Journal of Comparative Psychology
2003, Vol. 117, No. 3, 264–271

0735-7036/03/$12.00 DOI: 10.1037/0735-7036.117.3.264

Female Condition Influences Preferences for Sexual Dimorphism in Faces of Male Humans (*Homo sapiens*)

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In some species, female condition correlates positively with preferences for male secondary sexual traits. Women's preferences for sexually dimorphic characteristics in male faces (facial masculinity) have recently been reported to covary with self-reported attractiveness. As women's attractiveness has been proposed to signal reproductive condition, the findings in human (*Homo sapiens*) and other species may reflect similar processes. The current study investigated whether the covariation between condition and preferences for masculinity would generalize to 2 further measures of female attractiveness: other-rated facial attractiveness and waist-to-hip ratio (WHR). Women with high (unattractive) WHR and/or relatively low other-rated facial attractiveness preferred more "feminine" male faces when choosing faces for a long-term relationship than when choosing for a short-term relationship, possibly reflecting diverse tactics in female mate choice.

Recently, several researchers (e.g., Fink & Penton-Voak, 2002; Thornhill & Gangestad, 1999) have investigated the possibility that models of sexual selection developed by evolutionary biologists to explain mate choice in other species may be, to some degree, applicable to human mate choice. One topic that has received a great deal of attention from an evolutionary perspective is physical attractiveness. As the face appears to play a central role in human social interaction, empirical studies investigating physical attractiveness have predominantly focused on identifying attractive facial characteristics. Much of this research is based on evolutionary biological theories that suggest visual cues may advertise useful information to a potential mate, such as health or reproductive condition. Research with human participants has tended to stress the homogeneity of preferences across individuals and cultures, rather than looking at reasoned explanations for individual differences in attractiveness judgments. Some animal work, however, has stressed variability of preferences within species. The work reported here demonstrates variability in female preferences for male faces in humans that is in some respects reminiscent of results from studies of nonhuman species. The brief review below introduces the good genes model of sexual selection in both nonhuman and human species and presents work indicating that although useful, such models do not entirely encompass the diversity of preferences in humans or animals.

Good Genes Models of Sexual Selection in Nonhuman Species

Good genes models of sexual selection suggest that females should demonstrate preferences for markers of heritable quality in potential mates. These hypotheses have become more popular because of theoretical work suggesting such systems could evolve under conditions characterized by rapidly changing selection pressures (e.g., host–parasite coevolution; Andersson, 1994; Hamilton & Zuk, 1982; Kirkpatrick, 1996) and empirical demonstrations of heritability of fitness (e.g., Norris, 1993; Petrie, 1994). Good genes models predict female preferences for exaggerated secondary sexual characteristics in males, as such traits may be "honest signals" indicating desirable genetic qualities—such traits cannot be faked by individuals of lower "quality" because of their cost. Androgens are linked to the growth of secondary sexual characteristics in male mammals but have a suppressive action on active immune system function (Hillgarth & Wingfield, 1997). Traits that demonstrate successful development in the face of this immunosuppression are thought to represent an honest signal in males (Folstad & Karter, 1992) and are linked to mating success in a wide variety of species (Andersson, 1994).

Variation in Preferences in Nonhuman Species

Even in species in which females, by and large, express preferences for exaggerated secondary sexual characteristics, such preferences are not exclusive. Individuals use diverse reproductive strategies, rather than using a single "best" strategy (Gross, 1996). Although more studies have examined tactics within male mating strategies (e.g., fight–sneak, dominant–female mimic; for reviews, see Brockmann, 2001; Gross, 1996), variation in female sexual behavior also occurs. For example, in three-spined sticklebacks, parasites reduce the intensity of the red coloration around males' throats, and females preferentially mate with males with more intense color (Millinski & Bakker, 1990). This preference is modified by the viability of the female chooser (Bakker, Kunzler, & Mazzi, 1999). Females in better physical condition (high body weight to body size ratio) showed a greater preference for a red-throated model male, and those in worse condition showed a preference for a less intensely colored orange-throated model male.

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The help of R. Petronzio and G. Young in photography and data collection is greatly appreciated.

