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Human female orgasm and mate fluctuating asymmetry

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Abstract. Human, *Homo sapiens*, female orgasm is not necessary for conception; hence it seems reasonable to hypothesize that orgasm is an adaptation for manipulating the outcome of sperm competition resulting from facultative polyandry. If heritable differences in male viability existed in the evolutionary past, selection could have favoured female adaptations (e.g. orgasm) that biased sperm competition in favour of males possessing heritable fitness indicators. Accumulating evidence suggests that low fluctuating asymmetry is a sexually selected male feature in a variety of species, including humans, possibly because it is a marker of genetic quality. Based on these notions, the proportion of a woman's copulations associated with orgasm is predicted to be associated with her partner's fluctuating asymmetry. A questionnaire study of 86 sexually active heterosexual couples supported this prediction. Women with partners possessing low fluctuating asymmetry and their partners reported significantly more copulatory female orgasms than were reported by women with partners possessing high fluctuating asymmetry and their partners, even with many potential confounding variables controlled. The findings are used to examine hypotheses for female orgasm other than selective sperm retention.

The human female orgasm has attracted great interest from many evolutionary behavioural scientists. Several hypotheses propose that female orgasm is an adaptation. First, human female orgasm has been claimed to create and maintain the pair bond between male and female by promoting female intimacy through sexual pleasure (e.g. Morris 1967; Eibl-Eibesfeldt 1989). Second, a number of evolutionists have suggested that human female orgasm functions in selective bonding with males by promoting affiliation primarily with males who are willing to invest time or material resources in the female (Alexander 1979; Alcock 1987) and/or males of genotypic quality (Smith 1984; Alcock 1987). Third, female orgasm has been said to motivate a female to pursue multiple males to prevent male infanticide of the female's offspring and/or to gain material benefits from multiple mates (Hrdy 1981). Fourth, Morris (1967) proposed that human female orgasm functions to induce fatigue, sleep and a prone position, and thereby passively acts to retain sperm.

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Additional adaptational hypotheses suggest a more active process by which orgasm retains sperm. The 'upsuck' hypothesis proposes that orgasm actively retains sperm by sucking sperm into the uterus (Fox et al. 1970; see also Singer 1973). Smith (1984) modified this hypothesis into one based on sire choice; he argued that the evolved function of female orgasm is control over paternity of offspring by assisting the sperm of preferred sires and handicapping the sperm of non-preferred mates. Also, Baker & Bellis (1993; see also Baker et al. 1989) speculated that timing of the human female orgasm plays a role in sperm retention. Baker & Bellis (1993) showed that orgasm occurring near the time of male ejaculation results in greater sperm retention, as does orgasm up to 45 min after ejaculation. Orgasm occurring more than a minute before male ejaculation appears not to enhance sperm retention. Baker & Bellis (1993) furthermore argued that orgasms occurring at one time may hinder retention of sperm from subsequent copulations up to 8 days later.

In addition, a number of theorists have argued that human female orgasm has not been selected for because of its own functional significance and

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hence is not an adaptation. Rather, these theorists claim that female orgasm is an incidental by-product of male orgasm, which is an adaptation (e.g. Symons 1979; Gould 1987; Fox 1993).

The primary criterion by which features can be identified as adaptations is purposeful design (Williams 1966; Thornhill 1990). Is the feature designed to solve a particular problem posed by selective pressures? The functional hypotheses of human female orgasm suggest that it ought to have certain special design features. The by-product hypothesis predicts the absence of functional design in female orgasm. Human female orgasm clearly is not necessary for conception; hence, its function could not have arisen simply to ensure conception (Smith 1984; Baker & Bellis 1993). Perhaps the leading functional hypothesis is that human female orgasm is a female choice adaptation, designed to manipulate sperm competition and promote conception with males of high quality (Smith 1984; Baker & Bellis 1993). In hominid evolution, the primary context in which sperm competition has taken place is probably facultative polyandry, or copulation with an extra-pair male (Smith 1984). Female orgasm as a selective response thus may have evolved as a means by which females could favour sperm of an extra-pair male over that of an in-pair male, or vice versa.

Although extra-pair mating in humans may have evolved because of a number of potential benefits, a primary theory concerns good genes (Benshoof & Thornhill 1979; Smith 1984; Gangestad 1993). A woman who perceives her mate to be of low genetic quality may employ a strategy of garnering resources from her primary mate but having extra-pair sex with a male who is of higher genetic quality. These circumstances could have selected female design favouring retention of sperm from men who possess phenotypic markers of good genes. Baker & Bellis (1993) reported provisional support for these notions. In particular, women in multiple mating situations appear more likely to orgasm during copulation with extra-pair partners than with in-pair partners (see also Bellis & Baker 1990).

Currently, the leading theory of good genes sexual selection is the pathogen theory. Host–parasite coevolution maintains heritable pathogen resistance and, hence, viability in host populations. Thereby, sexual selection favours preferences for mates who possess honest indicators of pathogen resistance (Hamilton & Zuk 1982). A marker of male mating advantage in a variety of species may be fluctuating asymmetry, which is asymmetry of the two sides of bilateral characters (e.g. wings, fins, hands, feet, ears) for which the signed differences between the two sides have a population mean of zero and are normally distributed (Van Valen 1962). Because the two sides of such characters are not controlled by different genes, it is thought that fluctuating asymmetry represents imprecise expression of underlying developmental design because of developmental perturbations (developmental instability). Also, although a variety of factors can cause developmental perturbation (e.g. extreme environmental conditions, genetic mutations, toxins; see Parsons 1990), potentially important causes in natural populations are pathogens (e.g. Bailit et al. 1970; Parsons 1990; Møller 1992a). Within populations, fluctuating asymmetry can vary considerably across individual organisms. In a range of species, individuals' fluctuating asymmetry negatively predicts their fecundity, growth rate and survival (Mitton & Grant 1984; Palmer & Strobeck 1986; Parsons 1990; Thornhill 1992a, b; Thornhill & Sauer 1992). Reduced fluctuating asymmetry is associated with male mating success in a variety of species, including barn swallows, *Hirundo rustica* (Møller 1992b), scorpionflies, *Panorpa* spp. (Thornhill 1992a, b; Thornhill & Sauer 1992), *Drosophila* (Markow & Ricker 1992), non-human primates (Manning & Chamberlain 1993) and others (for reviews, see Møller & Pomiankowski 1993; Watson & Thornhill 1994). A meta-analysis of 29 studies of 13 species revealed a mean heritability of fluctuating asymmetry of 0.27 and an overall statistically significant effect size of 0.15 (Møller & Thornhill, in press). This heritability of fluctuating asymmetry is consistent with the good genes hypothesis of sexual selection.

