Chapter 12: Female orgasm

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Abstract

Male and female sexual experiences differ considerably, particularly with regards to orgasm. Research into the female orgasm tends to follow one of two lines of reasoning: the by-product explanation or the adaptation explanation. The by-product explanation posits that the female orgasm is a functionless by-product of women's early developmental similarity with men. By contrast, the adaptation explanation hypothesizes that female orgasm is an adaptation in its own, separate right. Supporters of the by-product explanation of female orgasm contend that because female orgasm is more difficult to induce than orgasm in men, is harder to produce via sexual intercourse than through masturbation, and is not necessary for reproduction, that it has not been designed via sexual selection. Supporters of the adaptation explanation of female orgasm, however, believe that female orgasm serves to increase fitness through one or more functions, such as through rewarding sexual behaviors, increasing pair bonds, augmenting the likelihood of conception, and/or working as a mate- or sire-selection mechanism. Here, the current literature on women's orgasmic experience and evidence in favor of both competing explanations are reviewed. It is concluded that a by-product explanation may not provide an adequate summation of the findings, although definite proof in favor of the adaptive design of female orgasm is lacking, and that female orgasm is an important, unique experience that is worthy of continued attention from researchers.

Keywords: Female orgasm, adaptation, by-product, sexual behavior, mate choice, sire choice, pair bonding.

1 Introduction

Female orgasm is accompanied by pleasure, relaxation (Hite, 1976), decreased activation of the cerebral cortex, increased activation of dopamine-related systems in the brain (Georgiadis et al., 2006, 2009), and behavioral responses, such as arching of the back and muscle tension (Komisaruk et al., 2006). Orgasm is also often associated with vocalizations (Hamilton and Arrowood, 1978), which are especially prevalent during penile-vaginal intercourse and may be under at least partial conscious control, providing women with an opportunity to manipulate male sexual behavior (Brewer and Hendrie, 2011). Women tend to additionally experience involuntary muscle contractions in the vagina and anus, and increases in blood pressure, heart rate, and respiration (Komisaruk et al., 2006; Masters and Johnson, 1966) at orgasm.

Sex hormone levels likely play an important role in women's orgasm frequency and individual experience. Oxytocin, a hormone that causes muscle contractions and increases gratification (Blaicher et al., 1999; Carmichael et al., 1987, 1994), but that is likewise involved in maternal care, pair bonding, and affiliation in female mammals (Campbell, 2008), is released at orgasm. Sexual activity may increase men's (Dabbs and Mohammed, 1992) and women's (van Anders et al., 2007) testosterone levels, and may also increase estradiol and decrease cortisol in women (van Anders et al., 2009). Androgen deficiency is one cause of female sexual dysfunction and female sexual dysfunction is often treated with testosterone (Apperloo et al., 2003). Trait testosterone (van Anders et al., 2007) and testosterone levels across the menstrual cycle (Bancroft et al., 1983) are positively associated with women's orgasm frequency. Women's testosterone levels are positively related to their reports of past sexual excitement (van Anders et al., 2009) and may also increase to a small extent at orgasm (Exton et al., 1999; van Anders et al., 2007). Recently, van Anders and Dunn (2009) found that women's estradiol level was

associated with their reported sexual desire and that women's testosterone level was associated with their reports of positive orgasm experience. In men, however, testosterone (not estradiol) level was associated with their reported sexual desire and was not related to their reports of orgasm experience. These findings highlight how male and female orgasmic experience may differ biologically, but they may also differ subjectively.

Women, in contrast to men, report that their orgasms can differ in intensity, location, sensory qualities, and in emotional components (Hite, 1976). For example, King et al. (2011) recently described four different classes of female orgasm. Women can also achieve orgasm in various ways. While stimulation of the glans of the clitoris is typically the fastest and most reliable way for a woman to orgasm, is not the only way (e.g., Bentler and Peeler, 1979; Schober et al., 2004), nor is it the only location at which women can experience orgasm. Different neural pathways in the vaginal area that are independent of the clitoral pathway can trigger orgasm, even in some (human and animal) cases where the spinal cord has been completely severed (Komisaruk et al., 1996; Komisaruk and Sansone, 2003; Komisaruk and Whipple, 2005; Komisaruk et al., 2004). Indeed, women with complete spinal cord injury at the tenth thoracic vertebrae (T10) or higher report sensations generated through vaginal-cervical stimulation, seemingly because of a pathway that can convey adequate sensory activity from the cervix to induce orgasm via the Vagus nerves (Komisaruk and Whipple, 2005).

Female orgasm does not occur with the same reliability as male orgasm, but not all researchers agree to what extent (e.g., Puts, 2006a; Wallen, 2006). Baker and Bellis (1993) found that nearly 50% of female orgasms occurred via masturbation, that approximately 35% of sexual intercourse did not result in orgasm for the woman, and that the woman usually climaxed first when copulatory orgasms did occur. Fisher (1973) reported that 20% of

women claim to never need clitoral stimulation in order to achieve orgasm, although Wallen (2006) later asserted that the number of women who achieve orgasm through penile-vaginal penetration alone might be as low as 6%. However, Fisher (1973) also found that 35% of women needed manual stimulation 50% or more of the time to achieve orgasm, a figure that Puts (2006a) used to state that 65% of women usually do not require manual clitoral stimulation to achieve copulatory orgasm. In line with this assertion, Tavris and Sadd (1977) found that 63% of women recount usually having an orgasm with intercourse and Lloyd (2005) estimated that 55% of women have orgasm with intercourse more than half the time. Finally, while Dawood et al. (2005) found that 34.7% of women never (13.7%) or rarely (21%) experienced orgasm via sexual intercourse, roughly the same number of women (36.3%) indicated that they usually (13.1%), almost always (17.9%), or always (5.3%) experience orgasm through sexual intercourse, with 82.8% of respondents indicating that they are capable of achieving orgasm this way.

