

# 50 The Adaptive Value of Women's Orgasm

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## 50.1 Introduction

Physiological response to orgasm is similar for men and women. Both sexes report pleasure, relaxation, feelings of release, involuntary muscle contractions, increased blood pressure and heart rate, rapid breathing, and behavioral responses (e.g., arching of the back, vocalizations) at orgasm (reviewed in Hite, 1976; Komisaruk et al., 2006; Masters & Johnson, 1966; Welling, 2014). The pattern of brain activation and deactivation is also similar across the sexes, with both men and women showing activation in the anterior medial cerebellum and deactivation in the left ventromedial and orbitofrontal cortex (Georgiadis et al., 2006, 2007, 2009). Women also experience involuntary muscle contractions in the vagina, anus, and pelvic floor muscles during orgasm (Grzybowska & Wydra, 2019; Komisaruk et al., 2006; Masters & Johnson, 1966). Despite the physiological similarities in orgasm in men and women, women report a larger variety of orgasm experiences compared to men, such as orgasms that differ in how they are induced, in their intensity, or even in their emotional experience (e.g., King et al., 2011; Hite, 1976). The fastest and most reliable way to induce orgasm in women is through stimulation of the clitoris (e.g., Schober et al., 2004), but women can experience orgasm through different neural pathways in the vagina that are independent of the clitoris. In fact, Komisaruk and colleagues (Komisaruk et al., 1996, 2004; Komisaruk & Sansone, 2003; Komisaruk & Whipple, 2005) have documented orgasm or orgasm-like sensations occurring in women with completely severed spinal cords through vaginal-cervical stimulation, which likely occur when sufficient stimulation travels to the brain via vagus nerve pathways. There are even reports of women experiencing orgasm through nongenital stimulation (e.g., breastfeeding) and from mental stimulation alone (discussed in Reed, 2010). This research suggests that the experience of orgasm is more complex for women than it is for men.

Several hormones play pivotal roles in orgasm (see Welling, 2014). For example, orgasm increases women's estradiol and decreases their cortisol (van Anders et al., 2009), which may increase sexual functioning (e.g., Berman, 2005) and desire (van Anders & Dunn, 2009), and reduce stress (e.g., Kirschbaum & Hellhammer, 2000). Similarly, prolactin, a hormone necessary for lactation, increases after orgasm in men and women, and may feedback to

dopaminergic neural systems to influence sex drive and sexual satisfaction (Krüger, Hartmann, & Schedlowski, 2005). However, oxytocin and testosterone have received the most attention with regard to women's orgasm. Oxytocin, a neuropeptide released by the pituitary, is released at orgasm in both sexes. It is known to influence maternal care, affiliative behaviors, and pair-bonding across several mammalian species (e.g., Campbell, 2008; Ferguson et al., 2002; Insel & Young, 2001; Lim & Young, 2006; Young & Wang, 2004), and may impact feelings of trust in humans (Kosfeld et al., 2005; but see Nave et al., 2015). Physiologically, women's increase in oxytocin at orgasm causes uterine contractions (Carmichael, 1987, 1994), which may help transport sperm up the reproductive tract (Fox, Wolff, & Baker, 1970; Wildt et al., 1998). Testosterone, on the other hand, increases with sexual activity (Dabbs & Mohammed, 1992; van Anders et al., 2007) and (to a small extent) at orgasm (Exton et al., 1999; van Anders et al., 2007), and serves an important function in sexual experience; trait (van Anders et al., 2007), state (Bancroft et al., 1983), and exogenously administered testosterone (e.g., Somboonporn, Bell, & Davis, 2005; Wierman et al., 2014) are positively associated with women's reported orgasm frequency, and sexual dysfunction is negatively associated and treated with androgens (e.g., Apperloo et al., 2003; Jayasena et al., 2019; Wählin-Jacobsen et al., 2017). Although serum testosterone does not correlate with overall sexual functioning among women in the general population (Davis et al. 2005; Santoro et al. 2005), women with higher testosterone report more positive orgasm experiences (van Anders & Dunn, 2009), and a single dose administration of exogenous testosterone increases female genital responsiveness, genital arousal, and subjective reports of "sexual lust" and "genital sensations" (Tuiten et al., 2000).

Orgasm is more difficult to induce in women compared to men, although the size of the discrepancy is debated (see Puts, 2006; Wallen, 2006; Welling, 2014). The likelihood of orgasm depends on many factors, such as mode of induction (e.g., oral sex, masturbation, penile–vaginal intercourse). Recently, Herbenick et al. (2018) conducted a large internet-based study using a sample of women aged eighteen to ninety-four years and found that, although 18.4% of women reported that coitus (i.e., penile–vaginal sexual intercourse) alone was sufficient to induce orgasm, 36.0% reported that clitoral stimulation improved (but was not necessary for) their orgasm and another 36.6% reported that clitoral stimulation was always necessary for coital orgasm. The percentage of women who achieve orgasm through coitus may be as low as 6% (Wallen, 2006) or closer to 100% (Marshall, 1971), but the majority of research finds incident rates closer to 50% (e.g., Dawood et al., 2005). This does not necessarily mean that only half of women are capable of coital orgasm. Rather, research suggests the majority of women can achieve orgasm this way; Lloyd (2005) estimated that approximately 55% of women experience orgasm with intercourse more than half the time, Tavris and Sadd (1977) found that 63% of respondents reported usually having an orgasm with