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Good Genes Sexual Selection and Male Facial Attractiveness in Humans

Although the correlation between attractiveness judgments and actual mate choice in humans is clearly not as direct as the link between preferences and sexual behavior in other species, it is evident that physical attractiveness is a contributing factor to mate choice in humans (see Buss, 1989, and Langlois et al., 2000, for an assessment of the importance of various factors in mate choice and a meta-analytic review of facial attractiveness literature, respectively). Given the importance of physical characteristics in human mate choice, several researchers have looked toward good genes models of sexual selection as a framework for studying sexual attraction (for a review, see Thornhill & Gangestad, 1999).

Facial masculinity has been proposed as a possible indicator of good genes, as masculine secondary sexual traits develop at puberty under the influence of sex steroids and hence may function as an honest signal (Thornhill & Gangestad, 1999). Although some studies find support for female preferences for facial masculinity, several others do not (for a review, see Penton-Voak & Perrett, 2001). For example, computer graphic studies using controlled manipulation of facial characteristics indicate that masculine faces are perceived as possessing negative personality traits and are not clearly preferred over more "feminine" male faces, which are seen as possessing prosocial, desirable personality characteristics (Perrett et al., 1998). In the light of these conflicting findings, it appears that good genes models cannot completely account for female judgments of male facial attractiveness. Some evidence suggests that males with markers of good genes are relatively less likely to invest in offspring, presumably as a profitable mating tactic, in evolutionary terms, is to expend resources on mating rather than parenting effort (for a review, see Gangestad & Simpson, 2000). Work in social psychology has also indicated that personality judgments based on facial information may have a "kernel of truth" (for a review, see Zebrowitz, 1998). Furthermore, links between high testosterone and failed marital relationships have been suggested (Booth & Dabbs, 1993). Good genes in male humans, then, may have a cost in terms of reduced paternal investment.

Variation in Women's Preferences of Male Faces

Recently, work on women's preferences for male faces has suggested that differing facial attractiveness judgments may reflect alternative tactics in a conditional mating strategy that trade off cues to good genes against other factors, such as paternal investment (Gangestad & Simpson, 2000; Gross, 1996). These studies suggest that women may switch tactics depending on their own personal situation and are reviewed below.

One example of variation in women's preferences for male faces has come from the demonstration of shifting female preferences for masculine traits across the menstrual cycle (Frost, 1994; Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak & Perrett, 2000). These changes in preferences for male faces occur in interaction with the specific context of the attractiveness judgment (short- or long-term relationship) and life-history factors (presence or absence of a partner; Little, Burt, Penton-Voak, & Perrett, 2002; Penton-Voak et al., 1999). Women prefer relatively masculine faces in the follicular phase of their menstrual cycle, especially when they have a long-term partner and are judging attractiveness for a short-term relationship. This finding has implications for the role of extra-pair copulations in the evolution of human sexuality: It is consistent with women selecting a relatively feminine face in a long-term partner, indicating possible future investment in offspring, and/or choosing relatively masculine men to father offspring to gain heritable immunocompetence benefits in the context of short-term relationships.

A further illustration of varying preferences that can be interpreted in terms of a conditional strategy demonstrated that women who consider themselves physically attractive show a greater preference for two proposed markers of phenotypic and genotypic quality in male faces: masculinity and symmetry (Little, Burt, Penton-Voak, & Perrett, 2001). The increased preference for masculine faces was seen only when women with high self-rated attractiveness were judging in the context of a long-term relationship. In short-term relationships, no effects of attractiveness were found, possibly as facial cues to paternal investment are less important to such judgments. If self-rated female attractiveness can be considered a measure of actual viability, these preferences could be considered analogous to varying preferences found in other species (e.g., Bakker et al., 1999). Clearly, in humans, the outcomes of social interactions are likely to influence preferences—some characteristics will increase demand for a particular individual as a mate, improving their "market value" (Pawlowski & Dunbar, 1999). High quality women may be more attracted to markers of quality in men because their own high quality means that lower paternal investment (or even desertion) is less detrimental. Alternatively, high quality men may be more willing to invest in (or not desert) high quality women compared with lower quality women. Conversely, women who perceive themselves as less competitive in the mating market may lack preferences for cues to good genes or actively prefer cues to direct benefits (such as paternal investment) in faces. Such "market forces" have been shown to influence men and women's behavior when seeking a romantic partner (Pawlowski & Dunbar, 1999).