Genetic, environmental (Dawood et al., 2005; Dunn et al., 2005), psychosocial (Cohen and Belsky, 2008; Harris et al., 2008), and cultural (Davenport, 1977) factors all appear to contribute to female orgasm frequency and experience, but the quality of the sexual experience undoubtedly plays an important role (Brody and Weiss, 2010; Puppo, 2011; Richters et al., 2006; Weiss and Brody, 2009). Although some women (Brindley and Gillian, 1982) and men (Rowland et al., 2010) are not capable of experiencing orgasm, reports on the proportion of women who have ever experienced orgasm, at least, may underestimate the amount of women capable of achieving orgasm (see also Puts, 2007; Puts et al., 2012a). For instance, Marshall (1971) reported that all women on the Polynesian island of Mangaia, a culture that places a high importance on men pleasing their female partners sexually, report achieving orgasm during intercourse. In Western populations, approximately 90-95 percent of

women have experienced orgasm, with close to 90 percent having experienced orgasm during intercourse (Lloyd, 2005). Furthermore, while cross-species comparisons will not be the focus of this chapter, it is important to mention that there is evidence of female orgasm within nonhuman primate species (reviewed in Allen and Lemmon, 1981; Puts et al., 2012a). Female gorillas (*Gorilla gorilla*) (Harcourt, Harvey, Larson, and Short, 1981; Nadler, 1976; Schaller, 1963) and chimpanzees (*Pan troglodytes*) (Allen and Lemmon, 1981; Hauser, 1990), among others (Puts et al., 2012a), also exhibit signs of orgasm, including changes in respiratory patterns, vocalizations, and vaginal contractions. This demonstrates that female orgasm may be more widespread than previously believed.

Women are more likely than men to fake orgasm (Muehlenhard and Shippee, 2010; Thornhill et al., 1995). Roughly half of all women admit to having faked an orgasm at some point (Darling and Davidson, 1986; Hite, 1976; Muehlenhard and Shippee, 2010; Wiederman, 1997) and one study found that women fake orgasm approximately 13% of the time (Thornhill et al., 1995). Women who began having sexual intercourse at a young age (Darling and Davidson, 1986; Davidson and Darling, 1988), who have more sexual partners (Davidson and Darling, 1988), and who act in less exclusive ways with their partners (Thornhill et al., 1995) tend to fake orgasm more often. Similarly, Wiederman (1997) found that women who have faked orgasm began having sexual intercourse at a younger age, were older, rated themselves as more facially attractive, reported more sexual partners, and scored higher on sexual esteem than women who had not faked orgasm. Just over half of women in one sample report that they fake orgasm because it is important to satisfy their partner (Darling and Davidson, 1986), but other reasons for faking orgasm include meeting a partner's expectations, to boost a partner's ego, and to increase sexual excitement (Muehlenhard and Shippee, 2010). These data underline the complexity of male-female sexual interactions.

Whether or not female orgasm serves an adaptive purpose has become a controversial topic (Alcock, 1980, 1987; Barash, 1977, 2005; Barash and Lipton, 2009; Beach, 1974; Eibl-Eibesfeldt, 1975; Gould, 1987; Hamburg, 1978; Judson, 2005; Morris, 1967; Puts and Dawood, 2006; Puts, 2006a, 2006b; Symons, 1979). Some scholars insist that female orgasm serves no evolutionary function (Lloyd, 2005; Wallen, 2006, 2007), while others believe it may serve one or more adaptive purposes (Baker and Bellis, 1993; Costa and Brody, 2007; Meston et al., 2004; Puts et al., 2012b; Shackelford et al., 2000; Singh et al., 1998; Smith, 1984; Thornhill et al., 1995; Wildt et al., 1998). Thus, there are two competing explanations for why women can experience orgasm: the adaptation hypothesis and the by-product hypothesis.

2 Adaptation versus by-product

An adaptation is any trait that increases the organism's inclusive fitness. Although environmental circumstances may play a vital role in their development (reviewed in Buss et al., 1998), adaptations are inherited, reliably developing traits that exist as a feature of a species through natural selection because they either directly or indirectly facilitated reproduction (Buss et al., 1998; Tooby and Cosmides, 1992; Williams, 1966). Put another way, "adaptation refers to any functional characteristic whose origin or maintenance must be explained by the process of natural selection" (Buss et al., 1998, p.536). For example, the common fear of spiders in humans would adaptively discourage dangerous behavior (i.e., handling potentially poisonous insects), and thus increase chances of survival. By-products, on the other hand, are characteristics that do not serve a specific function and do not solve adaptive problems. A by-product, also called a *spandrel*, is a trait that is not itself a product of natural selection, but instead arose as an indirect consequence of an adaptation (Buss et al.,

1998; Gould and Lewontin, 1979). A commonly used example of a by-product is the color of bones, which are white due to the fact that they contain large amounts of calcium, presumably selected because of properties such as strength and not color (Buss et al., 1998; Shackelford et al., 2012; Symons, 1992).