intercourse, and Dawood and colleagues (2005) found that approximately 83% of women report being capable of achieving coital orgasm. The discrepancies between studies in reported incidence of coital orgasm may be due to differences in methods (e.g., question phrasing; Shirazi et al., 2018), or a combination of cultural (Davenport, 1977; Marshall, 1971; Moreira et al., 2005), genetic (Burri et al., 2013; Dunn et al., 2005), environmental (Burri & Ogata, 2018; Dawood et al., 2005), and psychosocial (e.g., Cohen & Belsky, 2008; Harris et al., 2008; Wongsomboon, Burleson, & Webster, 2020) elements, which all factor into the frequency with which women experience orgasm. For example, rates of anorgasmia are higher among East Asian women compared to women from Western countries (Moreira et al., 2005), and field research on the Polynesian island of Mangaia, a culture that places a high emphasis on female sexual pleasure, reports that all women achieve coital orgasm (Marshall, 1971). Nonetheless, women most often achieve orgasm through masturbation, clitoral stimulation, oral sex, or a combination of these practices (e.g., Baker & Bellis, 1993; Richters et al., 2006).

Men are concerned with whether their female partner experiences a copulatory orgasm (McKibbin et al., 2010), yet more than half of women admit to having previously faked an orgasm (e.g., Ellsworth & Bailey, 2013; Muehlenhard & Shippee, 2010; Roberts et al., 1995; Wiederman, 1997) compared to only 25 percent of men (most of whom faked orgasm because of intoxication or because they had already orgasmed that day; Muehlenhard & Shippee, 2010). Women are able to pretend orgasm convincingly; men's estimates of their female partner's orgasm occurrence are higher than what actually occurs (Shirazi et al., 2018) and men's relationship satisfaction is related to whether their partner frequently appears to orgasm (i.e., not whether they actually orgasm; Kaighobadi et al., 2012). The motivations behind pretending to orgasm are varied. Individual differences such as first having sex at a younger age (Darling & Davidson, 1986; Davidson & Darling, 1988; Wiederman, 1997), holding anti-feminist views (Harris et al., 2019), having more sexual partners (Davidson & Darling, 1988; Wiederman, 1997), being older, having an attractive face, and being higher in sexual esteem (Wiederman, 1997) predict the likelihood a woman will pretend to orgasm. Men's interest in their female partner's orgasm (McKibbin et al., 2010) and the relatively commonplace occurrence of women faking orgasm (e.g., Ellsworth & Bailey, 2013) suggests that women's orgasm may serve an important purpose.

## 50.2 Adaptation vs. Byproduct

Orgasm in men makes obvious evolutionary sense because it leads to ejaculation, which is necessary for conception. However, orgasm in women is not necessary for conception, which has led to disagreement surrounding

whether female orgasm is an adaptation reflecting special design (reviewed by Welling, 2014). This disagreement boils down to two competing explanations for why female orgasm exists: the byproduct hypothesis and the adaptation hypothesis.

Adaptations are traits that either directly or indirectly increase an organism's inclusive fitness (i.e., their ability to pass on their genes – and the genes they share with close kin – to the next generation). Adaptations are inherited, reliably developing functional characteristics of a given species that are influenced by environmental pressures and that originate or are maintained by the processes of natural or sexual selection (see, e.g., Buss et al., 1998; Tooby & Cosmides, 1992). Adaptations can be physical (e.g., sharp claws for fighting, webbed feet for swimming, fur for warmth) or behavioral (e.g., common phobias such as fear of spiders, heights, or snakes). Some adaptations are sex-specific (see Rice & Chippindale, 2001), in which case genes for the adaptation are present in both sexes, but expression of the genes associated with the adaptation are regulated by sex steroid hormones (e.g., broader shoulders in men or broader hips in women).

Byproducts, also called spandrels, are distinct from adaptations in that they serve no function. Rather than being a product of natural selection, byproducts are indirect consequences of adaptations that serve no purpose on their own (Buss et al., 1998). The human navel is an example of a byproduct; it occurs where the umbilical cord was attached. Although the umbilical cord is an adaptation – allowing the transfer of vitamins and minerals from the mother to the fetus – the navel itself occurs as a consequence of that adaptation and does not itself enhance survival or inclusive fitness. Sexually antagonistic byproducts result from shared ontogeny between the sexes, such that genes that produce an adaptation in one sex can result in a byproduct in the other sex (Rice & Chippindale, 2001). With sexually antagonistic byproducts, the adaptation is the focus of strong selective pressures in one sex, but is often vestigial in the sex for which the trait is a byproduct. An example of a sexually antagonistic byproduct is male nipples, which arise because selection for nipples (used in breastfeeding) is so strong in women that they appear in men during early embryological development (discussed in Puts, Dawood, & Welling, 2012; Welling, 2014). Whether female orgasm is a byproduct or an adaptation has been debated. Next, we outline arguments in favor and against both perspectives.

### 50.2.1 Byproduct Explanation

The sexual anatomy of males and females is developmentally linked. Before approximately six weeks gestation, there is no gonadal differentiation between male and female fetuses. Once developing males are exposed to testosterone, the labioscrotal folds form the scrotum, the genital tubercle forms the penis, and the gonads descend into the scrotum. In developing females, the absence

of testosterone allows the labioscrotal folds to form the labia, the genital tubercle to form the clitoris, and the gonads to stay ascended. The byproduct hypothesis of female orgasm contends that the shared early development between the sexes has led to female orgasm as a sexually antagonistic byproduct of the male orgasm (Lloyd, 2005; Symons, 1979; Wallen & Lloyd, 2008). In other words, given that the male orgasm is necessary for reproduction and the female orgasm is not, proponents of the byproduct hypothesis argue that the female orgasm is a “happy accident” resulting from similar developmental anatomy. The three most prominent lines of evidence used to support this hypothesis are 1. the difficulty of achieving female orgasm through sexual intercourse, 2. the large variability in the occurrence of female orgasm, and 3. the unclear connection between female orgasm and reproduction (Lloyd, 2005).

