

The masculinity paradox: facial masculinity and beardedness interact to determine women's ratings of men's facial attractiveness

B. J. W. DIXSON*, D. SULIKOWSKI†, A. GOUDA-VOSSOS‡, M. J. RANTALA§ & R. C. BROOKS‡

*School of Psychology, University of Queensland, Brisbane, Qld, Australia

†School of Psychology, Charles Sturt University, Bathurst, NSW, Australia

‡Evolution & Ecology Research Centre, School of Biological, Earth & Environmental Sciences, The University of New South Wales, Kensington, Sydney, NSW, Australia

§Turku Brain and Mind Center, Section of Department of Biology, University of Turku, Turku, Finland

Keywords:

facial hair;
facial masculinity;
masculinity;
sexual selection.

Abstract

In many species, male secondary sexual traits have evolved via female choice as they confer indirect (i.e. genetic) benefits or direct benefits such as enhanced fertility or survival. In humans, the role of men's characteristically masculine androgen-dependent facial traits in determining men's attractiveness has presented an enduring paradox in studies of human mate preferences. Male-typical facial features such as a pronounced brow ridge and a more robust jawline may signal underlying health, whereas beards may signal men's age and masculine social dominance. However, masculine faces are judged as more attractive for short-term relationships over less masculine faces, whereas beards are judged as more attractive than clean-shaven faces for long-term relationships. Why such divergent effects occur between preferences for two sexually dimorphic traits remains unresolved. In this study, we used computer graphic manipulation to morph male faces varying in facial hair from clean-shaven, light stubble, heavy stubble and full beards to appear more (+25% and +50%) or less (−25% and −50%) masculine. Women ($N = 8520$) were assigned to treatments wherein they rated these stimuli for physical attractiveness in general, for a short-term liaison or a long-term relationship. Results showed a significant interaction between beardedness and masculinity on attractiveness ratings. Masculinized and, to an even greater extent, feminized faces were less attractive than unmanipulated faces when all were clean-shaven, and stubble and beards dampened the polarizing effects of extreme masculinity and femininity. Relationship context also had effects on ratings, with facial hair enhancing long-term, and not short-term, attractiveness. Effects of facial masculinization appear to have been due to small differences in the relative attractiveness of each masculinity level under the three treatment conditions and not to any change in the order of their attractiveness. Our findings suggest that beardedness may be attractive when judging long-term relationships as a signal of intrasexual formidability and the potential to provide direct benefits to females. More generally, our results hint at a divergence of signalling function, which may result in a subtle trade-off in women's preferences, for two highly sexually dimorphic androgen-dependent facial traits.

Correspondence: Barnaby J.W. Dixon, School of Psychology, McElwain Building, The University of Queensland, St Lucia, QLD 4072, Australia.
Tel.: +61 0423 701211; fax: +61 7 3365 4466;
e-mail: b.dixon@uq.edu.au

Introduction

Sexual selection via female choice has shaped the evolution of male ornamentation in many species (Andersson, 1994; Kokko *et al.*, 2003). Female preferences for attractive traits may evolve under indirect selection, wherein male ornaments signal aspects of underlying genetic quality (Kokko *et al.*, 2003). In other cases, female preferences for exaggerated ornaments evolve under direct selection, wherein male traits directly influence their fertility or survivability without necessarily being associated with any indirect benefits (Kokko *et al.*, 2003; Wong & Candolin, 2005). However, the relative importance of direct and indirect benefits in shaping the evolution of female preferences remains complex (Kokko *et al.*, 2006).

In humans, organizational effects of androgens during foetal development are associated with adult expression of male-typical (i.e. masculine) craniofacial shape (Whitehouse *et al.*, 2015), which includes an enlarged brow ridge, thicker jawline and longer face (Scott *et al.*, 2013). Androgenic effects on beard growth also have a strong genetic basis (Hamilton, 1964; Randall, 2008), and facial hair first appears early in pubertal development and is fully expressed at adulthood (Hamilton, 1958; Hamilton *et al.*, 1958). Facial shape and beardedness represent two of the most striking sexual dimorphisms expressed by humans. This dimorphism, and the extensive variation in facial shape and beardedness among men within and between populations, suggests that sexual selection has shaped their evolution.

Masculine-looking men are physically stronger (Fink *et al.*, 2007; Windhager *et al.*, 2011) and have better long-term health (Rhodes *et al.*, 2003; Thornhill & Gangestad, 2006) but do not exhibit more rapid immune responses than do less masculine-looking men (Rantala *et al.*, 2013). Experimentally exaggerating masculine facial shape in photographs enhances how old, sexually mature, masculine and socially dominant the photographed men appear to raters (Perrett *et al.*, 1998). Similarly, bearded men are rated as older, more masculine, more socially dominant and aggressive looking than clean-shaven men (Addison, 1989; Neave & Shields, 2008; Dixson & Vasey, 2012; Dixson & Brooks, 2013; Geniole & McCormick, 2015; Saxton *et al.*, 2016). Men with beards report higher feelings of masculinity (Wood, 1986), have higher testosterone (Knussman & Christiansen, 1988) and endorse more masculine gender roles than clean-shaven men (Oldmeadow & Dixson, 2016). Yet women's preferences for facial masculinity are mixed (Rhodes, 2006), or in some cases, masculinity reduces men's attractiveness (Perrett *et al.*, 1998; Geniole *et al.*, 2015). Likewise, beards enhance men's attractiveness over clean-shaven faces in some studies (Pellegrini, 1973; Reed & Blunk, 1990; Janif *et al.*, 2014;), but not others (Wogalter & Hosie, 1991;

Muscarella & Cunningham, 1996; Dixson & Vasey, 2012; Dixson *et al.*, 2013; Geniole & McCormick, 2015), and in some cases, there were no distinct preferences between beardedness and clean-shaven faces (Dixson & Brooks, 2013; Saxton *et al.*, 2016).

