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Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape

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Secondary sexual characteristics may indicate quality of the immune system and therefore a preference for masculinity may confer genetic benefits to offspring; however, high masculinity may be associated with costs of decreased paternal investment. The current study examined women's preferences for masculinity in male faces by using computer graphics to allow transformation between feminine and masculine versions of individual male faces. We found that preferences for masculinity are increased when women either have a partner or are considering a short-term relationship. Such preferences are potentially adaptive, serving to: (i) maximize parental investment and cooperation in long-term relationships by biasing choices towards feminine faced males, and (ii) maximize possible good-gene benefits of short-term or extra-pair partners by biasing choices towards masculine faced males. We also found that individuals using oral contraception do not show the above effects, indicating that such hormonal intervention potentially disrupts women's choices for evolutionarily relevant benefits from males.

Keywords: facial attractiveness; female preference; good-gene markers; partnership; context

1. INTRODUCTION

Studies examining biologically relevant aspects of facial attractiveness have focused on universally attractive features, characteristics that all individuals and human societies agree are attractive. An evolutionary view posits that individuals should agree on the characteristics that make up attractiveness. The high degree of agreement reported in attractiveness judgements from individuals within a particular culture, and also high agreement between individuals from different cultures, is consistent with an evolutionary interpretation of facial attraction (see Langlois *et al.* (2000) for a meta-analytic review).

Several researchers have proposed that the masculinity of human male faces is one such universally attractive trait. Theories of sexual selection predict that masculine male faces will be found attractive (e.g. Grammer & Thornhill 1994). Enlarged cheekbones, jaws and chins are examples of male secondary sexual characteristics influenced by the action of testosterone on human facial growth (Enlow 1990). Testosterone has been found to lower immunocompetence (Wedekind 1992; Hillgarth & Wingfield 1997) and so larger secondary sexual characteristics may reflect a healthier immune system because only healthy individuals can afford the high testosterone handicap necessary to produce such traits (Folstad & Karter 1992).

Although there is evidence that some masculine facial traits are attractive (e.g. Cunningham *et al.* 1990; Grammer & Thornhill 1994) other studies have also suggested that feminine shape characteristics in male faces are found more attractive than masculine characteristics (Berry & McArthur 1985; Cunningham *et al.* 1990; Perrett *et al.* 1998; Penton-Voak *et al.* 1999). This suggests male facial attractiveness judgements may depend on more than just cues to immunocompetence (good genes). One explanation of why masculine traits are not always attractive is that negative personality traits are associated with such features (Perrett *et al.* 1998). For example, Perrett *et al.* found that masculine male faces are perceived not only as more dominant but also as more likely to possess negative characteristics, such as lower honesty and lower warmth, and more likely to make bad parents than feminine male faces.

Studies of male facial masculinity and attractiveness have thus produced mixed results. It is possible, however, that male facial masculinity might differ in its attractiveness under different circumstances. Human males bring two factors to a parenting relationship: a level of paternal investment and potential heritable benefits (e.g. genes for high quality immune systems). The perceived high dominance and lower levels of cooperation point to lower paternal investment from the owners of masculine faces. Although females generally prefer long-term mating over short-term mating (Buss & Schmitt 1993), individuals differ in their inclination to take part in short- and long-term relationships (Gangestad & Simpson 1990; Simpson & Gangestad 1992). Depending on the type of relationship sought, masculine and feminine male faces are proposed to differ in their attractiveness to females. In the context of a short-term sexual relationship, the perceived cues to high paternal investment in the feminine faced male are of little value to a female. Females should therefore seek to maximize the genetic fitness of potential offspring if they are not extracting any other benefits from their mates

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and thus prefer more masculine males for short-term relationships. In long-term relationships, better parenting and increased cooperation may outweigh the benefits of genetic fitness, thereby enhancing the attractiveness of feminine-faced males.

