Adaptive Human Behavior and Physiology (2017) 3:304–320
DOI 10.1007/s40750-017-0070-3

ORIGINAL ARTICLE

Women's Preferences for Men's Facial Masculinity: Trade-Off Accounts Revisited

Iris J. Holzleitner[1] · **David I. Perrett**[2]

Received: 3 April 2017 / Revised: 16 June 2017 / Accepted: 19 June 2017 /
Published online: 12 August 2017

Abstract Studies on mate preferences have demonstrated that women's perception of male attractiveness is sensitive to men's facial masculinity, and that women's preferences for facial masculinity are subject to individual differences, such as own condition. These individual differences have been linked to potential trade-offs that women face given the hypothesized benefits and costs that masculinity may cue in a potential partner. Whereas most studies based conclusions regarding such trade-offs on shifts in mean preferences for a feminized vs. masculinized face shape, here we directly investigated attractiveness as a function of different levels of masculinity. Using computer-graphic methods, we manipulated the facial masculinity of men's 3D faces to vary between extremely feminine and hypermasculine, and assessed women's preferences for these different masculinity levels in the light of individual differences in self-rated attractiveness, financial worries, pathogen disgust sensitivity, self-reported health and relationship status. Our findings show that some individual differences shift preferences towards a generally lower or higher masculinity level, whereas others affect the tolerance to low vs. high levels of masculinity. We suggest that the use of preference curves allows for a more comprehensive investigation of how and why women's preferences for masculinity may shift under different contexts.

Keywords Masculinity · Attractiveness · 3D · Face shape · Individual differences

Electronic supplementary material The online version of this article (doi:10.1007/s40750-017-0070-3) contains supplementary material, which is available to authorized users.

✉ Iris J. Holzleitner
iris.holzleitner@glasgow.ac.uk

[1] Institute of Neuroscience & Psychology, University of Glasgow, 58 Hillhead Street, Glasgow G12 8QB, Scotland

[2] Perception Lab, School of Psychology & Neuroscience, University of St Andrews, St Mary's Quad, South Street, St Andrews KY16 9JP, Scotland

Introduction

Previous studies have argued that women's (and men's) preferences for potential mates' facial appearance have been shaped by sexual selection (e.g., Gangestad 1993; Grammer et al. 2003; Thornhill and Gangestad 1993, 1999). One trait that has received particular attention is men's (facial) masculinity, i.e. dimorphism in secondary sexual traits caused by sex-specific ratios of androgens and oestrogens, which affect both morphology and behaviour.

It has been hypothesized that women should find facial masculinity attractive in potential mates as masculinity may act as an honest signal of male health (e.g., Alonso-Alvarez et al. 2007; Folstad and Karter 1992; Moore et al. 2011a, b; Rantala et al. 2012; Wedekind and Folstad 1994; Foo et al. 2017; but see Scott et al. 2013), or as it may signal competitive ability to other men and is secondarily attractive to women (e.g., Puts et al. 2012; Scott et al. 2013). At the same time, it has been found that masculine facial traits increase both perceived dominance and negative attributions of male faces including decreased quality as a parent (e.g., Boothroyd et al. 2007; Borras-Guevara et al. 2017; Penton-Voak et al. 1999; Perrett et al. 1998). Indeed, high levels of testosterone have been linked to undesirable social traits such as aggression and decreased paternal investment (e.g., Booth and Dabbs 1993; Mascaro et al. 2013; Pollet et al. 2011). Thus, it has been suggested that women face a trade-off between less masculine but more agreeable, investing long-term partners and men whose more masculine appearance would indicate good male condition, but at the same time less socially desirable traits (e.g., Penton-Voak et al. 1999).[1] Women's trade-off regarding these costs and benefits has been suggested to be subject to a range of different factors which lead to differential preferences for masculinity within and between women, and that can be broadly summarized as internal factors (such as own condition), context (such as short- vs. long-term relationship contexts) and exposure (such as visual diet) (Little et al. 2011b). Previous studies thus broadly suggest that women's perception of male attractiveness is sensitive to facial cues of masculinity, and that there might be benefits and costs associated with choosing a (facially) feminine or masculine partner.

Most previous studies focused on how *mean* preferences for masculinity differ between, or shift within, women. That is, women were usually presented with either a two-alternative forced choice task in which the more attractive face is chosen between a feminized and masculinized version, or an interactive task, in which facial masculinity is increased or decreased by moving a computer mouse over the image until the face is most attractive. By comparing answers on this task between women, e.g., who rate themselves as more or less attractive, it was then tested whether more attractive women choose more masculine faces than less attractive women. As Jones et al. (2013) noted, the use of such experimental designs cannot answer the question of whether individual differences in relative preferences for, e.g., masculinized vs. feminized faces are driven by an increased attraction to masculine men and/or an increased aversion to feminine men.

[1] Note that a slightly different framework/interpretation is conceivable: women's trade-offs regarding male masculinity might "mirror" a trade-off in male life history strategy which is cued by masculinity via testosterone-mediated differential allocation of somatic resources to survival vs. reproductive, and mating vs. parenting efforts (e.g., Ellison 2003; Gangestad and Eaton 2013; Muehlenbein and Bribiescas 2005).

Here, we directly investigated potential differences in attraction to low and high levels of masculinity. We used computer-graphic methods to manipulate facial masculinity in a set of men's 3D faces, and asked women to rate these faces for their attractiveness. Determining the attractiveness of the same men at different levels of masculinity allowed us to establish how tolerance for low and high masculinity levels might shift depending on some of the factors previously established to impact on masculinity preferences. The following predictions were tested.

P1: Own Condition

Previous studies found that female self-rated attractiveness is positively associated with preferences for male facial (and vocal) masculinity (e.g., Kandrik and DeBruine 2012; Little et al. 2001; O'Connor et al. 2012; Smith et al. 2009; Vukovic et al. 2008). As physical attractiveness has been hypothesized to reflect "good condition", these findings have been interpreted as evidence that "high quality females" may be able to acquire both good genes and investment from "high quality males", whereas for women with lower mate value the costs of selecting a low investing partner might be higher than the heritable health benefits that this partner might provide (Little et al. 2001). We thus tested the prediction that women rating themselves as more attractive should show a reduced tolerance of low masculine male faces and/or a higher tolerance of highly masculine male faces than women perceiving themselves as less attractive.

