Adaptive Human Behavior and Physiology (2016) 2:26–43
DOI 10.1007/s40750-015-0029-1

ORIGINAL ARTICLE

Understanding the Prevalence of Sexual Dysfunctions in Women: an Evolutionary Perspective

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Received: 20 February 2015 / Revised: 17 May 2015 / Accepted: 8 June 2015 /
Published online: 18 June 2015

Abstract Epidemiological studies indicate that almost one in two women face some kind of sexual dysfunction. Given the importance of sexual functioning for successful reproduction, such a high prevalence is enigmatic. Selection forces should have reduced to a low frequency, or have eliminated completely from the gene pool, any alleles that predispose for sexual dysfunctions. Epidemiological studies indicate that this did not happen, and the present paper attempts to examine the reasons why. Based on anthropological and historical evidence, it is argued that in ancestral societies sexual motivation was a much weaker predictor of successful mating in women, than it is today in post-industrial societies. Accordingly, balancing selection has favored a female type of sexual behavior which is characterized by low sexual motivation. This low level of sexual motivation is not optimal in post-industrial societies where mate choice is not regulated, resulting in women, who have such predispositions, to be classified as suffering from a dysfunction. Predictions are derived from the proposed model, and matched with available evidence.

Keywords Sexual dysfunctions in women · Balancing selection · Ancestral neutrality · Sexual arousal disorder · Orgasmic disorder · Sexual pain disorder · Hypoactive sexual desire disorder

Introduction

Sexually reproducing species need to engage successfully in sexual intercourse for reproduction to take place. This means that good sexual functioning has considerable importance for individuals' fitness (i.e., their reproductive success), which translates into strong evolutionary pressures to remove from the gene pool any alleles that cause

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mechanisms regulating sexual behavior not to function properly. We would thus, expect a low prevalence of disorders which are characterized by a clinically significant disturbance in an individual's ability to respond sexually or experience sexual pleasure (see DSM 5, American Psychiatric Association 2013, for a detailed description of these disorders), a prediction which is not consistent with the findings of epidemiological studies of sexual functioning in women.

More specifically, in the USA, Shifren et al. (2008) estimated the overall prevalence of female sexual dysfunction to be 43.1 %, with the prevalence of low sexual desire to be 37.7 %, low arousal to be 25.3 % and orgasm difficulties to be 21.1 % (see also Laumann et al. 1999). In Britain, Mercer et al. (2003) estimated a lack of interest in sex to be 40.6 %, inability to experience orgasm to be 14.4 % and pain during intercourse to be 11.8 % women. In Norway, TrÆen and Stigun (2010) estimated prevalence of reduced sexual desire to be 37 %, difficulties in achieving orgasm to be 26 % and pain during intercourse to be 9 %. Similar prevalence rates were found in Australia (Ponholzer et al. 2005), Brazil (Abdo et al. 2004), China (Lau et al. 2005), Japan (Hisasue et al. 2005), Iran (Goshtasebi et al. 2009) and Egypt (Elnashar et al. 2007).

The purpose of this paper is to employ an evolutionary perspective in order to account for these high prevalence rates. It will be argued that these rates do not reflect genuine dysfunctions, in the sense that they are not the outcome of specific mechanisms not working properly, but they constitute normal variations in sexual functioning. It will be argued further that this variation may not be well adapted to the demands of the modern environment because it has evolved in a different one, and for this reason it is labeled as dysfunction.

In more detail, the high prevalence rates lead to the question of why selection forces have not eliminated, or reduced to very low frequencies in the population, alleles that predispose for sexual dysfunctions in women. One possibility is that there are not any such alleles for selection forces to remove; that is to say, individual differences in sexual functioning are not due to differences in genetic make-up, but due to differences in environmental conditions. This does not appear to be the case, as several studies have found evidence that the sexual functioning of women has a genetic component (e.g., Burri et al. 2012a; Zietsch et al. 2011). But even if certain environmental factors affected sexual functioning, there would be strong evolutionary pressure to evolve resistance to these factors, reducing in effect the prevalence of sexual dysfunctions to much lower than the observed levels.