An increased preference for genetic fitness over signs of parental investment would also be expected in extra-pair copulations when a woman has already acquired a long-term partner. Support for the notion that female preferences are variable according to the temporal context of relationships, and that females may aim to maximize genetic quality in extra-pair partners at peak fertility, has come from work related to the menstrual cycle. Women's menstrual cycles usually last between 21 and 35 days and most standard models of the menstrual cycle are based on a mean duration of 28 days. In such models, ovulation occurs on approximately day 14 at the end of the follicular phase (e.g. Chabbert-Buffert *et al.* 1998). Fertility is highest (where a woman is most likely to become pregnant after sexual intercourse) around the 12th day of the cycle during the follicular phase (Barrett & Marshall 1969). Although peaks in sexual desire and activity have been reported at different stages across the menstrual cycle (see Regan (1996) for a review), two studies have reported that women with partners may be more likely to engage in extra-pair sex at peak fertility (extra-pair copulation is 2.5 times more likely during the follicular phase than in the luteal phase (Bellis & Baker 1990; Baker & Bellis 1995)). These studies indicate a possible mechanism where women may maximize their chances of becoming pregnant with the offspring of males chosen for extra-pair affairs. Such males may be selected for possessing superior or alternative genes to the woman's current partner.

Women at mid-cycle do appear to be more sensitive to indirect genetic immunological benefits. Wedekind & Furi (1997) examined the influence of female major histocompatibility complex (MHC, a set of genes that play an important role in immune function) on male odour attractiveness, using T-shirts worn by males. They found a preference in females for the odours of males with dissimilar MHC profiles (offspring of partners with dissimilar MHC complexes are proposed to have an immune system better able to fight off infection) around day 12 of the women's menstrual cycle. Such preferences were not just absent but reversed in women using oral contraception, implying that the hormonal changes across the menstrual cycle play an important role in MHC odour preferences.

An example of women's preferences favouring signs of immunological quality at a time when they are most likely to become pregnant comes from the demonstration of shifting female preferences for masculine facial traits across the menstrual cycle (Frost 1994; Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000; Johnston *et al.* 2001). Recent research has revealed that female preference for male faces varies over the menstrual cycle. Despite a preference for feminine faces most of the time, during the follicular phase of the menstrual cycle when conception is most likely, women prefer relatively masculine faces (Penton-Voak & Perrett 2000; Johnston *et al.* 2001), particularly in the context of short-term relationships (Penton-Voak *et al.* 1999). Penton-Voak *et al.* also report non-significant trends to suggest that personal circumstances also influence face preferences: women currently in a relationship preferred marginally more masculine faces overall ($p = 0.07$), and tended to undergo a larger shift towards masculinity at peak fertility than women without partners ($p = 0.08$). Women using oral contraception showed no significant cyclic shifts in Penton-Voak *et al.*'s study.

A mixed strategy in female mate choice has been put forward as one explanation of females favouring masculinity at peak fertility (Penton-Voak *et al.* 1999; Penton-Voak & Perrett 2000). Females may choose a long-term partner on the basis of cooperation and high paternal care (indicated by a low masculine facial shape). When conception is most likely they may occasionally pursue additional relationships with males with proposed markers of good-genes for immunity, indicated by a relatively masculine face shape. Of course such a mechanism may also serve to maximize genetic benefits in offspring for women without partners.

The current study compared women's preference for masculinity in male faces in long- and short-term contexts to assess whether greater levels of masculinity are preferred for short-term partners compared with long-term partners. The study also examined partnership status to assess whether women with partners prefer more masculine faces than women without partners. Use of oral contraception has been found to influence women's preferences for potentially adaptive genetic benefits (e.g. Wedekind & Furi 1997; Penton-Voak *et al.* 1999) and the impact of this variable was also examined.

2. METHODS

(a) *Participants*

One hundred and fifty eight females, aged between 16 and 39 years (mean age = 21.7, s.d. = 4.8) took part in the experiment. The experiment was administered over the Internet. All participants were volunteers and were selected for reporting to be heterosexual and less than 40 years old.

(b) *Stimuli*

Five interactive face sequence trials were constructed using composite faces made from five groups of male and female faces. Each group of faces contributed to a single sequence trial and was made up of about 20 male and 20 female facial images of young adults in a neutral pose. To construct each sequence trial, 174 feature points were delineated on each face image in the group from which the average male and female shapes were then calculated. Using the linear difference between feature points in the average male and female shape, a sequence of 11 face shapes ranging from +50% masculinized to +50% feminized was constructed. The 11 images in the sequence were then produced by warping and then superimposing all of the male faces in the group into each of the face shapes. The images were made perfectly symmetrical by combining them with their mirror image prior to masculinity manipulation. For more details on the averaging and transforming techniques see Tiddeman *et al.* (2001). Figure 1 shows an example of a masculinized and feminized male face made using these methods. The final stimuli were five interactive tests which allowed for the on-screen transformation of a composite male face between a masculinized and feminized version of itself. These interactive tests were used in previous studies as follows: one Japanese group and one European group used in Perrett *et al.* (1998) and three other groups of European faces used in Penton-Voak *et al.* (1999).

