Cyclic Variation in Women's Preferences for Masculine Traits

Potential Hormonal Causes

David Andrew Puts
University of Pittsburgh

Women's preferences for several male traits, including voices, change over the menstrual cycle, but the proximate causes of these changes are unknown. This paper explores relationships between levels of estradiol, progesterone, luteinizing hormone, follicle stimulating hormone, prolactin, and testosterone (estimated using menstrual cycle information) and women's preferences for male vocal masculinity in normally cycling and hormonally contracepting heterosexual females. Preferences for vocal masculinity decreased with predicted progesterone levels and increased with predicted prolactin levels in normally cycling—but not hormonally contracepting—women. Adaptive explanations for menstrual variation in women's preferences for masculine traits are discussed and evaluated in light of these findings.

KEY WORDS: Good genes; Hormones; Masculinity; Mate choice; Menstrual cycle; Progesterone; Prolactin; Sexual selection; Vocal fundamental frequency; Voice pitch

W omen's mate preferences fluctuate across the menstrual cycle. Cyclic variation has now been demonstrated in women's preferences for masculine facial structure (Johnston et al. 2001; Penton-Voak and Perrett 2000, 2001; Penton-Voak et al. 1999), facial skin color (Frost 1994), body odors (Gangestad and Thornhill 1998; Grammer 1993; Thornhill and Gangestad 1999), and behavioral displays (Gangestad et al. 2004). Indeed, emerging evidence of a coherent pattern in cyclic variation in women's preferences for male traits includes the following elements: (1) Women's preferences for masculine traits increase with conception risk over the ovulatory cycle (facial structure, facial skin color, body odor; see above-cited references). (2) The trait is sexually dimorphic and sexually differentiates under the

"masculinizing" influence of androgens. This appears true of facial masculinity (reviewed in Penton-Voak and Perrett 2001), facial skin color (men universally have darker complexions than do women) (van den Berge and Frost 1986), and body odor, which differs by sex owing to the amounts of androstenone present in sweat (Grammer 1993).

Recently, Puts (2005) and Feinberg et al. (2006) demonstrated cyclic variation in women's preferences for masculine, low-pitch voices. In these studies, pitch was manipulated by shifting formant structure and fundamental frequency. (For a more complete description of pitch manipulations in Puts [2005], see Puts, Gaulin and Verdolini, in press.) Fundamental frequency (F_0) is the most salient acoustic parameter of voice and the one most closely associated with pitch (Banse and Scherer 1996). F_0 is highly sexually dimorphic (Klatt and Klatt 1990), sexually differentiates under the influence of androgens (Hollien, Green, and Massey 1994), and correlates with androgen levels in adult males (Dabbs and Mallinger 1999). Normally cycling (non–hormonally contracepting) women's preferences for low-pitch, masculine voices were greater in the fertile phase of the menstrual cycle (Puts 2005; Feinberg et al., 2006), and women preferred lower male voices primarily for short-term sexual relationships (Puts 2005).

EVOLUTIONARY EXPLANATIONS FOR CYCLIC PREFERENCE SHIFTS

Adaptation for Timing Genetic Recruitment

Several authors have suggested that such preference shifts are facultative adaptations to cyclic variation in the fitness payoffs associated with particular preferences (e.g., Gangestad and Thornhill 1998; Grammer 1993; Penton-Voak et al. 1999). Changing female preferences may function in recruiting males of high genetic quality when conception risk is greatest. The logic is that, although androgen-dependent traits (such as masculine smell, appearance, or voice) may signal heritable health (Folstad and Karter 1992), males offering such genetic benefits may be poor investors (Gangestad and Simpson 2000; Penton-Voak and Perrett 2001; Putz 2003). Without cues to good genes, women may be inclined to mate with investing males in non-fertile menstrual phases because this behavior increases access to resources while decreasing the risk of impregnation by genetically inferior males. Alternative explanations for cyclic variation in women's mate preferences can, however, be formulated.