Sex-specific adaptations can arise when alleles are expressed in both sexes, but are selected for one sex or the other (Rice and Chippindale, 2001). In these cases, selection can disrupt the expression of a sex-specific adaptation in the opposite-sex by regulating the associated genes with sex steroids, such as the evolution of wider hips in women, which evolved to more safely accommodate the head width of a fetus at birth (LaVelle, 1995). However, because of the genetic similarity between the sexes, genes that produce an adaptation in one sex can produce a trait that is not adaptive in the other, referred to as a sexually antagonistic by-product (Rice and Chippindale, 2001). A common example in humans is male nipples, which are clearly adaptive in women (used in breastfeeding), but serve no function in men (Fox, 1993; Puts et al., 2012a; Symons, 1979; Wallen and Lloyd, 2008). Like other by-products, selection also tends to reduce the expression of sexually antagonistic by-products, as demonstrated by male nipples being smaller than female nipples. Therefore, by-products often appear vestigial and do not appear to serve any relative function.

3 Female orgasm as a functionless by-product

Fisher (1930) argued that low genetic variation within a population implies strong selection. Following this hypothesis and observations of haplodiploid insects, Crespi and Vanderkist (1997) concluded that relatively high variability in traits indicated a lack of selection for functionality. The large variability in reports of incidence and method of achieving female orgasm (Dawood et al., 2005; Fisher, 1973; Lloyd, 2005; Symons, 1979; Tavris and Sadd,

1977) has led some to claim that female orgasm is reduced in comparison to male orgasm and, therefore, likely a by-product of the male ability to orgasm (Lloyd, 2005; Symons, 1979; Wallen and Lloyd, 2008). Arguably, the inconsistency of female orgasm, in comparison to male orgasm, may indicate that female orgasm is under significantly less selective pressure (Lloyd, 2005; Symons, 1979), which supports the idea that it was not selectively designed. If female orgasm was adaptively important and subject to strong selection pressure, the percentage of women who never experience orgasm, or who never experience it through intercourse, may be expected to be considerably lower. Eschler (2004) found that only one third (33.3%) of women indicated that vaginal stimulation led to orgasm, compared to 77.4% who indicated that manual clitoral stimulation led to orgasm. Wallen (2006) claims that 5-10% of women never experience orgasm under any circumstances and that approximately 75% of women never experience orgasm through penile-vaginal intercourse alone. Wallen (2006) goes on to argue that if female orgasm during intercourse ever conferred a reproductive advantage, orgasm would be more prevalent in modern women.

Gender in humans is determined at conception, but the early gonadal development of humans in utero is identical in both sexes and no physically dimorphic effects of the initial sex determination seem to occur until around 6 weeks (Blecher and Erickson, 2007). At this point in males, under the influence of testosterone, the labioscrotal folds fuse to form the scrotum, the genital tubercle becomes the penis and, later, the testes descend into the scrotum. In females, the labioscrotal folds do not fuse and form the labia, the genital tubercle forms the clitoris, and the ovaries do not descend (Blecher and Erickson, 2007). Given the homologous nature of male and female anatomical structures involved in orgasm and reproduction, it is evident that the ability of men and women to achieve orgasm is developmentally related. Wallen and Lloyd (2008) consequently looked at the variation in length in male and female

genital structures, finding that clitoral length was more variable than penile length. They argued that the marked variability in clitoral size suggests little or no selective pressure on its development and, by extension, on the development of female orgasm. However, Wallen and Lloyd (2008) have received some criticism for aspects of their study design and interpretation. Their argument assumes that clitoral/penile length are important for orgasmic potential, but current evidence suggests that neither penile (Lynch, 2008) nor clitoral length (Masters and Johnson, 1966) affects the ability to orgasm. As pointed out by Puts et al. (2012a), the assumption that increased variability in clitoral (versus penile) length is related to orgasm potential is flawed because the penis has the additional function of being necessary for both urination and sperm transfer. The clitoris also differs from the penis in the proportion that is external versus internal, making comparison possibly inappropriate (Lynch, 2008). Using volume instead of length, Lynch (2008) used the same data as Wallen and Lloyd (2008) and found no difference between variation in clitoral and penile volume. Hosken (2008) further highlights how it is unclear from Wallen and Lloyd's (2008) data whether allometric slope or the dispersion of the data drives the differences reported. The increased variance in clitoral versus penile length, therefore, is inadequate evidence to conclude definitively that selection did not favor the female orgasm.

Some have argued that the position of the clitoris is sexually dysfunctional in comparison to the penis because it requires extra stimulation that does not often occur naturally during penile-vaginal intercourse (Eibl-Eibesfeldt, 1989; Lloyd, 2005; Morris, 1985). This might suggest that the clitoris did not evolve to function in coital orgasm, thereby supporting the by-product hypothesis. Then again, this conclusion may be short-sighted because the position of the clitoris, while apparently inconvenient for consistent coital orgasmic stimulation, may reduce the risk of damage from vaginal tearing during childbirth (Potts and Short, 1999).

Moreover, because women are far more likely to experience multiple orgasms than men (Darling et al., 1991; Masters and Johnson, 1966; Sherfey, 1973), are widely capable of experiencing orgasm (Davenport,1977; Marshall, 1971), and seem to experience more complex, elaborate, and intense orgasms than men (Mah and Binik, 2001, 2002), some have reasoned that the female orgasm is not reduced compared to the male orgasm (Puts and Dawood, 2007; Puts et al., 2012a). Female orgasm may also serve one or more functions (e.g., sperm retention, Baker and Bellis, 1993) and may be facultative, reflecting possible aspects of female choice (Puts, 2007; Thornhill and Gangestad, 1996), potentially explaining the variation in women's orgasm frequency. Finally, if orgasm is maintained by a selection favoring male orgasm, there should be a strong positive correlation in orgasmic sensitivity between male and female relatives, but Zietsch and Santtila (2011) found no significant correlations in orgasmic function between opposite-sex twins or non-twin siblings. This finding contradicts the by-product hypothesis because it suggests that different genetic factors underlie male and female orgasmic function.

