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# Facial masculinity is related to perceived age but not perceived health

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#### **Abstract**

Variation in women's preferences for male facial masculinity may reflect variation in attraction to immunocompetence or to maturity. This paper reports two studies on (a) the interrelationships between women's preferences for masculinity, apparent health, and age in male faces and (b) the extent to which manipulating each of these characteristics affects women's attributions of the remaining characteristics. Both studies were carried out with a large sample of the general public (Studies 1a and 2a) and independently in a laboratory environment with smaller undergraduate samples (Studies 1b and 2b). In both samples, masculinity and age preferences were positively related, and masculinity preferences were not associated with preferences for apparent health. There was also a positive relationship between perceived age and perceived masculinity in both samples, but evidence for a link between perceptions of masculinity and health was equivocal. Collectively, these findings suggest that variation in women's preferences for masculine proportions in male faces

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reflect variation in attraction to male age and do not support a strict immunocompetence explanation of preferences for facial masculinity.

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#### 1. Introduction

Facial masculinity is due to the sexual dimorphism in facial features that emerges at puberty when boys' cranial bones grow, producing heavier brow-ridges, and larger jaws, while girls' faces grow less and retain small brows (leading to a perception of larger eyes), jaws, and noses (Enlow & Hans, 1996; Penton-Voak et al., 2001). Research has shown varying preferences for masculinity in male faces, with some studies finding a female preference for feminine-looking males (e.g., Perrett et al., 1998; Rhodes, Hickford, & Jeffery, 2000) and some a preference for masculine-looking males (e.g., Johnston, Hagel, Franklin, Fink, & Grammer, 2001). Rather than being arbitrary, however, women's preferences for masculinity in male faces vary systematically as a result of their own attractiveness (Little, Burt, Penton-Voak, & Perrett, 2001; Penton-Voak et al., 2003), the phase of their menstrual cycle (Johnston et al., 2001; Penton-Voak et al., 1999), and whether they have a partner (Little, Jones, Penton-Voak, Burt, & Perrett, 2002).

Two different explanations for the possible benefits of masculinity and femininity in male faces have been proposed. The "immunocompetence" explanation rests on a possible direct link between sex hormones and facial features, while the "neoteny" explanation rests upon the link between facial growth and age.

# 1.1. Immunocompetence

The Immunocompetence Hypothesis of Folstad and Karter (1992) proposes that secondary sexual features (those resulting from sex hormones) are honest signals of genetic quality because sex hormones, specifically testosterone, are deleterious to the immune system (Angele & Faist, 2000; Messingham, Shirazi, Duffner, Emanuele, & Kovacs, 2001). Only high-quality, healthy males may be able to tolerate the immunosuppressive effects of testosterone and develop exaggerated secondary sexual traits. Testosterone injections cause increased craniofacial growth (Verdonck, Gaethofs, Carels, & de Zegher, 1999), and jaw size and perceived facial masculinity are positively related to circulating testosterone levels in adult males (Chen, 2002; Penton-Voak & Chen, 2004). Attraction to masculine proportions in male faces may therefore reflect preferences for men displaying cues associated with immunity to infectious disease. This explanation has been widely adopted within facial attraction research (e.g., Johnston et al., 2001; Penton-Voak et al., 1999; Rhodes et al., 2000; Thornhill & Gangestad, 1999). Ratings of men's facial masculinity are also related to their rated apparent health (Johnston et al., 2001; Rhodes, Chan, Zebrowitz, & Simmons, 2003), as

well as actual medical health (Rhodes et al., 2003), which would seem to support an immunocompetence explanation. It should be noted, however, that in the wider literature, whether greater testosterone is associated with greater apparent health or reduced parasite load across individuals (as opposed to within individuals) is unclear, with mixed findings across different species (see Getty, 2002, for a review and possible reasons for this).