The research presented here aims to expand on the results reported by Little et al. (2001). This earlier study relied exclusively on self-reported measures of attractiveness, which are perhaps not the most reliable measure of putative female "mate value." Recent work has demonstrated that self-perceived attractiveness fluctuates over the menstrual cycle (Singh, Davis, & Randall, 2001). In conjunction with the previously reported cyclical variations in female preferences, these variations in self-perceived attractiveness suggest that the study by Little et al. (2001) may be somewhat confounded: Shifts in preferences for male faces may be due to cyclic factors rather than differences in self-perceived attractiveness. To investigate this possibility in the current study, we use two putative measures of female "condition": other-rated (rather than self-rated) attractiveness and waist-to-hip ratio (WHR). These measures are less susceptible to self-perception biases in self-report than those used by Little et al. (2001). A low WHR is thought to be an honest indication of the absence of pregnancy and also fertility (Zaadstra et al., 1993). Some evidence suggests that a high WHR indicates future health problems (Leibel, Edens, & Fried, 1989), and several studies suggest that WHR is a key characteristic in judgments of female attractiveness (e.g., Singh, 1995). This point of view is somewhat disputed: Other researchers suggest that WHR is at best a secondary cue to bodily attractiveness after body mass index (Tovee & Cornelissen, 1999). Furthermore, WHR seems to account for attractiveness better in western-

ized than other cultures (Yu & Shepard, 1998). Nonetheless, WHR does seem to account for a proportion of the variability in female attractiveness in the west and to be a somewhat useful indicator of health. Hence, we used WHR as a more objective measure of female condition than self-reported attractiveness.

It is hypothesized that women who are rated as more facially attractive by others or have a low (attractive) WHR (or both) will show stronger preferences for facial masculinity (a proposed marker of good genes in men). Secondarily, if other-rated facial attractiveness and WHR are indicators of female quality, we expect them to be related as hypothesized by Thornhill and Grammer (1999). Thornhill and Grammer proposed that female traits may represent "redundant signals" and that an assessment of several traits may provide a better estimate of a woman's reproductive status than one trait alone. A system that has evolved to use multiple cues to condition, rather than to rely on single traits, would presumably increase the reliability of mate quality appraisals.

Method

Participants

A total of 82 women (mean age = 20.2 years) volunteered to take part in this study. Informed consent was obtained from all participants at the beginning of the experimental session, in which participants were photographed and measured and took part in facial preference tests. Following an explanation of the procedure, 5 participants did not consent to being photographed but were measured. Twelve participants did not consent to being measured but were photographed. The participants were mainly undergraduate students at the University of St Andrews.

Photography and Measurement

The 77 consenting female participants were photographed under standard conditions with diffuse flash lighting from two lateral flashguns. Images were captured on a digital camera at a resolution of 1,200 × 1,000 pixels. Sitters assumed a neutral expression and removed occluding hair from the face as much as was possible. An additional image of the participant smiling was also captured. Participants were provided with a tape measure and instructed how to take both their waist and hip measurements.

Stimuli

Computer graphic techniques can be used to construct "average" male and female faces by digitally blending photographs of individuals of one sex. Sexual dimorphism in face shape can then be enhanced or diminished by measuring the geometrical differences between male and female face shapes and either exaggerating or decreasing them. For example, "masculinizing" a male face shape by increasing the differences between a male and female average increases the size of the jaw and reduces lip thickness, as male jaws are larger than female jaws and the lips of men are thinner than those of women. Of course, these are only two of many sexually dimorphic facial characteristics, all of which are manipulated simultaneously using this geometric technique.

Six interactive face sequence trials were constructed from six groups of male and female faces (a Japanese group and a Caucasian group as used in Perrett et al., 1998; three other groups of Caucasian faces as used in Penton-Voak et al., 1999; and an African–Caribbean composite generated from 20 Jamaican men with a mean age of 23.0 years and 20 Jamaican women with a mean age of 22.6 years). Each of the six sequences involved a continuum interpolating between and extrapolating beyond the average male and female face shape of one group. For every sequence, 174 feature points (with *X* and *Y* coordinates) were delineated on each face image (on the eyes, nose, lips, face outline, etc.) in the group. This information can be used to generate the average shape and feature configuration of the male and female faces within the group.