Fluctuating asymmetry may be a marker of male mating success in humans as well. Men who possess low fluctuating asymmetry tend to be judged more attractive than other men (Gangestad et al. 1994; Grammer & Thornhill 1994; Thornhill & Gangestad 1994). Moreover, they tend to have had relatively many sexual partners (Thornhill & Gangestad 1994), more extra-pair sexual relations and have had sex with women after shorter courtship (i.e. period of 'dating'; Gangestad & Thornhill, in press). No evidence suggests that these men invest more in

their relationships than do others and, in fact, in certain ways, they invest less. In particular, they appear to sexualize (e.g. flirt with) women other than their partner more than do other men (Gangestad & Thornhill, in press) and therefore may engage in greater efforts to mate outside the primary relationship.

If (1) low fluctuating asymmetry is a marker of male quality, independent of any investment he might provide, and (2) human female orgasm is a conditional response that has been designed to favour sperm of men who possess markers of quality, then women should orgasm during copulation with men who possess low fluctuating asymmetry more often than with men who do not. If Baker & Bellis (1993) are correct that orgasms occurring near the time of or after male ejaculation particularly favour sperm retention, then the frequency of female orgasms at these times should particularly correlate with partner fluctuating asymmetry. The current study attempts to test these predictions using data from reports of female orgasmic response from women and their male sexual partners. In examining the role of male fluctuating asymmetry in women's orgasms, we also consider a number of potential confounding variables (e.g. socioeconomic status, perceived future income, relationship investment behaviour, social potency, relationship length, women's and men's sexual experience and attitudes towards casual sex). Also, the data are used to examine the various functional hypotheses for female orgasm mentioned above.

METHOD

Subjects

Subjects were 86 heterosexual adult couples involved in sexually active, heterosexual romantic relationships. Subjects were recruited from introductory psychology courses at the University of New Mexico. This source is often used in scientific studies conducted in academic psychology research departments. At the University of New Mexico, introductory psychology students must meet a research requirement, and one way to meet the requirement is to be a subject in studies of the student's own choosing. Our subjects were self-selected, therefore, for participation in a study of physical features and romantic relationships for individuals who had been romantically involved for 1 month or more. Furthermore, they knew at the time they signed up for our study that they would be asked questions about sexual behaviour and history on a questionnaire. Average ($\pm$ SD) ages of men and women were 21.38 ± 3.66 and 20.28 ± 3.38, respectively (ranges 17–40 and 17–37). Relationships had a mean duration of 24 ± 20 months (range 2–108). Subjects were 53% Caucasian (N=46), 36% Hispanic (N=31), 6% native American (N=5), 2% Black (N=2), 1% Asian (N=1), and 1% other (N=1). Eight couples were married, four had had children together, and another four men and two women had had children with other partners. (An additional 18 couples were used in this study, but either had not engaged in sexual intercourse or did not fully complete the orgasm questionnaire; see Procedure.)

Procedure

Subjects reported for a questionnaire study in groups of one to four couples. Our study was approved by the Human Subjects Committee of the University of New Mexico. We guaranteed anonymity of their responses on the questionnaire, including that their partner would not know any of their responses. We told subjects of the sensitive nature of some of the questions (e.g. sexual history) and that if for any reason they wished to not answer certain questions, they could do so without penalty. Of individuals in couples who claimed that the relationship involved sexual intercourse, 100% of the women and 99% of the men answered all questions about actual female orgasm during intercourse. All of the women and 99% of the men answered a question about faked female orgasm. After reading and signing a consent form, each subject was escorted to his or her own room where they privately completed the questionnaire. Meanwhile, the experimenters (two at each data-collection session) interrupted each individual, one at a time, and took him or her to a different room where they measured fluctuating asymmetry and took a photograph. Subjects did not see their partner until both partners had turned in their questionnaires. After measurement and questionnaire completion, we told subjects the purposes, measures and procedures of the study, and answered subjects' questions. Finally, they were told that they could return the next semester after results were analysed to receive an

overview of the patterns in the data, though they would not be told of their individual results.

Questionnaire measures

We recorded the following measures.

(1) Basic information sheet, including age, height, weight, ethnicity and socioeconomic status of home of origin (upper class, upper-middle class, middle class, lower-middle class, lower class), marital status, duration of current relationship, number of offspring, and the number of offspring with the current partner. This basic information sheet also asked whether the subject had ever broken a foot, ankle, hand, wrist or elbow, or sprained any of these body parts, within the past 3 months. These reports were taken into account when we calculated our measure of fluctuating asymmetry (see below).

(2) Self- and partner-estimated future earnings. Each person was asked to estimate the yearly earnings they and their partners would achieve in 10 years. A small proportion (6%, $N=5$) put down outlying values (over \$100 000, up to \$500 000); hence we truncated the measure at \$100 000. Self- and partner-reports correlated 0.44 for men and 0.35 for women. We averaged the two reports to estimate perceived future earnings.

(3) Social potency scale of the adjective rating form of the multidimensional personality questionnaire (Tellegen & Waller, in press; A. Tellegen, unpublished data). A three-item adjective rating measure of social potency, patterned after a 26-item, true–false format scale. The three adjectives (accompanied by descriptions of the high and low scorers) were 'dominant', 'persuasive' and 'socially visible'. Internal consistency reliability was moderate (Cronbach's alpha=0.61).