Adaptation to Increase Probability of Conception

For example, the same reasoning can be used to hypothesize that menstrual changes in preferences for masculine traits function to promote insemination by fertile males: Females are predicted to select mates on both investment potential and fertility (Andersson 1994), but investing males are not necessarily highly fer-

tile, and vice versa. Because females may benefit from a male's fertility by reducing the number of unfertilized eggs (Halliday 1978) or by producing sons that are successful in sperm competition (Eberhard 1985), females should prefer highly fertile mates mainly for sexual relationships and near ovulation. Indeed, some evidence suggests that more masculine males are less investing (see above) but more fertile. Mifsud, Choon, Fang, and Yong (2001) found significantly higher free and total serum testosterone levels in fertile than in subfertile men, and several studies (Hiort et al. 2000; Mifsud et al. 2001; Milatiner et al. 2004) have found androgen receptor (AR) sensitivity to be positively related to male fertility, including sperm quality. Moreover, Manning and colleagues (1998) found that a more masculine ratio of the second and fourth manual digit lengths, a possible marker of prenatal testosterone, was associated with higher sperm numbers.

By-product of Hormone-Response Pattern Favored during Pregnancy

Cyclic variation in women's preferences for male traits may also represent a by-product of selection for changing preferences over the course of pregnancy. Changing hormone levels during pregnancy are related to aspects of women's reproductive psychology, such as postpartum feelings of attachment to their infants (Fleming et al. 1997), and may also mediate women's desires for relationships with particular types of males. For example, investing partners should be more valuable to females with infants than to those without dependent offspring, and changing hormone levels throughout pregnancy may increase desires for investing mates. Changing hormone levels during the menstrual cycle may thus cause a correlated—but not necessarily adaptive—cyclic shift in the preferences of non-pregnant women.

PROXIMATE MECHANISMS MEDIATING CYCLIC PREFERENCE SHIFTS

Determining which of these hypotheses is likeliest can be aided by a more complete understanding of the proximate mechanisms underlying menstrual variation in mate preferences. Although the underlying mechanisms are not known, it is plausible that such variation is mediated by changes in circulating hormone concentrations. For example, Frost (1994) found women's preferences for darker male faces to be greater during the menstrual phase when estrogen/progesterone ratio (E/P) is typically high than during the phase when this ratio is relatively low. However, additional hormones, including luteinizing hormone (LH), follicle stimulating hormone (FSH), testosterone (T), and prolactin (PRL), fluctuate over the menstrual cycle (see Franchimont et al. 1976 for a demonstration of cyclic fluctuation in PRL) and may mediate cyclic changes in preferences. Moreover, the hormones that mediate shifts in one preference might differ from those that mediate shifts in another.

It is generally difficult (and perhaps unethical) to manipulate hormone levels in order to test their effects on women's mate preferences. However, correlational studies

may be useful because different hormones exhibit different patterns of fluctuation across the menstrual cycle (Figure 1), and it is thus possible to correlate women's preferences with some hormones and not others. Unfortunately, hormone assays are costly, and without a priori knowledge, multiple hormones would have to be assayed in an exploratory study of cyclic variation in women's mate preferences, compounding costs.

One method for narrowing the search for the hormonal basis of cyclically fluctuating mate preferences is suggested by studies showing that female behavior and mate preferences vary with conception risk across the menstrual cycle (Chavanne and Gallup 1998; Gangestad and Thornhill 1998; Gangestad et al. 2004; Penton-Voak and Perrett 2000; Thornhill and Gangestad 1999). In these studies, women's positions within their cycles are estimated using menstrual cycle information obtained via questionnaires. Some studies (e.g., Gangestad and Thornhill 1998) then assign expected conception risk values to each woman based on her estimated position in her cycle and average daily values from published literature. That these methods give sufficient resolution is attested by the fact that significant relationships are observed between conception risk and preferences (e.g., Gangestad and Thornhill 1998; Gangestad et al. 2004; Puts 2005; Thornhill and Gangestad 1999). In the same way, expected hormone values may be assigned according to estimated position in the cycle. This technique was recently used by Fessler and Navarrete (2003) to estimate daily progesterone levels.

The present study thus employs a direct analogue of the methods used in the studies described above to present preliminary data on the hormonal mediation of cyclic variation in women's mate preferences. Estimated levels of cyclically fluctuating hormones (E, P, LH, FSH, T, and PRL) are used to predict preferences for vocal masculinity in normally cycling women, with women taking hormonal contraception serving as controls. Finally, the implications of these results for understanding the evolution of cyclic variation in women's preferences for masculine traits are discussed.

