

Menstrual cycle, trait estrogen level, and masculinity preferences in the human voice

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Abstract

Men with low testosterone (feminine men) invest in relationships and offspring more than men with high testosterone (masculine men). Women's attraction to testosterone dependent traits (e.g. masculine face shape) is enhanced during the late-follicular, fertile phase of the menstrual cycle. Attractive, feminine women have stronger preferences for masculine men as possible long-term partners than less attractive, masculine women. We manipulated 2 testosterone related vocal traits (voice pitch and apparent vocal-tract length) in voices to test if women prefer masculinized men's voices to feminized men's voices; masculinity preferences are enhanced at the fertile (late-follicular) menstrual cycle phase; the amount that masculinity preferences shift cyclically relates to average estrone-3-glucuronide concentration (the primary urinary metabolite of estrone, E3G). We found women displayed general masculinity preferences for men's voices; masculinity preferences were greater in the fertile (late-follicular) phase of the cycle than the non-fertile (early-follicular and luteal) phase; and this effect was most pronounced for women with low average E3G concentration. As feminine women (i.e. those with high average E3G levels) are most able to obtain investment even from masculine men, these women may not need to change their mating preference or strategy during the menstrual cycle as much as masculine women.

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Introduction

Masculine traits in men indicate long-term health (Rhodes et al., 2003), higher reproductive success (Mueller and Mazur, 1997, 1998; Pawlowski et al., 2000), but reduced commitment to relationships and offspring (Burnham et al., 2003; Gray, 2003; Gray et al., 2002, 2004). By contrast, feminine traits in men indicate a higher probability of relationship commitment and paternal investment (Burnham et al., 2003; Gray, 2003; Gray et al., 2002, 2004). Women exhibit stronger facial masculinity preferences during the most fertile phase of the menstrual cycle (late-

follicular phase) than at other times (Johnston et al., 2001; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999). Menstrual cycle shifts in facial masculinity preferences have been observed when women evaluated men's faces for short-term relationships (Penton-Voak et al., 1999) and when relationship context was not specified (Johnston et al., 2001; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999).

Masculinity in men's face shape is preferred by women more for short-term than long-term relationships (Johnston et al., 2001; Little et al., 2002; Penton-Voak et al., 1999, 2003). Preferences for male facial masculinity are influenced by the attractiveness and femininity of the female judges (Little et al., 2001; Penton-Voak et al., 2003). While relatively unattractive and masculine women demonstrated stronger preferences for masculine males as short-term

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partners than as long-term partners, the effect of relationship context on masculinity preferences was weaker for attractive, feminine women (Little et al., 2001; Penton-Voak et al., 2003). This effect of own condition on women's masculinity preferences is thought to occur because more attractive, feminine women may be better able to obtain investment from masculine men during long-term relationships (Clark, 2004; Gangestad and Simpson, 2000; Little et al., 2001; Penton-Voak et al., 2003). Given that attractive and feminine women have more stable masculinity preferences across relationship contexts than unattractive and masculine women, attractive and feminine women should show less variation in their preferences for masculine males during the menstrual cycle than unattractive and masculine women. Fundamental frequency (an acoustic measure of voice pitch) in men is negatively related to testosterone throughout pubertal development (Butler et al., 1989; Harries et al., 1997, 1998) and during adulthood (Dabbs and Mallinger, 1999). Collins (2000) and Feinberg et al. (2005) found that low fundamental frequency and large apparent vocal-tract length (indicated by narrow spacing of formant frequencies) independently predicted perceived masculinity. Fundamental frequency correlated negatively with attractiveness (Collins, 2000) and correlated with perceived dominance (Tusing and Dillard, 2000) of men's voices. Enhancing masculine characteristics in voices (lowering fundamental frequency and increasing apparent vocal-tract length) using Praat audio software (Boersma and Weenink, 2001) also increased women's attributions of masculinity and attractiveness to male voices (Feinberg et al., 2005). Moreover, male vocal attractiveness is highly related to masculinity (Collins, 2000; Feinberg et al., 2005) and men with attractive voices have more mating success than men with unattractive voices (Hughes et al., 2004).

