Evolution and Human Behavior 36 (2015) 249–255

Contents lists available at ScienceDirect

Evolution and Human Behavior

journal homepage: www.ehbonline.org

Original Article

Women's pathogen disgust predicting preference for facial masculinity may be specific to age and study design

Anthony J. Lee [a,*], Brendan P. Zietsch [a,b]

[a] School of Psychology, University of Queensland, St. Lucia 4072, Brisbane, Queensland, Australia
[b] Genetic Epidemiology Laboratory, QIMR Berghofer Medical Research Institute, Herston 4006, Brisbane, Queensland, Australia

ARTICLE INFO

Article history:
Initial receipt 12 November 2013
Final revision received 4 December 2014

Keywords:
Sexual dimorphism
Immunocompetence
Mate preferences
Pathogen avoidance
Good genes
Forced-choice

ABSTRACT

Facial masculinity in men is thought to be an indicator of good health. Consistent with this idea, previous research has found a positive association between pathogen avoidance (disgust sensitivity) and preference for facial masculinity. However, previous studies are mostly based on young adult participants and targets, using forced-choice preference measures; this begs the question whether the findings generalise to other adult age groups or other preference measures. We address this by conducting three studies assessing facial masculinity preferences of a wider age range of women for a wider age range of male faces. In studies 1 and 2, 447 and 433 women respectively made forced choices between two identical faces that were manipulated on masculinity/femininity. In study 1, face stimuli were manipulated on sexual dimorphism using age-matched templates, while in study 2 young face stimuli were manipulated with older templates and older face stimuli were manipulated using young templates. In the full sample for study 1, no association was found between women's pathogen disgust and masculinity preference, but when limiting the sample to younger women rating younger faces we replicated previous findings of significant association between pathogen disgust and preference for facial masculinity. Results for study 2 found no effect of pathogen disgust sensitivity on facial masculinity preferences regardless of participant and stimuli age. In study 3, the facial masculinity preferences of 386 women were revealed through their attractiveness ratings of natural (unmanipulated) faces. Here, we did not find a significant association of pathogen disgust on facial masculinity preferences, regardless of participant and stimuli age. These results call into question the robustness of the link between women's pathogen avoidance and facial masculinity preference, and raise questions as to why the effect is specific to younger adults and the forced-choice preference measure.

1. Introduction

Recent research has identified a link between women's pathogen avoidance and stronger preference for facial masculinity in a mate. For instance, DeBruine, Jones, Tybur, Lieberman, and Griskevicius (2010) conducted two studies investigating the link between women's pathogen disgust and their preference for facial masculinity. In study 1, 345 women were shown 20 pairs of the same face; one had been manipulated to be more masculine and the other more feminine. This study utilised a forced-choice preference measure where participants were asked which face they found more attractive. Results were that women higher in pathogen disgust (but not sexual or moral disgust) were more likely to choose the masculinised face as more attractive. In study 2, 74 women were given a choice between two unmanipulated faces that had been pre-chosen based on rated facial masculinity/femininity. Again, it was found that women with high pathogen disgust were more likely to choose the masculine face. This effect appears to persist across several levels of analysis, not only across individuals with differences in pathogen disgust predicting masculinity preference (DeBruine, Jones, Tybur et al., 2010; Jones, Fincher, Little, & DeBruine, 2013), but also across countries with different levels of national health predicting mean levels of masculinity preference for that nation (DeBruine, Jones, Crawford, Welling, & Little, 2010; Penton-Voak, Jacobson, & Trivers, 2004), and in response to pathogen cues (Lee & Zietsch, 2011; Little, DeBruine, & Jones, 2011).

The prominent theory behind these findings is that male facial masculinity is an indicator of good health and that women high in pathogen avoidance are therefore more likely to prefer a facially masculine partner. According to this theory, testosterone is an immunosuppressant and is also required in high levels to develop masculine facial features; as such, only males with good immune functioning are able to support the high levels of testosterone necessary to develop a masculine face. In this way, facial masculinity in men is thought to serve as an honest indicator of good health (Folstad & Karter, 1992; Zahavi, 1975). Consistent with this theory, facial masculinity has been found to be associated with objective (Gangestad, Merriman, & Thompson, 2010; Rantala et al., 2012; Rhodes, Chan, Zebrowitz, & Simmons, 2003; Thornhill & Gangestad, 2006) and perceived health (Rhodes et al., 2003; Scott, Swami, Josephson, & Penton-Voak, 2008). However, the underlying mechanism for this preference is unclear. Facial masculinity in men may represent heritable genetic quality that improves offspring's fitness; however, this 'good genes' theory has recently been questioned

* Corresponding author.
E-mail address: anthony.lee@uqconnect.edu.au (A.J. Lee).