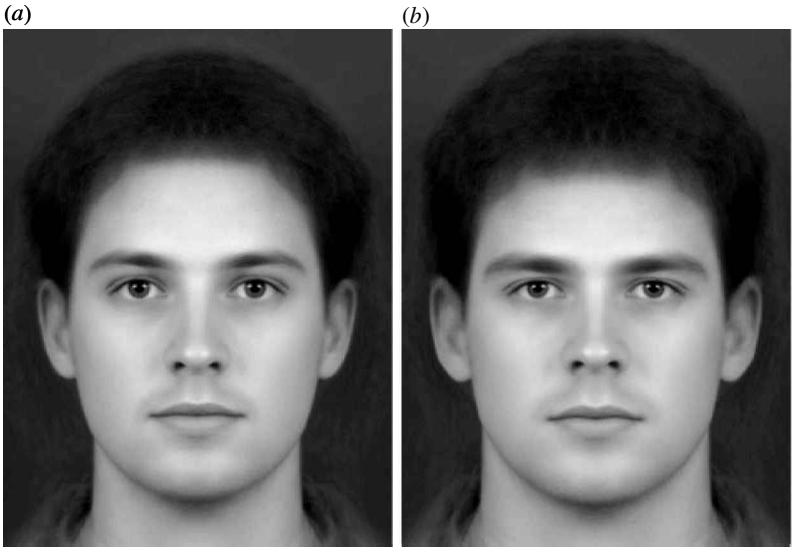

Figure 1. (*a*) 50% feminized male composite and (*b*) 50% masculinized male composite.

(c) *Procedure*

Participants were presented with five interactive face sequence trials followed by an on-screen questionnaire assessing age, sexuality, oral contraceptive use (yes/no), whether they had a current partner (yes/no), number of sexual partners and five questions assessed on a five-point scale, happiness with their current relationship (e.g. 1, very unhappy; 5, very happy), commitment to their current relationship, their physical attractiveness, their warmth, and their confidence. The face sequence interactive trials were presented in random order with participants being cued to make all their judgements based on either short- or long-term relationships by the message 'alter the face until you think it is closest to the appearance you would find attractive for a short- (or long-) term relationship' (i.e. the variable relationship context was manipulated between participants). Ratings for long or short term were run in two blocks; initially everyone rated for long-term relationships and later the experiment was changed to collect short-term ratings. During each trial left or right (counterbalanced between trials) mouse-movement altered the shape of the face in the on-screen image making it more or less masculine.

3. RESULTS

Only the data from participants who answered all questions could be entered into the analysis. Nine participants were removed for scoring 1 or 2 on either the relationship happiness scale (very unhappy, unhappy) or relationship commitment scale (very uncommitted, uncommitted). Individuals unhappy or uncommitted in their relationships may not rate faces as if they were in a relationship (i.e. they may be looking for a partner in order to leave the relationship or be contemplating leaving the current relationship anyway). Removing unhappy/uncommitted individuals increases the likelihood that remaining participants are rating for extra-pair partners rather than replacement partners. The highly skewed nature of scores on happiness/commitment scales (only nine subjects scored 1 or 2 on these scales and the majority of participants entered 5 on both scales) meant that it was not possible to assess if happiness/commitment was related to masculine preference in this sample. Two participants were also excluded as they reported being pregnant.

In order to assess any differences in personality/self-opinion between those using oral contraception and those not using oral contraception and those in relationships and those not in relationships, a $2 \times 2 \times 2$ multivariate ANOVA was carried out with three levels, 'context' (short-/long-term ratings), 'partnership status' (partner/no partner) and 'contraceptive use' (use/do not use) as the between-participant variables, and number of sexual partners, self-rated physical attractiveness, warmth, and confidence as the dependent variables. Age was entered as a covariate. Ten participants did not provide complete data for these questions and were excluded. This analysis produced only two significant results: significant effects of both age ($F_{1,140} = 54.6$, $p < 0.001$) and contraceptive use ($F_{1,140} = 9.2$, $p = 0.003$) were found for number of sexual partners. Age was positively correlated with number of sexual partners ($n = 150$, $r = 0.54$, $p < 0.001$), and women using oral contraceptive reported having had more partners than those not using oral contraceptive (4.5 and 2.6 mean number of partners respectively). All other effects and interactions were non-significant (all $p > 0.095$).