Testosterone enhances somatic tissue development (Notelovitz, 2002). Thus, vocal-tract length and testosterone are positively related (Fitch and Giedd, 1999). As vocal-tract length increases, formant dispersion decreases, closely spaced formants are associated with large body size in rhesus macaques (*Macaca mulatta*, Fitch, 1997), dogs (*Canis familiaris*, Riede and Fitch, 1999), and humans (*Homo sapiens*, Collins and Missing, 2003; Fitch and Giedd, 1999; Gonzalez, 2004). Other estimates of vocal-tract length predict body size in red deer (*Cervus elaphus*, Reby and McComb, 2003). Feinberg et al. (2005), Smith et al. (2005), and Fitch (1994) found that increasing apparent vocal-tract length in human voices increased perceived height. It is relevant here that Pawlowski et al. (2000) found that taller men had higher reproductive success.

Using voices manipulated in formant (vocal-tract length) and fundamental frequencies, we tested if women's preferences for masculine male and female voices were affected by menstrual cycle. In light of Feinberg et al. (2005) and Collins (2000), we predicted that masculinized men's voices would be preferred to feminized men's voices. Next we predicted that masculinity preferences for men's voices

would be stronger when conception risk is high (late-follicular phase) than when conception risk is low (early-follicular and luteal phases). This would parallel findings for facial masculinity.

Gangestad et al. (2004) found that women's preferences for dominant behavioral displays in video clips (including voices perceived as dominant) are strongest during the late-follicular phase of the menstrual cycle. Gangestad et al. (2004) did not test for variation in women's preferences for dominant voices. Also, Gangestad et al. (2004) did not determine whether their observed cyclic shift in attraction to dominance in men was due to a change in sensitivity to dominance across the menstrual cycle (see Macrae et al., 2002), or a change in attraction to dominance across the menstrual cycle. We sought to address the above by asking women to assess attractiveness and dominance of voices across the menstrual cycle and determining if sensitivity and/or attraction to dominance change cyclically.

Penton-Voak et al. (2003) found that waist-to-hip ratio negatively predicted women's preferences for masculinity in men's faces. Waist-to-hip ratio is negatively related to estrogen level (Jasienska et al., 2004). Therefore, we can predict that between women, average levels of estrogen metabolites would positively correlate with women's masculinity preferences in men's voices.

As feminine and attractive women showed the least variation when evaluating attractiveness of masculinized faces in long-term and short-term contexts (Little et al., 2001; Penton-Voak et al., 2003), we predicted that women with high average (trait) estrogen (an index of femininity and reproductive health in women, Jasienska et al., 2004; Moran et al., 1999; Zaadastra et al., 1993) would have relatively stable preferences for masculinity across the menstrual cycle. By contrast, we predicted that women with low average estrogen would show the most marked masculinity preference change across the cycle.

We tested for menstrual cycle shifts in both men and women's voices. If cyclic shifts are linked to mate-choice then such shifts would be present for men's but not women's voices. If may be however that menstrual cycle shifts have no costs, in which case, they could occur for both sexes of voices.

Materials and methods

Voice recordings

Four men's and 4 women's voices were recorded, speaking monophthong vowels "eh", "ee", "ah", "oh", and "oo" with an Audio-Technica AT4041 cardioid condenser microphone in a quiet room from a distance of approximately 20 cm. The voices were encoded directly onto computer hard disk in mono at 44.1 kHz sampling rate and 16-bit quantization using Sonic Foundry's Sound Forge 6.0. The voices, when manipulated, spanned the normal

range of fundamental frequencies of adult men and women (average pitch across all 5 vowels of manipulated voices in men: 105–142 Hz, $M = 121.91$ Hz, $SD = 3.45$; women: range 194–250 Hz, $M = 208.53$, $SD = 15.00$).

Acoustic measurements

All acoustic measurements and manipulations were conducted using Praat v4.0 (www.praat.org). Each vowel was measured separately. Fundamental frequency was measured using Praat's autocorrelation algorithm. Male fundamental frequencies were searched for between 65 and 300 Hz and female fundamental frequencies were searched for between 100 and 600 Hz. Fundamental frequencies were averaged across vowel sounds for each speaker.

The first (lowest) four formant frequencies of each vowel sound were measured in order to obtain estimates of vocal-tract length. Formant frequencies were measured using the Linear Predictive Coding Burg algorithm. The first set of predictions (using Praat's default input parameters) was plotted as dots overlaid on frequency-time spectrograms. Subsequently, Praat's input parameters (maximum formant and number of formants to search for) were adjusted to obtain the best visual fit of the predicted formants onto the observed formants (Feinberg et al., 2005). The algorithm produced a mean formant frequency, averaged across voiced windows of each vowel sound. Formant dispersion (the average distance between successive formants, Fitch, 1997) was used to estimate vocal-tract length. Formant dispersion (from Fitch, 1997) was calculated as $\frac{\sum_{i=1}^{N-1} F_{i+1} - F_i}{N-1}$ where F represents formant frequency i , and N is the number of formants measured (4). As per fundamental frequency, formant dispersion was averaged across vowels for each speaker.