http://dx.doi.org/10.1016/j.evolhumbehav.2014.12.001

(Scott, Clark, Boothroyd, & Penton-Voak, 2013), and recent evidence suggests that the genes increasing male facial masculinity are detrimental to female attractiveness, reinforcing doubt regarding the link between masculinity and good genes (Lee et al., 2014). Alternatively, indicators of good health may instead be preferred for more direct benefits (Scott et al., 2013; Tybur & Gangestad, 2011). For instance, men with cues to good health may be less likely to succumb to sickness themselves, reducing potential disease transmission to the choosing female. Also, one's ability to acquire resources is hampered while ill, and additional effort/resources are required to nurse a sick individual back to health. We note that it is also possible that facial masculinity may not represent past or current immunocompetence, but may still be associated with good genes or other direct benefits (e.g., facial masculinity may be associated with ability to physically compete intrasexually; (Puts, 2010). However, theory describing the association between pathogen avoidance and masculinity preference relies on facial masculinity being (or once being) associated with some health benefit (either directly or indirectly).

Despite several studies finding a link between women's pathogen avoidance and their preference for facial masculinity, the research has some limitations. First, studies supporting this association solely rely on a forced-choice task (i.e., participants are required to choose between two targets that differ on the trait of interest which is more attractive; (DeBruine, Jones, Crawford, et al., 2010; DeBruine, Jones, Tybur, et al., 2010; Jones et al., 2013; Little et al., 2011; Penton-Voak et al., 2004). Lee et al. (2013), which used a ratings paradigm, found no association between women's pathogen disgust and revealed preference for facial masculinity when 422 women rated realistic dating profiles. This could suggest that the influence of facial masculinity may be limited to the forced-choice study design.

Second, research in this area has also focused on young adults and often neglects older individuals. To illustrate this, the range of mean participant age of studies investigating the link between pathogen avoidance and preference for masculinity is 18.6 to 25.3 years (DeBruine, Jones, Crawford, et al. 2010; DeBruine, Jones, Tybur, et al., 2010; Jones et al., 2013; Lee & Zietsch, 2011; Lee et al., 2013; Little et al., 2011; Penton-Voak et al., 2004). Also, when reported, the age of facial stimuli used to assess masculinity preference is of young adults. Research investigating the link between health and facial masculinity has also been limited to participants in early adulthood or late adolescence (Gangestad et al., 2010; Rantala et al., 2012; Rhodes et al., 2003; Thornhill & Gangestad, 2006). Such an overrepresentation of young adults is problematic for several reasons: first, it is unclear if facial masculinity remains a cue to health in older men even though facial masculinisation, and hence the purported link with immunocompetence, occurs primarily during adolescence. Although evidence for a link between facial masculinity and health has been drawn only from samples of younger men, it has been implicitly assumed that facial masculinity indicates good health in male faces in general. If this were the case, we would expect that women's pathogen disgust should predict preference for facial masculinity regardless of age of the male. Second, restricting assessment of masculinity preferences to samples of young adults might obscure important evidence regarding the underlying mechanism for preferring facial masculinity. Young adults differ in motivations and priorities in mate preference compared to older individuals; for example, younger women within the reproductive age range may place greater importance on genetic quality compared to older women (Little et al., 2010). Therefore, we may expect a different pattern of results when testing different age groups, which in turn has implications for understanding the underlying mechanisms for preferring facial masculinity.

To address these limitations, we conducted three studies investigating the association between women's pathogen disgust and their preference for facial masculinity. In all three studies we include a much wider age of participants and target faces than has been included in previous studies. Studies 1 and 2 used a force-choice design with target faces manipulated on sexual dimorphism. Study 1 manipulated sexual dimorphism using morphological differences between male and female faces that matched the age of the stimuli, while in study 2 younger stimuli were manipulated on sexual dimorphism based on differences between older faces and older stimuli were manipulated based on differences between younger faces. Study 3 revealed preference for facial masculinity through attractiveness ratings (as oppose to using a forced-choice design) in natural (unmanipulated) faces.

2. Study 1

In study 1, we expand upon the first study presented in DeBruine, Jones, Tybur, et al., 2010. Here we assessed the association between the women's pathogen disgust on preference for facial masculinity in manipulated faces using a forced-choice paradigm with a wider range of ages for both participants and targets.

3. Method

3.1. Participants

A total of 478 women were recruited from https://www.MTurk.com, an online crowd-sourcing website in return for online credit. Participation was conditional on being female, heterosexual and residing in the United States. Participants missing data on any variable ($n = 12$), or who fell outside the selection criteria ($n = 19$) were removed from analysis; reducing the sample size to 447 ($n = 36.79$ years, $SD = 10.52$, age range = 20–66 years).