## 1.2. Neoteny

Manipulating sexually dimorphic characteristics in faces influences attributions of age, in addition to attributions of masculinity. Increasing feminine traits in faces decreases apparent age (i.e., increases attributions of youth; see e.g., Berry & McArthur, 1985, Perrett et al., 1998). Several researchers have emphasised neoteny, or "baby-facedness," rather than sexual dimorphism per se in their accounts of face preferences. For example, in a series of studies, Cunningham and various coworkers (Cunningham, Barbee, & Pike, 1990; Cunningham, Druen, & Barbee, 1997) suggested that "neotenous" facial features denote youth versus maturity and do not discuss neotenous features in terms of characteristics associated with femininity (see also Berry & McArthur, 1985; Jones, 1995). The "Multiple Fitness Model" (Cunningham et al., 1997) proposes that women prefer men with neotenous features because these features evoke feelings of nurturance, and youthful men are perceived as having the vigour required to raise children. In light of this, it is plausible that variation in preferences for sexual dimorphism in faces is a by-product of variation in preferences for facial cues associated with youth.

#### 1.3. Rationale

The purpose of Study 1 was to investigate the possible links between masculinity (face shape dimorphism, sensu Penton-Voak et al., 1999; Perrett et al., 1998) and age and apparent health (sensu Jones et al., 2001) in female preferences for male faces. Doing so allows the assessment of the functional similarity between masculinity and health/age (i.e., are they used in the same way for mate choice decisions), which is perhaps more informative to attraction research than assessing purely perceptual relationships. Apparent health in male faces is associated with indices of men's genotypic health (MHC heterozygosity: Roberts et al., 2003) and also related to putative indices of men's immune system strength (e.g., facial symmetry: Jones et al., 2001; Penton-Voak et al., 2001; Rhodes et al., 2001) and is therefore an appropriate trait to compare with masculinity when testing the immunocompetence explanation. If masculinity preferences are positively related to preferences for apparent health (but not preferences for older faces), this would support the models of variation in face preferences are positively related to preferences for apparent health), this would support the neoteny explanation of variation in face preferences.

Study 2 directly assessed the perceptual relationships between these characteristics in facial stimuli by examining the effects of manipulating masculinity on perceptions of health and age, and vice versa. Evidence that facial masculinity is associated with health

(but not age) would support the immunocompetence explanation. By contrast, evidence that facial masculinity is associated with age (but not apparent health) would support the neoteny explanation.

Participants in Studies 1a and 2a were members of the public recruited for online studies of face preferences. Participants in Studies 1b and 2b were undergraduate students recruited for a laboratory study of face preferences. Two sets of stimuli were used, which were manufactured from independent samples of face images, to establish if our findings were consistent across independent samples of faces (Studies 1a and 2a use Set A, while Studies 1b and 2b used Set B).

# 2. Study 1

This study investigated how variation in female preferences for facial masculinity relates to variation in preferences for health and age. If masculinity is a proxy for immunocompetence, then masculinity preferences should covary with preferences for apparent health. By contrast, the neoteny explanation predicts that masculinity preference should covary with age preference but does not predict a link between masculinity preference and health preference.

# 2.1. Study 1a

# 2.1.1. Participants

There were 645 female participants (mean age= $26.7\pm6.7$  years, range=16–45) recruited through the laboratory website and the media. The majority of participants reported being of Western origin (42.0% British, 25.5% European, 22.2% North American), and 84.7% reported being Caucasian. All participants reported being heterosexual.

## 2.1.2. Stimuli (Set A)

Three textured composite male base faces were created using the face processing package "Psychomorph" (for an explanation of the methods, see Tiddeman, Burt, & Perrett, 2001). The base faces are depicted in Fig. 1.

"Transforms" were then applied to the base faces to alter apparent masculinity, age, and health. The transformation process involved calculating the differences in skin colour, face shape, and skin texture between a prototype "source" face (e.g., a younger face) and a prototype "destination" face (e.g., an older face) and applying a proportion of that difference to the base face. The difference could be both "added to" the base face (a positive transform, e.g., aging the face) or "subtracted from" the base face (a negative transform, e.g., making the face look younger). After transformation, all images were masked that only the faces were visible (i.e., hair, neck, and ears were excluded) and were standardised to a size of  $400 \times 533$  pixels, with interpupillary distance being approximately 150 pixels.