Acoustic manipulations

All manipulations were carried out using Praat's Pitch-Synchronous Overlap Add (PSOLA) algorithm (www.praat.org). The manipulations (sensu Feinberg et al., 2005) were achieved by raising or lowering the entire sound spectrum (while preserving duration of utterance) such that the formant frequencies would produce the target vocal-tract lengths. Next, the fundamental frequency was manipulated (using the PSOLA algorithm, www.praat.org) to the appropriate values. To create feminized voices, the fundamental frequency of each voice was raised by 20 Hz and formant dispersion was increased by 50 Hz. To create masculinized voices, the fundamental frequency of each voice was lowered by 20 Hz and formant dispersion was decreased by 50 Hz. Here, each vowel's duration was normalized to 500 ms (using the PSOLA algorithm, www.praat.org) to control for variation in spoken vowel duration between individuals. Amplitude was normalized to 87 dB RMS. Table 1 displays descriptive statistics on

Table 1

Mean and standard deviation (in parentheses) of fundamental frequency (F0) and formant dispersion (Hz) of voices after acoustic manipulations

	Men's voices		Women's voices	
	Masculinized	Feminized	Masculinized	Feminized
F0 [Hz]	102 (3.36)	142 (3.54)	189 (13.91)	228 (16.09)
Fdisp [Hz]	1025 (72)	1124 (85)	1192 (50)	1299 (73)

acoustic properties of manipulated voices. Fig. 1 shows spectrograms of manipulated voices.

Participants

Twenty-six female participants aged 18 to 23 ($M = 19.5$, $SD = 1.29$) were screened for and satisfied the following criteria: reported they were heterosexual, were not using hormonal contraception (and had not been using hormonal contraceptives for 3 months), cycled regularly (self-report), had urine samples (without blood contamination), and reported no hearing problems.

Procedure

Female participants completed a block of testing once a week, for a period of 4–6 weeks. On each test day, participants provided a urine sample, completed voice preference tests, and completed a short questionnaire.

Hormone assays

We measured estrone-3-glucuronide (E3G), the primary urinary metabolite of estradiol and pregnanediol-3-glucuronide (P3G), the primary urinary metabolite of pregnanediol. Both E3G and P3G are most concentrated in early morning urine samples. Urinary creatinine concentration is a measure of urinary excretion rate (which can alter the concentration of metabolite in urine). Thus, to control for urinary excretion rate, E3G levels were divided by creatinine concentration levels (Hillier et al., 2002/2003). E3G and P3G are expressed as ratios: E3G:creatinine and P3G:creatinine. As both E3G and P3G were corrected for with creatinine, for brevity, henceforth, we discuss E3G:creatinine and P3G:creatinine as E3G and P3G concentration ratios.

Upon scheduling time of experimentation, prior to testing, participants were each given empty, sterilized urine collection vials. Women deposited approximately 25 ml of urine from mid-stream of their first urination on each day of testing. Urine was frozen at -20°C until time of analysis.

The assays used a direct competitive ELISA 96-well plate system. Urine samples, diluted in assay buffer, were incubated with labeled antigen [E3G or P3G conjugated to horseradish peroxidase] in the presence of rabbit anti-steroid antibody [respectively, anti-P3G antibody (RAB F 27/7/87) or anti-E3G antibody (RAB 1) (MRC/AFRC Comparative

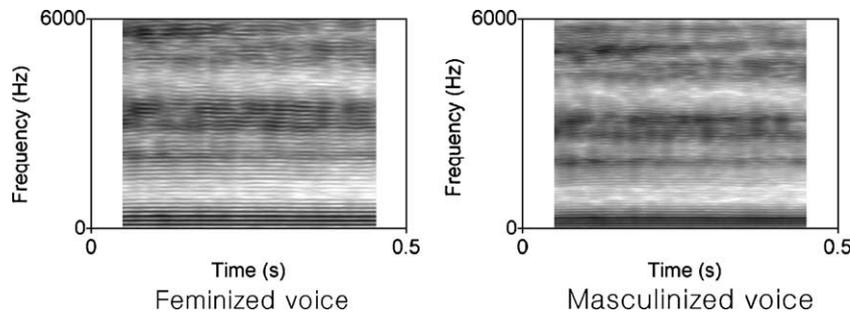


Fig. 1. Spectrograms of the vowel “ee” from one male speaker. Harmonics (thin horizontal lines) are integer multiples of the fundamental frequency (Ladefoged, 1996), thus change in pitch can be noted by the harmonic spacing. Formant frequencies are the thick, dark, horizontal bands. Therefore, formant dispersion can be seen by noting the spacing between formants.