To construct feminized and masculinized male face shapes, one must move every feature point on the average male face a prescribed distance along a vector toward its correspondent point on the aligned female average. A sequence of 11 face shapes ranging from 50% feminized (every point on the male face moved halfway along the vector toward the position of the equivalent point on the female face) to 50% masculinized (every feature point moved along the opposite vector) was constructed. The shape of each of the 11 images in each sequence were calculated using this technique. To create identical average male skin textures in each of these 11 faces, we "warped" (effectively stretched or shrunk) each male face that contributed to the male average to the average shape, and then all of the faces were superimposed into one final image. This ensures that the color information in discrete areas of the sitters' faces (for example, the lips) is blended with the appropriate color information from all the others. This procedure, explained technically in Rowland and Perrett (1995), ensures that the final images are sharp and realistic. Controlling for the influence of facial coloration and texture, characteristics that influence attractiveness independently of facial shape, allows the influence of facial shape on attractiveness judgments to be isolated. The images were made perfectly symmetrical by combining them with their mirror image prior to masculinity manipulation. This controls for the possibility that small asymmetries may be exaggerated when extrapolating beyond the average shape. Figure 1 shows sample images from each of the six continua, ranging from 50% masculinized images (the left column), through the average faces (the center column), to 50% feminized images (the right column). These transforms are holistic: Every feature that differs between the male and female averages varies simultaneously across the continuum.

Procedure

Masculinity preferences. Participants were presented with six interactive face-sequence trials followed by an on-screen questionnaire. Moving the mouse left or right altered the amount of the shape transform in the face displayed; for example, the far left mouse position resulted in the 50% feminized image being displayed, the far right mouse position resulted in the 50% masculinized position, and intermediate mouse positions resulted in intermediate face shapes. The face-sequence interactive trials were presented in random order with participants being cued to make judgments on the basis of 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." Short- and long-term relationships were defined before participants rated the faces:

> Short-term: You are looking for 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, an affair within a long-term relationship, and possibility of a one-night stand.
>
> Long-term: You are 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, someone you may consider leaving a current partner to be with, and someone you may, at some point, wish to marry (or enter into a relationship on similar grounds as marriage).

During each trial, left or right (counterbalanced between trials) mouse movement instantly altered the shape of the face in the on-screen image making it more or less masculine (Perrett et al., 1998). Participants were cued to rate attractiveness for either short- or long-term relationships as above. As relationship context (short or long) was manipulated between