A univariate 2×2 ANOVA was carried out with the two levels 'context' and 'partnership status' as the between-participant variables and femininity preference as the dependent variable. Separate analyses were carried out for women who did and did not report that they were using oral contraception. Age was entered as a covariate in both analyses due to its possible relationship with femininity preference and partnership status. A smaller number of women reported using oral contraception than reported not using it, meaning the statistical power in the oral contraception group was lower. The numbers of participants in the various conditions for the analysis can be seen in table 1.

For those women who reported not using oral contraception, a significant effect of both context ($F_{1,102} = 5.4$, $p = 0.022$) and partnership status ($F_{1,102} = 7.6$, $p = 0.007$) was found. No significant effect of age was found on masculinity preference ($F_{1,102} = 0.5$, $p = 0.50$) and there was

Table 1. Number of participants as split in the analysis.

oral contraception			*n*
no	context	short term	67
		long term	40
	partner	no	71
		yes	36
yes	context	short term	35
		long term	16
	partner	no	12
		yes	39

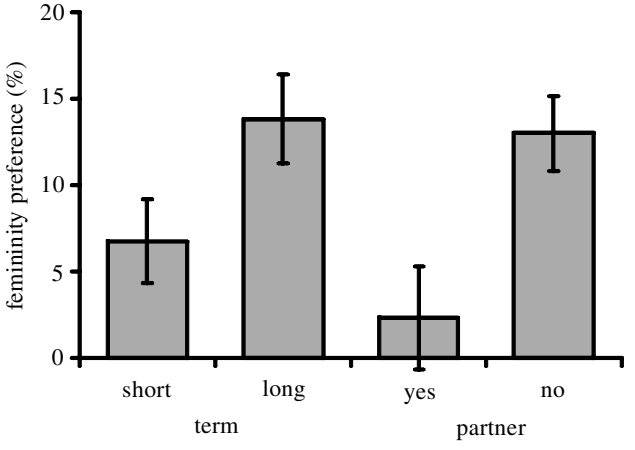

Figure 2. Mean femininity preferences (± 1 s.e.m.) in male faces for participants reporting they were not using oral contraceptives. Scores are presented separately for participants rating for short- and long-term contexts and for participants with and without partners.

no interaction between context and partnership status ($F_{1,102} = 0.2$, $p = 0.65$). These results reflect the lower preference for femininity in women judging for short-term relationships over women judging for long-term relationships and the lower preference for femininity in women with partners than women without partners (figure 2).

For those women who did report using oral contraception, there were no significant effects of context ($F_{1,46} = 0.9$, $p = 0.34$) or partnership status ($F_{1,46} = 1.3$, $p = 0.26$), and there was no interaction between context and partnership status ($F_{1,46} = 1.3$, $p = 0.25$) (figure 3). Comparing figures 2 and 3 shows the different preferences for masculinity in women using and not using oral contraception. A significant effect of age on masculinity preference was found in women not using contraception ($F_{1,46} = 4.9$, $p = 0.033$). Pearson correlations reveal a significant negative relationship between age and femininity preference overall ($n = 158$, $r = -0.20$, $p = 0.011$).

A univariate $2 \times 2 \times 2$ ANOVA with three factors, 'context', 'partnership status' and 'contraceptive use', with age as a covariate was carried out on the dependent variable of femininity preference to assess the effects of contraceptive use. Analysis revealed no significant effects of age ($F_{1,149} = 3.0$, $p = 0.087$), context ($F_{1,149} = 0.1$, $p = 0.76$), partnership status ($F_{1,149} = 0.2$, $p = 0.62$) or contraceptive use ($F_{1,149} = 0.1$, $p = 0.76$). There was a significant interaction between contraceptive use and context ($F_{1,149} = 3.9$, $p = 0.049$) and between contraceptive use and partnership