(4) Factor-analytically derived measures of investment behaviour. Each partner completed a series of measures about their own and their partner's behaviour in their relationship, including the relationship-specific investment inventory (B. Ellis, unpublished data), a series of measures of mate-retention tactics derived from Buss (1988) and a report of extra-pair sex. Self-partner composite measures were factor-analysed in a larger sample of 104 heterosexual couples within each sex to yield three factors: Nurturance/Commitment, marked by measures indicating a willingness to spend time with and money on the relationship, commitment to the relationship, concern for the partner's well-being; Non-exclusivity, marked by measures indicating a tendency to sexualize (for example, flirt with or attend to) individuals of the opposite sex other than the partner, deceive the partner or neglect the partner at social functions; Proprietariness, marked by measures indicating a tendency to monopolize the partner, be vigilant to the partner's interactions with potential rivals or deter potential rivals (S. W. Gangestad & R. Thornhill, unpublished data).

(5) The Rubin love scale (Rubin 1970). A 10-item face-valid measure of self-professed love for a romantic partner (Cronbach's alpha=0.83).

(6) Sexual behaviour and attitudes questionnaire. Subjects were asked a series of questions about their sexual history and attitudes. Embedded in this questionnaire were the five components of the sociosexual orientation inventory (SOI; Simpson & Gangestad 1991), including a brief three-item measure of attitudes toward sex without commitment: 'Sex without love is okay'; 'I can imagine myself being comfortable and enjoying casual sex with a different partner'; 'I would have to be closely attached to someone (both emotionally and psychologically) before I could feel comfortable and fully enjoy sex with him or her'. (Subjects responded to these items on a 1–9 scale, with 1='I strongly disagree' and 9='I strongly agree'; the last item was reverse-keyed.) In addition, we asked subjects their number of lifetime sex partners to date. We explicitly told subjects to count only heterosexual episodes and to exclude occasions in which sex was either exchanged for money or forced. Finally, we asked subjects their frequency of sexual intercourse in the last month. Men's and women's reports correlated 0.49 (Pearson's r); we treated the mean as a composite measure.

(7) Female orgasm questionnaire. Each partner was asked the percentage of overall time (in 10% increments) that the female partner orgasmed (a) during any sexual bout with the partner (including masturbation and oral sex); (b) during penile–vaginal sexual intercourse in particular; (c) before the partner during sexual intercourse; (d) after the partner during sexual intercourse; (e) at the same time as the partner during sexual intercourse. In addition, each partner was asked how often the female partner faked orgasm. In cases in which (c)–(e) summed to a value greater than (b), we transformed the values by taking the proportion

of each of (c)–(e) over their total and multiplying times (b). Using both partners' reports of orgasm increases the validity of our estimates.

Women's and men's reports correlated moderately for (a)–(e): Pearson's $r=0.51$, 0.47, 0.49, 0.52 and 0.24, respectively. Certain male–female discrepancies were due to cases in which women reported substantial faking that their partners did not detect. For instance, one woman reported that she never orgasmed but faked 100% of the time; her partner reported that she orgasmed 100% of the time and never faked. When we eliminated the 10 cases in which the proportion of total copulations the woman claimed to fake orgasm was more than 20% higher than that reported by the man (for example, 50% faked orgasm reported by the woman and 20% reported by the man would be a difference of 30%), the male–female correlations for (a)–(e) improved: Pearson's $r=0.62$, 0.58, 0.54, 0.60 and 0.28. To estimate these variables, then, we computed male–female composite measures as means, except in these 10 cases, for which we used the woman's report only. To the extent that each partner's report is somewhat valid (as reflected by the sizeable correlation between partners' reports) yet fallible, the composite measure should be more valid than either measure alone (Anastasi 1988).

Based on Baker & Bellis' (1993) work, we combined probability of copulatory orgasm coinciding with and following male ejaculation into a composite of (relatively) high sperm retention (HSR) orgasms. Orgasms occurring before male ejaculation were designated (relatively) low sperm retention (LSR) orgasms. Inter-rater reliabilities (Cronbach's alpha) for proportions of copulations associated with any orgasm, HSR orgasm, and LSR orgasm were 0.73, 0.74 and 0.70, respectively.

(8) Contraceptive use questionnaire. Women were asked which of several contraceptive methods were used during intercourse with their partners: pill (63%), condoms (31%), diaphragm (0%), IUD (0%), sponge/foam (4%) and other (7%). (Respondents could check more than one.) Because we did not include this questionnaire for the first several ($N=7$) couples and several women did not give responses about contraceptive methods, we missed 18 responses to this question. Preliminary analyses revealed that for no conceptive method did users significantly differ from non-users, either with respect to orgasm frequency (all $ts \leq 1.38$, NS) or mate fluctuating asymmetry (all $ts \leq 1.48$, NS). Any association between female orgasm and male fluctuating asymmetry then, appears not to be due to contraceptive method. Thus, we did not consider this variable in any of our main analyses.

Fluctuating asymmetry measures

After placing individuals into separate rooms to complete the questionnaires, the two experimenters interrupted each separately to measure fluctuating asymmetry. For these measurements, the subject was escorted to a separate room reserved for measurements alone. One of the two experimenters then measured the subject's left and right sides on seven bilateral characters: foot width, ankle width, hand width, wrist width, elbow width, ear length and ear width (see Thornhill & Gangestad 1994). We choose these traits because they show fluctuating asymmetry that has moderate heritability (Livshits & Kobylianski 1991). We made measurements with steel callipers to the nearest 0.01 mm. Because measurements may involve some measurement error, we re-measured when the left and right sides differed by more than 3 mm (determined from previous studies to be relatively extreme asymmetry; Thornhill & Gangestad 1994, unpublished data). Ten per cent of the measurements met this criterion. On such characters, we averaged the two measurements. We calculated a total fluctuating asymmetry index (FAI) for each subject by taking the absolute difference between the two sides on each character, dividing by the mean size of the character for the subject, and summing these values across the seven characters (Palmer & Strobeck 1986). We measured about one-third of the subjects, and assistants who did not know the research hypothesis took the other measures. In all cases, measures were taken without knowledge of the sexual behaviour of the subject or his/her partner.