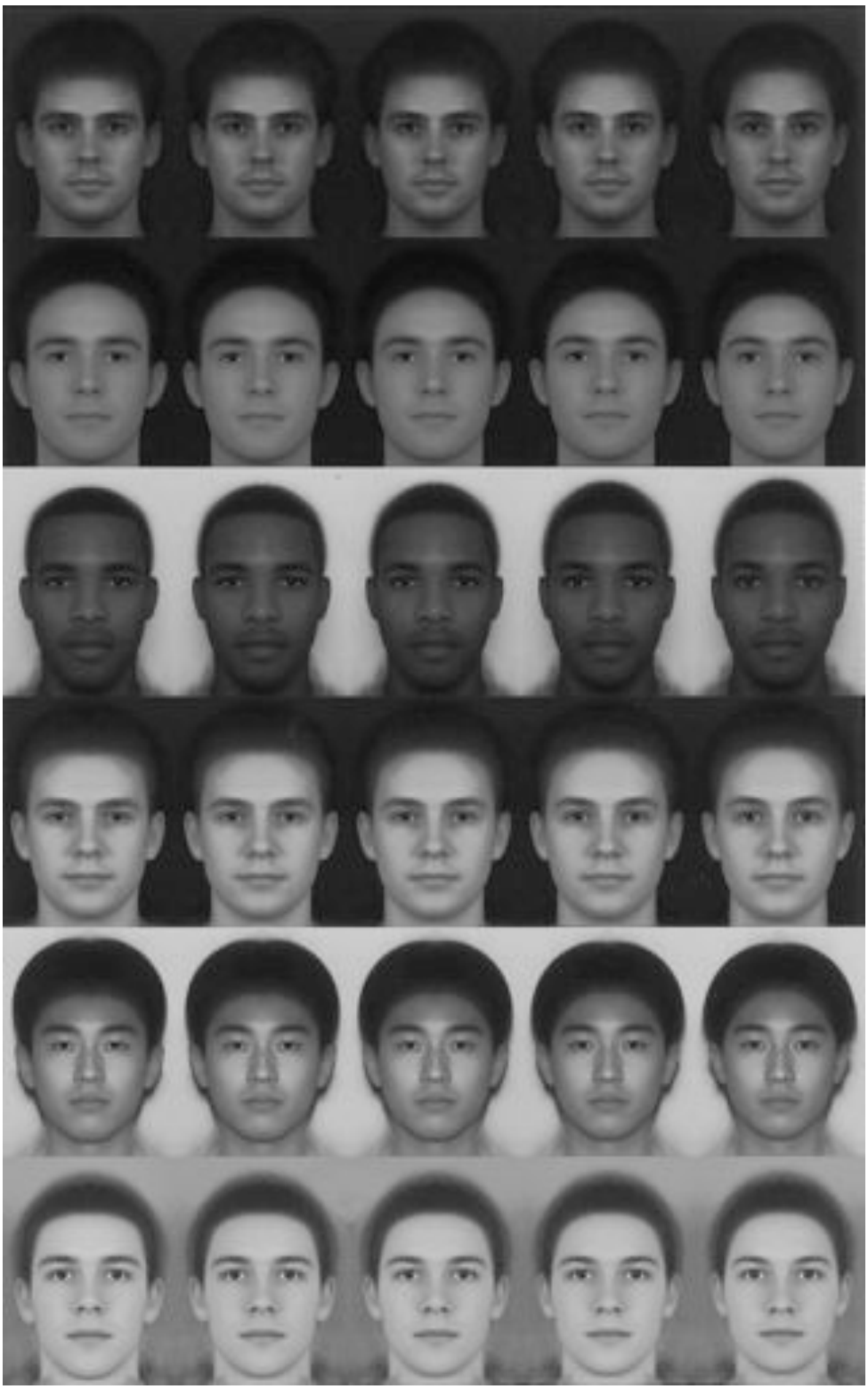

Figure 1. Representative images from each of the six continua used in the study. The five images from each set represent, from left to right, 50% masculinized images (the most masculine stimuli used in the experiment), 30% masculinized images, average images, 30% feminized images, and 50% feminized images (the most feminine stimuli used in the experiment). The left- and rightmost images of the second, fourth, and sixth rows are from "Menstrual Cycle Alters Face Preference," by I. S. Penton-Voak et al., 1999, *Nature, 399,* p. 741. Copyright 1999 by Nature Publishing Group (http://www.nature.com). Reprinted with permission. The center images of the first and fifth rows are from "Effects of Sexual Dimorphism on Facial Attractiveness," by D. I. Perret et al., 1998, *Nature, 394,* p. 885. Copyright 1998 by Nature Publishing Group (http://www.nature.com). Reprinted with permission.

participants, no participant rated faces for both short- and long-term relationships.

Self-rating of attractiveness. Following the masculinity preference tests, participants completed a brief, computer-based questionnaire in which two measures of self-rated attractiveness were taken: self-rated facial attractiveness and self-rated bodily attractiveness. Participants made each of these self-rated attractiveness judgments on a 7-point Likert scale, ranging from 1 (*very unattractive*) to 7 (*very attractive*).

Rating of photographs. An additional 28 undergraduate participants (13 women and 15 men) were recruited to judge the attractiveness of the 77 female photographs. Two images (one smiling and one neutral) of an individual were presented simultaneously on a computer monitor. Participants made a self-paced attractiveness judgment of each individual on a 7-point Likert scale, ranging from 1 (*very unattractive*) to 7 (*very attractive*), and then the next face pair was presented until all 77 women had been rated by each of the 28 participants. Order of presentation of the faces was randomized between raters. Interrater reliability was extremely high (Cronbach's $\alpha = .96$). A mean attractiveness score was calculated from this data for each of the 77 participants; this is referred to as "other-rated attractiveness" in subsequent analyses.