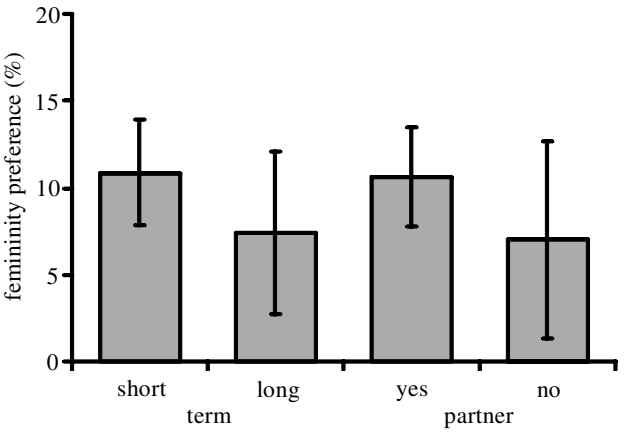

Figure 3. Mean femininity preferences (± 1 s.e.m.) in male faces for participants reporting they were using oral contraceptives. Scores are presented separately for participants rating for short- and long-term contexts and for participants with and without partners.

status ($F_{1,149} = 4.8$, $p = 0.030$). Comparing figures 2 and 3 it can be seen that these interactions reflect a reversal of the facial femininity preference results of the contraceptive-using group from the results of the group not using oral contraception. There was no significant interaction between context or partnership status ($F_{1,149} = 1.1$, $p = 0.29$) nor was there a significant three-way interaction between contraceptive use, partnership status and context ($F_{1,149} = 0.4$, $p = 0.51$).

4. DISCUSSION

The current study shows that human females have different preferences for femininity in male faces in relation to both the temporal context of the relationship they are assessing males for and in relation to their current partnership status. It was found that women showed a higher preference for male face masculinity when judging for short-term relationships than when judging for long-term relationships. A higher preference for male face masculinity was also found in women with partners than women without partners. We selected women who were happy in their current relationships. Our results may therefore reflect a choice for a potential extra-pair partner rather than choice for a potential replacement for their current partner. Changing preferences as the result of partnership or relationship context was only seen in women who reported not using oral contraception: women using oral contraception did not differ in their masculinity preferences across conditions.

The results show that women have different face preferences for short- and long-term mates. For example, Buss & Schmitt (1993) have found that women do in fact place greater emphasis on a male's physical attractiveness and physical prowess in the context of a possible short-term relationship. Scheib (2001) has also shown that when choosing for an extra-pair partner women are more likely to choose an attractive male lower on cooperation and parenting qualities over a less attractive male with higher cooperation and parenting qualities. In long-term contexts the reverse is true: women choose the less attractive but more cooperative man more often (Scheib 2001). The

effects in Scheib's study appear analogous to our finding that women trade-off good-genes for good parenting between short- and long-term contexts, although in Scheib's study the personality descriptions are explicit (presented in vignettes) rather than the implicit stereotypes associated with masculine faces (Perrett *et al.* 1998).

There is some indication that different women may even engage in different selection strategies. Women who are most willing to engage in short-term mating care more about a man's physical attractiveness than do women who are less willing to engage in short-term mating (Simpson & Gangestad 1992). Such findings may indicate alternative strategies: one that involves maximizing male gene quality for immunity by pursuing short-term relationships and one to maximize paternal investment by concentrating on long-term relationships and focusing less on cues to genetic immune quality.

That women with current partners prefer less feminine faces is also consistent with previous studies. For example, women have been found to prefer men with symmetrical bodies (symmetry being another proposed marker of genetic quality) as extra-pair partners (Thornhill & Gangestad 1994; Gangestad & Thornhill 1997). In the current study we might have expected to find an interaction between context and partnership status; those with partners showing the greatest shift towards masculinity preference when judging for short-term relationships. This interaction could be absent because women without a partner may always be influenced by their preferences for a long-term partner (Buss & Schmidt 1993). By contrast, women with partners may tend to consider a relationship outside their current partnership to be more likely to be short-term (i.e. when choosing a secondary potential partner women are not as constrained by their long-term preferences).

Changing preferences for masculinity in male faces highlights the importance of flexibility in women's mate choice. In humans, as with other species with bi-parental care, it is important, but not absolutely necessary, for a woman to obtain both paternal care and heritable benefits for her offspring. Masculine male faces and feminine male faces are associated with potential costs and benefits to the reproductive success of females (Perrett *et al.* 1998). Heritable immunocompetence benefits may be acquired from the owners of masculine faces but at the potential cost of lower paternal investment. It has been argued that high-quality males are less likely to invest in mates and instead pursue a strategy of maximizing their number of lifetime mates (Gangestad & Simpson 2000). Indeed, men with high body symmetry (a proposed marker of good-genes) appear less inclined to provide paternal care than other men (see Gangestad & Simpson (2000) for review). It is possible that some females may choose a long-term partner whose low masculine appearance suggests cooperation and extended paternal care and/or choose short-term partners whose higher facial masculinity may indicate better genetic quality. Females may thus trade-off heritable immunity benefits for the benefits of paternal investment. In the case of short-term mating or when a female has already acquired a long-term partner, the importance of paternal investment from a secondary partner is minimized and so females appear to favour male traits advertising heritable immunity benefits.