Part of this variation could be due to antisociality ascribed to masculine and bearded men. More masculine-looking men are rated as less warm, caring and romantic (Perrett *et al.*, 1998; Kruger, 2006), report greater interest and engagement in short-term than long-term relationships (Rhodes *et al.*, 2005; Provost *et al.*, 2006; Boothroyd *et al.*, 2007, 2008), and women accurately assign sexual infidelity in photographs of men varying in facial masculinity (Rhodes *et al.*, 2013). Given the importance of pair bonding in the evolution of human interpersonal relationships and child rearing (Marlowe, 2000; Chapais, 2008), a less masculine male partner may be more attractive than a highly masculine-looking man as a socially investing long-term mate (Perrett *et al.*, 1998). This double-edged sword to masculinity as a signal of men's mate qualities and women's mate preferences for masculine men remains a challenge to untangle in research in human mating behaviour (Scott *et al.*, 2010, 2013; Gangestad & Eaton, 2013).

Mating trade-off hypotheses suggest that women bypass the costly social traits associated with phenotypic masculinity to secure indirect genetic benefits that enhance offspring survival (Gangestad & Simpson, 2000). In support of this view, women's preferences for masculine faces, body shape, vocal pitch and scents are stronger when considering short-term than long-term relationships (Little *et al.*, 2002, 2011). However, preferences for facial hair follow the opposite pattern, becoming greater when considering long-term than short-term relationships (Neave & Shields, 2008; Dixson & Brooks, 2013). Men's facial hair is judged as most attractive when at intermediate levels between a clean-shaven appearance and full beardedness (Neave & Shields, 2008; Dixson & Brooks, 2013; Dixson *et al.*, 2013; Janif *et al.*, 2014; Saxton *et al.*, 2016; Dixson & Rantala, 2016), which coincides with the intermediate ratings of masculinity and dominance between the lowest ascribed to clean-shaven faces and the highest ascribed to full beardedness (Neave & Shields, 2008; Dixson & Brooks, 2013). Thus, there may be a threshold of facial hair density and facial masculinity at which beards operate as an attractive trait (Neave & Shields, 2008; Dixson & Brooks, 2013).

Sexual selection can act simultaneously on preferences for multiple sexual signals (Brooks, 2002; Blows *et al.*, 2003), via either multiple preferences or a single preference that is stimulated by multiple ornaments in concert (Jennions & Petrie, 1997; Brooks & Coultridge, 1999). It is possible that women's preferences for facial masculinity are higher when considering short-term mates as facially masculine men are costly as long-term

mates but may provide indirect benefits to offspring fitness, particularly under ecological conditions where survivability is compromised (DeBruine *et al.*, 2010). However, there is little evidence that beardedness reflects underlying genetic quality in the same manner as masculine craniofacial shape (Dixson & Rantala, 2016). Instead, beards have consistently been shown to enhance men's apparent age, masculinity, social dominance and aggressiveness intrasexually (Roll & Verinis, 1971; Kenny & Fletcher, 1973; Pancer & Meindl, 1978; Wood, 1986; Addison, 1989; Reed & Blunk, 1990; Wogalter & Hosie, 1991; Neave & Shields, 2008; Dixson & Vasey, 2012). There is some evidence that when the mating market is more male-biased, men choose to grow more facial hair, possibly due to increased intrasexual competition when females are scarcer (Barber, 2001).

In this study, we tested whether facial masculinity and beardedness interact to determine men's attractiveness for short-term and long-term relationships. We photographed men when clean-shaven, with 5 days of beard growth (light stubble), 10 days of beard growth (heavy stubble) and full beards of at least 1 month of growth. We then used computer graphic techniques (Perrett *et al.*, 1998), to manipulate facial shape at each level of beardedness to appear more (+25%, +50%) or less (-25%, -50%) masculine. We then collected attractiveness ratings from 8520 female participants, who were randomly assigned to treatments wherein they rated faces for either attractiveness in general, attractiveness for a short-term relationship or attractiveness for a long-term relationship. We aimed to test whether the different signalling functions of beards and facial masculinity were reflected in trade-offs in women's attractiveness judgments between different relationship contexts. We predicted that more masculine faces would be more attractive when considering short-term than long-term sexual relationships due to possible indirect benefits associated with androgenic markers of facial shape. Conversely, given that full beards may communicate aspects of intrasexual formidability rather than signalling genetic quality indirectly, we predicted that they would be considered more attractive for long-term than short-term relationships.

Materials and methods

Photographic stimuli

Thirty-six men (mean age + SD = 27.08 + 5.61 years) of European descent were photographed when clean-shaven, with 5 days of regrowth (light stubble), 10 days of regrowth (heavy stubble) and at least 4 weeks of untrimmed growth (full beard) posing neutral facial expressions in front view using a Canon digital camera (8.0 megapixels resolution), 150 cm from

the participant under controlled lighting (Janif *et al.*, 2014). From this pool, we randomly selected 16 men (mean age ± SD = 23.95 ± 3.43 years, range 20–31) to which we applied manipulations of facial masculinity.

Masculinity manipulation

Facial masculinity was manipulated via JPsychomorph software (Tiddeman *et al.*, 2001). A sexual dimorphism continuum was defined as the vector difference between an average male and an average female face, created by averaging 50 Caucasian male and 50 female face images, respectively, not including the stimulus identities of this study. The average male and female faces were matched for overall colour content using the Match Color tool in Photoshop (vCS5.1). This ensured that morphs created using this continuum would not differ in overall hue from their original image, but permitted variation of local colour cues that likely contribute to perceived facial structure.

The four images of each stimulus identity (clean-shaven, light stubble, heavy stubble and full beard) were each then morphed (using JPsychomorph) along this vector to create four additional images: two with masculinity increased by 25% and 50%, respectively, by morphing along either a quarter or half the length of the vector in the direction of the average male face and two with femininity increased by 25% and 50%, respectively, by morphing either a quarter or half the length of the vector in the direction of the average female face. Increases in masculinity resulted in narrower eyes, thicker and straighter brows, a thicker nasal bridge with narrower nostrils, less pronounced cheekbones, a narrower mouth and a larger, squarer jaw and chin, with the opposite changes accompanying feminization. A feminized and masculinized face is placed beside each other to illustrate these differences (Fig. 1a).