METHODS

Subjects

206 self-identified heterosexual female University of Pittsburgh undergraduates participated in this human subjects board–approved experiment. 142 subjects were normally cycling and not taking hormonal contraception, and the remaining 64 subjects were taking hormonal contraception at the time of the study. The mean age of non–hormonally contracepting subjects was 18.8 years (range = 18–30, s.d.= 1.7), and the mean age of hormonal contraceptive users was 19.8 (range 18–25, s.d. = 1.6).

Figure 1.   Daily hormone concentrations representing weighted averages from several published studies (Abraham 1974; Cooke et al. 1978; Franchimont et al. 1976; Judd and Yen 1973; and Midgley and Jaffe 1968).

A. Peptide Hormones
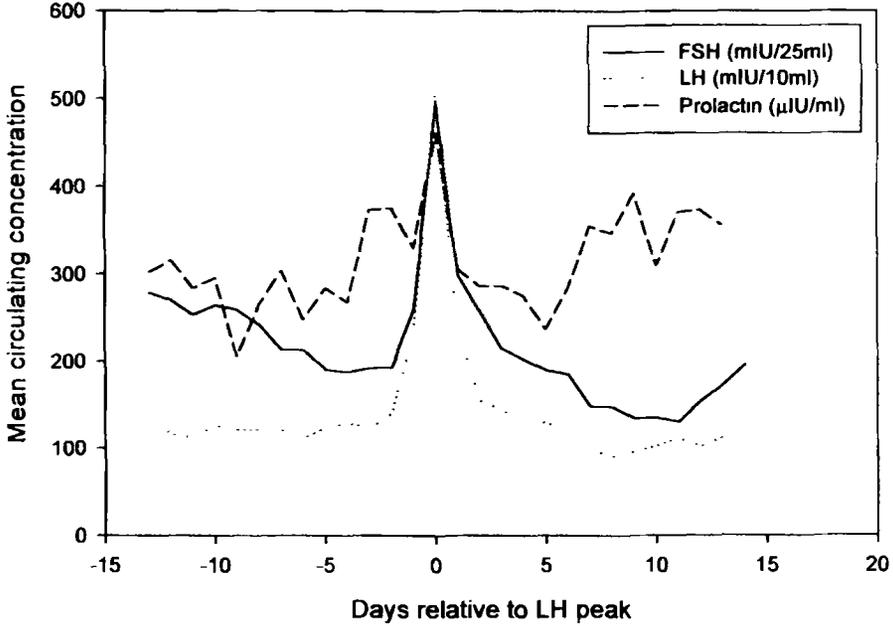
B. Steroid Hormones
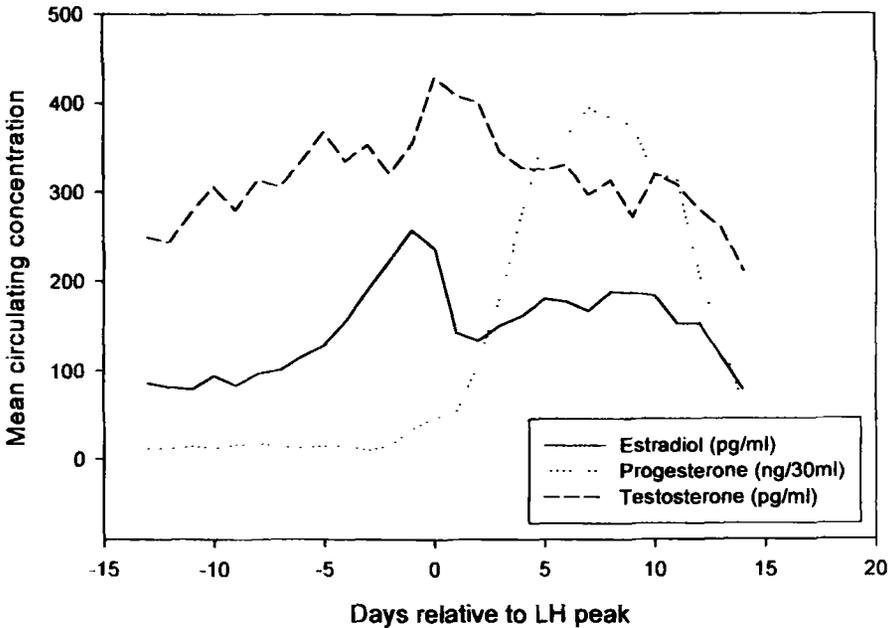
Procedures

Subjects attended one of 11 rating sessions held in classrooms equipped with audio equipment on which stimulus sets could be played.