3.2. Stimuli

Participants first completed a task measuring their preference for facial masculinity. Participants were randomly assigned to rate either the young or middle-aged male faces with neutral expressions from the FACES database (Ebner, Riediger, & Lindenberger, 2010). The young stimuli (aged between 19 and 31 years) set contained 27 faces, while the middle-aged (aged between 29 and 55) set contained 24 faces. Preference for facial masculinity was measured using a forced-choice task where participants were presented with two images of the same face side-by-side: one had been manipulated to be more masculine while the other more feminine. Participants were asked to rate which face they found more attractive on an 8-point scale (1 = *left is much more attractive*; 8 = *right is much more attractive*).

The masculinity/femininity of each photo was manipulated by morphing each individual face with a masculine or feminine template (similar to that used in Lee et al., 2013). To create the template faces, separate average faces for each sex and age group were made from 25 male and 25 female faces. Seventy facial landmarks were then manually placed on symmetrised versions of each averaged face, and the linear differences between facial landmarks for males and females within the same age group were calculated. These differences were then extended past the average face by 200% to produce a hyper-masculine/feminine template for each age group. To produce the masculinised face, each individual was morphed by 50% with the hyper-masculine template, while morphing each face by 50% with the hyper-feminised template produced the feminised image. This effectively manipulated face shape and colour along the dimension of objectively defined sexual dimorphism. All manipulation of images was conducted in the Fantamorph 5 software package. See Fig. 1 for example stimuli. The order in which face pairs were presented and the location of the masculinised face in each pair (left or right) were randomised for each participant.

Fig. 1. Feminised (left) and masculinised (right) faces of young (top) and middle-aged (bottom) male targets.

3.3. Measures

3.3.1. Pathogen disgust

The Three-Domain Disgust Scale (Tybur, Lieberman, & Griskevicius, 2009) contains 21 items measuring disgust across three factors, being moral, sexual, and pathogen disgust. While all three subscales were administered, here we focus on the pathogen disgust subscale (seven items), which refers to aversion to pathogen contagions that could threaten one's health. Participants rated their level of disgust on a 7-point scale (0 = *not at all disgusting*; 6 = *extremely disgusting*) on statements such as “Accidently touching a person's bloody cut.” The Three Domain Disgust Scale was administered as part of a larger set of questionnaires aimed at assessing preference for facial masculinity across a wide age group. Additional measures not focal to the hypothesis included measures of sociosexual orientation, participants' own masculinity/femininity, and information on contraception use and menstrual cycle.

3.4. Analysis

Each participant rated the total number of faces in either the young (27 faces) or old (24 faces) stimuli condition; this resulted in 11,332 observations. These data are hierarchical, such that each face pair rated by each participant (level 1) are nested in the participant themselves (Level 2). As such, we analysed the data using multilevel package in the R software package (for an explanation of this technique and its advantages over other approaches to analysing hierarchical data, see (Raudenbush & Bryk, 2002). In the model, the outcome variable was the rated preference for the masculinised face compared to the feminised face for each face pair. At level 2, pathogen disgust and participants' age were entered as continuous predictors with stimuli age as a dichotomous variable (0 = young stimuli; 1 = middle-aged stimuli). All interaction terms between level 2 predictors were also included. To aid interpretation, all continuous variables were standardised before being entered into the model. See the Supplementary Material (available on the journal's Website at www.ehbonline.org) for additional detail on the analyses conducted.

4. Results

The intra-class correlation (i.e., the proportion of the total variance that is between-rater variance) for masculinity preferences was .37. For full information on the random effects from the HLM analysis, see the Supplementary Materials (available on the journal's Website at www.ehbonline.org). Participants reported whether they used hormonal contraception (“Do you currently use hormonal contraception, such as birth control pills, a contraceptive injection, or a contraceptive implant?”) as well as their menopause status (“Have you gone through menopause?”). While we found a significant difference in age between women that used and did not use hormonal contraception [$t(469) = 7.17$, $p < .001$], and menopause status [$t(468) = -17.82$, $p < .001$], the pattern of results did not differ in models controlling for these variables. Therefore, we only report the original analyses here.

The fixed effects from the HLM analysis are reported in Table 1. Despite the masculine face being randomly presented on either the right or left side, participants showed a preference for faces on the right; therefore, we included presentation side as a level 1 predictor to control for this (0 = masculine face presented on the left; 1 = masculine face presented on the right). The only other significant predictor was stimuli age group, such that preference for facial masculinity increased when participants were rating the older stimuli set. Contrary to previous findings, there was no significant positive association between pathogen disgust and preference for facial masculinity. No interaction terms between predictors were significant.

Previous findings that women more sensitive to pathogen disgust prefer more masculine faces were derived from samples of only young women rating young stimuli. As a comparable analysis, we reran the above while only including young participants (<35 years old) who rated the young stimuli set ($n = 92$); we found a significant positive effect of pathogen disgust on preference for facial masculinity (Table 2). This may suggest that the influence of women's pathogen disgust on facial masculinity preferences in the forced choice design is limited to young people rating young stimuli. While we only report results from pathogen disgust here, we note that we did not find the same pattern of results with moral or sexual disgust.