The resultant morphs were then processed in Photoshop to ensure each had sharp edges at the sides of the neck, smooth pupils (by replacing irises in the morphs with irises from the original image) and were presented on a consistent neutral background colour (RGB: 193, 188, 182). Removal of artefacts around the neck and eyes ensured the morphs looked as much like unmanipulated photographs as the original images (Fig. 1b).

Experimental procedure

Data were collected online (www.socsci.com). Upon entry to the website participants first provided consent and were then randomly assigned to one of three conditions where they rated faces for either sexual attractiveness for a short-term sexual relationship, attractiveness for a long-term sexual relationship or sexual attractiveness without stipulating the length of the relationship.

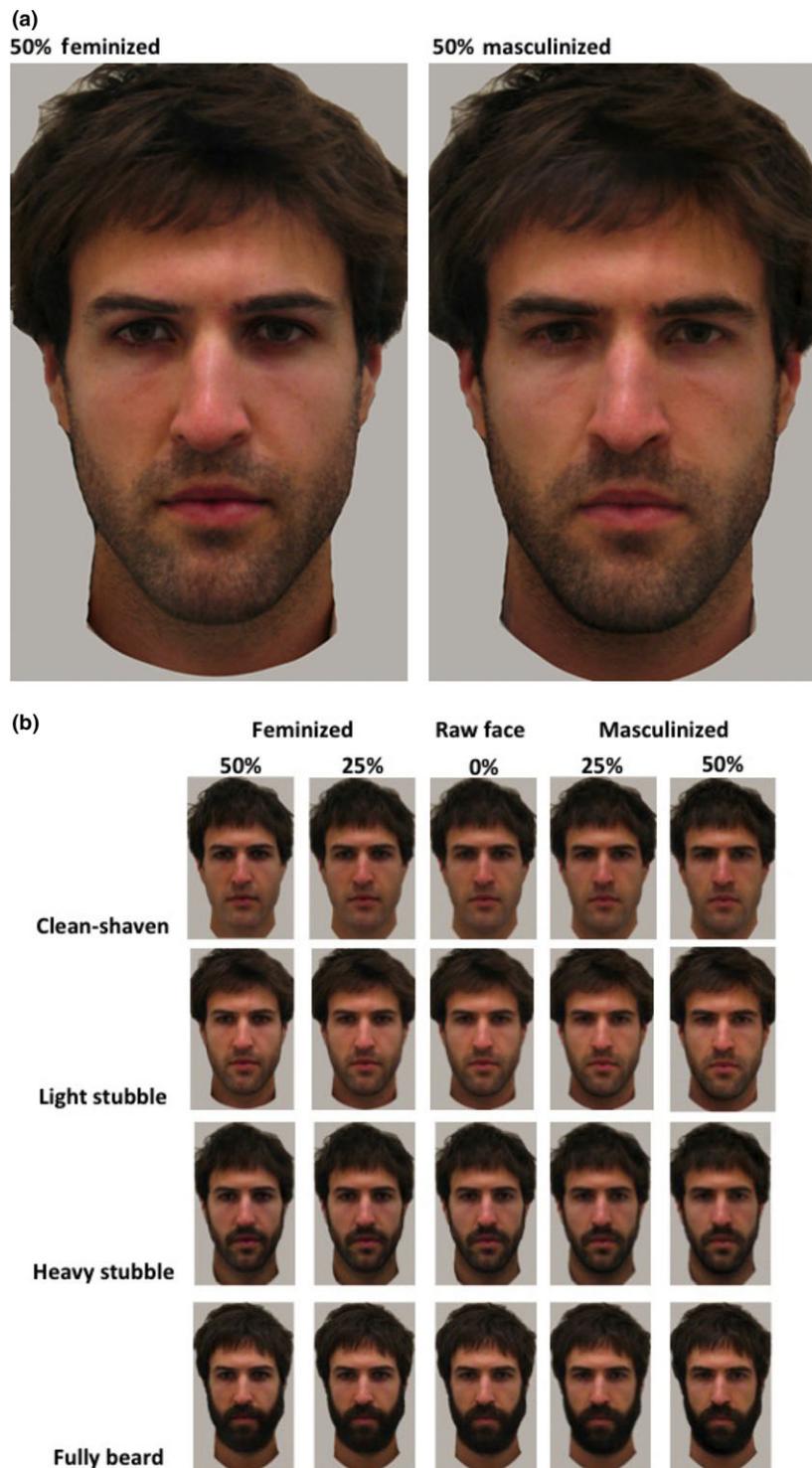


Fig. 1 Examples of the stimuli used in this study. The upper images (a) show an example of the morphing procedure. The images show the same individual morphed to appear 50% feminized on the left and 50% masculinized on the right. Increases in masculinity resulted in narrower eyes, thicker and straighter brows, a thicker nasal bridge with narrower nostrils, less pronounced cheekbones, a narrower mouth and a larger, squarer jaw and chin, with the opposite changes accompanying feminization. The lower panel of faces (b) show the full array of manipulations employed in this study. Images show the same individual in each of the four categories of facial hair (clean-shaven, light stubble, heavy stubble and fully bearded) manipulated to appear 25% and 50% less masculine (i.e. feminized) and 25% and 50% more masculine.

Prior to providing ratings, participants were given a written instruction taken from previous studies guiding them in how to apply the six-point Likert scales (0 = very low–10 = very high) for the rating condition

to which they were assigned. The ‘attractiveness’ condition asked participants to look at each face and rate it for sexual attractiveness using the scale immediately below (Dixson & Rantala, 2016). The ‘short-term

attractiveness' condition asked participants to rate the men when imagining the type of person who would be attractive in a short-term relationship. This implies that the relationship may not last a long time. Examples of this type of relationship would include a single date accepted on the spur of the moment and the possibility of a one-night stand (Little & Jones, 2012). The 'long-term attractiveness' condition asked participants to imagine they were looking for the type of person who would be attractive in a long-term relationship. Examples of this type of relationship would include someone you may want to move in with, settle down and, at some point, wish to marry [or enter into a relationship on similar grounds as marriage; (Little & Jones, 2012)].