In light of the above, the evidence in favor of the by-product hypothesis of female orgasm appears insufficient to declare female orgasm a "happy accident" with full certainty. Other evidence supports the alternative view that female orgasm is its own adaptation, separate from male orgasm.

4 Female orgasm as an adaptation

The most common reasons given by women as to why they would fake an orgasm are to keep their partner interested or excited, and to reduce the likelihood of a partner being unfaithful or of a partner defecting from the relationship (Muehlenhard and Shippee, 2010). It may not seem initially obvious why female orgasm would lead to an increase in male sexual

satisfaction or decrease the likelihood of male relationship defection, but if female orgasm serves any adaptive function, then men should have a vested interest in their partner's orgasm. Accordingly, McKibbin et al. (2010) found that partnered men who report higher relationship satisfaction also report greater interest in, and attentiveness to, their partner's copulatory orgasm than men who report lower relationship satisfaction, and that this relationship was strongest among men reporting a higher perceived risk of sperm competition through partner infidelity. Recently, Kaighobadi et al. (2012) tested the relationship between the frequency of faking orgasm and the frequency of reported mate retention tactics (behaviors designed to reduce the likelihood of a partner straying or being poached by a rival, Buss, 1988; Buss et al., 2008; Welling et al., 2011, 2012). They found that women who perceived a higher risk of partner infidelity were more likely to report faking orgasm and that women who reported greater probability of faking orgasm also reported performing more mate retention behaviors. Interestingly, there was also a relationship between faking orgasm and the frequency of negative mate retention behaviors, which was mediated by women's perceptions of the risk of partner infidelity. Kaighobadi et al. (2012) interpreted these findings as evidence that faking orgasm may be part of a broader strategy aimed at retaining one's mate, which may be performed by women who perceive a greater risk of their partner straying. If female orgasms are completely inconsequential, these findings become difficult to explain.

Hrdy (1996) suggested that female orgasm in primate females may have been adaptive for pre-hominid ancestors of *Homo sapiens*, meaning that the benefits were greater than any possible cost to reproductive success, although it may not be adaptive in all contexts. Thornhill and Gangestad (1996) further suggested the possibility that female orgasm may be functional for modern humans, but that its original function in pre-hominid ancestors may have been different than the function it serves now. In this case, the function of human female

orgasm may differ from functions that led to it in non-human primates. A secondary

adaptation, also called an *exaptation*, is an adaptation that originated as a by-product, but was

then modified over time by selection to serve a new, adaptive function (Gould and Vrba,

1982). One possible example of a secondary adaptation is the ability of most bird species to

fly. Some scholars (Ostrom, 1974, 1979; Rayner, 2001) believe that feathers originally

evolved for the purposes of insulation, but that eventually they also functioned with increasing

efficiency in flight for many bird species. Analogously, perhaps female orgasm began as a by-

product of male orgasm, but may have gradually been shaped as a secondary adaptation.

Adaptive explanations for female orgasm mainly center around four hypotheses: promotion

of future copulations, pair bonding, promotion of fertilization, and mate/sire selection. All

four propositions posit that female orgasm is an adaptation in its own right and not merely a

by-product resulting from similar ontogeny with men. Unlike the by-product explanation of

female orgasm, the different adaptive theories behind female orgasm are not necessarily

mutually exclusive.

4.1 Promotion of future copulations

Hypotheses surrounding the idea that orgasm promotes future copulations infer that the

intense pleasure associated with orgasm serves as a reward for engaging in sexual behaviors,

thereby promoting future sexual encounters. Because orgasm is accompanied by extreme

pleasure, feelings of release, and relaxation (Meston et al., 2004), the psychological rewards

may motivate people to continue to engage in sexual activity, which would augment fitness by

increasing the likelihood of sexual activity during fertile periods and, thus, possibly increase

conception rates. This principle can be applied to male orgasm as well as female orgasm

because the physiological aspects of male orgasm that lead to ejaculation need not necessarily

be accompanied by pleasurable sensations, which are not necessary for conception. For example, many species of fish fertilize eggs externally by ejaculating into the water without stimulation (Stockley et al., 1996). This introduces the possibility that the pleasurable sensations associated with orgasm in humans may function to increase both interest and likelihood of engaging in sexual behaviors. Psychological and affective rewards could also explain why women feel the urge to copulate outside the fertile window, when sexual intercourse carries no reproductive reward. Therefore, it is important to contemplate the psychological factors, as well as the biological ones, when considering the adaptive significance of orgasm.

Orgasmic sensations are greatly important to the majority of women. Eschler (2004) found that 75.8% of women rated having an orgasm with a partner as either somewhat or very important, while only 6% rated having an orgasm with a partner as somewhat unimportant or very unimportant. Additionally, 29.4% of women said it was very unlikely that they would enjoy sex without an orgasm, compared to only 9.1% who said it was very likely that they would still enjoy sex even if they did not have an orgasm. The feelings of release described by women who experience orgasm (Hite, 1976) could reward feelings of sexual desire by reducing sexual tension and increasing relaxation. Certainly, orgasm activates the dopamine-related ventral midbrain and right caudate nucleus, known to be involved in reward-driven learning and motivation (Georgiadis et al., 2006, 2009). Altogether, this research emphasizes the importance of women's subjective experience and pleasure in wanting to continue engaging in sexual activities and provides support for the assumption that orgasm acts as a reward for sexual behavior. Similarly, orgasm may motivate women to continue copulating until they achieve orgasm, thus increasing the likelihood that the man will have ejaculated, or it may encourage women to copulate again with men that have brought them to orgasm. This

latter explanation could function to encourage women to remain with their current partners, thereby promoting pair bonding for the purposes of later raising offspring.