5. Study 2

In study 1, we manipulated facial sexual dimorphism using templates that matched the age of the individuals in the stimuli. Given that there may be morphological differences between younger male and female faces compared to older male and female faces, an alternative interpretation may be that the effect of pathogen disgust on

Table 1
HLM (γ) coefficients (with standard errors) and associated *t* statistics for estimated fixed effects.

	γ (*SE*)	*t* (approx. *df*)	*p*-Value
Intercept	.02 (.03)	.51 (439)	.61
Pathogen disgust	.01 (.03)	.27 (439)	.788
Participant's age	-.04 (.03)	-1.30 (439)	.200
Stimuli age group	.23 (.06)	3.91 (439)	<.001***
Pathogen disgust × participant's age	-.04 (.03)	-1.40 (439)	.16
Pathogen disgust × stimuli age group	.01 (.06)	.22 (439)	.819
Participant's age × stimuli age group	.07 (.06)	1.21 (439)	.228
Pathogen disgust × participant's age × stimuli age group	.06 (.06)	1.00 (439)	.319
Presentation side	.07 (.02)	3.37 (446)	.001**

*p < .05, **p < .01, ***p < .001.

Table 2
HLM (γ) coefficients (with standard errors) and associated *t* statistics for estimated fixed effects when only including young participants rating young stimuli.

	γ (*SE*)	*t* (approx. *df*)	*p*-Value
Intercept	−.02 (.06)	−.36 (90)	.721
Pathogen disgust	.13 (.06)	2.04 (90)	.044*
Presentation side	.08 (.05)	1.41 (90)	.157

*p < .05, **p < .01, ***p < .001.

masculinity preferences may be specific to the morphological differences between younger male and female faces rather than the age of participants. We test this alternative in study 2, which is identical to study 1 except that older faces were manipulated using templates derived from younger faces, while younger stimuli were manipulated using templates derived from older faces.

6. Method

6.1. Participants

A total of 433 women were recruited from https://www.MTurk.com in return for online credit. Identical to study 1, participation was conditional on being female, heterosexual and residing in the United States. Participants missing data on any variable ($n = 22$), or who fell outside the selection criteria ($n = 16$) were removed from analysis; reducing the sample size to 395 ($n = 38.55$ years, $SD = 12.67$, age range = 18–75 years).

6.2. Stimuli

The faces and method of manipulating facial sexual dimorphism were identical to those of study 1, except for the templates used to manipulate sexual dimorphism of the young and older stimuli. While we used age-matched templates to manipulate facial masculinity/femininity in study 1, here we used the older templates to manipulate the younger faces, and the younger template to manipulate the older faces.

6.3. Procedure

The procedure for study 2 was identical to that of study 1.

6.4. Analysis

Each participant rated the total number of faces in either the young (27 faces) or old (24 faces) stimuli condition; this resulted in 10,093 observations. Analysis conducted was identical to study 1. See the Supplementary Material (available on the journal's Website at www.ehbonline.org) for additional details.

7. Results

The intra-class correlation (i.e., the proportion of the total variance that is between-rater variance) for masculinity preferences was .39, indicating there was significant variation in preferences between participants. Similar to study 1, we found a significant difference in age between women that used and did not use hormonal contraception [$t(392) = 6.67$, $p < .001$], and menopause status [$t(393) = -22.42$, $p < .001$]. Also similar to study 1, the pattern of results did not differ in models controlling for these variables. Therefore, we only report the original analyses here.

The fixed effects from the HLM analysis are reported in Table 3. No significant effects of participant or stimuli age, or pathogen disgust were found on masculinity preference, and there were no significant interactions. This suggests that the null finding with older adults in study 1 is not due to a difference in morphology between older male and female faces and younger male and female faces. It also suggests that the effects of pathogen disgust on young participants' preference for facial masculinity may only exist for young faces when the sexual dimorphism manipulation is also based on young faces.

Table 3
HLM (γ) coefficients (with standard errors) and associated *t* statistics for estimated fixed effects.

	γ (*SE*)	*t* (approx. *df*)	*p*-Value
Intercept	.01 (.04)	.06 (387)	.953
Pathogen disgust	.04 (.03)	1.36 (387)	.176
Participant's age	.05 (.03)	1.55 (387)	.123
Stimuli age group	−.07 (.07)	−.09 (387)	.278
Pathogen disgust × participant's age	−.02 (.03)	−.68 (387)	.496
Pathogen disgust × stimuli age group	.02 (.07)	.32 (387)	.752
Participant's age × stimuli age group	−.10 (.07)	−1.55 (387)	.123
Pathogen disgust × participant's age × stimuli age group	.04 (.07)	.67 (387)	.503
Presentation side	−.01 (.02)	−.14 (387)	.892

8. Study 3

In study 3, we use a different paradigm to test for the same associations between pathogen disgust and preference for facial masculinity. Here, participants rated the attractiveness of individually presented facial photos of males that naturally varied on facial masculinity and age in two face sets. From these attractiveness ratings we were able to infer preference for facial masculinity and test for any association with pathogen disgust.