2.1.2.1. Age. The prototype faces used for the age transforms were a composite of 19 males aged 8–12 years versus a composite of 15 males aged 45–55 years. All faces used in the

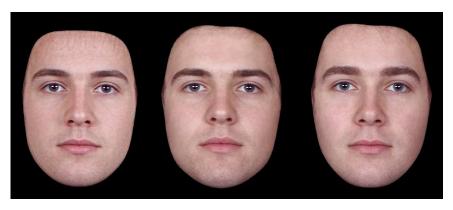


Fig. 1. Base faces made by combining the facial images of Caucasian adult males. Left–right: Male 1 (n = 66, mean age = 21.3±3.4), Male 2 (n = 12, mean age = 21.2±1.6), Male 3 (n = 12, mean age = 22.0±4.8).

transform composites were Caucasian with no facial hair. The base faces were transformed by adding and subtracting 15% of the difference between the two prototypes (see Fig. 2 for an example); colour, shape, and texture were all manipulated.

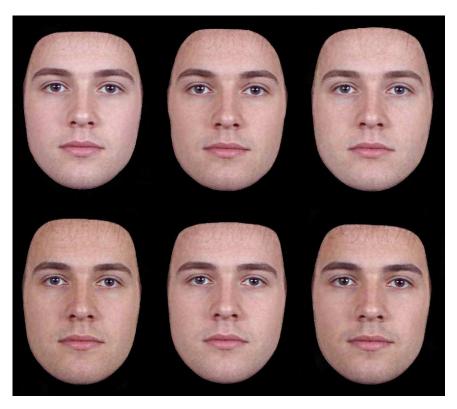


Fig. 2. Male 1 transformed to decrease and increase apparent age, masculinity, and health (Top row, left–right: young, feminine, unhealthy. Bottom row: old, masculine, healthy).

2.1.2.2. Masculinity. The prototypes used for the masculinity transform were a composite of 40 Caucasian females and a composite of 21 Caucasian males. Both prototypes consisted of individuals of the same age (mean 21.0 years) to manipulate masculinity without affecting apparent age. The shape of the faces was transformed 50% in each direction (see Fig. 2). Colour and texture were not changed, as this produces unrealistic changes to feminised images (e.g., abnormally light skin in the place of stubble).

2.1.2.3. Health. The prototypes used for the health transforms were composites of the faces judged most and least healthy from a set of 96 Caucasian male faces (healthy: n=15, mean rated health=5.0, mean age=20.5; unhealthy, n=15, mean rated health=3.2, mean age=22.2), all of whom had been rated by eight males and seven females for apparent general health on a Likert scale from 1 to 7 (where 1=very unhealthy and 7=very healthy). The three base faces were transformed 50% in each direction (see Fig. 2); colour, shape, and texture were all manipulated.

# 2.1.3. Stimulus validation

Using their own computers, a voluntary sample of 35 women (mean age= $26.4\pm9.4$ ) participated via the test website. After being asked their age, participants began the test. A pair of faces was presented using a Java applet, taking up most of the screen. Participants were asked to indicate which face was more masculine (when judging the three masculinity pairs) or healthy (when judging the three health pairs) on a scale underneath the faces, which had the following points from left to right: "much more" (left), "more," "slightly more," "guess (left)," "guess (right)," "slightly more," "more," "much more" (right; see Fig. 3 for the face preference version of the applet). The results were recorded as an eight-point scale, in which 0 represented a very confident choice for the "correct" face. Thus, a mean rating of 3.5 represented no perceived difference between the faces.