For a biological or psychological feature of an organism to be considered an adaptation, evolutionary scientists expect low genetic variation of that feature within a population, as well as a strong connection between that feature and reproduction (Fisher, 1930; Tooby & Cosmides, 1992; Williams, 1966). Such requirements cause researchers hesitation when considering female orgasm an adaptation because female orgasm does not reliably occur during vaginal (reproductive) intercourse. In fact, females achieve orgasm at a significantly lower rate than males (Eschler, 2004; Wallen, 2006). Eschler (2004) reported that only 33.3% of women experienced orgasm with no clitoral stimulation, and 77.4% of women reported experiencing orgasm with clitoral stimulation. Similarly, Shirazi and colleagues (2018) found that women’s online reports show orgasm during intercourse with no clitoral stimulation occurs as low as 21–30% of the time. On the other hand, reports of male orgasm during vaginal intercourse vary much less and occur much more easily. Proponents of the byproduct hypothesis consider this large sex difference to be strong evidence that female orgasm has received little to no selective pressure, claiming that if it had, it would be achieved as reliably as male orgasm. If there is such large variation in female orgasm, why then do many evolutionary scientists favor the adaptation hypothesis (e.g., Puts, Welling, Burriss, & Dawood, 2012; Puts & Dawood, 2006; Thornhill et al., 1995; Thornhill & Gangestad, 2008)?

A major reason why the idea that large variation in female orgasm is not entirely convincing as evidence for the byproduct hypothesis is that it leaves out the possibility that female orgasm systematically varies to confer reproductive advantages (Puts, Dawood, & Welling, 2012; Shackelford et al., 2000; Thornhill et al., 1995). Put another way, it is possible that female orgasm is so variable because its occurrence or absence alters the likelihood of producing offspring with higher genetic quality or with chosen suitors. Women report more intense orgasms (Gallup et al., 2014) and are more likely to experience orgasm when they are more physically attracted to their sexual partner (Puts, Welling, Burriss, & Dawood, 2012; Shackelford et al., 2000) and if their partner is very masculine (Puts, Welling, Burriss, & Dawood, 2012).

Although the byproduct hypothesis correctly points out that female orgasm occurs with high variation both between- and within-women, it is unsatisfactory in explaining why orgasms occur more frequently and intensely with partners possessing certain characteristics over others. Conversely, adaptationists argue that more frequent orgasms with more attractive partners could promote repeated mating with males of high genetic quality, thus highlighting a highly functional aspect of the female orgasm.

A key point of the byproduct hypothesis is that the female orgasm is a functionless and less consistent version of a male orgasm. Contrary to this view, Pavlicev and Wagner (2016) proposed that female orgasm predates human or primate lineages, and instead arose separately from the male orgasm. The authors make the argument that, because orgasm in women is accompanied by a hormonal surge similar to copulatory surges experienced by induced ovulation species (i.e., species in which copulation triggers ovulation), women's orgasm evolved as a modified version of induced ovulation. In this view, induced ovulation was ancestral, but became unnecessary with the evolution of spontaneous ovulation. They continue by suggesting that it is plausible that the female orgasm acquired new roles after spontaneous ovulation evolved, such as facilitating pair-bonding, encouraging repeated mating with males of high genetic quality, and sperm retention. Pavlicev and Wagner's (2016) argument requires future research; however, their reasoning suggests that female orgasm can simultaneously not be required for reproduction in modern humans and have evolved as a reproductive adaptation. Lastly, it is possible that male and female orgasm are ontologically related, but that the genetics that underlie them are different. Zietsch and Santtila (2011) found large genetic variation in male and female orgasmic function, as well as a nonsignificant correlation between the orgasmic function of opposite-sex twins. These results contradict the byproduct hypothesis because they suggest that selection pressures on the male orgasm do not impact female orgasmic function, which would be likely if the female orgasm was merely a byproduct of the male orgasm.

The byproduct hypothesis raises reasonable concerns with the hypothesis that the female orgasm is an adaptation. However, some of these concerns may not adequately challenge the adaptation hypothesis (Pavlicev & Wagner, 2016), and other evidence suggests that women's orgasm is functional (e.g., Puts & Dawood, 2006; Thornhill & Gangestad, 2008; Zietsch & Santtila, 2011). Next, we review lines of evidence that dispute a byproduct explanation of female orgasm.

### 50.2.2 Adaptation Explanation

Because the male orgasm is necessary for conception, it would be expected that women have a vested interest in their partner's copulatory orgasm. If the female orgasm serves no function on its own but is a nonfunctional byproduct

of strong selection for the male orgasm, it should not be expected that women's partners have significant investment in them achieving copulatory orgasm. Research finds, however, that women report only somewhat greater interest in their partners' achieving orgasm as compared to men (Barnett et al., 2018). Further, men's relationship satisfaction is associated with their partner's orgasm frequency and intensity (Ellsworth & Bailey, 2013), and attentiveness to their partner's next copulatory orgasm (McKibbin et al., 2010), suggesting that men have a vested interest in their partner's orgasm. If the female orgasm were simply a byproduct, it seems unlikely that its occurrence would be so important to heterosexual men.