It should be noted that the results of the study may not reflect that females with a partner or females rating for short-term relationships prefer masculinity; rather the results of the study may suggest that individuals without partners and those looking for men for long-term relationships prefer greater femininity, and hence positive personality attributes, in men. Females without partners and those rating for short-term relationships may not be as demanding of the overall preferred femininity in male faces, as they do not expect the relationship to last long or they already have a partner they are happy with and so this variable is simply not as important to them.

There are trends in the data to suggest that older individuals prefer more masculine faces (significant overall negative correlation between age and femininity preference). One obvious explanation may be that masculine faces appear older (Perrett *et al.* 1998). Older females may thus prefer older-looking male faces for a variety of reasons associated with assortative mating (individuals pair up with those possessing similar traits to themselves). Older individuals have also grown up under different environments and potentially different portrayals of beauty. For example, the males presented in Hollywood films are potentially different now from 20 years ago. Older individuals may also have needs in a partner that are different from those of younger individuals. Assortative mating for age, different media portrayals of beauty across time, and changing desires are all potential, and possibly additive, mechanisms to account for variations in preferences between younger and older participants.

Little *et al.* (2001) found that women who thought they were physically attractive preferred more masculine faces than those women who thought they were less physically attractive. The absence of a preference for proposed markers of good genes was interpreted as potentially adaptive for women of low mate value in order to avoid the costs of decreased parental investment/potential desertion from the owners of masculine features. The findings reported in this study appear independent of such effects given that self-rated attractiveness was not found to differ across those rating short- or long-term relationships, those with or without partners or those using and not using oral contraception.

The current study also demonstrates that use of oral contraception appears to disrupt potentially adaptive preferences. Women using an oral contraceptive displayed no effect of either context or partnership status, in fact their preferences appear to be in the reverse direction to women not using oral contraception. Woman using oral contraception also do not show potentially adaptive preferences for cycle-based attractiveness judgements of masculinity (Penton-Voak *et al.* 1999), odours associated with male facial symmetry (Thornhill & Gangestad 1999), and odour-based cues to MHC genes (Wedekind & Furi 1997). It is also worth noting that those using oral contraception reported having more lifetime partners than those not using oral contraception. This may indicate different lifestyle choices for those using and not using oral contraception. By reducing the consequences of casual sex, use of contraception may lead to more promiscuous behaviour, or else a desire to engage in sex with a greater number of partners may lead individuals to use oral contraception. It is possible then that it is not just the hor-

monal effects of contraceptive use that lead to different patterns of masculinity preference between contraceptive users and non-users in the current study—there may also exist behavioural differences between these groups which may also impact on preference. The impact of the use of oral contraception on actual mate choice remains to be seen but it is certainly an important avenue for future research given its impact on preferences for the potential to maximize offspring fitness.

The existence of different masculinity preferences emphasizes the importance of acknowledging the potential for strategy and flexibility in human mating. Women need not necessarily all have the same picture of the ideal man or one that remains stable throughout their life. Rather, women are influenced by environmental constraints, such as the likely relationship length, and by their own situational factors, such as whether they have a partner or not. The relationship context that a woman is currently interested in and partnership status may go some way in explaining some individual differences in face preference. That preference differences were not found in women using oral contraception implies that the preference changes found here may be related to hormonal status and also that oral contraceptive use may influence a woman's choice of mate. It must be stressed that there is no cause to believe that individuals are consciously aware of their preferences and the possible evolutionary advantages that different strategies of mate selection may confer. There is also no reason for the behaviour that the preferences may bring about to be considered moral or 'endorsed' by evolution.

REFERENCES

Baker, R. R. & Bellis, M. A. 1995 *Human sperm competition: copulation, masturbation, and infidelity*. London: Chapman & Hall.

Barrett, J. C. & Marshall, J. 1969 The risk of conception on different days of the menstrual cycle. *Popul. Studies* **23**, 455–461.