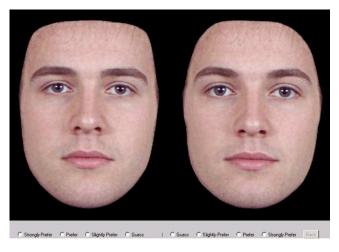


Fig. 3. The Java applet used throughout the study.

During presentation, the orders of face pairs and the left/right position of each face within the pairs were both randomised. Judgement order was fixed as health followed by masculinity and finally age. For the assessment of age, all six faces were presented at one time. Above each face was a box in which participants were asked to type the age they estimated that face to be.

The mean ratings by each participant for health and masculinity were calculated for each set of three pairs. Participants correctly identified the more masculine and healthy faces in that mean scores were significantly above 3.5 on both traits [masculinity: mean=4.39, t(34)=5.73, p<.001; health: mean=5.04, t(34)=7.93, p<.001]. Estimated ages of age stimuli were averaged for all "old" faces and for all "young" faces and compared using matched t tests; "older" faces were judged to be significantly older than the "younger" faces [mean perceived age gap=2.16 years, t(34)=5.12, p<.001].

# 2.1.4. Face preference test

Pairs were presented side by side in the same Java applet as was used for the stimulus validation (see Fig. 3). Results were recorded on an eight-point scale, where 0 represented a preference for feminine/young/unhealthy faces and 7 represented a preference for masculine/old/healthy faces. In the initial instructions, participants were told first to decide which of each pair "you find more attractive" and then to indicate the strength of that preference on the scale below the faces. The reminder "Please indicate which face you prefer and how much you prefer it, by clicking a point below" ran at the top of the screen throughout the test.

## **2.1.5.** Results

Mean scores were calculated for the participants' rated preference (0-7) averaged across all three pairs within each transform set (overall preference means: health mean= $5.03\pm1.08$ ; age mean= $3.82\pm1.42$ ; masculinity mean= $3.24\pm1.25$ ). Age preferences correlated significantly with masculinity preferences  $(r_s=.23,\ n=645,\ p<.001)$ , but there was no significant correlation between masculinity and health preferences  $(r_s=.02,\ n=645)$ . There was no effect of participant's age on their preferences (masculinity  $r_s=.02$ , age  $r_s=-.05$ , health  $r_s=.04$ , n=645), and correlations between preferences for masculinity, health, and age were equivalent when participant's age was partialled out.

# 2.2. Study 1b

To assess the replicability of Study 1a, Study 1b used an independent set of stimuli and a different participant group. It had the same design as Study 1a but was carried out within the University of St. Andrews on laboratory computers, rather than with the public via the Internet.

## 2.2.1. Participants

There were 160 heterosexual female participants (mean age= $20.73\pm1.97$  years, range=17-30) who were undergraduate students and completed the study in the laboratory.

## 2.2.2. Stimuli (Set B)

Eighteen base faces were constructed by averaging 10 randomly chosen faces. Six of these base faces were then transformed along the dimensions of masculinity (sexual dimorphism) and 6 were transformed on apparent health using the same methodology as in Stimuli Set A, but with new independent composites being used for the transforms. The masculinity and health stimuli have previously been reported by Cornwell et al. (2004) and Jones (2004), respectively. The only departure from the methodology used in Study 1a was in the age transforms applied to the remaining 6 base faces. The prototype faces used for the age transforms were a composite of 15 males aged 15–18 years versus a composite of 15 males aged 25–29 years. The base faces were transformed by adding and subtracting 30% of the difference between the two prototypes; as before, colour, shape, and texture were all manipulated.

## 2.2.3. Stimulus validation

Eleven women (mean age= $23.3\pm6.1$ ) assessed the health and masculinity of the health and masculinity stimuli, respectively. Testing took place in the laboratory on computers. The participants were presented with the face pairs and asked, within each pair, which looked more masculine/healthy. Face pairs were presented in a random order within each judgement block, and the order of judging masculinity and health was randomised. The computer returned the data as a dichotomous result in which 0 indicated a choice for the feminine or unhealthy face and 1 indicated a choice for the masculine or healthy face. For each participant, the proportion of masculine faces chosen over feminine faces and the proportion of healthy faces chosen versus unhealthy were calculated. Proportions were compared against chance (0.5) using one-sample t tests. Participants selected the correct faces significantly more than chance for both masculinity [mean=0.89, t(10)=8.48, p<.001] and health [mean=0.92, t(10)=9.04, p<.001].