Some asymmetry of skeletal characters may be due to breaks or sprains, not developmental instability. In previous research (Thornhill & Gangestad 1994), we did not take these factors into account, but this study attempted to do so. For any feature for which a subject reported a break (ever) or sprain (within the past 3 months) on one side, we assigned either the sex-specific mean asymmetry (in cases in which the asymmetry exceeded the mean) or the subject's measured

asymmetry (in cases in which the asymmetry was less than the mean asymmetry). In so doing, we assumed that breaks and sprains more often increased than decreased asymmetry. This procedure affected 4.7% of the fluctuating asymmetry calculations for individual characters (6.5% for men, 2.9% for women). The resulting measure of asymmetry correlated (Pearson's r) 0.94 and 0.96 with unaltered measures for men and women, respectively.

Given the small mean asymmetry of individual characters (less than 2 mm), measurement error is a potential concern. To assess inter-rater reliability, two experimenters who were blind to each other's measures took measurements for 47 individuals (23 men and 24 women). The intra-class correlation between the two measurer's FAIs for individuals was 0.63 (0.65 within each sex). Hence, inter-rater reliability for these measures of fluctuating asymmetry appears sufficient for correlational work. For individuals for whom we had two sets of measurements, we averaged across the FAIs. Because a subset of our measures thus had reduced measurement error because of aggregation, our reliability for FAI on the total sample was probably about 0.7.

Physical attractiveness ratings

After measuring a subject's fluctuating asymmetry, an experimenter took two black-and-white, head-on facial photographs of the subject, who was asked to retain a neutral expression. After processing, we selected one of the two photos of each individual for rating (the one that was most clearly head-on, in which the subject did not close his or her eyes or smile and for which the focus was best). Using these photos, the physical attractiveness of subjects was rated by 10 raters on a scale of 1 (least attractive) to 10 (most attractive). The 10 raters' judgements for each subject were summed to yield a composite attractiveness measure (Cronbach's alphas=0.74 and 0.89 for men and women, respectively). The raters were all naive to the research hypotheses and did not include individuals who conducted measurements of fluctuating asymmetry. Owing to camera mishaps, processing problems or unsuitable poses, we did not obtain ratings of 13 men and 12 women.

All statistical probabilities are two-tailed unless indicated otherwise. One-tailed values are reported only in cases of patterns predicted a priori.

RESULTS

Eighty-six of 104 couples reported that their relationship included copulation and completed the orgasm questionnaire. On average ($\pm$ SD), the 86 women claimed to orgasm during copulation $60 \pm 29.5\%$ of the time. Of these, $28 \pm 20.8\%$ occurred before male ejaculation, $14 \pm 11\%$ with ejaculation, and $19 \pm 17.4\%$ after ejaculation. The women claimed to fake orgasm during copulation somewhat more than men perceived them to fake, $13 \pm 19.9\%$ versus $10 \pm 16.3\%$, respectively. Owing to missing data, not all couples could be used in all analyses.

To examine the main hypotheses, we performed a series of multiple regression analyses. In a first analysis, we regressed percentage of copulations accompanied by female orgasm on male FAI, male age, male socioeconomic status of family of origin, male perceived future earnings, male social potency, male physical attractiveness, male relationship behaviour measures (Nurturance/Commitment, Non-exclusivity, and Proprietariness) and relationship duration (Table I).

With all other measures controlled, only a single measure significantly predicted reported female orgasm during copulation. As predicted, women with men who possessed lower fluctuating asymmetry were reported by both partners as having more orgasms during copulation (beta (standardized regression coefficient)$= -0.31$, $t = -2.41$, $df = 59$, one-tailed $P < 0.01$). Follow-up analyses revealed that this effect could not be attributed to the female or male report of copulatory orgasm alone. Two separate regressions replacing the composite measure of copulatory orgasm with either the female or the male report alone yielded significant effects of men's fluctuating asymmetry (betas$= -0.26$ and -0.24, respectively, Ps<0.05) and no other significant effects. Thus the effect of men's fluctuating asymmetry replicated across the two independent reports of copulatory orgasm.

As a group, male investment behaviour measures had particularly low predictive utility. We thus performed a second multiple regression, this time excluding these measures. Men's FAI once again emerged as the only variable significantly predicting female orgasm during copulation (beta$= -0.30$, $t = -2.54$, $df = 64$, one-tailed $P < 0.01$; all other betas<0.15, ts<1.19, NS).

Table I. Proportion of copulations reported to be accompanied by female orgasm predicted by men's fluctuating asymmetry and other features

Predictor variable	Beta	*t*	*P*
Men's features			
FAI	−0.31	−2.41	<0.01
Age	0.14	1.12	
SES	0.07	0.55	
Perceived future earnings	0.08	0.65	
Social potency	0.09	0.69	
Physical attractiveness	0.15	1.16	
Men's relationship behaviour			
Nurturance/commitment	−0.01	−0.07	
Non-exclusivity	0.11	0.71	
Proprietariness	−0.12	−0.13	
Relationship duration	0.12	0.90	

FAI: Fluctuating asymmetry index; SES: socioeconomic status of family of origin. Test on FAI one-tailed, all others two-tailed (although FAI also significant with two-tailed test). $df=59$. All *P*-values not listed were >0.10.

To examine HSR and LSR orgasms separately, we repeated the initial multiple regression analysis twice, each time substituting a specific orgasm measure for the total orgasm measure (Table II). With all other variables statistically controlled, men's FAI significantly predicted HSR orgasms (beta= −0.30, $t=-2.37$, $df=59$, one-tailed $P<0.02$). Although the sample effect was in the same direction, men's FAI did not significantly predict LSR orgasms (beta= −0.13, $t=-1.01$, NS) nor did any other variable. A comparison of these two effects yielded no significant difference ($t<1$). Men's physical attractiveness had a non-significant tendency to predict women's HSR orgasms (beta=0.21, $t=1.69$, $df=59$, $P<0.10$).