Bellis, M. A. & Baker, R. R. 1990 Do females promote sperm competition? Data for humans. *Anim. Behav.* **40**, 997–999.

Berry, D. S. & McArthur, L. Z. 1985 Some components and consequences of a babyface. *J. Pers. Soc. Psychol.* **48**, 312–323.

Buss, D. M. & Schmitt, D. 1993 Sexual strategies theory: an evolutionary perspective on human mating. *Psychol. Rev.* **100**, 204–232.

Chabbert-Buffert, N., Djakoure, C., Christin-Maitre, S. & Bouchard, P. 1998 Regulation of the human menstrual cycle. *Frontiers Neuroendocrinol.* **19**, 151–186.

Cunningham, M. R., Barbee, A. P. & Pike, C. L. 1990 What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *J. Pers. Soc. Psychol.* **59**, 61–72.

Enlow, D. H. 1990 *Facial growth*, 3rd edn. Philadelphia, PA: Harcourt Brace Jovanovich.

Folstad, I. & Karter, A. J. 1992 Parasites, bright males and the immuno-competence handicap. *Am. Nat.* **139**, 603–622.

Frost, P. 1994 Preference for darker faces in photographs at different phases of the menstrual cycle: preliminary assessment of evidence for a hormonal relationship. *Percept. Motor Skills* **79**, 507–514.

Gangestad, S. W. & Simpson, J. A. 1990 Toward an evolutionary history of female sociosexual variation. *J. Pers.* **58**, 69–96.

Gangestad, S. W. & Simpson, J. A. 2000 The evolution of human mating: trade-offs and strategic pluralism. *Behav. Brain Sci.* **23**, 573–644.

Gangestad, S. W. & Thornhill, R. 1997 The evolutionary psychology of extrapair sex: the role of fluctuating asymmetry. *Evol. Hum. Behav.* **18**, 69–88.

Grammer, K. & Thornhill, R. 1994 Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *J. Comp. Psychol.* **108**, 233–242.

Hillgarth, N. & Wingfield, J. C. 1997 Testosterone and immunosuppression in vertebrates: implications for parasite mediated sexual selection. In *Parasites and pathogens* (ed. N. E. Beckage), pp. 143–155. New York: Chapman & Hall.

Johnston, V. S., Hagel, R., Franklin, M., Fink, B. & Grammer, K. 2001 Male facial attractiveness: evidence for a hormone-mediated adaptive design. *Evol. Hum. Behav.* **22**, 251–267.

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallamm, M. & Smoot, M. 2000 Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychol. Bull.* **126**, 390–423.

Little, A. C., Burt, D. M., Penton-Voak, I. & Perrett, D. I. 2001 Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proc. R. Soc. Lond.* B **268**, 39–44.

Penton-Voak, I. S. & Perrett, D. I. 2000 Female preference for male faces changes cyclically: further evidence. *Evol. Hum. Behav.* **21**, 39–48.

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

Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D., Yoshikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L. & Akamatsu, S. 1998 Effects of sexual dimorphism on facial attractiveness. *Nature* **394**, 884–887.

Regan, P. C. 1996 Rhythms of desire: the association between menstrual cycle phases and female sexual desire. *Can. J. Hum. Sexuality* **5**, 145–156.

Scheib, J. E. 2001 Context-specific mate choice criteria: women's trade-offs in the contexts of long-term and extra-pair mateships. *Pers. Relation.* **8**, 371–389.

Simpson, J. A. & Gangestad, S. W. 1992 Sociosexuality and romantic partner choice. *J. Pers.* **60**, 30–52.

Thornhill, R. & Gangestad, S. W. 1994 Human fluctuating asymmetry and sexual behaviour. *Psychol. Sci.* **5**, 297–302.

Thornhill, R. & Gangestad, S. W. 1999 The scent of symmetry: a human sex pheromone that signals fitness? *Evol. Hum. Behav.* **20**, 175–201.

Tiddeman, B. P., Burt, D. M. & Perrett, D. I. 2001 Prototyping and transforming facial texture for perception research. *IEEE Comput. Graphics Applications* **21**, 42–50.

Wedekind, S. 1992 Detailed information about parasites revealed by sexual ornamentation. *Proc. R. Soc. Lond.* B **247**, 169–174.

Wedekind, C. & Furi, S. 1997 Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proc. R. Soc. Lond.* B **264**, 1471–1479.