Men's interest in their partner's orgasm combined with the relative inconsistency of heterosexual women's copulatory orgasms (e.g., Frederick et al., 2018) may partly explain why women are more likely than men to "fake" their orgasms (e.g., Muehlenhard & Shippee, 2010). Women report faking orgasm to hide their sexual disinterest or distraction, to improve their partner's sexual experience or protect their partner's ego, to manipulate their partner, to increase their own or their partner's arousal, to end sex, to meet their partner's expectations, and out of fear there is something wrong with them (Cooper et al., 2014; Goodman et al., 2017; Jonason, 2019; McCoy, Welling, & Shackelford, 2015; Muehlenhard & Shippee, 2010; Younis et al., 2018). Among the most common motivations women report for faking orgasm are pleasing their partner and preventing a partner from abandoning their relationship (Muehlenhard & Shippee, 2010), suggesting that women who fake their orgasms may primarily do so in an attempt to maintain their partner's investment. Kaighobadi and colleagues (2012) found that women who perceive a greater risk of their partner being unfaithful are more likely to report faking orgasms. Furthermore, these authors found that women who report greater likelihood of faking orgasm also report engaging in more mate retention behaviors (i.e., behaviors intended to prevent one's partner from abandoning a relationship; e.g., Buss, 1988). These findings suggest that women's orgasm is not merely a functionless byproduct.

Perhaps the female orgasm was initially a byproduct that was then modified or coopted to serve a function (i.e., a secondary adaptation or exaptation; Gould & Vrba, 1982)? If this is the case, the current function of the female orgasm may be different from its initial function among nonhuman primates (Thornhill & Gangestad, 1996). One possible example of a secondary adaptation is antlers in female caribou (i.e., reindeer), the only extant deer species in which females develop antlers. Although antlers likely originally evolved to aid in male–male competition (Clutton-Brock, 1982), the female caribou's antlers grow differently and are used within different contexts (Henshaw, 1968), suggesting they have been coopted as a secondary adaptation for females (Wheatley & Puts, 2015). Additionally, it is possible that the ability of most bird species to fly is a secondary adaptation. Some research suggests that feathers originally evolved to provide insulation, but were later coopted to

aid in flight (e.g., Rayner, 2001). The female orgasm may have once been a byproduct of the male orgasm, but may now serve a function of its own as a secondary adaptation.

Several lines of research investigating the origins of the female orgasm, however, argue that it is not a byproduct or secondary adaptation, but is instead an adaptation displaying special design. Four hypotheses (rewarding/reinforcing future copulations, pair-bonding, increasing conception probability, mate/sire choice) posit that the female orgasm evolved to solve a specific adaptive problem and increased reproductive success for ancestral women. Though these hypotheses, detailed below, posit different functions for female orgasm adaptive, they are not necessarily mutually exclusive.

### **50.2.3 Reward Value of Orgasm Increases Reproductive Success**

Orgasm is a desired outcome of sexual encounters for most women. One study found that only 6% of women rate having an orgasm during sexual intercourse as either somewhat or very unimportant, whereas 75.8% rate it as somewhat or very important (Eschler, 2004). Likewise, roughly 32% of women report they would be somewhat or very likely to enjoy sexual intercourse without an orgasm, compared to roughly 54% who would be somewhat or very unlikely to enjoy sex without an orgasm. Orgasm is an important sensation for many women that provides direct benefits to their sexual experiences, such as experiences of pleasure accompanied by sensations of ecstasy and relaxation (Mah & Binik, 2005.) In qualitative research conducted by Opperman and colleagues (2014), more than half of participants described their orgasm as “pleasure” or a “pleasurable” experience, suggesting that orgasm may act as a reward for reinforcing sexual activity. Specifically, orgasm may increase the probability of future sexual activity by serving as a positive reinforcer for the sexual behaviors that occurred before it (e.g., Pfaus et al., 2012). Further, activation of the left anterior insula (an area important for encoding emotional experiences, such as sexual behavior) is related to women's frequency and ease of orgasm, as well as satisfaction with their orgasm (Ortigue et al., 2007), suggesting that the reinforcing nature of orgasm is encoded in neural circuitry. Correspondingly, orgasm activates similar neural pathways within the brain as other reward experiences (e.g., gambling, drugs), specifically the dopaminergic pathways within the ventral midbrain and right caudate nucleus (Georgiadis et al., 2006, 2009). It is thus likely that the pleasure, ecstasy, and relaxation experienced from orgasm encourages future sexual behavior, possibly making sex during the fertile window (and thus conception) more probable.

Given that women report their orgasms to be pleasurable subjective experiences (e.g., Mah & Binik, 2005), it is possible that orgasm functions as a positive reinforcer that encourages women's future sexual behaviors and increases reproductive success. This could serve multiple functions by, for example, promoting continued copulation until orgasm is reached and a male partner

is more likely to have ejaculated, therefore making conception more likely. Copulatory orgasm may also encourage women to seek out more sex and sexual partners with whom they have experienced orgasm, possibly facilitating the development of a pair-bond to raise future offspring. This latter possibility has received empirical support (see, e.g., Young & Wang, 2004).

### 50.3 Female Orgasm as an Adaptation for Pair-bonding

Female orgasm may have evolved to strengthen the connection between mates, resulting in increased biparental care for offspring and enhanced individual fitness (Eibl-Eibesfeldt, 1989; Morris, 1967). Thornhill and Gangestad (1996) suggested that copulatory female orgasm may also assist pair-bonding by reducing female desire for multiple partners by facilitating a strong sense of intimacy with one or a few mates. Consequently, this may mean that a lack of copulatory orgasm also influences a woman's interest in extra-pair partners, which is plausible given the importance of orgasm in women's sexual satisfaction (Eschler, 2004) and that lower levels of sexual satisfaction are associated with infidelity (Buss & Shackelford, 1997; Mark, Janssen, & Milhausen, 2011). The frequency of female copulatory orgasm is uniquely associated with women's sexual satisfaction and sexual compatibility with their male partners (Klapilová et al., 2015). Women in longer marriages are also more likely to experience orgasm (e.g., Gebhard, 1966; Kinsey, Pomeroy, Martin & Gebhard, 1998; but see Laumann, Gagnon, Michael, & Michaels, 2000), which suggests that women may be more likely to orgasm with long-term partners with whom they are familiar and comfortable.