Finally we regressed the proportion of all sexual encounters that was reported to have led to female orgasms (including orgasms during intercourse) by men's features (e.g. FAI, age, socioeconomic status of family of origin and relationship behaviour), relationship duration and reported frequency of orgasms during sexual intercourse. By including this last variable, we effectively partialled out the relations between men's features and orgasms during intercourse, and, hence, examined in this analysis whether men's features predict reported female orgasms not during intercourse (e.g. through oral sex or masturbation). No male feature was significantly predictive (all betas<0.11, *t*s<1.03). In particular, men's FAI was not predictive of these orgasms (beta= −0.02, $t=-0.18$, $df=58$, NS). We have no evidence, then, that women with men of low fluctuating asymmetry are simply more orgasmic than other women.

Table II. Proportion of copulations reported to be accompanied by high sperm retention (HSR) and low sperm retention (LSR) female orgasms predicted by men's fluctuating asymmetry and other features

	HSR orgasms			LSR orgasms		
Predictor variable	Beta	*t*	*P*	Beta	*t*	*P*
Men's features						
FAI	−0.30	−2.36	<0.02	−0.13	−1.01	
Age	0.17	1.38		0.02	0.18	
SES	0.08	0.60		0.02	0.16	
Perceived future earnings	−0.09	−0.74		0.21	1.64	
Social potency	0.09	0.70		0.04	0.26	
Physical attractiveness	0.21	1.69	<0.10	−0.01	−0.06	
Men's relationship behaviour						
Nurturance/commitment	−0.17	−0.98		0.15	0.87	
Non-exclusivity	−0.01	−0.05		0.17	1.04	
Proprietariness	0.21	1.38		−0.24	−1.55	
Relationship duration	0.05	0.40		0.11	0.86	

FAI: Fluctuating asymmetry index; SES: socioeconomic status of family of origin. Test on FAI for HSR one-tailed, all others two-tailed. $df=59$. All *P*-values not listed were >0.10. Sperm retention was estimated from the timing of orgasm, after Baker & Bellis (1993).

Additional Analyses

Possibly, the relation between men's fluctuating asymmetry and their partner's orgasms is attributable not to fluctuating asymmetry or correlated indicators of developmental stability, but rather to correlated aspects of relationships that have their effects through processes having little to do with the theoretical notions we have set forth. Several possibilities come to mind.

(1) Sexual experience. Possibly, low-fluctuating-asymmetry men's partners are more likely to experience orgasm because one or both of the partners have had more sexual experience. In fact, men's fluctuating asymmetry is correlated with their number of sexual partners in each of three separate samples (Thornhill & Gangestad 1994; Gangestad & Thornhill, in press).

(2) Sexual frequency. Perhaps low-fluctuating-asymmetry men have sex with their partners more often than men with high fluctuating asymmetry, leading to greater experience with their partner and thereby greater likelihood of orgasm. Alternatively, perhaps low-fluctuating-asymmetry men have less frequent sex with their partners, such that sex has not become stale in their relationship and hence leads to more frequent orgasms.

(3) Partners' love for one another. Perhaps low-fluctuating-asymmetry men and/or their partners love each other more and hence are able to feel more comfortable about sex with the other, which leads to more frequent female orgasm.

(4) Attitudes towards sex. Perhaps low-fluctuating-asymmetry men or their partner's have more permissive attitudes towards sex even in the absence of love and commitment, and thus are able to relax more during sex, and hence have sex associated with more frequent female orgasm.

(5) Female's investment in the relationship. We had included measures of men's investment in their relationship in analyses reported above. Perhaps, however, men's fluctuating asymmetry is associated with their partners' investment in the relationship, which is associated with their involvement in the relationship, and thereby their likelihood of orgasm.

To attempt to control for these variables, we performed additional analyses. Specifically, we performed another set of regression analyses on reported copulatory female orgasm, with relationship duration, men's FAI, age, and physical attractiveness, both partners' investment measures, both partners' number of lifetime sex partners, frequency of sexual intercourse in the last month (mean of partners' reports), both partners' attitudes towards sex without commitment, and both partners' love scale (Table III). Results revealed that only one variable predicted reported female orgasm: men's FAI, beta $= -0.29$, $t = -2.10$, $df = 48$, one-tailed $P < 0.03$.

This analysis included more predictor variables (relative to subjects) than is generally recommended to achieve robust parameter estimates (more than one variable per five subjects), particularly when there exists substantial multicollinearity (Cohen & Cohen 1975). Two points, however, should be made. First, this analysis was not the primary analysis, but rather was a follow-up to one with a much smaller number of variables. It made sense, following the initial finding, to see whether the FAI effect would be removed by including more variables, and it was not. Second, exclusion of any subset of variables added for this analysis did not alter results in any substantive way; men's FAI remains significantly predictive. These facts indicated that the sheer number of variables in this analysis does not account for the FAI effect. Although we cannot rule out all possible confounding variables that may mediate the relationship between men's FAI (or associated markers of developmental stability) and their reports of partners' orgasms, these analyses strongly question a wide variety of major possibilities.

Analyses performed on reported HSR orgasms alone (while controlling for all variables listed above) also revealed a significant effect for men's FAI (beta $= -0.36$, $t = -2.56$, $df = 48$, one-tailed $P < 0.01$).