Table 1
Correlations Between Measures of Female Condition

Measure of condition	WHR	Self-rated facial attractiveness	Self-rated body attractiveness
Other-rated facial attractiveness			
r_s	−.276	.359	.227
p	.026	.001	.047
N	65	77	77
WHR			
r_s		.098	.202
p		*ns*	.09
N		70	70
Self-rated facial attractiveness			
r_s			.658
p			.001
N			82

Note. WHR = waist-to-hip ratio.

Results

Overall Preferences for Sexual Dimorphism in Male Faces

Masculinity–femininity preferences were calculated by averaging the mean preference across each of the six continua (Little et al., 2001; Penton-Voak et al., 1999). In the long-term condition, the mean preference was 7.70% feminized (one-sample t test against a null hypothesis of average, 0%), $t(35) = 3.25$, $p < .01$. In the short-term condition, the mean preference was 1.02% feminized (not significantly different to average), $t(45) = 0.44$, *ns*. Earlier studies using these graphics techniques did not distinguish between these two types of relationships. Therefore, a whole sample mean from 82 participants was calculated, giving an overall mean preference of 3.97% for feminized faces. This small preference is significantly different from a preference for average faces (one-sample t test against a hypothesized mean of 0%), $t(81) = 2.30$, $p = .02$. There was a marginally significant trend for more feminine faces to be selected in the long-term condition than in the short-term condition (independent samples t test), $t(80) = -1.98$, $p = .051$.

Relationships Between Self-Rated Attractiveness, Other-Rated Attractiveness, and WHR

The interrelationships between the two self-rated measures of physical attractiveness, WHR and other-rated facial attractiveness, are shown in Table 1. All correlations are Spearman's rho.

Self-rated body and facial attractiveness positively correlate with other-rated facial attractiveness. WHR has no relationship to self-perceptions of either face or body attractiveness but is negatively related to other-rated facial attractiveness. That is, as WHR increases (high values of WHR are thought to be less attractive than low values), other-rated facial attractiveness decreases.

Preferences for Masculinity and Measures of Mate Value

WHR and other-rated facial attractiveness are significantly correlated to women's preferences for male facial masculinity in the long-term conditions, as shown in Table 2. As WHR decreases or other-rated facial attractiveness increases, preferences for masculinity in male faces become more pronounced. No other significant relationships were found.

Alternative Analysis

Further understanding of the relationships between measures of female attractiveness and preferences for sexual dimorphism in male faces was sought by performing a secondary analysis. As WHR and other-rated facial attractiveness were correlated, an analysis of covariance (ANCOVA) was used in an attempt to dissociate the effects of the two measures of female condition on preferences for male faces.

A median split on the WHR of the women who provided measurements was performed, giving low and high WHR groups. A univariate ANCOVA with preference for masculinity as the dependent measure, WHR group (high or low) and relationship context (short or long term) as fixed factors, and other-rated facial attractiveness as the covariate demonstrated a significant main effect of context on preferences for masculine features, with stronger preferences for dimorphic features in the short-term context, $F(1, 69) = 7.40$, $p < .01$. A significant interaction between WHR group and relationship context was found, $F(1, 69) = 5.83$, $p < .02$. Inspection of Figure 2 (upper panel) suggests that this interaction was driven by more pronounced preferences for femininity in the high WHR group in the long-term context.

A similar median split on the mean other-rated attractiveness ratings of the participants was performed, giving low and high other-rated attractiveness groups of participants. A univariate ANCOVA with preference for masculinity as the dependent measure, other-rated attractiveness group (high or low) and relationship context (short or long term) as fixed factors, and WHR as the covariate demonstrated that preferences in the short-term context favored more masculine faces than preferences in the long-term context, $F(1, 64) = 6.68$, $p = .01$. A significant interaction between other-rated attractiveness group (high or low) and relationship context (short or long term) was found, $F(1, 64) = 5.96$, $p < .02$. Examination of Figure 2 (lower panel) suggests that this effect was driven by more pronounced preferences for femininity in the low other-rated attractiveness group in the long-term con-

Table 2
Correlations Between Measures of Female Condition and Preference for Masculinity in Short- and Long-Term Contexts

	Measures of female condition			
Context	WHR	Other-rated facial attractiveness	Self-rated body attractiveness	Self-rated facial attractiveness
Short term				
r_s	.245	−.165	.163	.067
p	*ns*	*ns*	*ns*	*ns*
N	39	42	46	46
Long term				
r_s	−.456	.405	.103	.184
p	.01	.016	*ns*	*ns*
N	31	35	36	36

Note. WHR = waist-to-hip ratio.

text. These two ANCOVAs suggest that both WHR and other-rated facial attractiveness have independent effects on female preferences for male faces in the context of a short-term relationship.