The age stimuli were validated by 16 women (mean age= $21.9\pm2.8$ ). Testing took place in the laboratory, on computers. The faces were presented individually in a random order. Beside each face was a box in which participants were asked to type the age they estimated that face to be. "Older" faces were judged to be significantly older than the "younger" faces [mean perceived age gap=2.28 years, t(15)=4.54, p<.001].

# 2.2.4. Face preference test

The face preference test was the same as used in Study 1a. However, this time, participants were given the test twice: once with the instruction to make the attractiveness judgement based on choosing a potential long-term partner and once based on choosing a potential short-term partner. The order of long- and short-term judgements was randomised.

## **2.2.5.** Results

Masculinity preference correlated significantly with age preference for short-term preferences ( $r_s$ =.22, n=160, p=.005) but not for long term ( $r_s$ =.05). There was no correlation between masculinity and health preferences (short term:  $r_s$ =.03; long term:  $r_s$ =.004). Participant's age did not correlate with any short-term preferences or with long-

term masculinity preferences (all  $r_s$ <.13), although younger women preferred younger ( $r_s$ =.18, p<.05) and healthier ( $r_s$ =.18, p<.05) long-term partners (correlations between preferences for masculinity, health, and age were equivalent when the participant's age was partialled out).

# 2.3. Discussion

Studies 1a and 1b found a link between preference for masculinity and preference for age in male faces, but no link between preference for masculinity and preference for health in male faces. The positive relationship between masculinity preference and age preference supports the discussion of youth and maturity related traits as a basis trcitivnessa of

#### 3.1.3. Procedure

Participants completed the experiment on their own computers. They were asked to estimate the ages of the six health (three healthy, three unhealthy) and six masculinity (three masculine, three feminine) stimuli in the same way as the participants in Study 1. They were then asked to decide which face of each age and health pair looked the most masculine, and which of each masculinity pair looked the healthiest using the same eight-point scale as in Study 1. All participants judged age, followed by masculinity, and then health. Interrater agreement was high for both masculinity and health ratings and for age estimates (all Cronbach's alphas >.85).

#### 3.1.4. Results

Each participant's age estimates were combined for the three high-masculinity and three low-masculinity faces separately. Similarly, pairs of age estimates were derived for the three high-health and the three low-health faces. Masculinity and health ratings for the three pairs were averaged into single composite scores separately for each judgement.

- 3.1.4.1. Age and masculinisation. A repeated measures t test showed that masculinised faces were perceived as significantly older than feminised faces [mean perceived age gap=1.72 years, t(46)=4.00, p<.001]. One-sample t tests showed that there was also a significant effect of manipulating facial age on perception of masculinity. As in Study 1, mean scores were compared against 3.5, which would indicate no perceived difference between the two faces. Mean scores for the age pairs were significantly above 3.5 [mean=5.10, t(46)=9.94, p<.001], showing that participants perceived the older faces as being more masculine.
- 3.1.4.2. Health and masculinisation. There was a significant effect of manipulating facial health on the perception of masculinity and also an effect of manipulating masculinity on the perception of health. Mean scores for masculinity ratings of health pairs were significantly above 3.5 [mean=4.59, t(46)=5.82, p<.001], showing that participants perceived the healthier males as more masculine. In contrast, mean scores for health ratings of masculinity pairs were significantly below 3.5 [mean=2.87, t(46)=4.26, p<.001], showing that participants perceived the more feminine faces as being healthier than the masculine faces.

# 3.2. Study 2b

## 3.2.1. Participants

There was a sample of 30 female undergraduate students (age range 21 to 50 years).