Potential Mediators

Although fluctuating asymmetry appears to predict reports of female orgasm independently of a variety of potential confounds, the fluctuating asymmetry measures we used are not observable in normal interaction; hence, certain other features might function as mediators of its relation to female orgasm. Men's FAI appears to predict both men's facial attractiveness (Gangestad et al. 1994; R. Thornhill & S. W. Gangestad, unpublished data) and their weight (Manning 1995), such that more symmetrical men are more attractive and heavier. In this sample, men's facial

Table III. Proportion of copulations reported to be accompanied by female orgasm predicted by men's fluctuating asymmetry and additional features

Predictor variable	Beta	*t*	*P*
Men's FAI	−0.29	−2.10	<0.03
Men's age	0.12	0.80	
Men's physical attractiveness	0.11	0.86	
Relationship duration	0.09	0.59	
Sexual experience			
Men's number of partners	0.15	0.97	
Women's number of partners	−0.19	−1.22	
Sex in the relationship			
Sex in the last month	−0.06	−0.42	
Partner's love			
Men's love	0.10	0.56	
Women's love	−0.11	−0.74	
Attitudes towards sex without commitment			
Men's attitudes	−0.09	−0.54	
Women's attitudes	0.12	0.71	
Partner's relationship behaviour			
Men's nurturance/commitment	−0.04	−0.20	
Men's non-exclusivity	0.34	1.58	
Men's proprietariness	0.15	0.70	
Women's nurturance/commitment	−0.04	−0.23	
Women's non-exclusivity	−0.15	−0.95	
Women's proprietariness	−0.28	−1.26	

FAI: Fluctuating asymmetry index. Test on FAI one-tailed, all others two-tailed (although FAI also significant with two-tailed test). $df=48$. All *P*-values not listed were >0.10.

attractiveness did not correlate with their fluctuating asymmetry (with age and age squared partialled out; partial $r=-0.01$, $df=86$, NS), although an aggregate analysis of three samples (including this one) revealed a small but significant average weighted (by sample size) correlation ($r=-0.15$, $df=173$, $P<0.05$: Gangestad & Thornhill, in press). Men's FAI did predict their weight, however (Pearson's $r=-0.25$, $df=100$, $P<0.01$), even when men's height was statistically controlled (partial $r=-0.25$, $df=99$, $P=0.02$; height did not predict FAI: $r=-0.09$, NS).

Might men's body mass account for the relationship between their FAI and reported copulatory orgasm? To address this question, we performed another regression analysis, this time including all men's features included in our original analysis (as in Table I), as well as both partners' weight and height, and women's facial attractiveness and FAI (see Table IV). Five variables significantly (or near-significantly) predicted reported frequency of copulatory female orgasm: men's FAI (beta$=-0.28$, $t=-2.12$, $df=50$, one-tailed $P<0.02$), men's weight (beta$=0.42$, $t=2.61$, $df=50$, $P<0.02$), men's physical attractiveness (beta$=0.29$, $t=2.00$, $df=50$, $P<0.051$), women's height (beta$=-0.44$, $t=-2.55$, $df=50$, $P<0.02$), men's height (beta$=-0.33$, $t=-1.99$, $df=50$, $P<0.052$). Interestingly, then, features found to be associated with men's fluctuating asymmetry (and hence cues of men's developmental stability; specifically, men's weight and physical attractiveness) did independently predict reported female orgasm. None the less, men's fluctuating asymmetry also independently predicted reported female orgasm. The entire relation between men's fluctuating asymmetry and reports of their partner's orgasms is not accounted for by these particular male features.

A regression analysis on reported HSR orgasms alone, including all variables listed above, yielded only one significant effect: men's FAI (beta$=-0.31$, $t=-2.32$, $df=50$, one-tailed $P<0.02$).

Faked Orgasms

As an exploratory analysis, we regressed frequency of reported faked orgasms on all male and

Table IV. Proportion of copulations reported to be accompanied by female orgasm predicted by men's and women's fluctuating asymmetry and other features, including weight and height

Predictor variable	Beta	t	P
Men's features			
FAI	−0.28	−2.12	<0.02
Age	0.05	0.36	
SES	0.19	1.32	
Perceived future earnings	0.03	0.23	
Social potency	0.08	0.59	
Physical attractiveness	0.29	2.00	<0.06
Weight	0.42	2.61	<0.02
Height	−0.33	−1.99	<0.06
Women's features			
FAI	0.07	0.58	
Physical attractiveness	0.19	1.23	
Weight	0.30	1.59	
Height	−0.44	−2.55	<0.02
Men's relationship behaviour			
Nurturance/commitment	−0.01	−0.04	
Non-exclusivity	0.11	0.68	
Proprietariness	−0.15	−0.91	
Relationship duration	0.04	0.27	

FAI: Fluctuating asymmetry index; SES: SES of family of origin. Test on FAI one-tailed, all others two-tailed (although FAI also significant with two-tailed test). $df=50$. All P-values not listed were >0.10.

female features included in our most expanded analysis above (see Additional Analyses). Only a single feature significantly predicted faked orgasms: female Non-exclusivity (beta=0.38, $t=-2.38$, $df=49$, $P<0.03$). Women who tend to act in less exclusive ways with their mate (e.g. flirted with other men or neglected their partners at social gatherings) tended to fake orgasms more often than other women. In light of the large number of variables included in this analysis and the fact that no a priori prediction was made with regard to this finding, however, this relationship must be interpreted very cautiously.

DISCUSSION

As predicted, when other potentially relevant male features, female features, and relationship characteristics were statistically controlled, women with men who possessed low fluctuating asymmetry self-reported and were reported by their partners to have had more orgasms during copulation than women with men possessing higher fluctuating asymmetry. Women with men of relatively low fluctuating asymmetry did not simply have more reported orgasms in general than other women; the reports indicate that the former women are only more orgasmic during copulation itself. In our sample, the increased reported copulatory orgasmic response of women with men of relatively low fluctuating asymmetry was greater for orgasms roughly categorized as high sperm retention orgasms by Baker & Bellis (1993), although we did not find a significant difference between the effects of men's FAI on high retention and low retention orgasms. This comparison is not a particularly sensitive one, however, given that our measure of timing was a very crude one. Baker & Bellis (1993) included orgasms occurring less than 1 min before male ejaculation as high sperm retention ones. Given that nearly half of the orgasms before ejaculation recorded by their informants occurred within this time span, many of the orgasms we categorized as low retention orgasms were probably miscategorized. Our findings support Smith's (1984) general notion that female orgasm evolved as a means by which women manipulate sperm competition occurring as a result of facultative polyandry. Furthermore, the pattern of our results is consistent with Baker & Bellis' (1993) specific hypothesis that timing of the orgasm plays a role in the manipulation, although we cannot offer these data as strong support for that claim.