Discussion

The principal aim of this study was to replicate and extend Little et al.'s (2001) study of preferences that appeared to demonstrate condition-dependent mate choice in women. Following the findings of this earlier study, we predicted that two measures of female mate value would predict women's preferences for masculinity in male faces. Consistent with this prediction, the current study demonstrates that both self-measured WHR and other-rated attractiveness are related to individual women's preferences for masculinity in male faces. Women rated low in facial attractiveness by others and women with a high WHR preferred more feminine faces in the context of a long-term relationship. These shifts in preferences are of approximately the same size as those that occur across the menstrual cycle (e.g., Penton-Voak et al., 1999). The shifts toward femininity from the short- to the long-term contexts for the high WHR and low other-rated facial attractiveness groups in the alternative analysis were 18% and 19%, respectively. The size of this difference perceptually is approximately the same as moving from the center images of Figure 1 to the images to their immediate right (illustrated difference, 20%). Women judged by others to be facially attractive and women with a low WHR did not vary in preferences across long- and short-term contexts. In contrast with the self-report measure of condition used by Little et al. (2001; self-rated attractiveness), here mate condition was assessed by more objective measures (WHR and other-rated attractiveness).

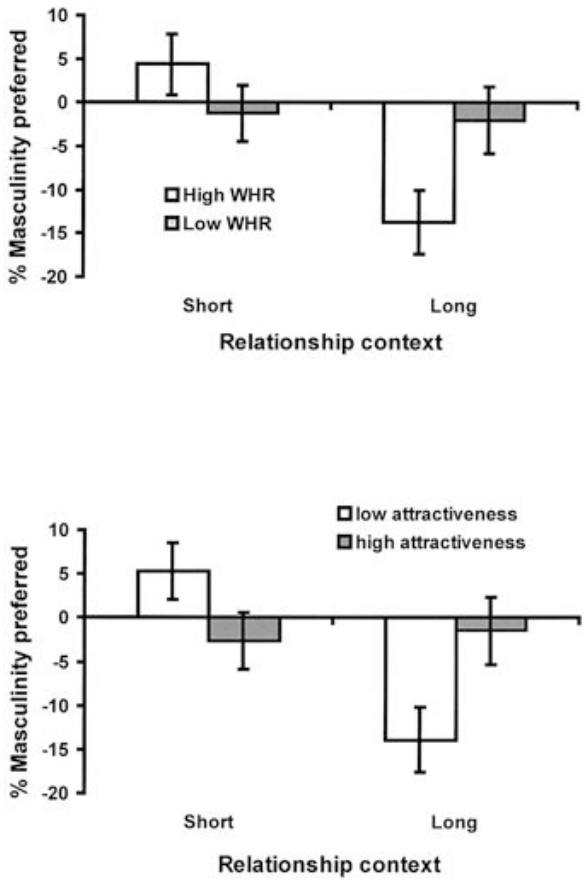

Figure 2. Percentage of male facial masculinity preferred in short- and long-term conditions by women grouped by waist-to-hip ratio (WHR; top) and other-rated facial attractiveness (bottom). Error bars represent standard errors.

The relationship between self-rated attractiveness and women's preferences for masculinity in male faces reported by Little et al. (2001) was not replicated here. This may, however, be due to the relatively small sample sizes in this experiment. Another possibility is that the differing participant selection methods used in the two studies led to samples that differed systematically; perhaps the country of origin of participants in the study by Little et al. (2001; who were recruited over the internet) differed. Although there is much cross-cultural consistency in attractiveness judgments, recent work has indicated subtle differences between cultures in preferences (Penton-Voak, 2001).