Another possibility is that sexual dysfunctions characterize predominantly post-menopausal women. That is, since in this case sexual dysfunctions are inconsequential for reproductive success, evolutionary forces would be weak in removing alleles that predispose for such dysfunction in older age. In this respect, the prevalence rate of these dysfunctions is very high among older women and very low among younger ones, accounting for the overall observed prevalence. Although, sexual dysfunction frequency increases with age (Laumann et al. 2005), the prevalence of sexual dysfunction remains high among younger women. For instance, Laumann et al. (1999) for the 18 to 39 age group, estimated lack of sexual interest to be 32 %, inability to achieve orgasm to be 27 %, and pain during sexual intercourse to be 18 %. Similar results were obtained by other studies (e.g., Mercer et al. 2003).

It may also be the case that sexual dysfunctions are caused by psychological disorders such as depression. For instance, studies suggest that half of women with major depression experienced desire and arousal problems (Kennedy et al. 1999). This argument predicts that the majority of women suffering from a sexual dysfunction also suffer from depression or another psychopathology which has not been caused by the sexual dysfunction. But this does not appear to be the case; that is, most women facing a sexual dysfunction do not have a preceding psychopathology (Wincze and Carey 2001). In any case, psychopathology is unlikely to account for the high prevalence of sexual dysfunctions. For instance, a Swedish study found that approximately 80 % of the women in the sample suffered from low sexual desire (Fugl-Meyer and Fugl-Meyer 1999). It is highly improbable however, that almost three quarters of the women in the sample suffered from depression or another mental disorder.

Overall, it is unlikely that traits which serve key evolutionary goals do not function properly in almost half of women. This changes the question from why evolutionary forces have not removed alleles that predispose for sexual dysfunctions from the population, to why it maintained alleles that predispose for such variation in sexual functioning. In turn, this raises the question of why much of this variation is considered dysfunctional. This paper aims to address these questions by proposing a model which combines the contributions of three different evolutionary models: It is going to be argued that most of the variation in sexual functioning is accounted for by balancing selection, with polygenic mutation and ancestral neutrality also having an important role.

The Evolutionary Logic of Sexual Motivation

In order to find mates and engage in sexual intercourse, women need to have mechanisms or adaptations to motivate them to do so. Sexual desire is such a mechanism, enhancing the motivation for sexual intercourse (Giles 2008; Toates 2014). For sexual intercourse to keep occurring however, another mechanism is required to reward women for doing so. Sexual arousal motivates sexual intercourse, by making it rewarding (Melis and Argiolas 1995; Wallen 1995). For instance, Meston and Buss (2007) found pleasure to be one of the main motives that drive women (and men) to have sex.

Orgasm, which can be defined as a peak sensation of intense pleasure (Meston et al. 2004), can be considered also as a mechanism for motivating and rewarding women for engaging in sexual intercourse (Lloyd 2005; Puts et al. 2012a, b). It has been argued that this mechanism further serves the function of enabling women to exercise mate choice. In particular, by investing more in their offspring, women become a scarce reproductive resource to which men strive to gain access (Trivers 1972). It pays then for women to be selective, and sexual functioning mechanisms enable them to exercise such a choice (Lloyd 2005; Puts et al. 2012a, b). Thus, women may be more likely to experience orgasm if they have sex with a man with desirable qualities. This argument was predominantly focused on orgasm, but it also applies to other mechanisms; for instance, women will feel a higher desire to have sex with a partner who has desirable traits such as high social status, and the experience will be more rewarding when they do so (McCabe and Cummins 1997).

In sum, there are at least three mechanisms which motivate women to seek sexual intercourse, namely sexual desire, sexual arousal and orgasm. It is no surprise then that sexual interest/arousal disorder, and orgasmic disorder refer specifically to dysfunctions of these mechanisms. A further sexual dysfunction is pain during sexual intercourse, which, although it does not directly reflect the operation of a sexual functioning mechanism, impairs motivation to engage in sexual activity (Wincze and Carey 2001).