Evidence indicates that women across cultures seek fewer short-term relationships than do men (Schmitt, Shackelford, & Buss, 2001), perhaps in part because casual sexual encounters are less likely to result in orgasm for women than for men (e.g., Armstrong, England, & Fogarty, 2012; England, Shafer, & Fogarty, 2008). Women also report enjoying romantic interactions more and regretting them less than they do hookups, which could be influenced both by the disparity in orgasm rate between the two relationship types and the negative stereotypes and reputation loss that can affect women (disproportionately compared to men) who do engage in hookups (Bogle, 2008). One effect of this orgasm disparity based on relationship type is that women may prefer to seek long-term, investing partners with whom increased orgasm rates may facilitate pair-bonding (for a review of the neurobiology underpinning romantic love and pair-bonding, see Zeki, 2007). There is some evidence that not only do women have more orgasms and are more sexually satisfied with long-term versus short-term partners, but that orgasm and sexual satisfaction are associated with greater relationship satisfaction and partner compatibility (e.g., Klapilová et al., 2015). Pair-bonded partners will be more likely to invest in potential offspring, provide biparental care, offer emotional and physical

support during the childbearing and rearing process, and perhaps (although not necessarily) provide financial support. Female orgasm may therefore be an adaptation that functions in the selection of long-term mates to bond women to certain partners (Beach, 1974).

Certain components of long-term, stable relationships may also promote female orgasm (Kontula & Mitettinen, 2016; Leonhardt et al., 2018). In a sample of over 10,000 Finnish women combined from multiple national studies, Kontula and Mitettinen (2016) found that experience and practice masturbating and experience with multiple partners during one's lifetime was not associated with more frequent female orgasm. Rather, certain relationship factors, such as good communication with partners and finding partners who were desirable and sexually skillful, were associated with increased orgasm rates for women. Data from the same set of studies indicated that single women were less likely to experience orgasm during intercourse than women who were in long-term relationships (e.g., married, cohabitating). About 40% of single women usually experienced copulatory orgasms, whereas women in long-term relationships experienced copulatory orgasm over 50% of the time. These results are similar to those obtained in a sample of Portuguese women, where researchers found that the frequency of penile–vaginal intercourse and frequency of orgasm from penile–vaginal intercourse were positively associated with several components of relationship quality (e.g., relationship satisfaction, intimacy, passion; Costa & Brody, 2007). Other research has shown that, at least in newly married couples, sexual communication positively predicts wives' sexual satisfaction and their frequency of orgasm (Leonhardt et al., 2018). This suggests that establishing effective communication with a partner is important to establishing a sexually satisfying relationship, and long-term pair-bonds may facilitate this type of communication more readily than do short-term relationships.

Some research has not found support for the association between female orgasm frequency and long-term relationship satisfaction. Although initial reports indicated that the wealth of a woman's partner (a potential indicator of investment likelihood or potential in a partner) was positively associated with orgasm frequency (Pollet & Nettle, 2009), research has since found that this relationship is confounded by the fact that women with wealthier partners are happier, younger, healthier, and better educated than women with lower-income partners (Herberich, Hothorn, Nettle, & Pollet, 2010). Other research has found no relationship between female orgasm frequency and indicators of male relationship investment potential. For example, Thornhill et al. (1995) found no relationship between women's orgasm frequency and relationship duration or love for one's partner. They also did not find that indicators of male investment potential or willingness (e.g., reported commitment, nurturance, reported love for one's partner, relationship duration) were associated with female orgasm frequency. Likewise, some research has found that women in long-term relationships report lower sexual satisfaction than women in short-term relationships, with an inverse relationship between relationship

length and sexual satisfaction (e.g., Laumann, Gagnon, Michael, & Michaels, 2000). The relationship between orgasm frequency and relationship type (casual versus committed sex) may also be moderated by individual differences in other factors. In a recent study, Wongsomboon and colleagues (2020) found that the gap in orgasm frequency between casual and committed relationships was moderated by women's sociosexual orientation (i.e., the degree to which someone is interested in pursuing casual, uncommitted sex). Women with more restricted sociosexual orientations experienced more orgasms in committed relationships, but women with less restricted sociosexual orientations experienced similar orgasm frequency in casual sexual encounters as they did in long-term committed relationships. The results from these studies collectively suggests that the relationship between female orgasm frequency in long-term partnerships is complex.