4.2 Pair bonding

Pair bonding theories suggest that the female orgasm evolved to strengthen the connection between mates, leading to greater biparental care of offspring and, by extension, enhanced fitness (Eibl-Eibesfeldt, 1989; Morris, 1967). Sexual arousal and orgasm deactivate a region in the human frontal cortex that overlaps the deactivated region observed in romantic love (Zeki, 2007). Thornhill and Gangestad (1996) suggested that copulatory orgasm may reduce the number of partners that women pursue by creating strong feelings of intimacy with one or only a few mates, but that a lack of copulatory orgasms may increase female infidelity. This hypothesis seems plausible given the importance of orgasm to women's sexual satisfaction (Eschler, 2004) and that sexual dissatisfaction is related to infidelity (Buss and Shackelford, 1997). Moreover, Gebhard (1966) found that women in longer marriages tended to experience more orgasms (see also Kinsey et al., 1953), which suggests that women may be more likely to orgasm with men they are comfortable and familiar with, or that long-term partners may be more likely to induce orgasm.

Across cultures (Symons, 1979), women are less likely than men to seek uncommitted sex (Clark and Hatfield, 1989; Oliver and Hyde, 1993), possibly in part because uncommitted sexual encounters (one-night stands) are unlikely to result in orgasm for the woman (Eschler, 2004) and may function to bond women to their investing partner, thus acting in selection of a long-term mate (Barash, 1977; Beach, 1974; Hamburg, 1978; Morris, 1967). It should be noted that the term investing is here used to refer to investment in the relationship via partner emotional and/or physical support and help with childrearing, but not necessarily financial

support since, as Hrdy (1997) pointed out, the presumed innate universal of women's preferences for wealthy mates may be facultative accommodations by women to constraints brought about by patriarchal monopolization of resources needed by women and their offspring to survive and reproduce. Indeed, the number of sex partners a woman has is increased in social settings in which each man has limited resources to provide in exchange for sexual access (Buss, 1994), suggesting that monopolization of resources can influence female reproductive strategy, possibly out of necessity, in ways that may not be directly comparable to social systems in ancestral times (O'Connell et al., 1999).

Other evidence indicates that women have more satisfying sex lives with long-term partners. Women believe that sexual encounters within a long-term relationship are more likely to result in orgasm (Eschler, 2004), premarital orgasms are more likely for women in stable relationships, and women's coital orgasm frequency is predicted by their active participation in sexual encounters and the duration of foreplay (Tavris and Sadd, 1977). Higher reported marital happiness is positively related to a higher percentage of penile-vaginal sexual intercourse that resulted in orgasm for the wife (Gebhard, 1966) and women in long-term relationships report greater emotional and physical satisfaction with their sex lives than women in comparatively shorter relationships (Laumann et al., 1994). In a sample of Portuguese women, both the frequency of penile-vaginal intercourse and the frequency of orgasm from penile-vaginal intercourse were positively associated with several aspects of relationship quality, and penile-vaginal orgasm frequency was negatively related to masturbation frequency (Costa and Brody, 2007). Coital orgasms are also more sexually satisfying to women than noncoital (i.e., clitoral) orgasms (Davidson and Darling, 1989). On the other hand, noncoital sexual behaviors with a partner were not correlated with any

measured dimensions of mate quality, although masturbation frequency was negatively related to reported love (Costa and Brody, 2007).

Still, other findings contradict the supposed relationship between female orgasm frequency and long-term relationship satisfaction. Despite initial reports that male income, a possible indicator of male investment potential, predicted female partner orgasm frequency (Pollet and Nettle, 2009), later work (Herberich et al., 2010; Pollet and Nettle, 2010) revealed that the association between partner wealth and female self-reported orgasm frequency was confounded by women with higher-income partners being healthier, happier, younger, and better educated than women with lower-income partners. Thornhill et al. (1995) found no association between women's orgasm frequency and either relationship duration of their professed love for their partner, nor did they find relationships between female orgasm frequency and male ratings of indicators of investment, such as reported commitment, nurturance, relationship duration, and reported love. Finally, Laumann et al. (1994) found a negative relationship between female orgasm frequency and relationship duration. These contradictory results suggest that relationship between pair bonding and orgasm may be more complex.

Some researchers have nominated the hormone oxytocin as responsible for, or encouraging of, pair bond formation in couples (Campbell, 2010; Fisher et al., 2006; Skuse and Gallagher, 2009), opening the possibility that sexual intercourse and orgasm may influence pair bonding via associated hormonal release (Puts et al., 2012a; Young and Wang, 2004). Oxytocin is released at orgasm in both sexes (Carmichael et al., 1987; Murphy et al., 1987) and in response to vaginocervical stimulation, lactation, and childbirth in women (reviewed in Komisaruk and Whipple, 2005). Oxytocin is also released during stress (Jezova et al., 1995),

may be involved in reducing anxiety (Heinrichs et al., 2009; McCarthy and Altemus, 1997), and it reduces activation of the amygdala (Kirsch et al., 2005), which is involved in the expression of fear and anxiety (Davis, 1992). Oxytocin also improves the ability to infer the mental state of others from social cues (Domes et al., 2007), increases prosocial behavior (Campbell, 2010; Heinrichs and Domes, 2008; Zak et al., 2007), and is higher in people reporting greater partner support (Grewen et al., 2005; Sanchez et al., 2009). Prenatal and postpartum oxytocin levels enhance the formation of maternal-infant bonds and reduce maternal stress reactivity, and the experience of being trusted and reciprocating trust seems to raise oxytocin levels (reviewed in Campbell, 2010). Similarly, oxytocin appears to be involved in the formation of pair bonds, sexual and affiliative behavior, and parenting behavior (Campbell, 2010; Carter et al., 1997; Carter et al., 1992; Curley and Keverne, 2005) in nonhuman animals. However, oxytocin levels have also been associated with greater interpersonal distress (Turner et al., 1999) and, in postmenopausal women, are negatively correlated with marriage quality, physically affectionate partner contact, and reports of partner relations (Taylor et al., 2006). Nonetheless, if oxytocin is involved in human pair bonding, orgasm may play an important role and may additionally function in promoting fertility via uterine contractions (Wildt et al., 1998).

