidence for the robustness of context effects. This interpretation is appealing as correlated masculine traits in humans are proposed to be, effectively, one signal of quality. While this is certainly a possibility, different dimorphic traits cannot straightforwardly be regarded as functionally or perceptually equivalent. Within a species, dimorphic traits can be intersexual cues of good genes, while others are primarily intrasexual signals and are not attractive ([Loyau et al. 2005](#); [Karubian et al. 2009](#)). Different masculine traits vary in their attractiveness; deep voices and tallness are usually attractive ([Collins 2000](#); [Nettle 2002](#)), and beards and male-pattern hair loss are often considered unattractive ([Muscarella and Cunningham 1996](#)).

Finally, context effects are consistent with nonimmunocompetence-based explanations. With regard to menstrual cycle effects; for example, cyclical changes are observed in a number of different female reproductive hormones, and these changes influence a broad range of cognitive, emotional, and sensory processes ([Dreher et al. 2007](#); [Farage et al. 2008](#); [Guillermo et al. 2010](#)). Which of these processes, if any, are subject to direct selection, and which are epiphenomena of other processes, is currently far from clear. Many alternative hypotheses of fertility shifts have been proposed; one among them being the hypothesis that mid-cycle preferences for masculinity facilitate conception by orienting women toward fertile partners ([Puts 2006](#)) or simply toward members of the opposite sex ([Macrae et al. 2002](#)). A further proposal is that menstrual shifts are an epiphenomenon of selection on the behavior of pregnant women ([Puts 2006](#); [Jones et al. 2008](#)) as progesterone is elevated during both the luteal phase of the menstrual cycle and during pregnancy.

Late-cycle preferences for femininity are proposed to reflect a greater orientation toward highly investing men among pregnant women ([Jones et al. 2008](#)), although this is not the only possible explanation, as pregnant women are avoidant of threats in general ([Lienard 2011](#)), and masculinity may be a cue of physical violence (see below for details). While there is currently limited empirical evidence regarding these hypotheses, their existence demonstrates that context effects alone do not constitute strong evidence for the immunocompetence hypothesis specifically.

IF MASCULINITY IS NOT PRIMARILY A SIGNAL OF IMMUNOCOMPETENCE, DOES IT MATTER AT ALL?

As patterns of facial masculinity preferences do not fit the immunocompetence hypothesis as well as is often assumed, and the importance of masculinity in attractiveness judgments may have been greatly overestimated (due to the methodologies employed in experimentation), attempts to explain the significance of masculinity variation primarily through female choice are weakened. An alternative (albeit extreme) possibility is that the variation has no significance; facial sexual dimorphism may act as a quick and useful signal of anatomical sex but beyond some discrimination threshold it may not carry any additional information at all. Essentially, the phenotype may simply drift at random, from one end of the male extreme to the other, under minimal selection and attended to by no one.

The problem with this interpretation is that masculinity variation may have some information value after all; in cultures around the world, facial masculinity is associated with perceptions of “prosocial orientation” (variously defined in different studies as social warmth, trustworthiness, and other related traits; e.g., [Perrett et al. 1998](#); [Penton-Voak and Scott 2010](#)). One possibility is that facial masculinity, via an association with testosterone, is being used as a cue of competitive status-seeking behaviors, including direct physical aggression. Morphological masculinity appears to influence perceived dominance ([Perrett et al. 1998](#); [Swaddle and Reiersen 2002](#); [Boothroyd et al. 2007](#)), which, in turn,

predicts future attainment of rank in certain environments (Mueller and Mazur 1996). Furthermore, humans can judge physical strength and fighting ability from faces alone (Sell et al. 2009). The obvious interpretation is that masculinity is not primarily relevant to female choice, but is relevant to direct male–male competition. This alternative has been proposed in a number of articles (Boothroyd et al. 2007, 2009; Sell et al. 2009; Puts 2010) and we believe that there is good reason to take it seriously.

MASCULINITY MAY BE A CUE OF CAPABILITY TO COMPETE INTRASEXUALLY

The evidence that masculinity is associated with aggressive/dominant behavior in men is at least as strong as the evidence for an analogous relationship between masculinity and health. Testosterone promotes male competitiveness and aggressive behavior, both in humans and other animals (see Mehta and Beer 2010 for review), and high testosterone is associated with aggression (Harris 1996; Azurmendi et al. 2006; Mehta and Beer 2010) and violent crime (Mazur and Booth 1998; Christiansen 2001; Booth et al. 2006). While situational variables appear to mediate the testosterone–aggression link, there nevertheless appears to be a reliable relationship between testosterone and probability of aggressive behavior in a given environment (Archer 2006, 2009). Testosterone administration increases self-reported aggression (Pope et al. 2000) and testosterone levels become elevated during exposure to contest situations, whether acute or chronic, direct, vicarious, or even anticipatory (Booth et al. 1989; Mazur et al. 1992; Archer 2006; Pound et al. 2009). If facial masculinity is related to adult testosterone levels, therefore, it could potentially serve as a physical cue of aggressively competitive behavior.