Some researchers have proposed that the neurohormone oxytocin may facilitate the formation of pair-bonds in couples (Campbell, 2010), and that the release of this hormone during orgasm may contribute to the process of pair-bonding in humans (Young & Wang, 2004). Oxytocin is released during sex and orgasm in both sexes and in response to vaginocervical stimulation, lactations, and childbirth in women (reviewed in Komisaruk & Whipple, 2005). Oxytocin is also released during stress (reviewed in Onaka, 2004) and has been shown to reduce the activity of the amygdala (e.g., Viviani et al., 2011; Spengler et al., 2017), which is involved in the expression and subjective experience of fear and anxiety. Administration studies of oxytocin in rats suggest that it buffers the activity of the HPA axis during stress by reducing stress-induced secretion of corticosterone (Windle, Shanks, Lightman, & Ingram, 1997). Oxytocin release may therefore have anxiolytic effects (see Khajehi & Behroozpour, 2018). Oxytocin has also been shown to improve the ability to infer the mental state of others (e.g., Domes et al., 2007; Riem, Bakermans-Kranenburg, Voorthuis, & van IJzendoorn, 2014; although see Radke & de Bruijn, 2015) and increase prosocial behavior (e.g., Riem, Bakermans-Kranenburg, Huffmeijer, & van Ijzendoorn, 2013; for comprehensive reviews, see Bartz, Zaki, Bolger, & Ochsner, 2011; Campbell, 2010), at least among in-group members (i.e., oxytocin increases parochial altruism; De Dreu et al., 2010). Within the context of romantic relationships, endogenous oxytocin is elevated during the initial stages of a new relationship (Schneiderman, Zagoory-Sharon, Leckman, & Feldman, 2012). Administration of oxytocin has been shown to influence how couples communicate with one another during relationship conflict and it buffers the effects of HPA activity during these relationship disputes (Ditzen et al., 2009) as well as enhances the stress-reducing influence of partner support during the experience of pain (Kreuder et al., 2019). In addition to its activity in humans, oxytocin and the oxytocin signaling system have been directly connected to pair-bond formation (e.g., Hammock & Young, 2006), sexual behavior (Carter, 1993), and parenting behavior (e.g., Fahrbach, Morrell, & Pfaff, 1984) in nonhuman animals. Oxytocin may play an important role in romantic relationship formation and duration in human

pair-bonding, although future research is necessary to further elaborate on the neural mechanisms underlying this relationship.

#### **50.4 Female Orgasm as an Adaption to Increase Conception Probability**

Theories that posit female orgasm evolved to facilitate fertilization of ova by sperm argue that female orgasm leads to physiological processes that enhance the probability of conception (Baker & Bellis, 1993; Levin, 2002; Meston et al, 2004; Singh, Meyer, Zambarano, & Hurlbert, 1998). According to this perspective, physiological changes that occur during orgasm (e.g., uterine contractions) make the transport of sperm towards the unfertilized egg easier. However, the fact that the large number of women who rarely or never obtain orgasm through penile–vaginal intercourse still manage to reproduce as well as those who do achieve orgasm during penile–vaginal intercourse calls this argument into question (Lloyd, 2005; Wallen, 2006), although research into the sources of this variation in orgasm rates yield interesting results. There is evidence that women are more likely to experience orgasm when they are fertile (e.g., Matteo & Rissman, 1984), likely due to endogenous changes in steroid hormones (e.g., estrogen, progesterone, testosterone) across the menstrual cycle (van Anders & Dunn, 2009), and there is limited evidence that women's desire to become pregnant is associated with their likelihood of orgasming shortly after their partner (Singh et al., 1998), when seminal fluid would be present in the reproductive tract. It should be noted, however, that the authors of this latter paper encouraged caution when interpreting their results, which were not adjusted for type 1 error and were underpowered. Although Baker and Bellis (1993) report that female orgasm that occurred between 1 minute before male ejaculation and 45 minutes after led to the retention of more semen, it is worth mentioning that of the nine couples who provided samples or estimates of semen “flowback” (a measure of semen retention), one couple provided 93 of the 127 data points used to measure whether female orgasm in proximity to male ejaculation had any effect on sperm retention. However, the pattern of results should still be of great interest to researchers, despite the limited sample size.

Some research has shown that both administration of exogenous oxytocin (Wildt et al., 1998) and orgasm (Fox, Wolff, & Baker, 1970; although note that the data for this study are from multiple copulations from only one couple) cause uterine contractions and subsequently change uterine pressure from outward to inward, which may create an “upsuck” of seminal fluids into the uterus that may reduce flowback of seminal fluids out of the vagina after ejaculation (Fox, Wolff, & Baker, 1970; Wildt et al., 1998). Because oxytocin induces uterine contractions that result in changes in uterine pressure, some authors have argued that orgasm may turn the uterus and fallopian tubes into

a sort of functional peristaltic pump (i.e., a positive displacement pump; Wildt et al., 1998; Zervomanolakis et al., 2007). Supplying endogenous oxytocin to women, mimicking the release of oxytocin during orgasm, causes uterine contractions to occur that increase the transport of seminal-like particles into the uterus during both the fertile and the nonfertile phases of the menstrual cycle (Wildt et al., 1998; Zervomanolakis et al., 2007, 2009). Interestingly, this transport is directed to the specific fallopian tube that would be releasing a developed ovum during the fertile phase of the cycle only. In other words, when there is potential for a developed egg cell to begin migrating down the fallopian tube, which occurs only during the late follicular phase, the uptake of seminal-like fluid occurs in an ipsilateral fashion (i.e., towards only one of the two fallopian tubes) towards the fallopian tube that will contain the ovum. The biological importance of the finding that seminal fluid may be directed to the fallopian tube associated with the ovulating ovary is underscored by the subsequent finding that pregnancy rate was higher in women who demonstrated ipsilateral seminal transport of fluid to the appropriate fallopian tube compared to women whose reproductive tract did not demonstrate lateralization of seminal fluid movement (Wildt et al., 1998; Zervomanolakis et al., 2007). There have been two studies that failed to find movement of semen-like substances through cervix following orgasm (Grafenberg, 1950; Masters & Johnson, 1966), although it is possible that because both studies placed a cap on the cervix that this could have impeded fluid movement (see Fox, Wolff, & Baker, 1970; Puts, Dawood, & Welling, 2012).