Overall, sexual dysfunctions are likely to reduce the willingness of women to engage in sexual intercourse, and compromise their capacity to exercise mate choice (Toates 2014; Wincze and Carey 2001). There are three evolutionary models which can potentially account for the fact that low sexual motivation (the term low sexual motivation will be preferred over sexual dysfunction to indicate a variation in, rather than a dysfunctional trait) has substantial costs, evolutionary forces can still favor it. The application of these models requires reconstructing ancestral human condition where selection forces have shaped mechanisms involved in sexual functioning. This can be done predominantly with the use of anthropological and historical evidence.

The Patterns of Mating During Human Evolution

The genus *Homo* appeared on earth approximately two million years ago, and for most of this period our ancestors were living is small bands of hunters and gatherers (Lee and Devore 1968). Thus, much of human evolution took place in ancestral foraging societies (Lee and Devore 1968; Tooby and Cosmides 1990). Accordingly, knowledge of the mating patterns prevailing at that time enables an understanding of the evolutionary history of adaptations related to sexual functioning. A good source of information is the anthropological record on the mating patterns of modern hunters and gatherers (Lee and Devore 1968). The way of life of modern foragers approximates the way of life of ancestral foragers, which means that typical patterns of mating in the former are likely to reflect typical patterns in the latter (Ember 1978).

Anthropological evidence from pre-industrial societies suggests that the choice of mates and the sexuality of women in ancestral times were regulated (Apostolou 2014; Stephens 1963). More specifically, one study collected evidence from a sample of 190 contemporary foraging societies and analyzed their mating patterns (Apostolou 2007). It was found that the most common mode of long-term mating (in approximately 70 % of the cases) was arranged marriage, where parents choose spouses for their children. In fewer than 5 % of cases, was the primary mode of marriage courtship, where children choose their own spouses with little input from their parents. Furthermore, in the vast majority of cases, men, mainly fathers, were in control of marriage arrangements. Phylogenetic analysis, which attempts to reconstruct the conditions prevailing in ancestral societies, has provided evidence that the patterns of mating found across modern foragers (e.g., arranged marriage) were also prevalent in ancestral ones (Walker et al. 2011).

A subsequent study revealed that the choice of mate is also heavily regulated in contemporary pre-industrial societies which base their subsistence on agriculture and animal husbandry (Apostolou 2010). In the same vein, one study coded the mating

patterns of 16 historical agropastoral societies covering a period of approximately 5000 years (Apostolou 2012). In all societies but one, the primary mode of long-term mating was arranged marriage, where fathers and other male relatives dominated marriage arrangements, and daughters were controlled more than sons. Comparisons between agropastoral and foraging societies suggests that parental choice is stronger in the former, indicating that it had also been stronger in the later stages of human evolution which followed the agricultural revolution approximately 10,000 years ago (Apostolou 2010).

In the pre-industrial context, women are married relatively early, while before marriage they are chaperoned by their parents to prevent sexual adventures from taking place (Apostolou 2014). The husband receives from the parents the right to have sexual access to their daughter, a deal that is usually sealed with the payment of the bridewealth, which women have limited capacity to resist (Goody and Tambiah 1973). In pre-industrial societies, it is usually the case that forcing sex on one's wife is not considered illegal (Bergen 1996; Russell 1990). Until recently, the law in most countries exempted men who forced sex on their wives from prosecution, and in many countries it still does (Hasday 2000; Freedman 2013).

In a context where mating is regulated, women still have some space to exercise choice. To begin with, they can engage in sexual relationships before their parents arrange a marriage. This is limited however, by the presence of chaperoning and the strong social control, and it is also risky as parents are likely to retaliate and punish their daughters severely if they find them flirting (Apostolou 2014; Perilloux et al. 2008). In many societies parents consult their daughters before choosing a husband for them, although the consent of the daughter is not usually a pre-requisite for the marriage arrangement to proceed (Apostolou 2010).