After being assigned to a rating condition, participants rated a total of 16 faces. One face was drawn at random, without replacement, from each of the 16 male models. Thus, the amount of facial hair (clean-shaven, light stubble, heavy stubble or full beard) and the degree of masculinity (−50%, −25%, neutral (raw face), +25%, +50%) were fully randomized across participants and across stimulus identities within each participant.

Participants

A total of 9991 participants (8699 female, 1292 male) completed this study. For this manuscript, we use only the response from women between 18 and 100 years of age whose Kinsey scale scores indicate they were at least as interested in men as they are in women (i.e. Kinsey *et al.*, 1948, 1–4). This left a sample of 8520 participants for analyses. Participants in this study were predominantly of European descent.

Statistical analyses

We fitted a linear mixed model, with the model (i.e. stimulus) and the rater identity as random effects, and beard (clean-shaven, light stubble, heavy stubble, full beard), masculinity (+50%, +25%, unmanipulated, −25%, −50%) and relationship context (attractiveness, short-term, long-term) as fixed effects.

Results

All of the fixed effects and their interactions were significant predictors of the ratings women gave the images (Table 1), except for the facial hair × facial masculinity × relationship context treatment interaction (Table 1). The significant main effect of masculinity reflects that unmanipulated faces were more attractive than 25% manipulations in either direction which were, in turn, more attractive than 50% manipulations in either direction. There was also a significant main effect of facial hair (Table 1), with heavy stubble

Table 1 Linear mixed model, with the model (i.e. stimulus) and the rater identity as random effects, and beard (clean-shaven, light stubble, heavy stubble, full beard), masculinity (+50%, +25%, unmanipulated, −25%, −50%) and relationship context (attractiveness, short-term, long-term) as fixed effects.

	d.f. _n	d.f. _d	F	P
Intercept	1	15.054	228.653	<0.001
Facial hair	3	127758.599	469.514	<0.001
Facial masculinity	4	127768.665	251.048	<0.001
Relationship context	2	8378.696	81.116	<0.001
Facial hair × facial masculinity	12	127767.474	8.284	<0.001
Facial hair × relationship context	6	127758.413	17.327	<0.001
Facial masculinity × relationship context	8	127768.523	3.120	0.002
Facial hair × facial masculinity × relationship context	24	127767.222	0.673	0.882

being most attractive followed by light stubble, then full beards and clean-shaven faces being least attractive of all (Fig. 2).

The significant facial hair × facial masculinity interaction (Table 1) reflects that extremely masculinized and, to an even greater extent, extremely feminized faces were least attractive when clean-shaven and that stubble, and to some extent full beards, dampen the polarizing effects of extreme masculinity and femininity, possibly by obscuring the facial features that contribute to these overall shape cues (Fig. 2).

There was also a significant facial hair × relationship context interaction (Table 1), so that preferences for light and heavy stubble were higher when rated for short-term than full beards and clean-shaven faces. Full beards and faces with stubble received higher ratings than clean-shaven faces for long-term than short-term relationships. Heavy stubble received the highest ratings for general attractiveness followed by full beards and light stubble, which were rated almost evenly, with clean-shaven faces being rated least attractive (Fig. 3a). Preferences for clean-shaven faces varied little with relationship context, but were least attractive when considering short-term relationships. The significant facial masculinity × relationship interaction (Table 1) appears to have been due to small differences in the relative attractiveness of each masculinity level under the three treatment conditions and not to any change in the order of their attractiveness (Fig. 3b). Finally, both Model ID and Participant ID had substantial effects on the variance in attractiveness scores (i.e. the variance component estimates were > 2 SE above zero).

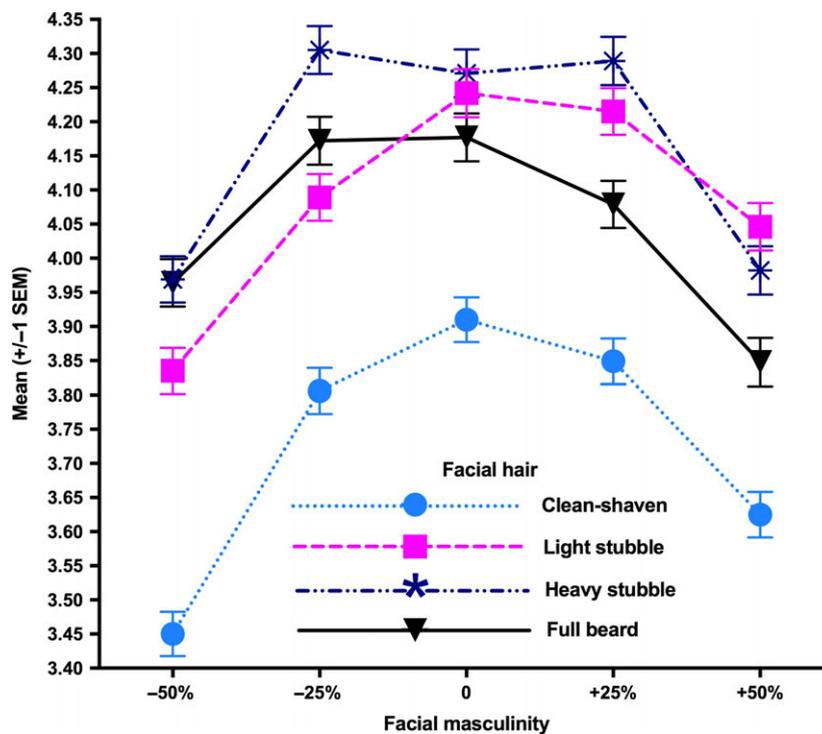


Fig. 2 Mean attractiveness ratings (± 1 SEM) of faces that had been morphed to appear more or less masculine by 50% and 25%. The value of '0' represents the 'raw' or unmanipulated faces (see Fig. 1 for examples of the stimuli). The separate lines depict the four levels of facial hair as they were rated across each level of facial masculinity. Ratings for clean-shaven faces are shown on a light blue dotted line with a circular symbol, light stubble on a pink dashed line with a square symbol, heavy stubble on a dark blue dashed and dotted line with an asterisk symbol and full beardedness on a solid black line with an inverted triangular symbol.