In addition to changes in uterine pressure that occur during orgasm, sexual arousal causes a physiological change in the vagina known as “vaginal tenting.” Vaginal tenting is caused by the inner third of the anterior wall of the vagina becoming elevated away from the posterior wall along with the uterus and cervix, which functionally moves the cervix away from pooling semen following male ejaculation (Levin, 2002; Masters & Johnson, 1966). Vaginal tenting may create a space for ejaculate to pool, which could decrease the flowback losses and provide time for the ejaculate to decoagulate through the process of capacitation (Eisenbach, 1995; Levin, 2002). Some researchers have argued that female orgasm may allow sperm to enter into the cervix by resolving vaginal tenting and bringing the cervix into contact with pooled sperm via contractions induced by orgasm (e.g., Welling, 2014). This contractile action during orgasm could move sperm from the vagina into the cervix, reduce flowback, and bring sperm closer to the fallopian tubes (Fox & Fox, 1971).

It should be noted that critics of theories of the female orgasm functioning as an adaptation to increase the likelihood of conception (e.g., Lloyd, 2005; Levin, 2011, 2016) have pointed out concerns regarding the quantity and quality of evidence used as support of this theory. For example, research investigating the flow of particles through the reproductive tract has observed movement in women who are at a basal, nonaroused state. Vaginal physiology changes during sexual arousal and orgasm (e.g., vaginal tenting), and

movement of seminal-like fluid through the reproductive tract may be different during arousal versus nonarousal (Levin, 2011). Regarding the experimental tests of oxytocin inducing uterine contractions that are meant to mimic the contractions that occur during orgasm, Levin (2011) also expressed concern about the supraphysiological amounts of oxytocin used to induce these uterine contractions. It is unclear whether the quantity of oxytocin administered by researchers is similar to the endogenous release of oxytocin caused by orgasm. Furthermore, other researchers have found that there is no substantial genetic link between female orgasm rate and number of offspring (Zietsch & Santtila, 2013), which one would expect based on the theory that female orgasm increases fertility. Still, others have suggested that uterine contractions that occur during orgasm may excite male ejaculation, potentially increasing the likelihood that a woman would be fertilized by her chosen partner (Meston et al., 2004). Perhaps, then, orgasm increases conception probability in a more complex way by functioning as a sort of mate- or sire-choice mechanism.

### **50.5 Female Orgasm as an Adaption for Selecting High-Quality Mates**

Orgasm may encourage women to mate with partners of high genetic or investment quality, thus resulting in indirect fitness benefits to women in the form of genetic or direct benefits provisioned by that male to potential resulting offspring (Alcock, 1980; Puts, Dawood, & Welling, 2012; Thornhill, Gangestad, & Comer, 1995). In most species, females are more selective about mates compared to males. Trivers' (1972) Parental Investment Theory provides an evolutionary framework to understand differences in mating and parental effort between sexes that has been used to explain sex differences in humans. According to Parental Investment Theory, women should be choosier when selecting partners compared to men because they stand to lose more (in terms of lifetime fitness) than men through inefficient allocation of mating versus parenting effort (e.g., Daly & Wilson, 1983; Trivers, 1972). This is due to their higher obligatory investment in gestation and lactation versus the minimum obligatory investment that males must contribute to reproduce (i.e., supplying viable sperm cells). It has been suggested that clitoral orgasm could facilitate female mate choice, as clitoral orgasm may help select for male partners who are willing to expend sufficient effort to induce orgasm, a signal of willingness to invest in his partner (Angier, 1999). The female mate choice hypothesis of orgasm supposes that orgasm should be more difficult for women to reach than men because they are choosier about potential partners and only those who possess traits indicative of higher genetic and/or relationship quality should be reliably able to induce orgasm. This choosiness should be most applicable to penile–vaginal intercourse because that could result in conception (Puts, 2007).

The mate choice/sire choice hypothesis is inclusive of other adaptive explanations of female orgasm. If orgasm is a mechanism by which women can select good long-term, investing partners, then it would be expected that orgasm also facilitates pair-bond formation between women and desirable long-term partners. If female orgasm reflects an index of male investment or mate quality, women should be less likely to orgasm with male partners who are less interested in pursuing long-term relationships and/or who are of lower mate quality. As previously mentioned, women are less likely to seek uncommitted sex than men (Clark & Hatfield, 1989; Schmitt et al., 2003), are less likely to orgasm during short-term relationships and hookups compared to men (Eschler, 2004), and are more likely to reach orgasm in long-term versus short-term relationships (Armstrong et al., 2012), suggesting that orgasm could influence women to seek out better quality long-term investing partners. Indeed, there is some evidence that orgasm quality varies by partner, and that partners who induce the highest orgasm rates have characteristics of a good long-term partner (e.g., warmth, faithfulness; Sherlock et al., 2016).

Although the mate choice perspective on female orgasm may not seem substantially different from the pair-bonding hypothesis outlined above, they vary in a subtle but distinct manner. The pair-bonding hypothesis states only that orgasm facilitates bonding between a woman and her male partner, whereas the mate choice theory of female orgasm posits that orgasm is more likely to happen when a man is already showing indicators of long-term investment potential. Alternatively, it is possible that female orgasm functions to select partners who are of high genetic quality, rather than of high investing quality. From this perspective, orgasm likelihood should depend less on indicators of investment willingness and potential, and more on cues of underlying genetic quality (e.g., indicators of current health, developmental stability, immune quality). This would also mean that orgasm might select more for sire quality than mate quality.