P2: Resource Availability

Previous studies suggest that priming women with cues to financial/environmental harshness decreases their masculinity preferences (Little et al. 2007, 2013b; see also Lee and Zietsch 2011), which has been interpreted as evidence that harsh environments may favour the choice of lower-quality but higher-investing (long-term) partners. Instead of priming participants with hypothetical scenarios, we tested whether perceived financial resource scarcity affects masculinity preferences. We asked women how much they worried about their future financial situation, and tested the prediction that women who worry more about their financial future show a higher tolerance/preference for low levels of masculinity than women who are less worried about their financial future.

P3: Pathogen Disgust Sensitivity

Facial masculinity has been linked to heritable good health. DeBruine et al. (2010) suggested that health benefits might offset the costs of high masculinity when pathogens are a greater concern, and studies have linked personal differences in sensitivity to pathogens (DeBruine et al. 2010; Jones et al. 2013) to an increased preference for masculine faces (see also Little et al. 2011a; but Lee and Zietsch 2015). We thus tested the prediction that women with higher pathogen disgust sensitivity show a higher preference/tolerance for high levels of masculinity than women scoring low on pathogen disgust sensitivity.

P4: Self-Reported Health

Based on the presumed link of masculinity and heritable health benefits, it could be predicted that for women with poor health, partner's masculinity, i.e. a cue to health, is of greater value than for women of self-reported good health (De Barra et al. 2013; Feinberg et al. 2012). It is possible that health might affect self-perceived mate value (Scott et al. 2008), and a prediction of the opposite direction is conceivable—that for women with poor health, and therefore lower mate value, the costs of choosing a highly masculine (and low-investing mate) outweigh benefits, reflected in a preference for feminine men. We therefore tested the general prediction that self-reported health affects masculinity preferences.

P5: Relationship Status

It has been suggested that women who are in stable long-term relationships would assess other men's attractiveness in the context of a potential extra-pair copulation, for which facial cues to parental investment (i.e. low masculinity) are less important, and facial cues to good health (i.e. high masculinity) are more important (Little et al. 2002; Sacco et al. 2012). Thus, we tested the prediction that women who are in happy, committed relationships should show a higher preference for/a higher tolerance towards high levels of masculinity than women who are currently single.

Methods

Participants

A total of 563 women were recruited through the Perception Lab website and through Amazon MTurk (Buhrmester et al. 2011). Amazon MTurk workers were paid $2.00 for their participation. Exclusions were made based on ethnicity (Caucasian only), age (only women in a reproductive age range, i.e. between ages 18 and 45), sexual orientation (only women who reported higher sexual attraction to men than women), hormonal contraceptive use (only women who reported not to be using hormonal contraceptives, e.g., Little et al. 2013a) and rating behaviour (only women who assigned more than two different values when judging men's attractiveness on the used 8-point Likert-type scale). Table 1 provides descriptive statistics for the sample before and after exclusions.

Table 1 Sample demographics before and after exclusions

	Before exclusions		Final Sample		
	Lab Website	MTurk	Lab Website	MTurk	Overall
N	267	296	112	112	224
M_{age}	24.98	37.08	24.41	33.97	29.19
SD_{age}	8.84	11.53	8.15	6.15	8.65

Stimulus Set

The stimulus set consisted of four base faces that were composites of four men each (see supplemental material). Base faces were manipulated in their masculinity by applying or subtracting the linear difference between the average male and female face shape from a set of faces used in a previous study (Holzleitner and Perrett 2016). With this difference corresponding to 100%, each base face was feminized and masculinized to cover a range of −100% to +200% sexually dimorphic shape in seven steps of 50%, resulting in 28 stimulus faces. Figure 1 shows one of the base faces at the seven different levels of masculinity. Note that transforming faces in this way changes face shape along the male-female axis while retaining identity.

Experimental Task

Women were asked to rate all 28 face images on their attractiveness on an 8-point Likert-type scale from 1–*Not at all attractive* to 8–*Very attractive*. Prior to the rating, participants were presented with 2D frontal images of all face models for one second each to provide an overview of stimulus variability. The 3D face stimuli were presented on a computer screen in randomized order. They were rotated from −45 to +45° from left to right while simultaneously being rotated from −15 to +15° up and down, resulting in the stimuli "bobbing" in a sinusoidal manner. Images were presented individually against a black background and remained visible until a rating was made.

Individual Differences

Prior to the experimental tasks, participants were asked to fill out a questionnaire on basic demographic information (age, gender, ethnicity). Participants then indicated their sexual orientation on a 7-point scale ranging from 1–*homosexual* to 4–*bisexual* to 7–*heterosexual* (Boothroyd et al. 2008; Moore et al. 2006). Only participants that reported a sexual orientation of 5 or above (i.e. a greater sexual attraction to men than women) were included in the subsequent analyses. Health was measured on a 5-point scale with the options 1–*Excellent,* 2–*Very good*, 3–*Good*, 4–*Fair* and 5–*Poor* (Jürges et al. 2008). Answers on the health item were reverse-coded for analysis, so that higher values corresponded to better health. Disgust sensitivity was measured with the seven-item pathogen disgust sensitivity scale (Tybur et al. 2009). Items were summed to give a disgust sensitivity score, with high values indicating high disgust sensitivity. If a participant did not rate all seven items, their pathogen disgust sensitivity was recorded

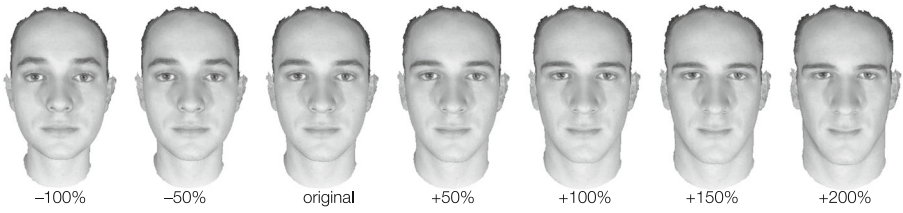

Fig. 1 One of the four base faces at the seven different levels of masculinity. Masculinity transforms were based on the difference in face shape between an average male (composite of 50 men) and an average female face (composite of 68 women, Holzleitner et al. 2016)

as missing. Participants rated their own attractiveness to the sex they were attracted to on a 7-point Likert-type scale ranging from 1–*Below average/Not so attractive* to 7–*Above average/Very attractive*. Participants were also asked about their relationship status: whether they were currently in a relationship, and if so how happy they were in the relationship (7-point Likert-type scale ranging from 1–*Very unhappy* to 7–*Very happy*) and how committed they felt to their relationship (7-point Likert-type scale ranging from 1–*Not committed at all* to 7–*Very committed*). Only women who reported to be committed to and happy in their current relationship (values of 4 or above on the respective scales) were included in the analysis of the effect of relationship status (Little et al. 2002). To approximate perceived environmental harshness, participants were asked to report how much they worried about their future financial situation when thinking ahead (7-point Likert-type scale ranging from 1–*I worry a lot* to 7–*I'm not worried at all*). Answers were reverse-coded so that higher values corresponded to more reported worries. Finally, participants were asked whether they were currently using hormonal contraceptives, and whether they had answered all questions truthfully (all women in the final sample—i.e. after the described exclusions—indicated they had).