Women can also exercise choice through divorce. Divorce is found in almost all human societies, and in most of the cases women have the right to initiate it (Betzig 1989). Although subsequent marriages are also likely to be arranged by their families, divorce gives considerable latitude to women to exercise choice, as parents usually have little say in such decisions (Apostolou 2014). Women can also exercise choice in extramarital relationships which are found in almost all pre-industrial societies (Broude 1980). They risk paying however, a high price if such a relationship is revealed. In particular, adultery can to lead to divorce (Betzig 1989), or to severe punishment of women, including body mutilation or even death (Frayser 1985). Furthermore, women can exercise choice in subsequent marriages when they are more independent from their parents, their parents are absent due to death, or they are too physically weak to impose their will (Apostolou 2014).

In sum, the anthropological and historical records of pre-industrial societies indicate that extensive free mate choice is an evolutionary novel phenomenon found predominantly in post-industrial societies. Sexual motivation mechanisms evolved in a context where the mate choices of women were regulated, an insight that can lead to solution of the puzzle of the high prevalence of sexual dysfunctions. This solution involves combining the insights gained from the anthropological and historical records with three different evolutionary models that will be discussed next.

Evolutionary Models

Balancing Selection

The predominant view on the prevalence of psychological disorders among evolutionary psychiatrists and evolutionary psychologists is the balancing selection model (Barrantes-Vidal 2004; Longley 2001; Wilson 1998). In this model, alleles that predispose an individual towards a disorder in certain instances may increase fitness. There are several ways that this can happen, one being the heterozygote advantage. In sickle-cell anemia those who are homozygous for the common allele (AA) at the b-hemoglobin locus are susceptible to malaria, whereas those homozygous for the less common allele (aa) are more likely to die from sickle-cell anemia. Nevertheless, heterozygotes (Aa) have an advantage over the other two as they do not develop anemia, and they are much more resistant to malarial infection. It has been argued that certain mental disorders such as schizophrenia (Huxley et al. 1964) and depression (Wilson 2001) are maintained in the population by such heterozygote advantage.

In negative frequency-dependent selection the fitness of alleles increases as they become rarer. Thus, an equilibrium is reached where both alleles that predispose for a given dysfunction and those that do not co-exist (Morris and Watson 2011). For instance, Mealey (1995) argued that psychopathy persists in the population at a low frequency for this exact reason. That is, individuals with this trait increase their fitness considerably by exploiting and taking resources from others, but this trait is less effective when it becomes common in the population and others become more vigilant of it.

Polygenic Mutation

For the genetic material to pass to future generations it needs to copy itself multiple times, which means that the human genome is susceptible to copy errors or mutations. Mutations usually decrease fitness (Eyre-Walker and Keightley 2007) so, evolutionary forces remove them from the genome. But this process takes time, which is contingent on how harmful a mutation is; that is, it takes longer for less harmful mutations to be removed from the population. For instance, a theoretical model calculated that a mutation causing a 1 % reduction in fitness will pass approximately through 100 individuals before it is eliminated from the population (García-Dorado et al. 2003).

Some theoretical papers have centered on the role of mutations in maladaptive human traits (e.g., Gangestad and Yeo 1997). The basic idea behind these models is that the heritability of these traits is due to a large number of harmful alleles which are individually very rare at any given locus, but which are collectively common across loci (Keller and Miller 2006). There is some evidence in favor of this model for serious mental conditions such as schizophrenia (Sipos et al. 2004).

Ancestral Neutrality

A further possibility is ancestral neutrality; that is, alleles for traits which are maladaptive in a modern post-industrial context may not had been maladaptive in ancestral environments. For instance, it has been argued that individuals with schizophrenia

living in ancestral times were valued as shamans and were not socially and sexually ostracized as it is the case today (Polimeni and Reiss 2002). In the same vein, alleles that increase the risk of mental disorders in a modern post-industrial context, may not have had such an effect in ancestral environments.