There is a body of indirect evidence suggesting that when women are maximally fertile they may be more likely to engage in coitus, and possibly experience orgasm, with males who possess indicators of high genetic quality. At peak fertility, women are more likely to experience orgasm (Matteo & Rissman, 1984), report being less committed to their current romantic partners (Jones et al., 2005), and may be more interested in extra-pair partnerships (Gangestad, Thornhill, & Garver-Apgar, 2002, 2005; Grebe, Thompson, & Gangestad, 2016; Haselton & Gangestad, 2006; but see Pillsworth, Haselton, & Buss, 2004), although this latter relationship depends on the quality of their current partner (Gangestad et al., 2005; Pillsworth & Haselton, 2006). Women's preferences for cues to male genetic quality are also sensitive to fertility status, and women experience an increase in preference for indicators of high genetic quality when fertility is high, such as male facial symmetry (e.g., Little, Apicella, & Marlow, 2007; Little, Jones, Burt, & Perrett, 2007; Penton-Voak et al., 1999; although see Petters, Simmons, & Rhodes, 2009),

masculinity (Feinberg et al., 2006; Johnston et al., 2001; Jones et al., 2005; Little, Jones, & Burriss, 2007; Penton-Voak et al., 1999; Welling et al., 2007; but see Marcinkowska, Galbarczyk, & Jasienska, 2018; Jones et al., 2018), and dominance (Havlicek, Roberts, & Flegr, 2005; Gangestad et al., 2004). Symmetry, for example, is a putative indicator of underlying genetic quality because developmental perturbations may influence the degree to which the left and right side of the body develop dissimilarly (Møller, 1997; Møller & Pomiankowski, 1993). In humans, symmetry is considered attractive (Grammar & Thornhill, 1994; Little, Apicella, & Marlowe, 2007; Little, Jones, & Burriss, 2007; Little, Jones, Burt, & Perrett, 2007) and fluctuating asymmetry is negatively associated with mating success (Bogaert & Fisher, 1995; Thornhill & Gangestad, 1994). Women's extra-pair partners may be more symmetric than their in-pair partner (Gangestad & Thornhill, 1997), and those with more symmetric partners report more orgasms than do women with relatively more asymmetric partners (Thornhill, Gangestad, & Comer, 1995). Physical attractiveness, which is also considered a putative cue of underlying mate quality (Fink & Penton-Voak, 2002; Grammar, Fink, Møller, & Thornhill, 2003; Rhodes, 2006) and has been linked to sperm quality (Soler et al., 2003, although see Peters, Rhodes, & Simmons, 2008; Soler et al., 2014), is also positively associated with women's frequency and timing of orgasm (Puts, Welling, Burriss, & Dawood, 2012). Specifically, women with more attractive partners are more likely to orgasm at the same time or soon after their partner compared to women with less attractive partners, which may decrease semen flowback and increase the likelihood of conception. Additionally, women with more masculine and dominant partners experienced more frequent and earlier-timed orgasms (relative to their male partner's orgasm timing), suggesting that orgasm frequency is positively associated with sire quality. That women are more likely to seek extra-pair partners during periods of high fertility, show an increase in preference for indicators of high genetic quality in partners during this time, and are more likely to orgasm from high quality male partners (Puts, Welling, Burriss, & Dawood, 2012; Thornhill, Gangestad, & Comer, 1995) supports the hypothesis that female orgasm is a mechanism of sire choice.

## 50.6 Conclusion

As outlined above, research into women's sexual experience has yielded several theories regarding the function (or lack thereof) of female orgasm. The evidence that female orgasm may be adaptive, be it through increased pair-bonding, increased likelihood of conception, encouraging sex with high quality partners, or by reinforcing sexual behaviors in general, is too plentiful to be dismissed. However, considerable research remains to be conducted. For example, research documenting differential sexual experience with

attractive and unattractive men, or more masculine versus more feminine men, is lacking. Similarly, results from studies investigating female orgasm as a sire choice mechanism may have alternative explanations. More dominant and masculine men have more sexual experience (e.g., Keller et al., 1982; Perusse, 1993; Puts et al., 2006), and it is possible that this sexual experience is driving the difference in orgasm frequency described in prior studies linking male attractiveness to orgasm frequency in women (e.g., Puts, Welling, Burriss, & Dawood, 2012). Given that women find masculine men more sexually attractive (Little et al., 2002), the earlier timing of female orgasm with partners whom they consider attractive may not be related to increasing sperm retention (and increased probability that that individual will sire offspring), but rather associated with sexual excitability and arousal. Moreover, more research on the biological relevance of women's orgasm and orgasm timing is necessary to determine the contribution they make to conception. This area of research is in need of replications with larger samples and clear/transparent methodologies. In fact, recent evidence (Shirazi et al., 2018) indicates that questionnaire semantics influence the way that both male and female participants respond to self-report measures of orgasm, the most common method by which participants provide information about orgasm frequency, quality, and timing.

It is also possible that orgasm facilitates conception, not through an upsuck mechanism, but because it releases endorphins, which are known to increase tolerance to pain and promote feelings of euphoria, and oxytocin, which has anxiolytic effects (reviewed in Khajehei & Behroozpour, 2018). Oxytocin also reduces cortisol, psychosocial stress (Heinrichs et al., 2003), and blood pressure (Bumann & Uvnäs-Moberg, 2020). Importantly, psychological stress can have a large detrimental impact on conception (see Campagne, 2006), and so orgasm may increase conception probability by promoting relaxation and reducing stress. Women are also more likely than men to fall asleep after sexual intercourse, and orgasm increases postcopulatory somnolence (Gallup, Platek, Ampel, & Towne, 2020), the result of which may be a reduction in flowback prior to sperm capacitation (i.e., postcoital sleeping may allow more sperm to travel into the female reproductive tract while the woman is lying down). These and other possibilities should be considered in future research. Fundamentally, regardless of the mechanism or mechanisms through which women's orgasm is adaptive, there is an abundance of evidence suggesting that it functions to improve women's fitness.

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