Analyses

We used linear mixed models to analyse facial attractiveness as a function of masculinity. Attractiveness ratings (1–8) were entered as the dependent variable, and masculinity level as a predictor. As we anticipated the relationship of attractiveness and masculinity to be curvilinear, we also entered a quadratic masculinity term. The seven masculinity levels (−100% to +200%) were recoded to be centred on the unaltered masculinity level and span a unit of 1 (−2/6 to 4/6). Continuous predictor variables were standardized before entering them as fixed effects, and allowed to interact with both linear and quadratic masculinity terms. For all models, random intercepts and slopes were specified maximally (Barr 2013; Barr et al. 2013). Full model specifications, outputs and the data itself are given in the supplemental materials.

To visualize the effects of predictors on attractiveness as a function of masculinity, curves were fitted based on the estimated slopes from the linear mixed effect models for the predictor at its sample minimum and sample maximum. The local maximum of the function (for values corresponding to the range of presented masculinity levels, −2/6 to 4/6, and the predictor at its lowest, or highest value) was graphically illustrated. All analyses were carried out using *R* (R Development Core Team 2015), and the *R* packages *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2015). All *p*-values reported are two-tailed.

Control Variables

In a first step, we tested for the effects of two control variables: age, and sexual orientation. Several studies have indicated a positive correlation of age and masculinity preferences within a reproductive age range (Little et al. 2001, 2002, but see, e.g., DeBruine et al. 2006 for a null-finding regarding age); Batres et al. (in submission) observed that in women who identified their sexual orientation as 5, 6 or 7 on the 7-point sexual orientation scale used in the current study, sexual attraction to men and masculinity preferences were

positively associated. The effects of age and sexual orientations were thus tested in a preliminary model by adding them as fixed effects and allowing each of them to interact with both the linear and quadratic masculinity level terms.

Results and Discussion

Preliminary Analysis: Attractiveness as a Function of Masculinity

We first predicted ratings of attractiveness by entering men's level of facial masculinity as a linear term. Re-running the model including the quadratic term significantly increased model fit (AIC 20638 vs. 19898, $\chi^2 = 748.69$, $p < .001$). In a further step, the two control variables (participant age and sexual orientation) were added to the model and allowed to interact with both linear and quadratic masculinity terms.

We found no significant main effect of age, nor a significant interaction of age and masculinity in predicting attractiveness (all $t \leq 1.37$, all $p \geq .174$). Sexual orientation did not have a significant main effect or interaction with the quadratic masculinity term (both $t \leq 0.70$, both $p \geq .434$), but significantly interacted with the linear masculinity term ($t(221) = 2.53$, $p = .012$; see supplemental material). Figure 2a visualizes the effect of sexual orientation on masculinity preference curves.

The initial analysis of women's attractiveness ratings as a function of masculinity level showed that, as predicted, men's facial masculinity was related to women's ratings of attractiveness in a curvilinear fashion. Very low and very high levels of masculinity were rated as relatively unattractive. For strictly heterosexual women, attractiveness ratings peaked at a level of +87% masculinity, i.e. clearly above zero. This is in line with findings from previous studies that have reported a general preference for masculinity/masculine traits (Cunningham et al. 1990; Gillen 1981; Grammer and Thornhill 1994; Koehler et al. 2004; Neave et al. 2003; Rhodes et al. 2003, 2007; Saxton et al. 2009; Scheib et al. 1999), but in contrast to other studies which reported that overall, women prefer a close to average or slightly feminine male face shape (Little et al. 2001; Penton-Voak et al. 2004, 2003; Perrett et al. 1998; Rhodes et al. 2000; Scott et al. 2010). Our results might differ from these latter findings because we used an asymmetric range of masculinity (−100% to +200%). Presented with more masculinized compared to feminized faces, participants might have shifted their preferences towards a higher level of masculinity/the average of the presented range (+50%).

Age We found no effect of age on women's masculinity preferences. In subsequent analyses, age was thus not controlled for unless previous findings suggested an interaction of age with the variable of interest.

Sexual Orientation The more women were exclusively sexually attracted to men, the more attractive they found highly masculine faces: the turning point of the quadratic function for strictly heterosexual women was at a higher masculinity level than for women who reported the most attraction to women. Cost/benefit functions of masculinity appeared not to differ; rather the whole preference curve was shifted towards a higher level of masculinity. Thus, even within women who might report their sexual orientation as "heterosexual" when only given the options of homosexual/bisexual/