9. Method

9.1. Participants

Participants were 486 females recruited from MTurk in return for online store credit. Participants who did not identify as a heterosexual female ($n = 31$), were missing data on any variable ($n = 60$), did not pass control questions that indicated paying attention to items ($n = 4$), or fell outside the age range of 18–50 years ($n = 5$) were removed from analysis. This reduced the sample to 386 ($M = 34.99$, $SD = 8.23$).

9.2. Stimuli

Participants rated faces from two stimuli sets for a total of 91 faces. The order in which stimuli sets were presented and also the order of faces within each set were randomised. Participants rated each face on attractiveness of a 100-point slide scale (0 = very unattractive; 100 = very attractive).

9.2.1. Face set 1

The first face set was the FACES database used in study 1 (Ebner et al., 2010). Precise ages of each target face were not provided, but instead were separated two age groups. As in study 1, there were 27 faces between the ages of 19 and 31 years, and 24 faces between the ages of 39 and 55 years (coded as 0 = younger group, 1 = older group). Online volunteers (17 males, 21 females, $M = 26.00$, $SD = 7.27$) pre-rated each face on facial masculinity.

9.2.2. Face set 2

The second set contained 40 faces evenly ranging in age from 18 to 55 years collected from an online database. Precise ages of the individuals when photographs were taken were known for this set, so it was possible to include stimuli age as a continuous variable. These faces were also pre-rated on facial masculinity by 54 online volunteers ($M = 23.69$, $SD = 9.21$).

9.3. Measures

After rating faces on attractiveness, participants completed the Three Domain Disgust Scale as described in study 1. No other measures were included in the survey.

9.4. Analysis

Similar to study 1, a hierarchical linear model was used to analyse the data where each face rated (level 1) was nested in the participants themselves (level 2). For face set 1, there were 15,440 observations, while there were 19,686 observations for face set 2. As with study 1, we analysed the data using hierarchical linear modelling using the multilevel package in the R software package. In the model, the outcome variable was the ratings of attractiveness. At level 2, participants' age and pathogen disgust were entered as predictors, while level 1 predictors included pre-rated facial masculinity and stimuli age. All interaction terms between predictors were also included in analysis. To aid interpretation, all continuous variables were standardised before being entered into the model. See the Supplementary Material (available on the journal's Website at www.ehbonline.org) for additional detail on the analyses conducted.

10. Results

We first analysed the two face sets separately; however, the pattern of results of both sets was fairly similar, so we report here an analysis that combined both face sets (for the results of the analyses where face sets were kept separate, see the Supplementary Materials available on the journal's Website at www.ehbonline.org). In order to combine face sets, stimuli ages from face set 2 were dichotomised to as closely match face set 1 as possible (0 = 18–35 years; 1 = 36–55 years). The intra-class correlation (i.e., the proportion of the total variance that is between-rater variance) for attractiveness rating was .29. For full information on the random effects from the HLM analysis for the combined face sets, see the Supplementary Materials (available on the journal's Website at www.ehbonline.org).

The fixed effects from the HLM analysis are reported in Table 4. We found main effects of all predictors; overall, older participants and those with lower pathogen disgust gave higher attractiveness ratings. Younger and more feminine stimuli also received higher attractiveness ratings. Importantly, and contrary to previous work, we did not find an overall significant interaction between pathogen disgust and facial masculinity on attractiveness ratings, and the association was not significantly moderated by either participants' age or stimuli age. Also, contrary to the results from study 1, the relationship between pathogen disgust and preference for facial masculinity remained non-significant when only looking at younger participants' (<35 years old) ratings of younger stimuli (<35 years old). Thus, when not using the forced-choice paradigm, we find no evidence for an association between pathogen disgust and preference for facial masculinity regardless of the age of the participants or stimuli.

There were also three significant two-way interactions; as these are not pertinent to the main hypotheses the nature of these interactions are only described briefly here. First, older participants rated older faces significantly less negatively compared to younger participants. There was also a significant interaction between stimuli age and facial masculinity, such that facial masculinity was not associated with attractiveness in older faces, but was negatively associated with attractiveness in younger faces. Finally, there was a significant interaction between participants' age and pathogen disgust, such that younger participants with high pathogen disgust gave higher attractiveness ratings compared to all older participants, or young participants with low pathogen disgust. This pattern of results is specific to pathogen disgust, and not sexual or moral disgust.