Discussion

Sexual selection has shaped the evolution of attractive ornaments and weaponry across many taxa (Andersson, 1994; Kokko *et al.*, 2003). In humans, considerable debate surrounds whether men's androgen-dependent facial traits were shaped by female choice as attractive ornaments or via intrasexual selection as communicators of status, dominance and aggressiveness (Archer, 2009; Puts, 2010; Scott *et al.*, 2013). How masculine facial features (shape and beardedness) determine men's attractiveness has presented somewhat of a paradox in studies of human mate preferences. On the one hand, male-typical features may signal men's age, sexual maturity and aspects of masculine social dominance (Puts, 2010; Dixson & Vasey, 2012), underlying health (Rhodes *et al.*, 2003; Thornhill & Gangestad, 2006), and are, in some cases, associated with men's mating success (Barber, 2001; Hill *et al.*, 2013). Yet on the other hand, these masculine traits are associated with aspects of aggressiveness and reduced paternal investment (Perrett *et al.*, 1998; Kruger, 2006). Our data suggest a possible divergence of signal function between masculine facial shapes, which is linked to aspects of genetic quality such as health but reduced paternal investment, and tends to be preferred by women for short-term relationships; and facial beardedness, which is more strongly associated with social dominance than underlying health and may be more strongly preferred for long-term relationships.

We found that light and heavy stubble faces were more attractive than either full beards and clean-shaven faces, consistent with recent studies (Neave & Shields, 2008; Dixson & Brooks, 2013; Janif *et al.*, 2014). Masculine faces were judged as least attractive, followed by feminized faces, with unmanipulated faces rated most attractive, which also replicates the general patterns reported elsewhere (Rhodes, 2006). However, we found subtle interactions between facial masculinity and beardedness that differed depending upon whether stimuli were judged for short-term, long-term or general attractiveness. Our findings suggest that sexual selection may have shaped different preference functions in women when judging different androgenic secondary sexual traits in men.

Previous research has shown that ratings of men's masculinity increase in a linear fashion with facial hair and that women's attractiveness judgments peak at intermediate levels of facial hair or 'stubble' (Neave & Shields, 2008; Dixson & Brooks, 2013). This suggests that facial hair functions as an attractive trait when the costs of masculinity are attenuated. In the current study, we experimentally manipulated underlying facial masculinity and facial hair in concert and found that facial masculinity and beardedness interact to determine men's facial attractiveness. Heavy stubble and full beards attenuated the effects of relatively small changes in facial shape on attractiveness judgements, perhaps by effectively masking the subtle morphological differences between the original faces and the 25%

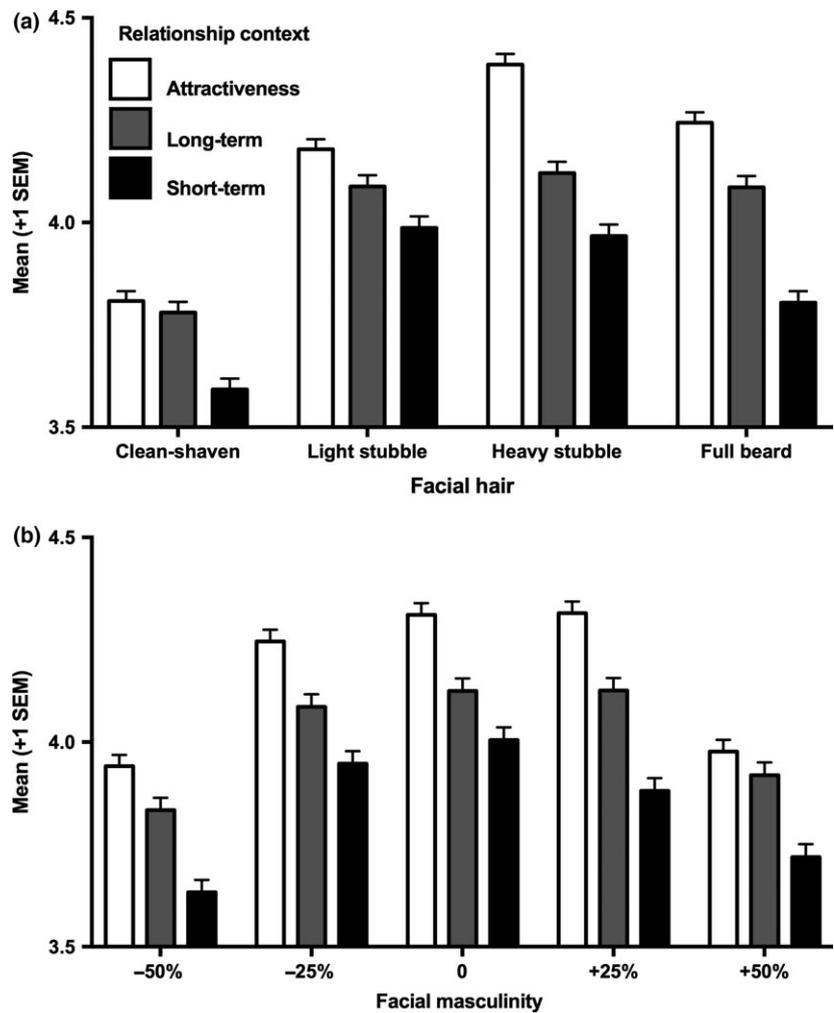


Fig. 3 Panel a shows the mean ratings (+1 SEM) of faces varying in facial hair (clean-shaven, light stubble, heavy stubble and fully bearded). Panel b shows the mean ratings (+1 SEM) of faces manipulated to appear -25% and -50% less masculine (i.e. feminized) and 25% and 50% more masculine. The value of '0' represents the 'raw' or unmanipulated faces (see Fig. 1 for examples of the stimuli). In both panels, data are split by the experimental rating treatments to which participants were assigned, with open bars representing ratings of general attractiveness, dark grey bars depicting ratings when considering attractiveness for a long-term relationship and black bars depicting ratings for attractiveness when considering a short-term relationship.

masculinized and feminized versions. Thus, beards may mask the unattractive features of having overly feminine or masculine face shapes. The apparent shifts in attractiveness peak towards more feminine faces with more facial hair (Fig. 2), suggesting that there may be a threshold of facial masculinity at which facial hair operates as an attractive trait (Neave & Shields, 2008; Dixon & Brooks, 2013), but beyond which the additive effects of facial shape and facial hair on perceived masculinity have a deleterious impact on subjective attractiveness ratings.