Physiology Research Group, Institute of Zoology, London)]. Bound and free antigens were separated using solid-phase goat anti-rabbit immunoglobulin (IgG). The plates were washed and bound antigen was detected by incubation with the substrate *o*-phenylenediamine and the developed reaction was detected using a plate reader at 492 nm.

Intra- and inter-assay variations (CVs) were assessed by multiple analyses of a number of samples. The samples (low, medium, and high concentrations) were aliquoted and stored at -20°C , a new aliquot being used for each assay. For intra-assay variation, three samples were assayed 10 times within the same assay. This was repeated on four occasions over a period of 2 weeks. For inter-assay variation, three samples were assayed in 42 assays over a period of 8 weeks. The intra-assay CV was less than 10% on each occasion. The intra-assay CV was greater than 10% on only two occasions (11.2 and 12.9%). At the three levels: low, medium, and high, the intra-assay CVs for E3G were 11.0, 6.4, and 4.8%, respectively. At the three levels, low, medium, and high, the intra-assay CVs for P3G were 10.6, 69.6, and 45.5%, respectively.

Voice ratings

Each stimulus was composed of five vowels from each speaker (in the order “ah”, “ee”, “eh”, “oh”, “oo”, presented at 500 ms intervals). The order of stimuli was randomized. Participants were allowed ad-lib repetitions of each voice, played at an adjustable volume via headphones, to ensure that ratings were private. To ensure further privacy, computer stations were separated by screens. Participants were instructed to select their rating of each voice for attractiveness and dominance on 7 point scales on the computer monitor (1 = very unattractive, 7 = very attractive; 1 = very subordinate, 7 = very dominant). Men and women’s voices were rated in 2 separate blocks, the order of which was randomized.

Questionnaires

In addition to hormonal analysis, menstrual cycle information was collected via self-report (diary data). To

determine day of menstruation and length of menstrual cycle, participants reported the number of days since the onset of their last period of menstrual bleeding and their average menstrual cycle length. Date of onset of period following study completion was also collected via email. We calculated cycle day by the backwards counting method (see Gangestad et al., 2004). Additionally, participants reported hormonal contraceptive use (current or in the last 3 months). Sexual orientation was reported on a 7 point scale (1 = completely homosexual, 4 = bisexual, 7 = completely heterosexual). Age was also self-reported.

Menstrual cycle classification

From diary data, test days between 14 and 21 days until next onset of menses (i.e. the late-follicular phase) were first assigned to the high conception risk group and all other days assigned to the low conception risk group (Penton-Voak et al., 1999). Subsequently, diary data were verified using P3G ratios (sensu Jones et al., 2005). If participants whose diary data indicated that they were in the late-follicular phase did not have P3G concentration ratios <0.5 , we classified data from these times as non-fertile.

Eleven women completed testing in the fertile phase only once, 12 completed testing in the fertile phase twice, and 2 women completed testing in the fertile phase 3 times. Two women completed testing in the non-fertile phases twice, 10 completed testing in the non-fertile phases 3 times, and 13 women completed testing in the non-fertile phases 4 times. Where women completed testing in more than one fertile and/or non-fertile phase, average scores (within each phase) were used (sensu Jones et al., 2005). Differences between phases in number of times participants were tested reflect the fact that only 1 week was used to categorize the fertile phase, whereas 3 weeks were used to categorize non-fertile phases.

Statistical analysis

Mean ratings for each listener were calculated by averaging attractiveness ratings of the 4 same-sex voices of each manipulation type (masculinized or feminized)

every time they rated voices for each cycle phase (fertile or non-fertile). When participants did not rate all voices, they were excluded from that specific analysis. Our hypotheses contained directional predictions thus allowing one-tailed probability estimates. To increase the robustness of the reported effects, and to reduce probability of type 1 errors, two-tailed probability estimates were used.