Masculine facial anatomy is more robust than feminine anatomy, which may reflect an ability to withstand direct competition rather than merely the propensity to engage in it (Puts 2010). This need not imply that masculinity is a reliable cue of “quality”, however, as testosterone levels may be responsive to quality-independent factors such as the frequency of aggression in the local population (Qvarnstrom and Forsgren 1998) and individual (developmental) exposure to conflict (Mazur and Booth 1998; Archer 2009). Masculinity may therefore reflect a strategic, rather than (entirely) quality-dependent reallocation of resources away from certain types of demand (e.g., maintaining health) and toward others (surviving violent conflict).

While it is difficult to demonstrate that masculinity is a “better” cue of aggression than of health, there are reasons to treat this as plausible. Convergent sources of evidence relating to spatial geography, phylogeny, and anatomy suggest that men’s morphology may have been subject to stronger intrasexual than intersexual selection (Puts 2010) and may convey more information about competitiveness than about heritable viability as a result. This would not make humans an oddity, as honest signaling of dominance is observed in many species and may be more common than honest signals of health (Johnstone 1995). While participant’s attributions are not a decisive test of actual relationships (Kruger 2006), we note that masculinized faces are judged to be dominant and aggressive in populations from a wide range of socio-ecologies (Perrett et al. 1998; Swaddle and Reiersen 2002; Boothroyd et al. 2007; Penton-Voak and Scott 2010), and that the effects are stronger and more consistent than those regarding health or attractiveness (Perrett et al. 1998; Boothroyd et al. 2005; DeBruine et al. 2006; see Puts 2010).

FEMALE RESPONSES TO MASCULINIZED STIMULI MAY REFLECT PREFERENCES FOR COMPETITIVE MATES

Women may not appear to attend greatly to masculinity when making attractiveness judgments of real faces in which other cues (such as color) are available, but responses to artificially masculinized stimuli are clearly patterned (within experiments, at least) and require explanation. One possibility is that the variation observed in the attractiveness of masculinity in these experimental contexts may reflect the costs and benefits associated with a mate’s potential success in intrasexual competition.

Observed responses to masculinized stimuli are broadly consistent with this hypothesis, and arguably more so than with an immunological one. An aggressiveness hypothesis can, for example, more readily accommodate the fact that women often prefer feminized to masculinized faces in experiments, even for short-term relationships. One reason for this is that aggressiveness—unlike health—could theoretically impose indirect costs upon mates. Aggressiveness has heritable components (DiLalla 2002; Brendgen et al. 2006; Baker et al. 2008) and may be positively or negatively predictive of intrasexual competitive success, depending on context (Johnson et al. 2007; Mehta et al. 2009; McIntyre et al. 2011). When status is based on “prestige” or cooperation, rather than direct competition, aggressiveness is associated with poor outcomes so that mating with an aggressive male could produce less successful offspring. In addition to this, aggressive males may impose direct costs such as violence and disease risk that—unlike low parental investment—are pertinent to short-term matings (Qvarnstrom and Forsgren 1998). These considerations make it theoretically plausible that women should sometimes be averse to cues of aggression, even for short-term relationships, and indeed preferences for less-dominant males have been observed in a number of low-investing species (Qvarnstrom and Forsgren 1998; Ophir and Galef 2003).

Consideration of the costs and benefits associated with aggressiveness could also account for observed individual variation in preferences for masculinity such as relationship-context effects. As noted above, aggression may be directed toward one’s mate, but may also be predictive (either positively or negatively, depending on environment) of intrasexual competitive success, and hence of access to resources. Whether having an aggressive mate represents a net direct cost or benefit is therefore likely to be population specific, but in environments where it represents a net direct cost, aversion to masculinity should be stronger in long-term contexts. Evidence suggests that in many Western populations, aggressive men may indeed impose a net direct cost on their partners (Sutherland et al. 1998; Coker et al. 2000; Campbell 2002), and this could explain why Western women are particularly averse to masculinized stimuli when thinking about long-term relationships. In populations where aggressiveness is a net direct benefit, however, this pattern may be reversed, which may explain why relationship-context effects are inconsistent across cultures (Yu et al. 2007; Penton-Voak and Scott 2010).