## 3.2.2. Stimuli (Set B)

The same stimuli were used as in Study 1b, that is, six masculinity pairs, six health pairs, and six age pairs.

#### 3.2.3. Procedure

The participants completed the task on computers in departmental laboratories. They rated the masculinity and health of the stimuli as in Study 2a. However, rather than guessing the ages of the stimuli, they compared each pair and rated which of the faces appeared older, using the same method as for the masculinity and health ratings. The order of rating health, masculinity, and age was randomised.

#### 3.2.4. Results

- 3.2.4.1. Age and masculinisation. Mean scores for the age ratings of the masculinity pairs did not differ significantly from 3.5 [mean=3.71, t(29)=1.01], showing that participants perceived neither face as being older. Mean scores for the masculinity ratings of the age pairs were significantly above 3.5 [mean=5.04, t(29)=11.12, p<.001], showing that participants perceived the older faces as being more masculine.
- 3.2.4.2. Health and masculinisation. Mean scores for masculinity ratings of health pairs were significantly above the indifference point of 3.5 [mean=3.99, t(29)=2.24, p<.05], showing that participants perceived the healthier males as more masculine. Mean scores for health ratings of masculinity pairs did not differ from 3.5 [mean=3.51, t(29)=0.06], showing that neither face appeared healthier.

Table 1 gives a summary of the results of Study 2.

## 3.3. Discussion

The purpose of Study 2 was to assess the degree to which masculinity is associated with perceptions of age and health. It was found that masculinity and age in faces are perceptually related. Artificially "aging" a face caused increased attributions of masculinity in both stimulus sets, while masculinising the shape of a face led to an increase in perceived age in Study 2a. As the composites used in the masculinity transformation were of males and females of the same age, this demonstrates that masculinisation has an effect on perceived age independent of actual age. The lack of effect in Study 2b could be due to the different rating method: In Study 2b, participants rated which face within each pair looked older, while in Study 2a, they estimated the ages of each face separately.

Table 1 Summary of results of Study 2 (cross-rating stimuli) and stimulus validations (Study 1)

Older faces	look:
Masculine	
Older	
Masculine	
Older	
	Older

When participants rated health and masculinity, increasing the masculinity of a face shape either decreased perceptions of health (Study 2a) or had no effect at all (Study 2b). In contrast, increasing perceived health increased perceived masculinity in both Studies 2a and 2b. While this ambiguous result does not necessarily contradict the Immunocompetence Hypothesis (because the signal need not represent actual "parasite load," nor be consciously perceivable), it does contrast with the findings of correlational study of Rhodes et al. (2003) and the computer graphic study of Johnston et al. (2001). This contradiction and the ambiguity in the current results may be because the health transforms manipulated shape, colour, and texture, while the masculinity transform changed only the shape of the faces and features. Thus, healthy, dark skin might suggest masculinity, while the lack of change in skin texture in masculinity transforms could obscure an apparent health difference. However, in previous work suggesting that masculinity is linked to genotype quality (e.g., Penton-Voak et al., 1999), researchers also manipulated only the sexual dimorphism of face shape. Therefore, while the masculinity stimuli may lack a degree of ecological validity, the current result (that masculinisation has no clear effect on perceived health) is still important when considering previous mate choice studies.

#### 4. General discussion

These studies investigated the proposal that attraction to facial masculinity could be due to either an attraction to advertised immunocompetence or a by-product of attraction to maturity. Study 1 showed, using two independent stimulus sets, that masculinity and age have a similar impact on attraction but that apparent facial health affects attraction independently of facial masculinity. While the association between masculinity and age preferences does not mean that facial age and facial masculinity are the same, these findings do suggest that the two traits are used in similar ways when judging faces; indeed, Study 2 suggests that perceptions of age and masculinity relate to similar features in the face.