According to mating strategy theories, when opting for short-term relationships, women may bypass the social costs of potentially reduced paternal investment and select masculine mates to secure indirect benefits from higher quality mates (Gangestad & Simpson, 2000). Although preferences for masculine faces were reportedly stronger when considering short-term than long-term relationships (Little *et al.*, 2002, 2011), we found that ratings for all faces were lowest when considering shorter-term attractiveness than other

rating conditions. Further, preferences for somewhat more masculine men were higher for general sexual attractiveness and long-term relationship ratings than when rating for short-term relationships, wherein slightly feminine-looking and unmanipulated faces were most attractive. Extremely masculine and extremely feminine-looking males were least attractive, irrespective of relationship context. However, although we used well-established techniques to morph faces to vary in masculinity, whether or not our experimental approach extends to natural variation in craniofacial morphology will be important for future research to determine. Previous studies have reported that preferences for men's beards are stronger than for clean-shaven faces when considering long-term relationships (Neave & Shields, 2008; Dixon & Brooks, 2013). In the current study, stubble was judged as most attractive overall and received higher ratings for short-term relationships than full beards, which were more attractive for long than short-term relationships.

The apparently divergent effects of facial shape and facial hair on attractiveness ratings for long- and short-term relationships suggest that these characteristics do not simply constitute redundant cues of masculinity. Although both traits emerge during adolescence under the actions of androgens, the mechanisms by which androgens exert their effects differ. Testosterone likely has organizational effects during foetal development that result in more male-typical features in adulthood (Whitehouse *et al.*, 2015) and total testosterone at puberty augments masculine facial characters (Verdonck *et al.*, 1999). In contrast, beard hair follicles express terminal hairs under the dual actions of testosterone and its 5α -reductase metabolite dihydrotestosterone (Randall, 2008). Thus, craniofacial masculinity may vary independently of the ability to grow a full beard, and women's mate preferences may differ for each trait owing to the different information contained within each signal. For example, men with more masculine faces tend to report less interest in long-term relationships, more interest in short-term relationships and a greater number of short-term mates than less masculine men (Rhodes *et al.*, 2005; Boothroyd *et al.*, 2008). Studies, with the exception of the current one, have repeatedly shown that masculine men are more attractive to women when judging for short-term rather than a long-term relationship (Little *et al.*, 2011). A full beard, therefore, conveniently masks the masculine facial shape that women tend not to find attractive for a long-term prospect while simultaneously signalling sexual and social maturity and, potentially, a greater likelihood and capacity to invest.

Men have a similar degree of visually conspicuous secondary sexual trait development as those nonhuman primate species where males live in large multilevel social systems with some degree of polygyny (Dixson *et al.*, 2005; Grueter *et al.*, 2015). Like other nonhuman primates, the role of conspicuous sexually dimorphic traits like facial hair in determining male attractiveness to females remains to be fully understood (for reviews see Grueter *et al.*, 2015). However, beards consistently render men with an older, more masculine, socially dominant and aggressive appearance (Neave & Shields, 2008; Dixson & Vasey, 2012; Sherlock *et al.*, 2016), suggesting a strong role of intrasexual selection in shaping its evolution. Success in intrasexual competition may result in direct benefits to females such as resource quality and holding potential that enhance offspring survivability (Wong & Candolin, 2005). Thus, beards may be more attractive to women when considering long-term than short-term relationships as they indicate a male's ability to successfully compete socially with other males for resources. Interestingly, a longitudinal analysis of men's facial hair fashions in London from 1871 to 1972 revealed that beards became more common when the marriage market was more male-biased and the degree of intrasexual competition to attract

mates was augmented (Barber, 2001). Taken together, findings highlight an important role of intrasexual selection in shaping the signalling value of men's beards.

With respect to the evolution of secondary sexual characteristics more broadly, the apparently divergent signalling functions of two androgen-dependent traits emphasize the importance of understanding the developmental and physiological mechanisms leading to the expression of such traits (McNamara & Houston, 2009). Differential effects of beardedness and masculine facial shape on female preferences only appear paradoxical if one presumes that all androgen-dependent traits simply indicate a males' masculinity on a single dimension. This, of course, is not the case. Masculinity itself is not a defined trait, but a linguistic shorthand for any number of traits that are sexually dimorphic, and that vary between individual males. Understanding the mechanisms by which such traits manifest can help illuminate their potential signal content to both same and opposite-sex receivers and thus informs theories about their evolution.

Any evolutionary account of the selective pressures giving rise to men's beardedness is complicated by temporal variation within and between populations in grooming patterns. Given the current and past findings that men are less attractive when clean-shaven than when they are stubbled or bearded (Neave & Shields, 2008; Dixson & Brooks, 2013; Janif *et al.*, 2014), the widespread popularity of shaving remains an important paradox for research to address. One possible explanation hinted at by our findings is that unmanipulated faces do better than small manipulations (25% feminized or masculinized) in clean-shaven and lightly stubbled men, but that this advantage disappears in more heavily stubbled and fully bearded men. If facial hair growth masks small variations in facial masculinity, and, ostensibly, other sources of similar variation, then perhaps it obscures the signalling value of the face to women and to other men. It would then be to the advantage of men with attractive faces and for women in general to impose on the men around them norms of shaving or hair removal. The relationship between local economic and demographic conditions and facial hair growth is a topic just starting to receive attention (Janif *et al.*, 2014), and future research should attend to how social and cultural dynamics interact with the evolved signalling value of facial hair to shape patterns of beard grooming.

Acknowledgments

This study was approved by the Human Ethics Committee at the University of New South Wales (#1876). This study was supported by an ARC Discovery Grant to RCB and BJWD and a University of Queensland Postdoctoral Fellowship to BJWD.