4.3 Promotion of fertilization

Promotion of fertilization theories hypothesize that female orgasm leads to physiological processes that enhance the likelihood of conception via easier transport of sperm towards the unfertilized egg (Baker and Bellis, 1993; Fox et al., 1970; Levin, 2002; Meston et al., 2004; Singh et al., 1998; Wildt et al., 1998). According to Lloyd (2005), the fact that the low number of women who reliably achieve orgasm through penile-vaginal intercourse reproduce as well as the women who rarely or never experience orgasm brings the adaptive nature of the

female orgasm into question, at least with reference to conception (see also Wallen, 2006).

However, there is evidence that women are more likely to experience orgasm when they are

fertile (Matteo and Rissman, 1984; Udry and Morris, 1968), likely because of changes in

hormone levels across the menstrual cycle (van Anders and Dunn, 2009). Female orgasm

activates the paraventricular nucleus (Komisaruk et al., 2004), which is involved with

oxytocin release (Fliers et al., 1985; Powell and Rorie, 1967), and activates the cingulate

cortex and medial amygdala (Komisaruk et al., 2004), which may cause uterine contractions

(Beyer et al., 1961; Setekleiv, 1964). Moreover, women's desires to become pregnant are

associated with their likelihood of achieving orgasm shortly after their partner (Singh et al.,

1998) when sperm would already be present in the reproductive tract. Indeed, Baker and

Bellis (1993) found that female orgasms that climaxed between 1 minute before the male

ejaculated and 45 minutes after led to the retention of more sperm, while either no orgasm or

one occurring more than one minute before the male ejaculated led to comparatively low

sperm retention.

Both orgasm (Fox et al., 1970) and oxytocin (Wildt et al., 1998) released at orgasm (Blaicher

et al., 1999), cause uterine contractions and change uterine pressure from outward to inward,

creating an "upsuck" of seminal fluids into the uterus (Fox et al., 1970; Wildt et al., 1998)

that may reduce the amount of sperm that flows back out of the vagina (i.e., "flowback"). The

oxytocin-induced contractions in the uterus and oviducts also seem to act directly in

transporting sperm, turning the uterus and fallopian tubes into a sort of functional peristaltic

pump (Wildt et al., 1998; Zervomanolakis et al., 2007, 2009). Mimicking oxytocin release at

orgasm by administering hormones to women induces uterine contractions and transports

seminal-like particles up into the uterus during both the luteal (infertile) and follicular

(fertile) phases of the menstrual cycle, but that transport is directed into the specific fallopian

tube that would be releasing an egg during the fertile phase of the cycle only (Wildt et al., 1998; Zervomanolakis et al., 2007, 2009). The biological significance of this finding is demonstrated by the observation that the pregnancy rate was higher in women who demonstrated transport of fluid into the appropriate fallopian tube than in those women who failed to exhibit lateralization (Wildt et al., 1998; Zervomanolakis et al., 2007). Although two studies failed to find movement of semen-like substances through the cervix following orgasm (Grafenberg, 1950; Masters and Johnson, 1966), the significance of these null findings has since been contested (see also Puts and Dawood, 2006; Puts et al., 2012a) because both studies placed a cap over the cervix, which may have prevented the flow of fluids (Fox et al., 1970). Finally, while oxytocin may be released during sexual stimulation without orgasm (Lloyd, 2005), uterine contractions (Komisaruk et al., 2006), uterine suction (Fox et al., 1970), and oxytocin release (Carmichael et al., 1994) have been found to increase following orgasm. Therefore, peristaltic contractions, like those experienced at orgasm, should increase the chance of fertilization by way of decreasing the distance sperm need to travel to reach the dominant follicle.

During sexual arousal a physiological change known as "vaginal tenting" occurs in which the inner third of the anterior wall of the vagina becomes elevated away from the posterior wall along with the uterus and cervix, thereby removing it from the pool of semen (Levin, 2002; Masters and Johnson, 1966). This may function to create a space for the ejaculate to pool, thus reducing flowback losses (Baker and Bellis, 1995; Levin, 2002) and to provide time for the ejaculate to decoagulate (Levin, 2002). Human sperm cannot fertilize an ovum immediately, but requires time within the female reproductive tract to acquire the ability to fertilize, a process called *capacitation* (Eisenbach, 1995; Levin, 2002). Female orgasm may allow earlier entry of sperm into the cervix by resolving the vaginal tenting that accompanies

sexual arousal (Puts et al., 2012a), which would remove sperm from the vagina into the

cervix, help decrease the flowback of sperm, and bring sperm closer to the fallopian tubes

(Fox and Fox, 1971). Additionally, Meston et al. (2004) suggested that vaginal contractions

may excite male ejaculation, possibly increasing the odds that the woman will be fertilized by

her chosen partner, and the secretion of prolactin at orgasm may increase sperm capacitation

(see also Reyes et al., 1979). These findings compliment previous findings on the uptake of

sperm into the cervix and oviducts via uterine contractions associated with orgasm and point

out the probable importance of the role of female mate choice for procreation.