Stimulus Sets. 111 males were recorded (mean recording length = 20.5 seconds) as they participated in an unscripted dating game scenario by describing themselves to a female whom they were told might choose them for a date (described in Putz et al. 2004). Average fundamental frequency (F_0) was measured from each recording using Praat voice analysis software (mean $F_0 = 112.7$ Hz, range = 82.9–158.9 Hz). Because female preferences for vocal masculinity were later measured as a function of the recordings' F_0, it was desirable to increase the total F_0 range available for ratings, thus increasing the potential for F_0 to affect ratings. The total F_0 range of recordings was increased to 78.2–168.4 Hz by both raising and lowering each recording by one semitone (without affecting speed) using the sound-editing program CoolEdit 2000. Voice manipulations also shifted formant structure, an acoustic correlate of vocal tract length, but these shifts were in the same direction as F_0, producing either lower/more masculine voices or higher/more feminine voices (see Puts et al., in press). Owing to experimenter error, one recording was not lowered. Thus, 332 recordings were produced (111 raised, 111 unmodified, and 110 lowered). Recordings were divided into nine sets of 30 and two sets of 31 recordings (11 total stimulus sets) so that each set included (*a*) no more than one version of a single male's recording and (*b*) nearly equal numbers of raised, lowered, and unmodified recordings (from different males). Manipulations produced obvious pitch differences between otherwise identical recordings, but all recordings sounded "natural," and consequently no rater reported any suspicion of recordings having been altered.

Rating Vocal Attractiveness. Subjects received rating sheets for rating the sexual attractiveness and long-term relationship attractiveness of male voice recordings. The experimenter explained the importance of obtaining independent ratings and directed raters not to react audibly or visibly to recordings or to pay attention to others. The experimenter then played a compact disc of the following: (1) a description of the stimulus set: approximately 30 recordings of men attempting to win a date with a woman, (2) directions to rate each man's attractiveness for both a "short-term, purely sexual relationship, such as a one-night stand" and a "long-term, committed relationship"; (3) five sample recordings illustrating the range of variation; (4) 30 or 31 modified and unmodified courtship recordings of males, each followed by 10 seconds of silence for rating; and (5) directions for filling out a questionnaire at the end of the rating packet. All recorded instructions were spoken by a 25-year-old female in a pleasant, professional tone. Subjects assessed attractiveness by placing a mark anywhere on a line from "extremely unattractive" to "extremely attractive." One hundred unlabelled tick marks on each line enabled the experimenter to assign

values from 0 to 100 for attractiveness ratings according to the placement of the rater's mark. Owing to a missing rating sheet, one subject rated only 24 recordings.

Questionnaires.   After rating the recordings, subjects were also asked the length of their typical menstrual cycle, the number of days since the onset of their last menstrual bleeding, and whether or not they were currently using a hormonal contraceptive.

Data Treatment

Preferences for Male Vocal Masculinity.   Because it is highly conspicuous, sexually dimorphic, and androgen-dependent, F_0 was used as a measure of vocal masculinity. Both the magnitude and strength of individual subjects' preferences for masculine voices were measured. Preference magnitude, measured by the slope of a female's attractiveness ratings regressed on F_0, is the degree to which a change in F_0 (and its verbal and acoustic correlates) predicts a change in a female's attraction. Preference strength, measured by the correlation between F_0 and a female's ratings, is the extent to which F_0 (and its verbal and acoustic correlates) accurately predicts a female's attraction. Because low F_0 represents high vocal masculinity, the sign of preference measures was reversed for clarity. Thus, preferences for more-masculine voices are positive in sign, whereas preferences for less-masculine voices are negative in sign. The magnitude and strength of subjects' preferences were measured for both short-term, sexual and long-term, committed mating contexts. Consequently, for each subject, four preference measures were calculated: short- and long-term preference magnitude, and short- and long-term preference strength.