There is little evidence in this study to support an Immunocompetence explanation of female attraction to facial masculinity. Neither stimulus set showed any correlation between masculinity preferences and preferences for apparent health, and increasing facial masculinity did not increase perceived health (although healthier faces did look more masculine). This does not rule out a link between masculinity and real or underlying health, but these results suggest apparent health is of limited importance in masculinity preferences with regard to facial shape.

Given these results, the question is then raised as to the validity of theories relying on "good-genes" explanations of attraction to facial masculinity. Cunningham et al. (1997) did not rely on "good-genes" in that they suggested that women trade off the virility, strength, and status of mature males with the fact that neotenous faces trigger the nurturance instinct. This does not, however, explain why women who consider themselves to be unattractive would be more drawn to neoteny more than other women are (Little et al., 2001) or why women would require a stronger partner at peak fertility points in their menstrual cycle (Penton-Voak et al., 1999). It may be that maturity and/or masculinity is associated with some other feature

that is both heritable and associated with greater reproductive success in offspring possessing that feature. For instance, dominance and status may be heritable and may be associated with higher potential or real reproductive success (e.g., Mueller & Mazur, 1997; Pérusse, 1993). If this is the case, masculine men could still be attractive in short-term contexts for their "good," high-status genes, which they would pass on to "sexy sons" (sensu Weatherhead & Robertson, 1979), but would remain less attractive in long-term contexts because their high reproductive success comes at the expense of potentially reduced paternal investment in offspring. As has been previously shown, facial masculinity is perceived as being associated with increased dominance but decreased suitability to be a father (Perrett et al., 1998). Alternatively, a simple "Fisherian" female bias in favour of masculinity could produce a similar pattern (for avian evidence of the impacts of arbitrary attractiveness on sexual strategy and paternal care, see Burley, Parker, & Lundy, 1996; Magrath & Elgar, 1997).

Collectively our findings suggest that the assumption that a preference for masculinity in males is due to a preference for immunocompetence should be treated cautiously; the present data fail to support this view. Indeed, there is also a lack of strong evidence for a link between testosterone and immune function in humans (Angele & Faist, 2000) and mammals in general (Roberts, Buchanan & Evans, 2004). Facial attraction researchers should perhaps consider alternative advantages and disadvantages of facial masculinity, such as dominance and sexy-sons, versus paternal investment.

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#### References

- Angele, M. K., & Faist, E. (2000). Gender-specific immune response following shock: clinical and experimental data. European Journal of Trauma, 26, 267–277.
- Berry, D., & McArthur, L. (1985). Some components and consequences of a babyface. Journal of Personality and Social Psychology, 48, 312–323.
- Burley, N. T., Parker, P. G., & Lundy, K. (1996). Sexual selection and extrapair fertilization in a socially monogamous passerine, the zebra finch (Taeniopygia guttata). Behavioral Ecology, 7, 218–226.
- Chen, J. Y. (2002). Does testosterone affect bony structures in the face? Are women sensitive to testosterone markers in the face? Paper presented at the 14th Annual Meeting of the Human Behavior and Evolution Society. New Brunswick, NJ: Rutgers.
- Cornwell, R. E., Boothroyd, L. G., Burt, D. M., Feinberg, D. R., Jones, B. C., Little, A. C., Pitman, R. C., Whiten, S., & Perrett, D. I. (2004). Concordant preferences for opposite-sex signals? Human pheromones and facial characteristics. Proceedings of the Royal Society of London Series B, Biological Sciences, 271, 635–640.
- Cunningham, M., Barbee, A., & Pike, C. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. Journal of Personality and Social Psychology, 59, 61–72.