4.4 Mate selection: Sire and mate choice

Theories surrounding mate/sire selection purport that female orgasm functions to encourage

repeated sex with either high quality or investing males, or that high quality or investing

males are better able to induce orgasm, which serves to increase the fitness of resulting

offspring through genetic and/or other benefits associated with the high quality or investing

father (Alcock, 1980; Alexander, 1979; Puts et al., 2012b; Shackelford et al., 2000; Thornhill

et al., 1995). Women stand to lose more than men through an inefficient allocation of mating

effort due to their higher investment in childrearing via gestation and lactation, leading

women to be choosier than men regarding mate choice (Clark and Hatfield, 1989; Daly and

Wilson, 1983; Schmitt, 2005; Trivers, 1972). Angier (1999) suggested that the clitoral

orgasm's function may reflect this choosiness, with the clitoris responding only when the

male partner has expended sufficient effort as to demonstrate his willingness to invest in his

partner. Female orgasm acting as a mate/sire choice mechanism supposes that orgasm should

be more difficult for women to achieve because they are choosier about mate choice than men

(Allen and Lemmon, 1981; Hosken, 2008; Puts et al., 2012a) and that this choosiness should

be most applicable to penile-vaginal intercourse that may result in conception (Puts, 2007).

Unlike other adaptive explanations of the female orgasm, the mate/sire choice hypothesis hinges on orgasm also functioning in either a pair bonding capacity (if orgasm functions in mate choice and women use orgasm to choose investing males) or a promotion of fertilization capacity (if orgasm functions in sire choice and women orgasm more with genetically fit men). If female orgasm reflects male investment, women should be less likely to orgasm with males who are not interested in a long-term relationship. In fact, women are less likely to seek uncommitted sex (Clark and Hatfield, 1989; Oliver and Hyde, 1993; Symons, 1979) and are less likely to orgasm during short-term sexual encounters than men (Eschler, 2004), indicating that orgasm in women may function in part to seek out a long-term, investing partner. This argument differs from the pair bonding hypothesis in a subtle way: while the pair bond hypothesis stipulates that orgasm functions to bond a woman to a man or vice-versa, the mate choice hypothesis stipulates that orgasm is more likely to happen when a man is already showing long-term investment potential. This would explain the strong associations between relationship length, aspects of relationship quality in a long-term partner, and orgasm frequency (Costa and Brody, 2007; Gebhard, 1966; Laumann et al., 1994). Alternatively, orgasm could function in the selection of a high quality mate, rather than an investing mate, per se. Under this view, orgasm likelihood would depend less on male investment and more on cues to underlying quality, and by extension would be more relevant to sire choice than long-term mate choice.

Indirect evidence suggests that women may be more likely to copulate with, and possibly experience orgasm with, high quality men at ovulation. Women report being less committed to their partners (Jones et al., 2005) and may be more likely to seek extra-pair copulations (Bellis and Baker, 1990; Gangestad et al., 2002, 2005) (but see Pillsworth et al., 2004) at peak

fertility. Women are also more likely to experience orgasm near peak fertility (Matteo and Rissman, 1984; Udry and Morris, 1968) and demonstrate increased preference for cues to male mate quality at peak fertility, including cues to male symmetry (Little and Jones, 2011; Little et al., 2007) (but see Koehler et al., 2002, 2006), masculinity (Feinberg et al., 2006; Frost, 1994; Johnston et al., 2001; Jones et al., 2005; Little et al., 2007, 2008; Penton-Voak and Perrett, 2000; Penton-Voak et al., 1999; Puts, 2005; Welling et al., 2007), and dominance (Gangestad et al., 2004). If women are more likely to orgasm with high quality men (Garver-Apgar et al., 2006; Puts et al., 2012b; Shackelford et al., 2000; Thornhill et al., 1995), are more attracted to cues to high male quality at peak fertility, and are more likely to seek extra-pair sex at peak fertility, this could support the premise that female orgasm functions in sire choice. Furthermore, it could provide additional evidence of a dual mating system, whereby women seek good genes for potential offspring while fertile through extra-pair sex, but seek longer-term mating opportunities with investing males at other points in the cycle (reviewed in Gangestad and Thornhill, 2008).

One putative cue to underlying quality is symmetry, as any deviation from bilateral symmetry implies developmental instability on the part of the organism (Møller, 1997; Møller and Pomiankowski, 1993; Parsons, 1990, 1992). Fluctuating asymmetry is negatively related to male mating success in humans (Bogaert and Fisher, 1995; Thornhill and Gangestad, 1994) and is considered attractive by women (Gangestad et al., 1994; Grammer and Thornhill, 1994; Little et al., 2007; Thornhill and Gangestad, 1994). Women's extra-pair sexual partners tend to have low fluctuating asymmetry (Gangestad and Thornhill, 1997), and women may be more likely to orgasm with extra-pair, versus in-pair, males (Baker and Bellis, 1993), alluding to the conclusion that women may have more orgasms with symmetrical companions. Indeed, Thornhill et al. (1995) found that women coupled with men lower in fluctuating asymmetry