A similar reasoning may also be applied to preference shifts observed across menstrual-cycle stages. In populations where aggressive males confer net indirect benefits, these benefits are most likely to be realized during the fertile stage of a woman’s cycle; at other times, the cost-benefit ratio of mating with an aggressive male will be higher, making them less attractive. Consistent with this suggestion, we note that in Western populations, preferences for behavioral cues of aggressiveness and for the odor of self-rated dominant men have been observed

to increase both during ovulation and in short-term mating contexts (Gangestad et al. 2004, 2007; Havlicek et al. 2005), whereas preferences for apparent health in faces appear to increase during the luteal phase of the menstrual cycle (Jones et al. 2005). Note that this argument does not necessarily imply that aggressive mates will actually be preferred when a woman is fertile; the indirect benefits offered may still not be substantial enough to overcome the costs, even if they do a better job of mitigating them.

Finally, an aggressiveness hypothesis may also account for intergroup variation in preferences. In a cross-cultural comparison of 30 countries, DeBruine et al. (2010a) found that average national masculinity preferences were predicted by an index of national health, in line with Penton-Voak et al. (2004) prediction that masculinity, as a cue of heritable good health, will be more valued in regions where health is relatively poor. A reanalysis of this data (Brooks et al. 2011), however, showed that income inequality—proposed by some authors (Daly and Wilson 2001) to predict the strength of male–male competition—was an excellent predictor of masculinity preferences and significantly better than national health. Subsequent analyses focusing on data from USA suggested that health may also play a role in predicting intergroup variation in preferences (DeBruine et al. 2011), and that, within a Western culture, priming pathogen-related cues increases preferences for masculinity (Little et al. 2010), but the equivocal nature of the findings mean that at present it remains difficult to exclude any particular interpretation.

CONCLUSIONS AND FUTURE DIRECTIONS

There is nothing fundamentally wrong with the immunocompetence hypothesis as a logical argument, either in its original manifestation or in the form of the trade-off proposal. However, its popularity may not be proportionate to the strength of the supportive evidence. At present, there is little direct evidence of a link between facial masculinity and immunocompetence in humans, and the evidence from the animal literature regarding general relationships between dimorphism, testosterone, and disease is complex and difficult to interpret. In the absence of direct support for the operation of immunocompetence signaling in humans, preference studies are a potential source of insight into the functional significance of masculine morphology, but these provide limited evidence of the robust effects that would be expected if masculinity were an important cue of immunocompetence. Crucially, women do not appear to base facial attractiveness judgments on masculinity as much as previously thought, and may ignore it altogether.

These considerations cast doubt on the claim that facial masculinity is an important intersexual signal. While it is difficult to definitively exclude the possibility that preferences for health are driving observed preferences for artificially masculinized stimuli, most patterns of results are compatible with multiple explanatory frameworks. However, reverse engineering the function of preferences is not straightforward, and it is not clear that the immunocompetence hypothesis is superior to other alternatives based on current evidence. A plausible alternative hypothesis is that women's responses to masculinized stimuli may reflect preferences for intrasexual competitiveness, and this alternative explanation, although far from established, warrants greater research attention than it currently receives. Designing experiments that aim to discriminate between competing hypotheses should be a goal of future work, although not an easily attained one.

Despite the lack of evidence supporting an immunocompetence account of facial masculinity, it is quite possible that this could prove to be a useful explanation of observed preferences for other sexually dimorphic traits in humans, such as voice pitch, color cues, and body size. As in the facial attractiveness literature, however, care should be taken not to accept the immunocompetence hypothesis as supported without due evidence and consideration of viable alternatives.

More generally, the findings described above highlight the importance of ensuring adequate cross-cultural and ecological validity in attractiveness research (Penton-Voak 2011). Evolutionary approaches to attractiveness have, to date, devoted a great deal of attention to explaining variation in responses to theoretically driven experiments in which manipulated stimuli are judged. This approach is commendable, but there is a relative lack of data addressing the importance of given traits in real mate choice or even in attractiveness judgments of naturally varying stimuli. In counterpoint, a complementary approach is to identify traits that contribute to attractiveness by post hoc analysis of the traits that contribute to attractiveness ratings in large face sets (Chen and Zhang 2010; Said and Todorov 2011). Currently, these approaches do not always converge on similar conclusions about the traits that are actually important in attractiveness judgments, which must raise some concerns. The use of more ecologically valid stimuli, investigations of real mate choice (or, perhaps more practically, “mate choice” constrained by the researchers, such as in “speed dating” studies), and cross-cultural evidence from outside of Western/postindustrial populations would strengthen claims in this area considerably.

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