Hormonal Status.   Menstrual cycle information was used to estimate hormonal status by first estimating each subject's distance (in days) from the midcycle LH peak (D_{LH}) (e.g.,–2 indicates two days before, and 2 indicates two days after, the LH peak). This was accomplished by estimating the onset of the subject's next menstrual bleeding and assuming that the LH peak occurs 15 days prior (Bakos et al. 1994). D_{LH} values were then transformed into their expected equivalents in a 28-day cycle $(D_{LH(28)})$ as follows. If $D_{LH} < 0$, then

$$D_{LH(28)} = D_{LH}[13 / (c - 15)]$$

where c is the subject's average menstrual cycle length (in days). Thus, D_{LH} was multiplied by the average number of days in a 28-day cycle prior to the LH peak, divided by the expected number of days in a c-day cycle prior to the LH peak. This preserved distance from LH peak as a percentage of the follicular phase (the phase prior to and including the LH peak day). Because most between-female menstrual cycle variation occurs during the follicular phase (Nelson 2000:318), luteal phase D_{LH} values (those after the expected LH peak day) and D_{LH} values of zero were not adjusted. Thus, if $D_{LH} \geq 0$, then $D_{LH} = D_{LH(28)}$.

Expected hormone levels were assigned according to $D_{LH(28)}$ using daily hormone concentrations from several published studies (Abraham 1974; Cooke et al. 1978; Franchimont et al. 1976; Judd and Yen 1973; Midgley and Jaffe 1968), averaging values across studies, and weighting each study's values by the number of subjects in that study. The hormones estimated (and the number of subjects measured for the hormone across studies) were E ($N = 34$), P ($N = 23$ for follicular phase, 34 for luteal phase), LH ($N = 34$), FSH ($N = 34$), PRL ($N = 14$), and T ($N = 12$) (Figure 1). Because a PRL value for day $D_{LH(28)} = 15$ could not be obtained from the cited studies, this value was interpolated as the average of the two adjacent days (days 14 and –13). Treating this value as missing data did not alter the results.

In order to obtain more reliable hormonal status estimates, 52 women with cycle lengths differing by more than 3 days from a 28-day cycle were eliminated from analysis. A further 15 women who reported that more than one of their average cycle lengths had elapsed since the onset of their last menstrual bleeding were also eliminated, resulting in a sample population of 96 normally cycling and 43 hormonally contracepting subjects.

Statistical Analysis

Eliminating subjects on the basis of long or short menstrual cycle length has the advantage of increasing the reliability of hormonal status estimates, but it also has the disadvantage of decreasing sample size. Consequently, two differentially inclusive sets of analyses were performed: one for all subjects whose average cycle length was 25–31 days and a second for only those whose cycles were 27–29 days in length. Linear relationships between preference measures and individuals' hormone levels, independent of the effects of other estimated hormones, were analyzed via multiple regression. Because these analyses were exploratory and did not test specific hormonal hypotheses, statistical corrections (e.g., Bonferroni corrections) for multiple tests were not used. All p-values are two-tailed and considered statistically significant if < 0.05.

RESULTS

Multiple regression collinearity diagnostics revealed that expected LH and FSH values were highly correlated (see also Figure 1). Because LH always exhibited a higher variance inflation factor (VIF) (between 11.6 and 14.6), LH was eliminated from all multiple regressions. Bivariate correlations revealed that LH did not correlate significantly with any measure of women's preferences for either group of subjects (those using and those not using hormonal contraceptives). The removal of LH from multiple regressions resulted in a VIF < 3.0 for all variables in all subsequent analyses, and thus analyses are unlikely to be confounded by collinearity between independent variables.