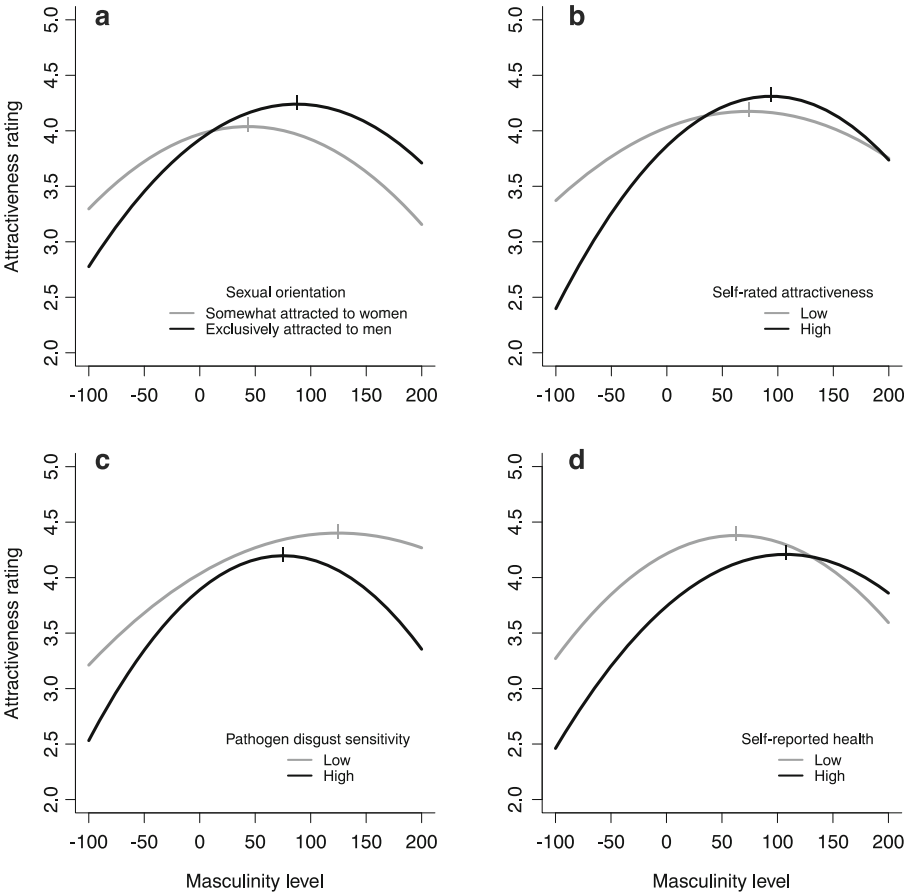

Fig. 2 Male attractiveness as a function of facial masculinity and women's individual differences in sexual orientation (**a**), self-rated attractiveness (**b**), pathogen disgust sensitivity (**c**) and self-reported health (**d**). Curves show masculinity preferences at the sample minimum and maximum values for the respective predictor variables

heterosexual, variation in the extent to which women feel attracted to men appears to impact on their masculinity preferences.

Sample sizes for the different sexual orientation categories were relatively small and unbalanced (on the 7-point scale, 18 women indicated their sexual orientation as *5,* 49 as *6* and 157 as *7*, i.e. "strictly" heterosexual). Thus, it was decided to restrict subsequent analyses to women who identified themselves as strictly heterosexual (7 on the 7-point scale, $N = 157$).

P1: Own Condition

One woman did not report her self-rated attractiveness. The sample size was thus $N = 156$. The mean self-rated attractiveness was 4.5 ± 1.2, with values ranging from 1 to 7. The model revealed a significant interaction of self-rated attractiveness with the

linear masculinity term ($t(154) = 2.04$, $p = .043$). Neither the main effect of self-rated attractiveness ($t(154) = -0.40$, $p = .687$), nor its interaction with the quadratic masculinity term ($t(154) = -1.86$, $p = .065$) were significant. Figure 2b visualizes preference curves for women who rated themselves lowest (1) and highest (7) on attractiveness.

Previous studies have suggested that women with a lesser mate value might opt for less masculine but more pro-social long-term mates (Little et al. 2001). Our findings suggest a different interpretation—the preference curves show that both women of self-rated low and high attractiveness show a similar level of attraction to highly masculine men. It seems that it is not the costs of high levels of masculinity that differ for women depending on their perceived individual condition; rather, there seems to be a difference in the costs associated with choosing a very feminine mate. More attractive women showed less tolerance to lower levels of masculinity than less attractive women, and their attractiveness ratings increased more steeply with increasing masculinity. Although the interaction with the quadratic masculinity term was not significant, our results also tentatively suggest that more attractive women show a greater range in their ratings of attractiveness (a steeper curve), which might indicate they are more discriminatory than less attractive women when it comes to men's facial masculinity.

P2: Resource Availability

One woman did not report her financial worries; the final sample size was thus $N = 156$. The mean reported financial worries was 3.5 ± 1.8, with values ranging from 1 to 7. We found no significant main effect of financial worries on attractiveness ratings, nor an interaction with the linear or quadratic masculinity term (all $t \leq 1.594$, all $p \geq .113$).

Based on previous findings, we expected to see that women who worry more about their financial future would show a higher preference for low levels of masculinity than women who are less worried about their financial future, but found no significant effect (see below).

P3: Pathogen Disgust Sensitivity

Six participants did not respond to all pathogen disgust questionnaire items. The final sample size was thus $N = 151$. The mean pathogen disgust sensitivity was 25 ± 8, with values ranging from 2 to 42. We found no significant main effect of pathogen disgust sensitivity, nor a significant interaction with the linear masculinity term (both $t \leq .77$, both $p \geq .440$), but a significant interaction of pathogen disgust sensitivity and the squared masculinity term ($t(149) = -2.19$, $p = .030$, see Fig. 2c). As a recent study suggested that pathogen disgust sensitivity might interact with age in predicting masculinity preferences (Lee and Zietsch 2015), we also re-ran the model with a three-way interaction of age, disgust sensitivity and masculinity level; age had no significant effect on its own or in any interaction, whereas the pattern of results for disgust sensitivity remained unchanged (see supplemental material).

We predicted that women with higher pathogen disgust sensitivity would show a higher preference/tolerance for high levels of masculinity than women scoring low on this measure. We did not find evidence for this prediction in the analysis of preference curves; indeed, our results were reversed with respect to our prediction and previous findings. Peak preferences actually appeared to be higher for women *low* on disgust

sensitivity, although it is important to note that the interaction with the linear masculinity term was not statistically significant. The significant effect we did observe, i.e. the interaction of pathogen disgust sensitivity and the quadratic masculinity term, translates to an increasingly steep, more closed preference curve with increasing pathogen disgust sensitivity, which might be interpreted as perceptions of attractiveness increasingly being sensitive to facial masculinity.

P4: Self-Reported Health

One woman did not report her health; the final sample size was thus $N = 156$. The mean self-reported health was 3.8 ± 0.9, with values ranging from 2 to 5. Neither the main effect of health ($t(154) = -1.66$, $p = .098$), nor its interaction with the linear ($t(154) = 1.82$, $p = .071$) or quadratic masculinity term ($t(154) = 0.12$, $p = .904$) were significant in predicting attractiveness.

Although non-significant, our findings tentatively suggest similarities in the effects of self-reported health and self-rated attractiveness (see Fig. 2d). With increasing self-reported health, women's preferences shifted towards higher levels of masculinity; the peak masculinity preference level was higher for women of better compared to poorer health. This is in line with reasoning that opinions about health might either affect, or help to form, perceptions of women's own condition (Scott et al. 2008), but our finding contrasts with predictions made regarding the importance of male masculinity as a cue to health (De Barra et al. 2013; Feinberg et al. 2012). From the condition perspective, women who view themselves as attractive and healthy should prefer more masculine partners, yet from the immunocompetence perspective it is women who have had poor health who are thought to prefer more masculine partners. It is important to note that our measure of women's health might have confounded infectious diseases (to which immunocompetence predictions relate) and other aspects of health, such as injuries or long-term conditions unrelated to infectious disease.

P5: Relationship Status

Relationship status was missing for 11 women; the final sample size was thus $N = 146$ (59 single women, 87 partnered women). Relationship status had neither a main effect on ratings of male attractiveness nor any interaction with masculinity level terms in predicting women's ratings of attractiveness (all $t \leq 1.11$, all $p \geq .267$).