Some evidence to suggested perceived masculinity from subjective ratings might measure a different construct to objective structural masculinity (Scott, Pound, Stephen, Clark, & Penton-Voak, 2010). To address this we ran an additional analysis using objectively derived facial masculinity scores from landmark coordinates. Here, we found a significant positive correlation between rated masculinity and objective masculinity in men ($r = .38$, $p < .001$). The pattern of results for objective masculinity, pathogen disgust, participant age and stimuli age is the same pattern found with rated masculinity reported above, which suggests that results are not specific to subjectively rated masculinity. For full details of analyses conducted with objective facial masculinity see the Supplementary Materials (available on the journal's Website at www.ehbonline.org).

Table 4
HLM (γ) coefficients (with standard errors) and associated *t* statistics for estimated fixed effects.

	γ (*SE*)	*t* (approx. *df*)	*p*-Value
Intercept	−.01 (.03)	−.23 (382)	.820
Pathogen disgust	−.14 (.03)	−5.24 (382)	<.001***
Participant's age	.10 (.03)	3.60 (382)	.004**
Facial masculinity	−.03 (.01)	−4.51 (382)	<.001***
Stimuli age group	−.82 (.02)	−39.28 (382)	<.001***
Participant's age × facial masculinity	.004 (.01)	.56 (382)	.572
Participant's age × stimuli age group	.07 (.03)	3.33 (382)	.009**
Pathogen disgust × participant's age	−.06 (.03)	−2.21 (382)	.028*
Pathogen Disgust × Facial Masculinity	.003 (.01)	.40 (382)	.686
Pathogen disgust × stimuli age group	.004 (.02)	.22 (382)	.823
Facial masculinity × stimuli age group	.03 (.01)	2.49 (382)	.013*
Pathogen disgust × participant's age × facial masculinity	.01 (.01)	1.38 (382)	.168
Pathogen disgust × participant's age × stimuli age group	.000 (.02)	.02 (382)	.983
Pathogen disgust × facial masculinity × stimuli age group	.003 (.01)	.30 (382)	.767
Participant's age × facial masculinity × stimuli age group	−.01 (.01)	−1.26 (382)	.206
Pathogen disgust × participant's age × facial masculinity × stimuli age group	.01 (.01)	.63 (382)	.530

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.01$.

11. Discussion

Contrary to predictions based on previous research, we did not find an overall link between women's pathogen disgust and preference for facial masculinity in any of the three studies. Previous research that found a link between pathogen avoidance and masculinity preferences used only young adult participants assessing young adult targets, and relied solely on the forced-choice design. We replicated that specific effect in study 1 when we only considered younger women who rated younger male targets in the forced-choice design (as per previous studies in which the effect was found), but despite large samples the association was not observed in older participants, or for older stimuli, or in study 2 when younger faces were manipulated using sexual dimorphism based on older faces. Also, there were no significant effects of pathogen disgust for any participants or stimuli when the forced-choice design was not used. Our results suggest that the association between women's pathogen avoidance and preference for masculinity may be quite age- and methodology-specific.

The results from study 1 suggest that any association between pathogen disgust and women's masculinity preference is age-dependent (though, given that we were unable to find such a pattern in study 2 and 3, any claim of an age-dependent link is tentative). If an age-dependent link does exist, it implies that the inferences normally drawn from the link—i.e., that facial masculinity indicates good health in men and that women have evolved mate preferences that are calibrated to their degree of pathogen avoidance—may not apply to older adults. First, it needs to be established whether masculinity is associated with health in older men as well as younger men. The studies that found a link between male facial masculinity and health used young samples (Gangestad et al., 2010; Rantala et al., 2012; Rhodes et al., 2003; Thornhill & Gangestad, 2006), though even then the link is controversial as other studies have found null effects (Thornhill & Gangestad, 2006; van Anders, 2010) or even negative association (Booth, Johnson, & Granger, 1999; Muehlenbein & Bribiescas, 2005)—but future studies should endeavour to investigate older as well as younger men.

If any link between facial masculinity and health is age-dependent, one possible explanation could be that, because testosterone-dependent masculinisation of face shape occurs primarily during adolescence, facial masculinity best indicates immunocompetence during adolescence and the period immediately following (young adulthood), whereas by later-adulthood the link has deteriorated. This is supported by results from study 2, where pathogen disgust did not influence sexual dimorphism differences based on older faces, even with young participants rating young stimuli. In later-adulthood, characteristics other than facial masculinity might better indicate current health in men—this may include facial skin colour or texture, or facial symmetry, as these may be traits more readily influenced by health perturbations faced in adulthood compared to facial sexual dimorphism.