This study also contributes data on preferences for feminine male faces that are consistent with previous work. Overall preferences for femininity in faces are comparable with those reported in Perrett et al. (1998) and other studies using stimuli constructed in this way, although the preferences for femininity are smaller than those in some previous work. Other secondary findings of note are the correlations between the various measures that are suggested to indicate female mate value: self-reported facial and bodily attractiveness, WHR, and other-rated facial attractiveness. Self-reported and other-rated attractiveness are related, although not especially

highly, indicating the value of obtaining other-rated attractiveness judgments in addition to self-reports. WHR, an index thought by several researchers to be closely related to female bodily attractiveness, was not significantly correlated to female self-perceptions of bodily attractiveness. WHR did, however, predict other-rated facial attractiveness. This finding is consistent with other work that used both body and face stimuli in male preference tests. Thornhill and Grammer (1999) found a correlation between the rated body attractiveness (when faces were masked in the stimuli) and facial attractiveness (when bodies were masked in the stimuli) in a sample of 92 women and correlations between WHR and body attractiveness but not a direct correlation between WHR and other-rated facial attractiveness as found here.

The finding that WHR and other-rated facial attractiveness are related to female judgments of male facial attractiveness can be interpreted with respect to the literature reviewed in the introduction. Both factors have been considered to be honest signals of female mate value. If this is the case, such visible signals allow women to assess their own mate value in relation to potential competitors. The outcome of such social comparison may allow women to switch tactics dependent on their status in a manner consistent with models of status-dependent tactic selection as suggested by Gross (1996) and as has been reported in nonhuman species (Bakker et al., 1999). In species with complex social organization and biparental care, it is in the reproductive interests of a woman to obtain both paternal care and heritable benefits in offspring. Men in possession of putative indicators of good genes, however, appear less inclined to provide paternal care than other men (Gangestad & Simpson, 2000). Women may assess their own status, or mate value (with or without any conscious awareness), and either trade off cues to heritable benefits against cues to paternal investment in potential partners or try to extract both heritable benefits and paternal care from a high quality man if possible. Whether any conscious awareness of such processes occurs is of secondary importance to the potential evolutionary consequences of such behavior, but it is interesting to note that women's actual preferences appear to change in an experimental situation in which there are no costs to choosing any male face (such as rejection in real partner-choice situations). Although only suggestive, this finding seems inconsistent with a conscious decision to prefer "nice" (feminine) rather than "handsome" (masculine) men in the face of competition.

As in the study by Little et al. (2001), it is clear that the relationship context is of primary importance to these shifts in women's preferences. The long-term/short-term distinction is controversial in research in human mating, as many short-term relationships develop into long-term relationships and the motivations and expectations at the start of relationships may change over time. Although we accept that the distinction between the two relationship types is not a precise definition, it should be noted that in a number of experimental situations, women have shown different preferences when cued to long- or short-term contexts (e.g., Penton-Voak et al., 1999). Additionally, the differences between preferences in long- and short-term contexts are consistent with a status dependent trade-off for good genes against expected paternal investment in humans. Less attractive women (either bodily or facially) seem to change their preferences when choosing partners for a long-term relationship.

A speculative interpretation of the second analysis suggests that less attractive women may not be able to compete with more attractive women for men who offer cues to high heritable quality. Hence, when selecting partners for long-term relationships, less attractive women choose more feminine men, who may be less likely to desert and are less likely to be selected by more attractive women as partners. Such mate choice may result in stable pair-bonds, which benefit offspring through extended paternal investment. In short-term relationships, however, less attractive women pick relatively masculine men, maximizing possible good genes benefits in a context in which paternal investment is not an issue. Conversely, more attractive women, who may be able to extract long-term investment from masculine men (presumably males of high mate quality), choose similar faces in the context of both long- and short-term relationships.

Although any potential adaptive value of these varying preferences is unknown at this point, it is clear that the findings reported here indicate that female preferences for male faces are more complex than some contemporary accounts suggest. For example, theories suggesting that attractiveness judgments reflect universal (i.e., condition-invariant) image processing strategies (e.g., Ghirlanda, Jansson, & Enquist, 2002) fail to predict the condition-dependent effects found here, despite their undoubted ability to account for many findings in facial perception.

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Received December 10, 2001
Revision received September 26, 2002
Accepted September 29, 2002 ■