Previous studies found that single women preferred less masculine men than partnered women (Little et al. 2002; Sacco et al. 2012). No evidence for an effect of relationship status was apparent in the current study. We note that this discrepancy is likely due to the fact that we did not assess attractiveness in different relationship contexts (i.e. short- and long-term relationship context) in our rating task; previous studies suggested that the effect of relationship status might be contingent on the type of relationship for which attractiveness is assessed (Little et al. 2002).

Combining Different Predictors into One Model

In a final step, we used explanatory factor analysis to test whether some of the individual differences we recorded (i.e. age, self-rated attractiveness, financial worries, pathogen

disgust sensitivity, self-reported health) might be tapping into the same underlying constructs. We extracted two factors using varimax rotation that cumulatively explained 38% of the variance in the tested predictor variables (see supplemental material).

Factor 1, which we labelled "Condition", showed positive loadings for self-rated attractiveness (.88) and self-reported health (.55), as well as a small negative loading for financial worries (−.28); factor 2 showed a positive loading on financial worries (.77), a small negative loading on health (−.25) and a small positive loading on disgust (.23), and was labelled "Concerns". The factor solution did not account for much of the variance in age and disgust sensitivity (uniqueness of .99 and .95, respectively). Bartlett scores for the two factors for each participant were entered into a model with the linear and quadratic masculinity terms to predict attractiveness, and allowed to interact with both linear and quadratic masculinity terms. No other predictors were included in this model.

"Condition" showed a significant interaction with the linear masculinity term ($t(145) = 2.01$, $p = .046$); the main effect ($t(145) = -0.51$, $p = .612$) and interaction with the quadratic masculinity term ($t(145) = -1.78$, $p = .077$) were both non-significant. "Concerns" showed a significant interaction with the quadratic masculinity term ($t(145) = -2.29$, $p = .023$); the main effect of "Concerns" ($t(145) = 0.55$, $p = .586$) and the interaction with the linear masculinity term ($t(145) = -0.26$, $p = .797$) were non-significant.

Figure 3 visualizes the effects of Condition and Concerns on preference curves. In line with the observed individual effect of self-rated attractiveness, higher Condition shifted preferences to higher masculinity levels. Although the interaction with the quadratic masculinity term was not significant, our findings tentatively suggest that higher Condition leads to a decreased tolerance of low masculinity levels compared to lower Condition.

Concerns mainly loaded on financial worries. We had asked women for their financial worries as an approximation to perceived resource scarcity. Contrary to our prediction, we observed that women with high Concerns/financial worries do not actively appear to prefer low levels of masculinity, but more strongly dislike high

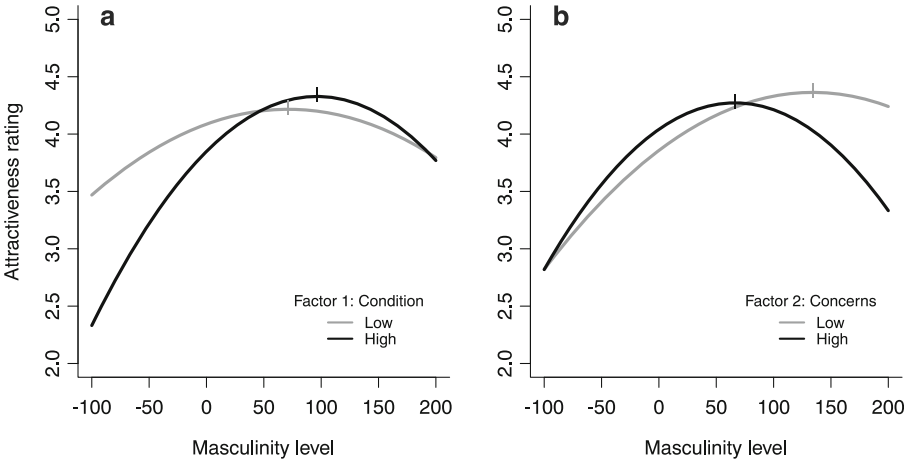

Fig. 3 Masculinity preference curves for women scoring lowest and highest on the two factors identified in the exploratory factor analysis, "Condition" (**a**) and "Concerns" (**b**)

levels of masculinity compared to women with fewer Concerns. The significant interaction with the quadratic masculinity term suggests that in women with lower compared to higher Concerns/financial worries, perceptions of male attractiveness are more sensitive to facial masculinity. Moore et al. (2006) found that women in control of financial resources placed greater importance on men's physical appearance—from the current work, this may translate to greater attraction to high levels of masculinity.

It is notable that when analysed as an individual variable, financial worries had no significant effect, whereas the effect of Concerns/financial worries was significant when controlling for Condition, which suggests that the effect of (financial) concerns was unmasked by accounting for individual women's self-perceived mate value. The conjoint analysis of the effects of the two factors also reveals that self-perceived condition and financial concerns make independent contributions to influence women's attraction to males.

Conclusion

"Point measures" of masculinity preferences from experimental designs such as interactive or two-alternative forced choice tasks can reveal how individual differences shift preferences towards lower or higher masculinity. Such methods, however, do not allow interpretation of the changes in attitudes to low or high levels of facial masculinity. To our knowledge, the current study is the first to test how women's masculinity preferences for men's faces change across multiple levels of masculinity.[2]

We investigated whether individual differences change the shape of masculinity preference curves, i.e. whether women might differentially trade off costs and benefits potentially associated with choosing a facially feminine vs. masculine mate. Modelling and plotting preference curves allowed for a more refined investigation of previously established effects. As previously suggested but not explicitly tested, our approach has shown that some parameters do indeed change women's tolerance towards low vs. high levels of masculinity (self-perceived condition and worries about financial resources), whereas other aspects merely shift the overall level of masculinity preferences (variation in the extent to which women feel exclusively attracted to men).

These findings are important because of their theoretical implications: for example, they suggest that self-perceived condition does not change the benefits associated with choosing a very masculine mate. Instead, self-rated attractiveness appears to change the costs of choosing a very feminine mate; for less attractive women it seems less costly to choose a (facially) very feminine man than for more attractive women. This might make it necessary to reconsider previous narratives which have argued that cues to prosociality (less masculinity/higher femininity) are actively preferred by less attractive women. We note that the minor effect self-rated attractiveness had on peak masculinity preference in our study is not necessarily in conflict with previous studies that found significant differences in the preferences of more and less attractive women: the steeper preference function for low levels of masculinity in more attractive women can lead to

[2] Note that Johnston et al. (2001) used preference curves to visualize how social perception of men's faces changed across different masculinity levels in a between-subject design. We used a within-subjects design.

the finding of a large preference difference when using a two-alternative forced choice task using stimuli that range between ±50%, i.e. a low range of masculinity.