reported more orgasms than women coupled with relatively asymmetric men. Physical attractiveness is another putative measure of underlying genetic quality (Fink and Penton-Voak, 2002; Grammer et al., 2003; Rhodes, 2006; Scheib et al., 1999; Shackelford and Larsen, 1999; Thornhill and Gangestad, 1999), which may be related to semen quality (Soler et al., 2003) (but see Peters et al., 2008). Shackelford et al. (2000) found that women were more likely to have experienced orgasm at last copulation if they rated their partner as more attractive (see also Thornhill et al., 1995), even after controlling for relationship satisfaction, relationship duration, and age. More recently, Puts et al. (2012b) found that women with more attractive partners reported more frequent orgasms during or after male ejaculation, which is within the optimum window for sperm retention described by Baker and Bellis (1993). In addition, a principle component composed of several measures of masculinity (another presumed marker of men's genetic quality, Fink and Penton-Voak, 2002; Gangestad and Simpson, 2000; Rhodes et al., 2003) and dominance was related to more frequent and earlier-timed orgasms in women. That men's attractiveness and masculinity predicted their female partners' orgasm frequency was taken as evidence by Puts and colleagues that male sire quality increases incidences of female orgasm. Assuming that female orgasm increases the probability of conception, selective orgasms with suitors of higher genetic quality, rather than indiscriminant orgasms, could increase the probability of impregnation by genetically fit men, thereby augmenting offspring viability through the associated genetic benefits.

Past work, however, has provided little information about the differences in subjective sexual experience between women mated to attractive versus unattractive men and those mated to masculine versus more feminine men. For example, possible differences in penis size between subgroups of men may be a factor in female sexual satisfaction or male sexual confidence (Brody and Weiss, 2010; Costa et al., in press; Lever et al., 2006). For instance, Costa et al.

(in press) found that a longer penis was related to greater vaginal orgasm frequency, but not to the frequency of clitoral orgasms. Also, more attractive and more masculine/dominant men tend to have more sexual experience (Keller et al., 1982; Puts et al., 2006; Rhodes et al., 2005), and this greater experience could lead to better sexual techniques or duration. Finally, that women with masculine partners are more likely to climax before their partners (Puts et al., 2012b) may be better explained by sexual excitability than an adaptation to acquire good sire genes for offspring. Earlier timed orgasms are associated with greater sexual arousal, and more physiological and psychological sexual satisfaction (Darling et al., 1991), but orgasm more than one minute prior to male ejaculation may not increase chances of conception (Baker and Bellis, 1993). When taken with the findings that masculine men are considered sexually attractive by women (Little et al., 2002), the earlier timing of female orgasms with masculine partners (Puts et al., 2012b) may not necessarily be related to conceiving with masculine men. More research on the circumstances leading to, and timing of, female orgasm, and its relationship with conception, is clearly needed.

Perhaps the best evidence for the hypothesis that female orgasm functions in selecting a father with good genes comes from a study by Garver-Apgar et al. (2006) on major histocompatibility complex genes. Genetic complementarity at the major histocompatibility complex (MHC, also called human leukocyte antigen, or HLA) may be beneficial for offspring. MHC molecules mediate interactions between white blood cells (cells of the immune system that are involved in defending the body against infections, diseases, and foreign materials) and other cells. Selection of an MHC-dissimilar (i.e., compatible) mate increases the heterozygosity of offspring at the MHC, thereby decreasing the chances that the offspring will have a weak immune system or suffer genetic consequences of inbreeding (Havlíček and Roberts, 2009). Garver-Apgar et al. (2006) found that women mated with an

MHC-compatible partner experienced more orgasms, but only during the fertile phase of the ovulatory cycle. If orgasm and conception are related, then these findings are evidence that orgasm may function in selecting good genes for offspring. This is, however, a speculative argument in need of further investigation.

5 Conclusions

Because there is evidence in favor of more than one of the above hypothesized functions of the female orgasm, it is again important to stress that more than one function could be correct and that seemingly different functions could be related. For example, it is possible that orgasm in women functions to encourage sexual behavior more generally (i.e., as a reward for, and reinforcement to continue, sexual behavior that may result in conception), but that it also promotes fertilization with chosen sires, potentially of higher genetic quality (Garver-Apgar et al., 2006; Puts et al., 2012b; Shackelford et al., 2000; Thornhill et al., 1995), during peak fertility when orgasm is more easily induced (Matteo and Rissman, 1984; Udry and Morris, 1968) and attraction to men of high genetic quality highest (e.g., Gangestad and Thornhill, 2008). Female orgasm may simultaneously foster pair bonds with chosen long-term partners at nonfertile points in the cycle, potentially via oxytocin release (Campbell, 2010; Fisher et al., 2006; Skuse and Gallagher, 2009), when orgasm induction may take relatively more specialized partner attention. Otherwise, perhaps female orgasm was originally a by-product that has been shaped as a secondary adaption over time, or, alternatively but perchance unlikely, that it no longer functions in the capacity for which it was designed.

Although the available evidence is not wholly conclusive, there is strong evidence to suggest that a by-product explanation of female orgasm alone may be insufficient. Certainly, more research is needed. For example, if inducing orgasm (or even uterine contractions) increases

the likelihood of pregnancy relative to no orgasm, as some work suggests (Wildt et al., 1998), this would be compelling evidence that orgasm promotes conception. Relatedly, whether the timing of female orgasm relative to male orgasm influences conception (Baker and Bellis, 1993) could be tested, as could whether variation in the level of oxytocin released during coital orgasm correlates with a woman's feelings towards her partner. These and other research hypotheses surrounding the utility of female orgasm should be investigated cross-culturally and across different mammal and primate species. Such comparative work will improve our understanding of the physiology and purpose of the female orgasm, and enable a better insight into our species' evolved sexual responses. Indeed, it is clear from current work that female orgasm is a complex, unique experience worthy of the continued attention from investigators.

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