As for why older women might not show an effect, this could be because older women are less likely to reproduce and so heritable immunocompetence is of less relevance (assuming facial masculinity is associated with good genes). This explanation is congruent to findings that women's facial preferences can differ according to reproductive capability, such as between childhood and adolescence (Saxton, Caryl, & Roberts, 2006), or between pre-menopausal and post-menopausal women (Jones, Vukovic, Little, Roberts, & DeBruine, 2011; Vukovic et al., 2009), and is consistent with the finding that the association between women's pathogen avoidance is also specific to male faces (Little et al., 2011). Alternatively, older women's preferences may be primarily calibrated for choosing older male partners in whom the link between facial masculinity and health has deteriorated, or perhaps the null effect is a side-effect of hormonal changes that occur during women's later-adulthood. Changes to hormonal levels due to the menopause process can begin around age 35 years (Al-Assawi & Palacios, 2009), and hormone status, which can be influenced by contraception use or the menstrual cycle, has also been associated with changes in women's facial masculinity preferences (Little, Burriss, Petrie, Jones, & Roberts, 2013; Welling et al., 2007). However, the relationship between hormones and our findings is unclear, as while we found significant associations between age, and hormonal contraception use and rate of menopause in studies 1 and 2, controlling for these did not influence the pattern of results.

Results from study 2 suggest that the age-dependent effect in study 1 is not solely due to different sexual dimorphism transforms being applied to older and younger face (i.e., the sexual dimorphism templates used for the manipulation matched that of the age group). In addition, in study 1 we found no relationship of pathogen disgust on masculinity preference for older participants rating the younger faces (which we would expect if the effect was based solely on the younger manipulation; the effect with older participants rating younger faces in fact trends in the opposite direction). Thus, these results may further suggest the sexual dimorphism between younger faces and not between older faces may be a cue to health. Given that previous studies that have purported a link between pathogen avoidance and masculinity preference often use a sexual dimorphism transform based on young faces, this raises further issues if the effect cannot generalise to other sexual dimorphism manipulations.

In addition, contrary to findings from forced-choice studies of young participants rating young stimuli in previous papers and here in study 1, we did not find any association between pathogen disgust and revealed preference for facial masculinity in study 3. Study 3 used a standalone-rating design in which participants' preferences are inferred from their rating of each standalone facial photo, rather than a forced choice between two photos. Studies that have found an association of pathogen disgust with masculinity preference have exclusively used the forced-choice design (DeBruine, Jones, Crawford, et al., 2010; DeBruine, Jones, Tybur, et al., 2010; Jones et al., 2013; Little et al., 2011), while another study using a different paradigm failed to replicate the association (Lee et al., 2013). This may suggest that the effect is specific to the forced-choice design.

One possible explanation for this specificity is that the forced-choice design is more sensitive at detecting a true association, and that associations tested via standalone attractiveness ratings lack sufficient power. This possibility is made less likely by the fact that studies using the ratings paradigm have used unusually large sample sizes to compensate for this (studies using a rating paradigm now have an average $n = 362$, compared to previous forced-choice studies that have an average $n = 133$; (DeBruine, Jones, Tybur, et al., 2010; Jones et al., 2013; Lee et al., 2013; Little et al., 2011; Penton-Voak et al., 2004) and that we would expect results to at least trend in the predicted direction for study 3 ($N = 386$), which they do not. Alternatively, the forced-choice design may tap slightly different construct than the ratings paradigm—for example, a forced choice between two adjacent faces seems more likely to be affected by conscious awareness of differences in masculinity than standalone ratings of random faces. However, it should be noted that previous research has found that masculinity preference measured by a forced-choice design is associated with masculinity preference measured using other methods (DeBruine et al., 2006). We also note that when we refer to the literature relying on the forced-choice paradigm, we are specifically discussing the effect of women's pathogen avoidance on facial masculinity preferences. Associations have been found between pathogen avoidance and women's preferences in other domains that are measured using other paradigms; for instance, pathogen avoidance has been shown to influence stated masculinity preferences (Jones et al., 2013), preference for adiposity (Fisher, Fincher, Hahn, DeBruine, & Jones, 2013), and preference for physical attractiveness (Gangestad & Buss, 1993; Lee et al., 2013) when they are measured using a ratings paradigm.

Regardless, these results question the generality of the association between pathogen disgust and facial masculinity preferences, and further research is needed using other methodologies, as well as participants and stimuli of a wider range of ages. These studies highlight the complexities of human mate choice, particularly surrounding pathogen avoidance and preference for facial masculinity. Individual differences in pathogen disgust sensitivity might be important in the quest to understand the interrelation of sexual selection and facial masculinity, but to this purpose it is important to establish the generality or specificity of any association with women's facial masculinity preferences. Our findings point towards a quite specific association for young people judging young stimuli in a forced-choice design, but further research is needed to interrogate this further.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2014.12.001.