One benefit of previously employed two-alternative forced choice tasks using feminized/masculinized faces is that manipulated faces are equal in their prototypicality, or averageness (Little and Hancock 2002). This is significant, as previous studies have demonstrated that prototypicality impacts on perceptions of attractiveness, whereby averageness increases attractiveness (though the most attractive faces are not necessarily average; Langlois and Roggman 1990; Perrett et al. 1994; DeBruine et al. 2007). The current study presented participants with male faces that were manipulated to range in sexual dimorphism from −100% to +200% of masculinity, including the original, unmanipulated masculinity level (0%). This raises the possibility that our computer-graphic manipulation of masculinity also changed stimuli's facial prototypicality, thereby confounding effects of masculinity and facial averageness. The appeal of averageness might explain why, compared to previous studies, we found a very strong preference for masculinity across all women. Yet, it does not easily explain our findings on individual differences in preferences, such as that women who differ in their (exclusive) attraction to men differed in their peak masculinity preference level, or that women low and high on self-rated attractiveness showed different preferences for low but not high levels of our manipulation. We also note that there is evidence to suggest that sexual dimorphism and distinctiveness form independent dimensions of male facial appearance (Komori et al. 2011; O'Toole et al. 1998). Nonetheless, an explicit test of the effect of sexual dimorphism manipulations on facial prototypicality when working with a range of masculinity levels might be warranted in future studies.

Our exploration of masculinity preferences was not entirely comprehensive, as we did not explore the effects of two previously established influences on women's attractiveness judgments: relationship context, as well as the effects of male-on-female violence. Relationship context, i.e. whether women judge men's attractiveness as potential short- or long-term partners, has been shown to moderate women's preferences such that women have been found to prefer more feminine faces in a long- as compared to short-term context (e.g., Little et al. 2002; Scott et al. 2008). Importantly, relationship context has also been found to interact with other aspects that impact on women's masculinity preferences, such as individual condition (Little et al. 2001; Penton-Voak et al. 2003; Scott et al. 2008), environmental condition (Little et al. 2007) and relationship status (Little et al. 2002). While this omission of relationship context in our study is likely to explain our failure to replicate an effect of relationship status on masculinity preferences, we nonetheless found effects for individual condition and one aspect of environmental condition (perceived financial harshness) that are consistent with previous findings. The other independent influence on masculinity preferences our study did not investigate is perceived threat of violence and/or sexual coercion. Two recent studies found that women's masculinity preferences decrease when primed with images of male-on-female aggression (Li et al. 2014) or when exposed to higher levels of violence (Borras-Guevara et al. 2017).

In summary, we attempted to define women's preferences across a range of masculinity levels. Our analysis shows that masculinity preferences are, as has often been assumed, indeed a quadratic function and that both high and low levels of masculinity are unattractive. Our research shows that attraction can change as a function of masculinity in a variety of ways including a change in the tolerance towards high or low masculinity, which has previously been theorized but not explicitly tested.

Acknowledgements We thank Sean Talamas for help in recruiting MTurk participants.

Compliance with Ethical Standards

Conflict of Interest The authors state that there is no conflict of interest.

References

Alonso-Alvarez, C., Bertrand, S., Faivre, B., Chastel, O., & Sorci, G. (2007). Testosterone and oxidative stress: The oxidation handicap hypothesis. *Proceedings of the Royal Society B: Biological Sciences, 274*, 819–825. doi:10.1098/rspb.2006.3764.

Barr, D. J. (2013). Random effects structure for testing interactions in linear mixed-effects models. *Frontiers in Psychology, 4*(328), doi:10.3389/fpsyg.2013.00328.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255–278. doi:10.1016/j.jml.2012.11.001.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi:10.18637/jss.v067.i01.

Booth, A., & Dabbs, J. M. (1993). Testosterone and men's marriages. *Social Forces, 72*, 463–477.

Boothroyd, L. G., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007). Partner characteristics associated with masculinity, health and maturity in male faces. *Personality and Individual Differences, 43*, 1161–1173.

Boothroyd, L. G., Jones, B. C., Burt, D. M., DeBruine, L. M., & Perrett, D. I. (2008). Facial correlates of sociosexuality. *Evolution and Human Behavior, 29*, 211–218.

Borras-Guevara, M. L., Batres, C., & Perrett, D. I. (2017). Aggressor or protector? Experiences and perceptions of violence predict preferences for masculinity. *Evolution and Human Behavior, 38*(4), 481–489. doi:10.1016/j.evolhumbehav.2017.03.004.

Buhrmester, M., Kwang, T., & Gosling, S. D. (2011). Amazon's mechanical Turk: a new source of inexpensive, yet high-quality, data? *Perspectives on Psychological Science, 6*, 3–5. doi:10.1177/1745691610393980.

Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male physical attractiveness. *Journal of Personality and Social Psychology, 59*, 61–72.

De Barra, M., DeBruine, L. M., Jones, B. C., Mahmud, Z. H., & Curtis, V. A. (2013). Illness in childhood predicts face preferences in adulthood. *Evolution and Human Behavior, 34*, 384–389. doi:10.1016/j.evolhumbehav.2013.07.001.

DeBruine, L. M., Jones, B. C., Little, A. C., Boothroyd, L. G., Perrett, D. I., Penton-Voak, I. S., et al. (2006). Correlated preferences for facial masculinity and ideal or actual partner's masculinity. *Proceedings of the Royal Society B: Biological Sciences, 273*, 1355–1360. doi:10.1098/rspb.2005.3445.

DeBruine, L. M., Jones, B. C., Unger, L., Little, A. C., & Feinberg, D. R. (2007). Dissociating averageness and attractiveness: attractive faces are not always average. *Journal of Experimental Psychology: Human Perception and Performance, 33*(6), 1420. doi:10.1037/0096-1523.33.6.1420.

DeBruine, L. M., Jones, B. C., Tybur, J. M., Lieberman, D., & Griskevicius, V. (2010). Women's preferences for masculinity in male faces are predicted by pathogen disgust, but not by moral or sexual disgust. *Evolution and Human Behavior, 31*, 69–74. doi:10.1016/j.evolhumbehav.2009.09.003.

Development Core Team, R. (2015). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Ellison, P. T. (2003). Energetics and reproductive effort. *American Journal of Human Biology, 15*, 342–351. doi:10.1002/ajhb.10152.