Although modern post-industrial environments are radically different from ancestral ones, it is unlikely that alleles that increase the risk of mental disorders today were neutral in ancestral times (Keller and Miller 2006). Nevertheless, traits which in a contemporary context impair fitness considerably, may have done less so in ancestral times.

Ancestral neutrality is related to mismatch theory: a mismatch between ancestral and modern environments explains why traits may have been selected for (or ignored) ancestrally, but are reproductively costly now. For instance, strong preferences for sugar and fat has been favored in ancestral environments to motivate seeking energy-rich food, but these preferences may not work in a fitness-increasing way in modern context where such foods are readily available, as they can lead to diabetes and obesity (Breslin 2013).

The next section will examine how each of the models can contribute to our understanding of the observed prevalence rates of sexual dysfunctions.

Assessing the Contributions of Each Model

Balancing Selection and Ancestral Neutrality

In a context where mate choice is regulated, women who have low motivation to seek sexual intercourse enjoy several advantages. To begin with, they face less friction with their parents as they will be unlikely to engage in pre-marital sex which is not approved by them. In addition, they will be more likely to accept a husband that their parents have selected for them, even if he is physically unattractive, and they will be less likely to divorce him if he does not satisfy them sexually. They will also be less likely to seek sexual satisfaction in extramarital relationships, and thus they will be less likely to suffer punishment or divorce from their husbands. In addition they will be less likely to be infected with sexually transmitted diseases, and they will be less likely to get pregnant by someone who is unwilling to stay with them and invest in their children.

Women with low sexual motivation also suffer costs however. The cost which appears to be the heaviest, and which makes the prevalence of this trait puzzling, is exclusion from mating and sexual intercourse. Nevertheless, the key insight from the anthropological and historical records is that during the period of human evolution, a high level of sexual motivation was not required for a woman to find a partner and have sex. This is because it is usually parents who find husbands for their daughters and grant them sexual access rights. This means that for most of human evolution this cost has not been substantial. There are other costs that women with low sexual motivation are likely to suffer, however.

First, they will be more susceptible to their parents' control, who exercise in-law choice not always in their daughters' best interests (Apostolou 2011; Buunk et al. 2008). For instance, they will be more likely to accept a husband who is not particularly attractive, and they will be less likely to divorce him, if he does not satisfy them

sexually. This is because, women who are not particularly interested in having sex, will be less concerned about how attractive prospective sexual partners are. Second, they will have a lower capacity to sexually satisfy their husbands (see Brezsnyak and Whisman 2004), something that is likely to cause friction in the marriage, and to lead their husbands to abandon them or seek sexual outlets outside the marriage. If their husbands die or leave them, and their parents are also dead or unable to arrange another marriage, women may effectively place themselves out of the mating market, due to the possible inadequacy of their sexual motivation to drive them to seek new partners. That is, a woman who experiences a low sexual desire, is unable to reach orgasm and experiences pain during sexual intercourse, will not have a strong incentive to seek a partner.

Furthermore, women derive several advantages from engaging in extramarital relationships. First, as men are willing to have casual sexual intercourse with women of lower mate value, women engaging in such relationships can obtain better genes for their children than the ones offered by their husbands (Benshoof and Thornhill 1979; Buss 2003). This is particularly so in the context where marriage is regulated, and parents do not place much emphasis on the genetic quality of their sons-in-law (Apostolou 2011); thus, women can balance the costs of parental choice by seeking better genetic quality in extramarital partners (Apostolou 2014). In addition, by engaging in extramarital relationships women can gain resources, but also establish a network of men who can support them or marry them if their husbands abandon them or die (Buss 2003). Accordingly, women with low sexual motivation are less likely to receive these benefits because they are less likely to engage in such relationships.