Few other male features significantly predicted the occurrence of reported female orgasm. Our results provide some evidence that men's weight and physical attractiveness predict copulatory female orgasm frequency independent of male body symmetry. Future research may address the robustness and theoretical interpretation of these relations.

Self-report data can be obtained only in animal behaviour research on humans, and provide one way to address hypotheses about humans. Although self-reports alone may contain errors of unknown magnitude, our use of reports by both partners allowed us to examine the validity of individual reports. Women's own reports and the reports of their partners correlated substantially (about 0.6). Unless the errors in reporting covaried across partners (an unlikely scenario), each set of reports (the women's and the men's) must be substantially valid. Moreover, if each set of

reports is nearly equally fallible, the average of the two reports should be more valid than either report alone. If we assume that errors in the two reports are uncorrelated, the square root of Cronbach's alpha provides an estimate of the correlation of the averaged reports with the 'true' rate of orgasm (Anastasi 1988): in this case, 0.85, the square root of 0.73. Despite being based on retrospective reports, then, internal analyses of our data suggest that our measures are highly valid. None the less, future studies might attempt to gather more accurate data by asking couples over an extended period to fill out a questionnaire pertaining to the female's sexual response on a day-to-day basis. Such an approach may complement the retrospective approach we used.

Of course, even our internal analyses reveal that our measures are not perfectly valid. For a variety of reasons (e.g. deception, faulty memory) retrospective reports are less than perfect. None the less, it seems unlikely that false reporting of orgasms could account for the relationship between men's body symmetry and female orgasm. To do so, errors in the reports would have to correlate with men's body symmetry, an unlikely situation. Moreover, the reporting errors would have to correlate across women's and men's reports for the effect of men's fluctuating asymmetry replicated across reports. Although we can readily imagine that either partner could falsely report orgasm frequency, it seems unlikely that the reporting errors of one person would substantially correlate with those of the other, and each with men's fluctuating asymmetry. After all, neither men nor their partners knew their body symmetry. Also, although male subjects and their partners can observe the male's physical attractiveness, ratings of male physical attractiveness did not correlate with body symmetry in this study. Once again, however, additional studies using alternative methodologies should complement the procedures we used.

Some concern has been expressed to us about how much can be learned from studies of college undergraduates. Although we appreciate the need to replicate this study on a wider sample of people, there is no theoretical reason to expect that college students do not show species-typical sexual responses. Thus, these results cannot be rejected because they were obtained using college undergraduates.

Our results can be used to examine hypotheses that suggest that female orgasm is an adaptation whose function is other than selective sperm retention. The hypothesis that female orgasm functions to create and maintain the pair bond does not explain variability in the female sexual response. Nor does it account for the pattern we have found between male symmetry and increased orgasm. There is nothing explicit about selective bonding in the traditional pair bond hypothesis for orgasm (Morris 1967; Eibl-Eibesfeldt 1989).

Smith (1984) suggested that female orgasm has two design features: (1) it preferentially retains sperm of males of high phenotypic quality and (2) it promotes differential bonding with such males. As mentioned, our results are consistent with point (1). They may also be consistent with point (2). Oxytocin may mediate both effects. Oxytocin, a hypothalamic hormone stored in the neurohypophysis until its release into circulation, could be directly involved in ejaculate choice by women. Circulating oxytocin controls smooth muscle contractions of the uterus at parturition and smooth muscle contractions that eject milk (Insel 1990). Circulating oxytocin increases during the human female sexual response, peaking at orgasm, and is believed to facilitate orgasmic contractions of the smooth muscles of the uterus and vagina (Carmichael et al. 1987; Carter 1992). These contractions may lead to sperm retention. Oxytocin also affects attraction to and acceptance and nurturance of offspring by female mammals (Insel 1990; Panksepp 1992), and recent research implicates oxytocin in heterosexual pair bonding in prairie voles (Carter et al. 1992). If oxytocin promotes conditional and selective affiliation with sexual partners, presence or absence of orgasm could be an important proximate cause of female mate choice. We found no evidence that female orgasm is associated with greater investment by women in their romantic relationships or greater love for the male partner. Thus, if oxytocin facilitates differential bonding with men of high genotypic quality, the bonding apparently does not result in greater love or investment.

The hypothesis that female orgasm promotes preferential bonding with males who are capable or willing to invest (Alexander 1979; Alcock 1987; also see Konner 1990) predicts that male love/investment will correlate with women's orgasm frequency. Our results do not support this prediction. Orgasm frequency in women was unrelated

to the three measures of relationship investment by men: men's love, men's socioeconomic status of family or origin, and men's perceived future earnings. It is possible that male wealth or status or general male investment potential in our sample of young men varied too little to allow detection of a relationship between female orgasm and male investment. Additional studies are needed to examine this relationship. Recent theory and empirical results suggest, however, that females will have evolved to trade off male investment for male genetic quality (Gangestad 1993); thus there may be little reason to expect female copulatory orgasm to relate to male investment per se.

One version of the hypothesis that female orgasm promotes preferential bonding with investing males could involve male investment in the form of foreplay and extra-copulatory sexual play in general. We did not collect data on foreplay, but there is no reason to believe that symmetrical men engage in more or more stimulating foreplay than asymmetrical men. Our finding that symmetrical men are quicker to copulate in romantic relationships (Gangestad & Thornhill, in press) suggests that courtship investment is reduced in these men, but does not directly address their sexual techniques immediately preceding or otherwise surrounding copulation.