Average (trait) E3G concentration was computed by calculating the mean of the previously computed average fertile level and average non-fertile E3G concentration from all urine samples collected from each participant. Analyses using either average late-follicular E3G, or average non-fertile (late-follicular and luteal) E3G produced comparable results. One-sample Kolmogorov–Smirnov tests revealed that all variables were normally distributed (all $P > 0.05$).

Results

Initially, tests for main effects of the vocal manipulations on attractiveness and dominance, collapsed across menstrual cycle phases, were evaluated using paired sample t tests. These results are displayed in Table 2. In both sexes, masculinized voices were rated more dominant than feminized voices. Women preferred masculinized men's voices to feminized men's voices. We also observed a significant preference for feminized women's voices.

Late-follicular and non-fertile E3G concentration ratios were positively correlated with non-fertile E3G concentration ratios ($r_{25} = 0.598$, $P = 0.002$). Average E3G concentration ratios did not correlate with average male vocal masculinity preferences ($r_{25} = -0.126$, $P = 0.517$). Late-follicular and non-fertile P3G concentration ratios were not significantly correlated ($r_{25} = 0.307$, $P = 0.136$).

To evaluate possible individual differences in size of cyclic shifts in masculinity preferences, masculinity preference scores were created by subtracting attraction (or dominance attribution) to feminized voices from that of masculinized voices (sensu Feinberg et al., 2005). These masculinity preference scores were entered into mixed-model ANOVAs for evaluation of condition-dependent menstrual cycle shifts in masculinity preferences. A paired sample t test showed that the fertile and non-fertile groups did not differ significantly in order of testing ($t_{23} = 1.172$, $P = 0.253$).

Table 2

Paired sample t tests, comparing attributions of attractiveness and dominance to voices varying in masculinity

		Difference in means (masculine–feminine)	t value	P value
Men's voices	Attractiveness	0.901	6.07	<0.0001
	Dominance	1.334	9.83	<0.0001
Women's voices	Attractiveness	-0.314	-2.25	0.036
	Dominance	1.08	9.15	<0.0001

A mixed-design ANOVA [within-subject factor: menstrual cycle phase (fertile/non-fertile), covariate: average E3G concentration] revealed a main effect of menstrual cycle phase on masculinity preferences ($F_{1,23} = 7.447$, $P = 0.012$). Masculinity preferences were elevated in the late-follicular (fertile) menstrual cycle phase. The main effect of menstrual cycle on vocal masculinity preferences was qualified by average E3G concentration ($F_{1,23} = 5.948$, $P = 0.023$). Women with low E3G concentration showed stronger cyclic shifts in preferences for masculinity in men's voices than women with high E3G concentration (see Fig. 2).

Mixed-design ANOVAs [within-subject factor: menstrual cycle phase (fertile/non-fertile), covariate: average P3G concentration] diminished the strength of the previously observed menstrual cycle shift in vocal masculinity preferences ($F_{1,23} = 3.823$, $P = 0.063$). There was no significant interaction between average P3G and menstrual cycle shifts for vocal masculinity preferences ($F_{1,23} = 32.732$, $P = 0.112$).

Mixed-design ANOVAs [within-subject factor: menstrual cycle phase (fertile/non-fertile), covariates: either average E3G or average P3G] revealed no menstrual cycle shift in dominance attributions to men's or women's voices, or femininity preferences in women's voices (all $F < 1.75$, $P > 0.2$).

Discussion

We found that masculinizing male voices increased their attractiveness, replicating findings by Feinberg et al. (2005). We also found that masculinized male and female voices were perceived as more dominant than feminized voices. This supports findings that pitch of voice was negatively correlated with attributions of dominance in men's voices and contradicts findings that pitch of voice and dominance ratings were not associated in women's voices (Tusing and Dillard, 2000). Our finding supports research showing that other testosterone dependent traits predict dominance (Mazur and Booth, 1998; Mueller and Mazur, 1996; Swaddle and Reiersen, 2002).

We found that women prefer vocal masculinity in men (but not women) more when fertile than non-fertile. This extends to the vocal domain, findings by Penton-Voak et al. (1999), Penton-Voak and Perrett (2000), and Johnston et al. (2001), who found that women increased their facial masculinity preferences at peak fertility.

As masculinized men's voices were rated more dominant than feminized voices, menstrual cycle shifts in preferences for dominant sounding voices were observed, supporting findings by Gangestad et al. (2004). Attributions of dominance to voices varying in pitch and apparent vocal-tract length did not change across the menstrual cycle. Dominance itself (or masculinity) becomes more attractive to women when fertile. Women did not become more sensitive to dominance in voices when fertile.