Feinberg, D. R., DeBruine, L. M., Jones, B. C., Little, a. C., O'Connor, J. J. M., & Tigue, C. C. (2012). Women's self-perceived health and attractiveness predict their male vocal masculinity preferences in

different directions across short- and long-term relationship contexts. *Behavioral Ecology and Sociobiology, 66*, 413–418. doi:10.1007/s00265-011-1287-y.

Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist, 139*, 603–622. doi:10.1086/285346.

Foo, Y. Z., Nakagawa, S., Rhodes, G., & Simmons, L. W. (2017). The effects of sex hormones on immune function: a meta-analysis. *Biological Reviews, 92*(1), 551–571. doi:10.1111/brv.12243.

Gangestad, S. W. (1993). Sexual selection and physical attractiveness - implications for mating dynamics. *Human Nature, 4*, 205–235. doi:10.1007/BF02692200.

Gangestad, S. W., & Eaton, M. A. (2013). Toward an integrative perspective on sexual selection and men's masculinity. *Behavioral Ecology, 24*, 594–595. doi:10.1093/beheco/ars096.

Gillen, B. (1981). Physical attractiveness. *Personality and Social Psychology Bulletin, 7*, 277–281. doi:10.1177/014616728172015.

Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *Journal of Comparative Psychology, 108*, 233–242. doi:10.1037/0735-7036.108.3.233.

Grammer, K., Fink, B., Moller, A. P., & Thornhill, R. (2003). Darwinian aesthetics: sexual selection and the biology of beauty. *Biological Reviews, 78*, 385–407.

Holzleitner, I. J., & Perrett, D. I. (2016). Perception of strength from 3D faces is linked to facial cues of physique. *Evolution and Human Behavior, 37*(3), 217–229. doi:10.1016/j.evolhumbehav.2015.11.004.

Holzleitner, I. J., Hunter, D. W., Tiddeman, B. P., Seck, A., Re, D. E., & Perrett, D. I. (2014). Men's facial masculinity: when (body) size matters. *Perception, 43*, 1191–1202. doi:10.1068/P7673.

Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: evidence for hormone-mediated adaptive design. *Evolution and Human Behavior, 22*, 251–267. doi:10.1016/S1090-5138(01)00066-6.

Jones, B. C., Feinberg, D. R., Watkins, C. D., Fincher, C. L., Little, A. C., & DeBruine, L. M. (2013). Pathogen disgust predicts women's preferences for masculinity in men's voices, faces, and bodies. *Behavioral Ecology, 24*, 373–379. doi:10.1093/beheco/ars173.

Jürges, H., Avendano, M., & MacKenbach, J. P. (2008). Are different measures of self-rated health comparable? An assessment in five European countries. *European Journal of Epidemiology, 23*, 773–781. doi:10.1007/s10654-008-9287-6.

Kandrik, M., & DeBruine, L. M. (2012). Self-rated attractiveness predicts preferences for opposite-sex faces, while self-rated sex-typicality predicts preferences for same-sex faces. *Journal of Evolutionary Psychology, 10*, 177–186. doi:10.1556/JEP.10.2012.4.2.

Koehler, N., Simmons, L. W., Rhodes, G., & Peters, M. (2004). The relationship between sexual dimorphism in human faces and fluctuating asymmetry. *Proceedings of the Royal Society B: Biological Sciences, 271*, S233–S236.

Komori, M., Kawamura, S., & Ishihara, S. (2011). Multiple mechanisms in the perception of face gender: Effect of sex-irrelevant features. *Journal of Experimental Psychology. Human Perception and Performance, 37*, 626–633. doi:10.1037/A0020369.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2016). lmerTest: tests in linear mixed effects models. R package version 2.0-33. https://CRAN.R-project.org/package=lmerTest.

Langlois, J. H., & Roggman, L. A. (1990). Attractive faces are only average. *Psychological Science, 1*(2), 115–121. doi:10.1111/j.1467-9280.1990.tb00079.x.

Lee, A. J., & Zietsch, B. P. (2011). Experimental evidence that women's mate preferences are directly influenced by cues of pathogen prevalence and resource scarcity. *Biology Letters, 7*, 892–895. doi:10.1098/rsbl.2011.0454.

Lee, A. J., & Zietsch, B. P. (2015). Women's pathogen disgust predicting preference for facial masculinity may be specific to age and study design. *Evolution and Human Behavior, 36*, 249–255. doi:10.1016/j.evolhumbehav.2014.12.001.

Li, Y., Bailey, D. H., Winegard, B., Puts, D. A., Welling, L. L. M., & Geary, D. C. (2014). Women's preference for masculine traits is disrupted by images of male-on-female aggression. *PloS One, 9*, e110497. doi:10.1371/journal.pone.0110497.

Little, A. C., & Hancock, P. J. B. (2002). The role of masculinity and distinctiveness in judgments of human male facial attractiveness. *British Journal of Psychology, 93*, 451–464. doi:10.1348/000712602761381349.

Little, A. C., Burt, D. M., Penton-Voak, I. S., & Perrett, D. I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society B: Biological Sciences, 268*, 39–44.

Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society B: Biological Sciences, 269*, 1095–1100.

Little, A. C., Cohen, D. L., Jones, B. C., & Belsky, J. (2007). Human preferences for facial masculinity change with relationship type and environmental harshness. *Behavioral Ecology and Sociobiology, 61*, 967–973.

Little, A. C., DeBruine, L. M., & Jones, B. C. (2011a). Exposure to visual cues of pathogen contagion changes preferences for masculinity and symmetry in opposite-sex faces. *Proceedings of the Royal Society B: Biological Sciences, 278*, 2032–2039.

Little, A. C., Jones, B. C., & DeBruine, L. M. (2011b). Facial attractiveness: evolutionary based research. *Philosophical Transactions of the Royal Society, B: Biological Sciences, 366*, 1638–1659. doi:10.1098/rstb.2010.0404.

Little, A. C., Burriss, R. P., Petrie, M., Jones, B. C., & Roberts, S. C. (2013a). Oral contraceptive use in women changes preferences for male facial masculinity and is associated with partner facial masculinity. *Psychoneuroendocrinology, 38*, 1777–1785. doi:10.1016/j.psyneuen.2013.02.014.

Little, A. C., DeBruine, L. M., & Jones, B. C. (2013b). Environment contingent preferences: Exposure to visual cues of direct male-male competition and wealth increase women's preferences for masculinity in male faces. *Evolution and Human Behavior, 34*, 193–200. doi:10.1016/j.evolhumbehav.2012.11.008.

Mascaro, J. S., Hackett, P. D., & Rilling, J. K. (2013). Testicular volume is inversely correlated with nurturing-related brain activity in human fathers. *Proceedings of the National Academy of Sciences, 110*(39), 15746–15751. doi:10.1073/pnas.1305579110.