Acknowledgments

We thank Lennan Petersen for help with data collection for study 1, and Harry Pan for help with stimuli creation.

References

Al-Assawi, F., & Palacios, S. (2009). Hormonal changes during menopause. *Maturitas*, *63*, 135–137.

Booth, A., Johnson, D. R., & Granger, D. A. (1999). Testosterone and men's health. *Journal of Behavioral Medicine*, *22*(1), 1–19.

DeBruine, L. M., Jones, B. C., Crawford, J. R., Welling, L. L. M., & Little, A. C. (2010a). The health of a nation predicts their mate preferences: Cross-cultural variation in women's preferences for masculinized male faces. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1692), 2405–2410.

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*(1592), 1355–1360.

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

Ebner, N., Riediger, M., & Lindenberger, U. (2010). FACES—A database of facial expressions in young, middle-aged, and older women and men: Development and validation. *Behavior Research Methods*, *42*, 351–362.

Fisher, C. I., Fincher, C. L., Hahn, A. C., DeBruine, L. M., & Jones, B. C. (2013). Individual differences in pathogen disgust predict men's but not women's, preferences for facial cues of weight. *Personality and Individual Differences*, *55*(7), 860–863.

Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. *American Naturalist*, *139*(3), 602–622.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology*, *14*, 89–96.

Gangestad, S. W., Merriman, L. A., & Thompson, M. E. (2010). Men's oxidative stress, fluctuating asymmetry and physical attractiveness. *Animal Behaviour*, *80*, 1005–1013.

Jones, B. C., 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*(5), 373–379.

Jones, B. C., Vukovic, J., Little, A. C., Roberts, S. C., & DeBruine, L. M. (2011). Circum-menopausal changes in women's preferences for sexually dimorphic shape cues in peer-aged faces. *Biological Psychology*, *87*, 453–455.

Lee, A. J., Dubbs, S. L., Kelly, A. J., von Hippel, W., Brooks, R. C., & Zietsch, B. P. (2013). Human facial attributes, but not perceived intelligence, are used as cues of health and resource provision potential. *Behavioral Ecology*, *24*(3), 779–787.

Lee, A. J., Mitchem, D. G., Wright, M. J., Martin, N. G., Keller, M. C., & Zietsch, B. P. (2014). Genetic factors increasing male facial masculinity decrease facial attractiveness of female relatives. *Psychological Science*, *25*(2), 476–484.

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*(6), 892–895.

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

Little, A. C., DeBruine, L. M., & Jones, B. C. (2011). 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*(1714), 2032–2039.

Little, A. C., Saxton, T. K., Roberts, S. C., Jones, B. C., DeBruine, L. M., Vukovic, J., et al. (2010). Women's preferences for masculinity in male faces are highest during reproductive age range and lower around puberty and post-menopause. *Psychoneuroendocrinology*, *35*, 912–920.

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

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.

Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, *31*(3), 157–175.

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*(694).

Raudenbush, S. W., & Bryk, A. S. (2002). *Hierarchical linear models: Applications and data analysis methods* (2 ed.). Thousand Oaks, California: Sage Publications.

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Proceedings of the Royal Society of London B*, *270*, S93–S95.

Saxton, T. K., Caryl, P. G., & Roberts, S. C. (2006). Vocal and facial attractiveness judgments of children, adolescents and adults: The ontogeny of mate choice. *Ethology*, *112*(12), 1179–1185.

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*(3), 579–589.

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*(10), e13585.

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*(4), 289–296.

Thornhill, R., & Gangestad, S. W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior*, *27*, 131–144.

Tybur, J. M., & Gangestad, S. W. (2011). Mate preferences and infectious disease: Theoretical considerations and evidence in humans. *Philosophical Transactions of the Royal Society of London. Series B-Biological Sciences*, *366*(1583), 3375–3388.

Tybur, J. M., Lieberman, D., & Griskevicius, V. (2009). Microbes, mating, and morality: Individual differences in three functional domains of disgust. *Personality Processes and Individual Differences*, *97*(1), 103–122.

van Anders, S. M. (2010). Gonadal steroids and salivary IgA in healthy young women and men. *American Journal of Human Biology*, *22*, 348–352.

Vukovic, J., Jones, B. C., DeBruine, L. M., Little, A. C., Feinberg, D. R., & Welling, L. L. M. (2009). Circum-menopausal effects on women's judgements of facial attractiveness. *Biology Letters*, *5*(1), 62–64.

Welling, L. L. M., Jones, B. C., DeBruine, L. M., Conway, C. A., Law Smith, M. J., Little, A. C., et al. (2007). Raised salivary testosterone in women is associated with increased attraction to masculine faces. *Hormones and Behavior*, *52*, 156–161.

Zahavi, A. (1975). Mate selection—Selection for a handicap. *Journal of Theoretical Biology*, *53*(1), 205–214.