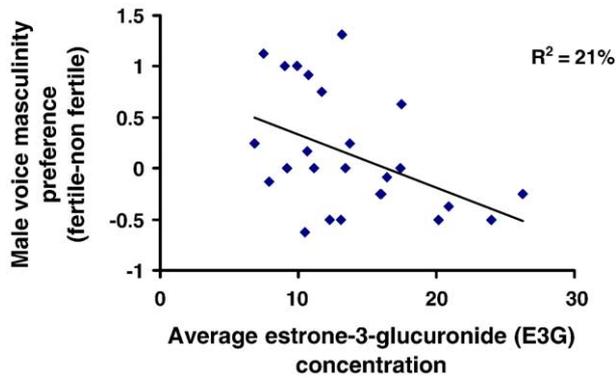


Fig. 2. Average estrogen predicts size of menstrual cycle shifts in male masculinity preferences. Women with low average estrogen showed the biggest cyclic shifts in masculinity preferences.

Average E3G concentration across the entire cycle did not predict vocal masculinity preferences as might be predicted from Penton-Voak et al. (2003). We found, however, that women with higher E3G concentration exhibited the smallest menstrual cycle shifts in vocal masculinity preferences. If the cost associated with choosing masculine men as long-term partners is lower for feminine and attractive (high estrogen) women, i.e. they are more able to secure masculine men for long-term partners (Gangestad and Simpson, 2000; Little et al., 2001; Penton-Voak et al., 2003), menstrual cycle shifts in masculinity preferences may not surface. If the cost associated with choosing masculine men as long-term partners is higher for masculine and unattractive (low estrogen) women, menstrual cycle shifts in masculinity preferences may be more pronounced.

Within-individual change in progesterone appears to be more important for within subject changes in mate preferences during the menstrual cycle than change in estrogen level (in Jones et al., in press). Between-individual variation in estrogen (or concentration of estrogen metabolites), however, appears to be a better predictor of between subject variation in the magnitude of cyclic shifts in masculinity preferences than between subjects variation in progesterone level.

It should be noted that there are perceptual scales of pitch (e.g. ERB, Bark, Mel; Stevens, 1998; Traunmüller, 1990), different than the Hz scale. Absolute frequency changes may be easier to detect in masculinized voices than in feminized voices and in male than female voices. Therefore, our manipulations may not have been perceptually equivalent. We found, however, that the manipulations were strong enough to drive attributions of dominance in both sexes. Therefore, it is unlikely that perceptual differences in pitch between the manipulations of men and women's voices were the reason we observed no cyclic shifts in masculinity preferences in women's voices.

As menstrual cycle affected attributions of attractiveness but not attributions of dominance, our results cannot be explained by a decrease in cortical sensitivity to sounds

varying in pitch at the luteal phase (Walpurger et al., 2004). In other words, if general acoustic sensitivity underlies our results then we would expect equal cyclic change in attraction to women's voices and dominance attributions to men and women's voices. This did not occur. The absence of menstrual cycle effects on women's preferences for manipulated masculinity in women's voices supports the idea that the findings reported here are mate-choice relevant.

Although not investigated here, the present results may be qualified by relationship context. Penton-Voak et al. (1999) found that menstrual cycle shifts in masculinity preferences were more pronounced when women were evaluating faces in a short-term context than a long-term context. Clark (2004) found that masculine women (as indicated by digit-ratio and mental-rotation ability) had less restricted socio-sexual inventory scores (e.g. preferred and had more short-term relationships) (see Gangestad and Simpson, 2000) than feminine women. Hughes and Gallup (2003) found that feminine women (as indicated by waist-to-hip ratio) were more likely to be in long-term relationships than masculine women. Therefore, women preferring short-term relationships should show larger cyclic shifts in masculinity preferences than women preferring long-term relationships. The impact of relationship desired, or considered, remains to be evaluated in future studies.

In summary, menstrual cycle shifts in masculinity preferences were found in men's but not women's voices. The size of cyclic shifts was smaller in women with high average levels of estrogen metabolites. Feminine and attractive women may secure masculine men as long-term partners (Little et al., 2001; Penton-Voak et al., 2003). Thus, when trade-offs between male genetic quality and paternal investment are less of an issue (e.g. for attractive, feminine high estrogen women), menstrual cycle shifts in preferences for masculinity may be less pronounced. Future studies on menstrual cycle shifts in preferences should consider underlying condition as a qualifying factor to help unravel the mystery of female mate preferences.

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