- Cunningham, M., Druen, P., & Barbee, A. (1997). Angels, mentors, and friends: trade-offs among evolutionary, social and individual variables in physical appearance. In J. Simpson, & D. Kenrick (Eds.), Evolutionary Social Psychology. Mahwah, NJ: Lawrence Erlbaum (pp. 109–140).
- Enlow, D. H., & Hans, M. G. (1996). Essentials of Facial Growth. Philadelphia: Saunders.
- Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. American Naturalist, 139, 603-622.
- Getty, T. (2002). Signaling health versus parasites. American Naturalist, 159, 363-371.
- Johnston, V., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: evidence for hormone-related adaptive design. Evolution and Human Behavior, 22, 251–267.
- Jones, B. C. (2004). Pregnancy, menstrual cycle and hormonal contraceptive use alter attraction to apparent health in faces. Paper presented at the 16th Annual Meeting of the Human Behavior and Evolution Society, Berlin, 2004.
- Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Facial symmetry and judgements of apparent health. Evolution and Human Behavior, 22, 417–429.
- Jones, D. (1995). Sexual selection, physical attractiveness and facial neoteny. Current Anthropology, 36, 723-748.
- 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 of London Series B, Biological Sciences, 271(S4), 233–236.
- 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 of London Series B, 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 of London Series B, 269, 1095–1100.
- Magrath, M. J. L., & Elgar, M. A. (1997). Paternal care declines with increased opportunity for extra-pair matings in fairy martins. Proceedings of the Royal Society of London Series B, 264, 1731–1736.
- Messingham, K., Shirazi, M., Duffner, L., Emanuele, M., & Kovacs, E. (2001). Testosterone receptor blockade restores cellular immunity in males mice after burn injury. Journal of Endocrinology, 169, 299–308.
- Mueller, U., & Mazur, A. (1997). Facial dominance in Homo sapiens as honest signalling of male quality. Behavioral Ecology, 8, 569–579.
- Penton-Voak, I. S., & Chen, J. Y. (2004). High salivary testosterone in linked to masculine male facial appearance in humans. Evolution and Human Behavior, 25, 229–241.
- Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., & Perrett, D. I. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. Proceedings of the Royal Society of London Series B, Biological Sciences, 268, 1617–1623.
- Penton-Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P., & Perrett, D. I. (2003). Measures of female condition influence preferences for sexual dimorphism in faces of male Homo sapiens. Journal of Comparative Psychology, 117, 264–271.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L., & Minimasawa, R. (1999). Menstrual cycle alters face preference. Nature, 399, 741–742.
- Perrett, D. I., Lee, K., Rowland, D., Yoshikawa, S., Burt, D. M., Henzi, S., Castles, D. L., & Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. Nature, 394, 884–887.
- Pérusse, D. (1993). Cultural and reproductive success in modern societies: Testing the relationship at the proximate and ultimate levels. Behavioral and Brain Sciences, 16, 267–322.
- 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 Series B, 270, S93–S95.
- 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.
- Rhodes, G., Zebrowitz, L., Clark, A., Kalick, S., Hightower, A., & Mckay, R. (2001). Do facial averageness and symmetry signal health? Evolution and Human Behavior, 22, 31–46.

- Roberts, C., Petrie, M., Gosling, M., Perrett, D., Little, A. C., Jones, B., Penton-Voak, I., & Carter, V. (2003). Human facial attractiveness and the MHC. Paper presented at the 15th Annual Meeting of the Human Behavior and Evolution Society. Lincoln, NE: University of Nebraska-Lincoln.
- Roberts, M. L., Buchanan, K. L., & Evans, M. R. (2004). Testing the immunocompetence handicap hypothesis: a review of the evidence. Animal Behavior, 68, 227–239.
- Thornhill, R., & Gangestad, S. (1999). Facial attractiveness. Trends in Cognitive Sciences, 3, 452-460.
- Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial textures for perception research. IEEE Computer Graphics and Applications, 21, 42–50.
- Verdonck, A., Gaethofs, M., Carels, C., & de Zegher, F. (1999). Effect of low-dose testosterone treatment on craniofacial growth in boys with delayed puberty. European Journal of Orthodontics, 21, 137–143.
- Weatherhead, P. J., & Robertson, R. J. (1979). Offspring quality and the polygyny threshold: the sexy son hypothesis. American Naturalist, 113, 201–208.