Table 1.   Results of Multiple Regressions of Vocal Masculinity Preference Measures Regressed on Estimated Hormone Levels in Non-Hormonally Contracepting Women with Average Reported Cycle Lengths of 25–31 Days and 27–29 Days

	N	Short-Term Strength		Long-Term Strength		Short-Term Magnitude		Long-Term Magnitude	
		t	β	t	β	t	β	t	β
25–31 day cycles									
Progesterone	96	–3.15**	–0.39	–3.13**	–0.38	–2.79**	–0.35	–2.53*	–0.32
Prolactin	96	1.03	0.13	1.39	0.18	0.96	0.13	1.70†	0.22
27–29 day cycles									
Progesterone	60	–2.42*	–0.36	–2.78**	–0.41	–2.03*	–0.30	–2.33*	–0.34
Prolactin	60	2.04*	0.32	2.37*	.0.32	2.24*	0.35	2.82**	0.43

† = $p < 0.10$, * = $p < 0.05$, ** = $p < 0.01$

Women with Cycle Lengths between 25 and 31 Days

Multiple regression models using E, FSH, P, PRL, and T as independent variables significantly predicted short- and long-term preference strength ($F_{5, 90} = 2.70$, adjusted $r^2 = 0.082$, $p = 0.025$, and $F_{5, 90} = 2.69$, adjusted $r^2 = 0.082$, $p = 0.026$, respectively), but not short- and long-term preference magnitude ($F_{5, 90} = 2.20$, adjusted $r^2 = 0.060$, $p = 0.061$, and $F_{5, 90} = 2.19$, adjusted $r^2 = 0.059$, $p = 0.062$, respectively) in normally cycling women with cycle lengths between 25 and 31 days. Of the hormones examined, only P significantly predicted vocal masculinity preferences (Table 1). As shown in Table 1, P significantly predicted short- and long-term preference strength ($p = 0.002$ for both) and short-term and long-term preference magnitude ($p = 0.007$ and 0.031, respectively). In women taking hormonal contraceptives ($N = 43$), no model was statistically significant, and no individual hormone significantly predicted preferences.

Women with Cycle Lengths between 27 and 29 Days

When only women with cycle lengths between 27 and 29 days were included in the analysis, multiple regression hormonal models significantly predicted all measures of preference for vocal masculinity in normally cycling women: for short- and long-term preference strength, $F_{5, 54} = 3.05$, adjusted $r^2 = 0.148$, $p = 0.017$, and $F_{5, 54} = 3.32$, adjusted $r^2 = 0.165$, $p = 0.011$, respectively, and for short- and long-term preference magnitude, $F_{5, 54} = 3.28$, adjusted $r^2 = 0.162$, $p = 0.012$, and $F_{5, 54} = 3.59$, adjusted $r^2 = 0.180$, $p = 0.007$, respectively. Both P and PRL significantly predicted all preference measures (Table 1). P significantly predicted short- and long-term preference strength and short- and long-term preference magnitude (p

= 0.019, 0.007, 0.047, and 0.024, respectively). For PRL, the p values were 0.046, 0.021, 0.029, and 0.007, respectively. Again, in hormonally contracepting women ($N = 39$), no model was statistically significant, and no hormone significantly predicted preferences for vocal masculinity.

DISCUSSION

In the present study, only estimated P and PRL levels significantly predicted females' preferences for male vocal masculinity, and only in women who were not using hormonal contraception. High P levels were associated with preferences for males with less masculine (higher) voices, whereas high PRL ratios were associated with preferences for males with more masculine (lower) voices. These results parallel those of Frost (1994), who found women's interest in lighter (less masculine) photographs of male faces to be greater during the phase of the menstrual cycle in which P levels are high.

Although P was a significant predictor of preferences for vocal masculinity both in women with 25–31 day cycles and in those with 27–29 day cycles, PRL significantly predicted preferences only in the more restrictive (27–29 day cycle) group. A likely reason for this difference can be inferred from Figure 1. Whereas P increases soon after the LH peak and remains elevated throughout the majority of the luteal phase, PRL levels are elevated only for a day or two around the LH peak. PRL levels are thus more susceptible to errors introduced by estimating the offset from the midcycle LH peak on a 28-day cycle ($D_{LH(28)}$, see Methods) in women whose actual cycle lengths differ substantially from 28 days.

Different hormonal contraceptives deliver different hormones (P vs. both E and P) at different levels, but all hormonal contraceptives function to suppress ovulation by damping normal cyclic hormonal fluctuations. Thus, no relationships between the vocal masculinity preferences of women taking hormonal contraception and expected hormone levels (if they were not taking hormonal contraception) were predicted or found.