Moore, F. R., Cassidy, C., Law Smith, M. J., & Perrett, D. I. (2006). The effects of female control of resources on sex-differentiated mate preferences. *Evolution and Human Behavior, 27*, 193–205. doi:10.1016/j.evolhumbehav.2005.08.003.

Moore, F. R., Cornwell, R. E., Law Smith, M. J., Al Dujaili, E. A. S., Sharp, M., & Perrett, D. I. (2011a). Evidence for the stress-linked immunocompetence handicap hypothesis in human male faces. *Proceedings of the Royal Society B: Biological Sciences, 278*, 774–780.

Moore, F. R., Law Smith, M. J., Taylor, V., & Perrett, D. I. (2011b). Sexual dimorphism in the female face is a cue to health and social status but not age. *Personality and Individual Differences, 50*, 1068–1073.

Muehlenbein, M. P., & Bribiescas, R. G. (2005). Testosterone-mediated immune functions and male life histories. *American Journal of Human Biology, 17*, 527–558.

Neave, N., Laing, S., Fink, B., & Manning, J. T. (2003). Second to fourth digit ratio, testosterone and perceived male dominance. *Proceedings of the Royal Society B: Biological Sciences, 270*, 2167–2172. doi:10.1098/rspb.2003.2502.

O'Connor, J. J. M., Feinberg, D. R., Fraccaro, P. J., Borak, D. J., Tigue, C. C., Re, D. E., et al. (2012). Female preferences for male vocal and facial masculinity in videos. *Ethology, 118*, 321–330.

O'Toole, A. J., Deffenbacher, K. A., Valentin, D., McKee, K., Huff, D., & Abdi, H. (1998). The perception of face gender: the role of stimulus structure in recognition and classification. *Memory and Cognition, 26*, 146–160. doi:10.3758/BF03211378.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., et al. (1999). Menstrual cycle alters face preference. *Nature, 399*, 741–742.

Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P., & Perrett, D. I. (2003). Female condition influences preferences for sexual dimorphism in faces of male humans (*Homo sapiens*). *Journal of Comparative Psychology, 117*, 264–271.

Penton-Voak, I. S., Jacobson, A., & Trivers, R. (2004). Populational differences in attractiveness judgements of male and female faces: comparing British and Jamaican samples. *Evolution and Human Behavior, 25*, 355–370.

Perrett, D. I., May, K. A., & Yoshikawa, S. (1994). Facial shape and judgements of female attractiveness. *Nature, 368*, 239–242. doi:10.1038/368239a0.

Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D., Yoshikawa, S., Burt, D. M., et al. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature, 394*, 884–887.

Pollet, T. V., der Meij, L. V., Cobey, K. D., & Buunk, A. P. (2011). Testosterone levels and their associations with lifetime number of opposite sex partners and remarriage in a large sample of American elderly men and women. *Hormones and Behavior, 60*, 72–77.

Puts, D. A., Jones, B. C., & DeBruine, L. M. (2012). Sexual selection on human faces and voices. *Journal of Sex Research, 49*, 227–243. doi:10.1080/00224499.2012.658924.

Rantala, M. J., Moore, F. R., Skrinda, I., Krama, T., Kivleniece, I., Kecko, S., et al. (2012). Evidence for the stress-linked immunocompetence handicap hypothesis in humans. *Nature Communications, 3*. doi:10.1038/ncomms1696.

Rhodes, G., Hickford, C., & Jeffery, L. (2000). Sex-typicality and attractiveness: are supermale and superfemale faces super-attractive? *British Journal of Psychology, 91*, 125–140. doi:10.1348/000712600161718.

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society B: Biological Sciences, 270*, S93–S95. doi:10.1098/rsbl.2003.0023.

Rhodes, G., Yoshikawa, S., Palermo, R., Simmons, L. W., Peters, M., Lee, K., et al. (2007). Perceived health contributes to the attractiveness of facial symmetry, averageness, and sexual dimorphism. *Perception, 36*, 1244–1252.

Sacco, D. F., Jones, B. C., DeBruine, L. M., & Hugenberg, K. (2012). The roles of sociosexual orientation and relationship status in women's face preferences. *Personality and Individual Differences, 53*, 1044–1047. doi:10.1016/j.paid.2012.07.023.

Saxton, T. K., Little, A. C., Rowland, H. M., Gao, T., & Roberts, S. C. (2009). Trade-offs between markers of absolute and relative quality in human facial preferences. *Behavioral Ecology, 20*, 1133–1137. doi:10.1093/beheco/arp107.

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society B: Biological Sciences, 266*, 1913–1917.

Scott, I. M. L., Swami, V., Josephson, S. C., & Penton-Voak, I. S. (2008). Context-dependent preferences for facial dimorphism in a rural Malaysian population. *Evolution and Human Behavior, 29*, 289–296.

Scott, I. M. L., Pound, N., Stephen, I. D., Clark, A. P., & Penton-Voak, I. S. (2010). Does masculinity matter? The contribution of masculine face shape to male attractiveness in humans. *PloS One, 5*. doi:10.1371/journal.pone.0013585.

Scott, I. M. L., Clark, A. P., Boothroyd, L. G., & Penton-Voak, I. S. (2013). Do men's faces really signal heritable immunocompetence? *Behavioral Ecology, 24*, 579–589. doi:10.1093/beheco/ars092.

Smith, F. G., Jones, B. C., Little, A. C., DeBruine, L. M., Welling, L. L. M., Vukovic, J., et al. (2009). Hormonal contraceptive use and perceptions of trust modulate the effect of relationship context on women's preferences for sexual dimorphism in male face shape. *Journal of Evolutionary Psychology, 7*, 195–210. doi:10.1556/JEP.7.2009.3.1.

Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty - averageness, symmetry, and parasite resistance. *Human Nature, 4*, 237–269.

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences, 3*, 452–460.

Tybur, J. M., Lieberman, D., & Griskevicius, V. (2009). Microbes, mating, and morality: individual differences in three functional domains of disgust. *Journal of Personality and Social Psychology, 97*, 103–122. doi:10.1037/a0015474.

Vukovic, J., Feinberg, D. R., Jones, B. C., DeBruine, L. M., Welling, L. L. M., Little, a. C., et al. (2008). Self-rated attractiveness predicts individual differences in women's preferences for masculine men's voices. *Personality and Individual Differences, 45*, 451–456. doi:10.1016/j.paid.2008.05.013.

Wedekind, C., & Folstad, I. (1994). Adaptive or Nonadaptive immunosuppression by sex hormones? *The American Naturalist, 143*, 936–938.