References

- Addison, W.E. 1989. Beardedness as a factor in perceived masculinity. *Percept. Mot. Skills* **68**: 921–922.
- Andersson, M.B. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Archer, J. 2009. Does sexual selection explain human sex differences in aggression? *Behav. Brain. Sci.* **32**: 249–266.
- Barber, N. 2001. Mustache fashion covaries with a good marriage market for women. *J. Nonverbal Behav.* **25**: 261–272.
- Blows, M.W., Brooks, R. & Kraft, P.G. 2003. Exploring complex fitness surfaces: multiple ornamentation and polymorphism in male guppies. *Evolution* **57**: 1622–1630.
- Boothroyd, L.G., Jones, B.C., Burt, D.M. & Perrett, D.I. 2007. Partner characteristics associated with masculinity, health and maturity in male faces. *Pers. Individ. Dif.* **43**: 1161–1173.
- Boothroyd, L.G., Jones, B.C., Burt, D.M., DeBruine, L.M. & Perrett, D.I. 2008. Facial correlates of sociosexuality. *Evol. Hum. Behav.* **29**: 211–218.
- Brooks, R. 2002. Variation in female mate choice within guppy populations: population divergence, multiple ornaments and the maintenance of polymorphism. *Genetica* **116**: 343–358.
- Brooks, R. & Couldrige, V. 1999. Multiple sexual ornaments coevolve with multiple mating preferences. *Am. Nat.* **154**: 37–45.
- Chapais, B. 2008. *Primeval Kinship. How Pair-Bonding Gave Birth to Human Society*. Harvard University Press, Cambridge, MA.
- DeBruine, L.M., Jones, B.C., Crawford, J.R., Welling, L.L.M. & Little, A.C. 2010. The health of a nation predicts their mate preferences: crosscultural variation in women's preferences for masculinized male faces. *Proc. R. Soc. Lond. B* **277**: 2405–2410.
- Dixson, B.J. & Brooks, R.C. 2013. The role of facial hair in women's perceptions of men's attractiveness, health, masculinity and parenting abilities. *Evol. Hum. Behav.* **34**: 236–241.
- Dixson, B.J.W. & Rantala, M. 2016. The role of facial and body hair distribution in women's judgments of men's sexual attractiveness. *Arch. Sex. Behav.* **45**: 877–889.
- Dixson, B.J. & Vasey, P.L. 2012. Beards augment perceptions of men's age, social status, and aggressiveness, but not attractiveness. *Behav. Ecol.* **23**: 481–490.
- Dixson, A.F., Dixson, B.J. & Anderson, M.J. 2005. Sexual selection and the evolution of visually conspicuous sexually dimorphic traits in male monkeys, apes, and human beings. *Ann. Rev. Sex. Res.* **16**: 1–17.
- Dixson, B.J., Tam, J.C. & Awasthy, M. 2013. Do women's preferences for men's facial hair change with reproductive status? *Behav. Ecol.* **24**: 708–716.
- Fink, B., Neave, N. & Seydel, H. 2007. Male facial appearance signals physical strength to women. *Am. J. Hum. Biol.* **19**: 82–87.
- Gangestad, S.W. & Eaton, M.A. 2013. Toward an integrative perspective on sexual selection and men's masculinity. *Behav. Ecol.* **24**: 594–595.
- Gangestad, S.W. & Simpson, J.A. 2000. The evolution of human mating: trade-offs and strategic pluralism. *Behav. Brain. Sci.* **23**: 573–587.
- Geniole, S.N. & McCormick, C.M. 2015. Facing our ancestors: judgements of aggression are consistent and related to the facial width-to-height ratio in men irrespective of beards. *Evol. Hum. Behav.* **36**: 279–285.
- Geniole, S.N., Denson, T.F., Dixson, B.J., Carré, J.M. & McCormick, C.M. 2015. Evidence from meta-analyses of the facial width-to-height ratio as an evolved cue of threat. *PLoS ONE* **10**: e0132726.
- Grueter, C.C., Isler, K. & Dixson, B.J. 2015. Are primate badges of status adaptive in large groups? *Evol. Hum. Behav.* **36**: 398–406.
- Hamilton, J.B. 1958. Age, sex and genetic factors in the regulation of hair growth in man: a comparison of Caucasian and Japanese populations. In: *The Biology of Hair Growth* (W. Montagna, R.A. Ellis, eds), pp. 399–433. Academic Press, New York, NY.
- Hamilton, J.B. 1964. Racial and genetic predisposition. *Clin. Obstet. Gynecol.* **7**: 1075–1084.
- Hamilton, J.B., Terada, H. & Mestlert, G.E. 1958. Studies of growth throughout the life span in Japanese: II. Beard growth in relation to age, sex, heredity, and other factors. *J. Gerontol.* **13**: 269–281.
- Hill, A.K., Hunt, J., Welling, L.L., Cárdenas, R.A., Rotella, M.A., Wheatley, J.R. et al. 2013. Quantifying the strength and form of sexual selection on men's traits. *Evol. Hum. Behav.* **34**: 334–341.
- Janif, Z.J., Brooks, R.C. & Dixson, B.J. 2014. Negative frequency-dependent preferences and variation in male facial hair. *Biol. Lett.* **10**: 20130958.
- Jennions, M.D. & Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* **72**: 283–327.
- Kenny, C.T. & Fletcher, D. 1973. Effects of beardedness of person perception. *Percept. Mot. Skills* **37**: 413–414.
- Kinsey, A.C., Pomeroy, W.B. & Martin, C.E. 1948. *Sexual Behavior in the Human Male*. Saunders, Philadelphia, PA.
- Knussman, R. & Christiansen, K. 1988. Attributes of masculinity and androgen level. *Homo* **39**: 45–50.
- Kokko, H., Brooks, R., Jennions, M.D. & Morley, J. 2003. The evolution of mate choice and mating biases. *Proc. R. Soc. Lond. B* **270**: 653–664.
- Kokko, H., Jennions, M.D. & Brooks, R. 2006. Unifying and testing models of sexual selection. *Annu. Rev. Ecol. Evol. S.* **37**: 43–66.
- Kruger, D.J. 2006. Male facial masculinity influences attributions of personality and reproductive strategy. *Pers. Relatsh.* **13**: 451–463.
- Little, A.C. & Jones, B.C. 2012. Variation in facial masculinity and symmetry preferences across the menstrual cycle is moderated by relationship context. *Psychoneuroendocrinology* **37**: 999–1008.
- Little, A., Jones, B., Penton-Voak, I., Burt, D. & Perrett, D. 2002. Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proc. R. Soc. Lond. B* **269**: 1095–1100.
- Little, A.C., Connely, J., Feinberg, D.R., Jones, B.C. & Roberts, S.C. 2011. Human preference for masculinity differs according to context in faces, bodies, voices, and smell. *Behav. Ecol.* **22**: 862–868.
- Marlowe, F. 2000. Paternal investment and the human mating system. *Behav. Processes.* **51**: 45–61.
- McNamara, J.M. & Houston, A.I. 2009. Integrating function and mechanism. *Trends Ecol. Evol.* **24**: 670–675.