These results should be replicated using hormone assays. However, potential sources of error in hormone level estimation generated by the present methods (including absence of ovulation and inaccurate reporting of menstrual cycle variables by subjects in the present study and measurement errors in the hormonal studies consulted) should introduce noise rather than contribute to significant relationships between hormone level estimates and mate preferences.

Possible Neural Mechanisms

At present, it is unclear by which neural mechanisms fluctuating P and PRL levels may modify women's mate preferences, but some informed speculation is possible. Progesterone mediates sexual behaviors in female mammals (Nelson 2000; Takahashi 1990) and may affect preferences by regulating the transcription of re-

ceptors for neurotransmitters implicated in female sexual behavior, including ace-
tylcholine, GABA, serotonin, oxytocin, and CCK (McEwen 1988). Potential sites
of such effects include the anterior hypothalamus, ventromedial-ventrolateral hy-
pothalamus, medial preoptic area, amygdala, and midbrain central gray area, which
are regions involved in regulating female sexual behavior (Nelson 2000:322) and in
which target cells for P are concentrated (Blaustein 1996; Pfaff and Conrad 1978).

In contrast to progesterone, prolactin is normally associated with nonsexual func-
tions, such as maternal behavior, appetite and food intake, and suppression of fertil-
ity during pregnancy and lactation (reviewed in Bole-Feysot et al. 1998). In humans,
prolactin levels rise gradually throughout pregnancy and remain elevated until nursing
is completed (Nelson 2000:363). PRL probably contributes to maternal functions
by acting on cells in the arcuate, periventricular, and preoptic nuclei of the hypo-
thalamus, where PRL receptor expression occurs in diestrous (sexually inactive)
rats and increases during pregnancy (Pi and Grattan 1999). Of special interest to the
present research is the action of PRL during the fertile phase of the ovulatory cycle
corresponding to behavioral estrus in rats. Estrogen levels increase during the ovu-
latory phase in rats, stimulating behavioral estrus (Nelson 2000:281), and thus pos-
sible sites of fertile phase PRL activity include those brain regions in which prolactin
receptor expression has been detected in estrogen-treated rats. These areas include
the supraoptic, suprachiasmatic, ventrolateral preoptic, and ventromedial preoptic
nuclei (Pi and Grattan 1998).

Further research, including functional neural imaging studies in humans and
experimental hormonal manipulations in appropriate animal models, is needed to
elucidate the specific proximate mechanisms underlying menstrual variation in
women's mate preferences.

Ultimate Causes

Although several plausible ultimate-level hypotheses predict cyclic variation in
women's mate preferences, the present study provides support for some of these
hypotheses and contradictory evidence to at least one other. This variation in women's
mate preferences does not appear to be a by-product of an adaptation inducing
women to choose more-investing, less-masculine mates in response to the demands
of child-rearing. First, progesterone levels drop precipitously at parturition (Nelson
2000). According to the present research, this should increase preferences for mas-
culine males at a time when less-masculine, more-investing mates would be advan-
tageous, and putative genetic benefits from masculine males could not be obtained.
Second, as noted above, prolactin levels rise during pregnancy and remain elevated
throughout nursing—a hormonal state that the present data indicate should also
*increase preferences for more-masculine, less-investing males when the reverse
would seem to be most beneficial.* On the other hand, the present study supports
hypotheses that women's preferences have been shaped by selection to increase the
probability of mating with masculine males during the fertile phase of the ovula-

tory cycle. First, progesterone levels are low during the fertile phase of the ovulatory cycle, which the present results indicate should lead to higher preferences for masculine males. Second, prolactin levels peak at midcycle, and this should also increase preferences for masculine males near ovulation, when women are most fertile. Whether this increased preference for masculine males during peak fertility represents an adaptation to recruit high-quality genes for offspring or merely to mate with fertile males is not at present clear. The degree to which these findings generalize to cyclic variation in women's preferences for male traits other than vocal masculinity also awaits further investigation.

David Puts received his doctorate in biological anthropology from the University of Pittsburgh in 2004 (under the name David Andrew Putz). He is interested in sexual selection and human sex differences; has written a textbook on human sexuality; and is currently a postdoctoral fellow in neuroscience in the laboratory of Marc Breedlove and Cynthia Jordan at Michigan State University researching the development of sex differences in the brain and behavior.

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