Hrdy (1981) suggested that female orgasm promotes pursuit of multiple partners by females, which either reduces male infanticide of a female's offspring by confusing paternity or results in more material benefits from multiple compared to single mates. This idea appears to be inconsistent with our findings. Hrdy's hypothesis seems to predict that orgasm frequency in women will correlate positively with women's lifetime number of sex partners. Alternatively, it could be argued that women who have many mates are unusually resistant to orgasm and pursue it via sexual variety, which would predict a negative correlation between orgasm frequency and lifetime partner number. We found no relationship, positive or negative, between lifetime sex partner number and orgasm frequency in women. We should add that Hrdy herself has not applied her hypothesis to women, only to other female primates (personal communication). She has proposed that female orgasm is an atavistic trait in women, but is an adaptation in other female primates (Hrdy 1981). Our results suggest, however, that human female orgasm is an adaptation whose evolutionary function is selective sperm retention.

Other ideas concerning the possible causes of human female orgasm have been suggested to us. One view is that female orgasm is dependent upon how relaxed a woman is during sex or on how comfortable she is with her mate in general. We found no evidence that orgasm frequency is related to partners' love for one another, attitudes towards sexual permissiveness of women (or men), female or male investment in the relationship, or copulatory frequency in the last month. A related idea is that the form of contraception will influence how relaxed women are about having sex and thus will affect orgasmic response. We found no evidence for a relationship between contraception type and female orgasm. Further research may examine other hypothetical causes of female orgasm.

Human female orgasm is not functionally designed for conception per se because orgasm is not necessary for conception (e.g. Smith 1984; Baker & Bellis 1993). The notion that human female orgasm positively influences conception ignores the strong selection on males to conceive. The evolutionarily stable strategy of male mating effort is to inseminate fertile females effectively. Selection on males will lead to male sexual adaptations designed for high conception. Female mechanisms that digest, manipulate or nourish sperm are most likely sire-choice mechanisms (Thornhill 1983).

Our findings suggest that human female orgasm is designed to retain sperm of men of high developmental stability, and perhaps the sperm of men who are facially attractive and large in body size. Men's facial attractiveness has been shown to correlate positively with their body symmetry but not in this sample. Men's weight, however, correlated positively with their body symmetry in this sample. When symmetry is controlled, our findings indicate that men's attractiveness and weight each covary positively with female orgasm frequency.

The positive relationship between reported female orgasm and male body symmetry is unlikely to be explained as an incidental effect or by-product of object or mate recognition. This hypothesis has been offered as an alternative explanation to good genes mate choice for female preference of symmetrical males (Enquist & Arak 1994; Johnstone 1994). The body asymmetries that

we measured are small (e.g. a small difference in hand width) and are apparently not used in mate choice. Conceivably, body features that are visually assessed in mate choice, for example faces, may correlate with the measured body features; but how a preference for symmetrical body form would cause a greater orgasm response in women mated to symmetrical men remains to be detailed.

Our results place in question the traditional hypothesis that human female orgasm is an incidental effect of male orgasm (Symons 1979; Gould 1987; Fox 1993). Both Symons and Fox emphasized the greater similarity between women's orgasm and the orgasm of pre-pubescent males (boys) than between the orgasms of women and men. Neither boys' nor women's orgasms involve ejaculation; both boys and women exhibit multiple orgasms and very prolonged periods of high erotic sensation (lengthy plateau phase). According to Symons and Fox, the orgasms of both pre-pubescent males and women are incidental, non-functional consequences of adaptive orgasm in men.

The similarity between women's and boys' orgasms suggest to us that boys' sexual experiences might be a training ground for assessment of true orgasm in sexual partners at maturity. One hypothesized evolutionary function of human feelings is that they allow one to model the minds of other individuals and thereby adaptively increase the predictiveness of others' behaviour (Humphrey 1986; Alexander 1989). This view of feelings leads us to speculate that the orgasmic experiences of boys may be similar to those of women because of design. Boys' orgasms may allow them to personally experience female orgasm, which could improve their ability to distinguish true female orgasm from mere sexual arousal of women and from faked orgasms.

Alexander (1979) proposed that female orgasm increases paternity reliability for the male mate by signalling the female's sexual satisfaction with the mate. Our results support this hypothesis in that they imply that males may have gained reproductively in human evolutionary history by distinguishing female orgasm from mere female arousal because orgasm is associated with sperm retention and thus, presumably, with increased probability of paternity. Also, the results showed moderate positive correlations between men's and women's reports of female orgasm frequency and timing, suggesting that men have knowledge of their partner's orgasms, which is expected if female orgasm conveys information to males. Moreover, although preliminary, our results suggest an advantage to men of distinguishing true from faked orgasm. Women who sexualize males other than the pair-bond mate report more faked orgasms. Thus, faked orgasm may correlate with lower reliability of paternity.

Although copulatory female orgasm may signal enhanced paternity reliability to a mate, our results do not support the idea that copulatory female orgasm is a female signal of phenotypic quality. There was no effect of female body symmetry on reported copulatory orgasmic frequency. The negative relationship between women's height and their copulatory orgasmic frequency is difficult to interpret.

Female orgasm outside humans, especially in non-human primates, has been a topic of controversy (Alexander 1979; Lancaster 1979; Symons 1979; Hrdy 1981; Fox 1993). Our results suggest that female orgasm will occur in mammals in which females mate with multiple males whose ejaculates commonly overlap temporally inside individual females. In female primates, for example, orgasm is predicted in species with multiple sexually active males comprising the social unit (e.g. the chimpanzee, *Pan troglodytes*), but not in harem species in which one male monopolizes sexual access to fertile females (gorilla, *Gorilla gorilla*) or monogamous species with large, dispersed territories (e.g. the siamang, *Symphalangus syndactylus*). The occurrence of female orgasm across mammal species is predicted to be positively related to the development of sperm competition adaptations in males. This prediction is complicated by the fact that orgasm is only one way for females to adjust the outcome of sperm competition during or after mating and thus select the fittest sire. Thornhill (1983) used the term 'cryptic' choice for the many types of female adaptations that may operate during and after mating by which multiply mating female animals might select a fit sire.

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