- Muscarella, F. & Cunningham, M.R. 1996. The evolutionary significance and social perception of male pattern baldness and facial hair. *Ethol. Sociobiol.* **17**: 99–117.
- Neave, N. & Shields, K. 2008. The effects of facial hair manipulation on female perceptions of attractiveness, masculinity, and dominance in male faces. *Pers. Individ. Dif.* **45**: 373–377.
- Oldmeadow, J.A. & Dixon, B.J. 2016. The association between men's sexist attitudes and facial hair. *Arch. Sex. Behav.* **45**: 891–899.
- Pancer, S.M. & Meindl, J.R. 1978. Length of hair and beardedness as determinants of personality impression. *Percept. Mot. Skills* **46**: 1328–1330.
- Pellegrini, R.J. 1973. Impressions of the male personality as a function of beardedness. *Psychology* **10**: 29–33.
- Perrett, D.I., Lee, K.J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D.M. *et al.* 1998. Effects of sexual dimorphism on facial attractiveness. *Nature* **394**: 884–887.
- Provost, M., Kormos, C., Kosakoski, G. & Quinsey, V. 2006. Sociosexuality in women and preference for facial masculinization and somatotype in men. *Arch. Sex. Behav.* **35**: 305–312.
- Puts, D.A. 2010. Beauty and the beast: mechanisms of sexual selection in humans. *Evol. Hum. Behav.* **31**: 157–175.
- Randall, V.A. 2008. Androgens and hair growth. *Dermatol. Ther.* **21**: 314–328.
- Rantala, M.J., Coetzee, V., Moore, F.R., Skrinda, I., Kecko, S., Krama, T. *et al.* 2013. Adiposity, compared with masculinity, serves as a more valid cue to immunocompetence in human mate choice. *Proc. R. Soc. Lond. B* **280**: 20122495.
- Reed, J.A. & Blunk, E.M. 1990. The influence of facial hair on impression formation. *Soc. Behav. Person.* **18**: 169–175.
- Rhodes, G. 2006. The evolutionary psychology of facial beauty. *Ann. Rev. Psychol.* **57**: 199–226.
- Rhodes, G., Chan, J., Zebrowitz, L.A. & Simmons, L.W. 2003. Does sexual dimorphism in human faces signal health? *Proc. R. Soc. Lond. B* **270**: S93–S95.
- Rhodes, G., Simmons, L.W. & Peters, M. 2005. Attractiveness and sexual behavior: does attractiveness enhance mating success? *Evol. Hum. Behav.* **26**: 186–201.
- Rhodes, G., Morley, G. & Simmons, L.W. 2013. Women can judge sexual unfaithfulness from unfamiliar men's faces. *Biol. Lett.* **9**: 20120908.
- Roll, S. & Verinis, J.S. 1971. Stereotypes of the scalp and facial hair as measured by the semantic differential. *Psychol. Rep.* **28**: 975–980.
- Saxton, T.K., Mackey, L.L., McCarty, K. & Neave, N. 2016. A lover or a fighter? Opposing sexual selection pressures on men's vocal pitch and facial hair. *Behav. Ecol.* **27**: 512–519.
- 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**: e13585.
- Scott, I.M.L., Clark, A.P., Boothroyd, L.G. & Penton-Voak, I.S. 2013. Do men's faces really signal heritable immunocompetence? *Behav. Ecol.* **24**: 579–589.
- Sherlock, J.M., Tegg, B., Sulikowski, D. & Dixon, B.J. 2016. Facial masculinity and beardedness determine men's explicit, but not their implicit, responses to male dominance. *Adapt. Hum. Behav. Physiol.* 1–16.
- Thornhill, R. & Gangestad, S.W. 2006. Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evol. Hum. Behav.* **27**: 131–144.
- Tiddeman, B., Burt, M. & Perrett, D. 2001. Prototyping and transforming facial textures for perception research. *Comput. Graph. Appl. IEEE* **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. *Eur. J. Orthod.* **21**: 137–143.
- Whitehouse, A.J.O., Gilani, S.Z., Shafait, F., Mian, A., Tan, D.W., Maybery, M.T. *et al.* 2015. Prenatal testosterone exposure is related to sexually dimorphic facial morphology in adulthood. *Proc. R. Soc. Lond. B* **282**: 20151351.
- Windhager, S., Schaefer, K. & Fink, B. 2011. Geometric morphometrics of male facial shape in relation to physical strength and perceived attractiveness, dominance, and masculinity. *Am. J. Hum. Biol.* **23**: 805–814.
- Wogalter, M.S. & Hosie, J.A. 1991. Effects of cranial and facial hair on perceptions of age and person. *J. Soc. Psychol.* **131**: 589–591.
- Wong, B. & Candolin, U. 2005. How is female mate choice affected by male competition? *Biol. Rev.* **80**: 559–571.
- Wood, D.R. 1986. Self-perceived masculinity between bearded and nonbearded males. *Percept. Mot. Skills* **62**: 769–770.

Received 16 May 2016; revised 19 July 2016; accepted 29 July 2016