An additional cost to low sexual motivation women is likely to be a reduced ability to exert mate choice via female orgasm. Orgasm can work as a mate choice mechanism, with women tending to experience orgasm with fitness-increasing mates, and less so with mates who are not fitness-increasing (Baker and Bellis 1993). This being the case, women with a reduced capacity to experience orgasm may also suffer from a reduced capacity to distinguish between mates.

These costs to women with low sexual motivation are the benefits of women with high sexual motivation. To begin with, they will be less likely to accept mates of low genetic quality imposed by their parents, and will be more likely to divorce husbands who are not attractive or committed enough to satisfy them sexually. They will also be more likely to sexually satisfy their husbands (Brezsnyak and Whisman 2004), reducing the likelihood that the latter will seek sexual satisfaction in an extramarital partner or in another wife. They can also obtain good genes, resources, and support from extramarital partners. Moreover, if they find themselves in a situation where their husbands are dead or abandon them, they will be motivated by their high sexual desire to seek others partners instead of staying single.

Nevertheless, women with high sexual motivation also suffer costs. To begin with, they will be prone to engage in pre-marital relationships, resulting in conflict with their parents. They are also likely to experience a reduction in their mate value if they acquire a reputation of loose sexual behavior. They may also refuse a husband who is not attractive or divorce him if he does not satisfy them sexually, causing further conflict with their parents. Moreover, they will be likely to engage in extramarital relationships, risking divorce and severe punishment from their husbands. In addition, they will be more likely to catch sexually transmitted diseases, and to get pregnant by

someone who is not optimal for them (see Kafka 2010 for a review of the costs of high sexual motivation in a post-industrial context).

Overall, there is not a single female morph (i.e., a type of woman distinguished by her level of sexual motivation) which is always better off than another. On this basis, it is hypothesized that evolutionary forces will maintain alleles for both morphs in the population. Another way to put this, is that there are at least two evolutionary niches in the population, one for women with low sexual motivation and one for women with high sexual motivation. Where a species occupies multiple niches, a polymorphic equilibrium (i.e., two or more distinct specializations) is usually more optimal than a monomorphic one (i.e., a single specialization) as specialists are more efficient than generalists (Wilson 1994 see also Figueredo et al. 2009). The relative frequency of each morph depends on the frequency of the other, and the equilibrium will be determined by local conditions that define the size of each evolutionary niche (i.e., frequency dependent selection).

In particular, as women with high sexual motivation become more common in the population, the friction between parents and their daughters will increase, extramarital relationships will become more frequent, the rate of unwanted pregnancies and the spread of sexually transmitted diseases will increase. In consequence, women with low sexual motivation will tend to be valued more by parents, husbands and society in general. For instance, parents, as well as social institutions such as the law and the church, would not punish these women for undesirable sexual behavior.

This will give a selective advantage to this female morph which will increase in frequency in the population. But as it becomes more common and the high sexual motivation morph becomes rarer, the value ascribed to low sexual motivation will decline since extramarital relationships, unwanted pregnancies, sexual transmitted diseases and conflict with parents become less common. In addition, men will have a harder time finding women to satisfy them sexually, increasing the value they place on such women. Women with high sexual motivation will also suffer less cost from adultery and sexually transmitted diseases, as husbands will be less vigilant for extramarital relationships and the frequency of sexually transmitted diseases will be low. Thus, women with high sexual motivation will enjoy a selective advantage and the frequency of this morph will increase in the population. Eventually, an equilibrium will be reached where a proportion of the female population will have low sexual motivation and the other a high sexual motivation.

The important point is that the optimum equilibrium in ancestral times was different from the optimum equilibrium in modern times in post-industrial societies. This is because the weakening of parental choice and the strengthening of female choice have dramatically reduced the niche for low sexual motivation. As this happened relatively recently, evolutionary forces have not been able to adjust the relative frequencies of genes that code for sexual motivation mechanisms to the new equilibrium, meaning that there is a substantial proportion of women with a sexual motivation which is below what is now optimal.

Ancestral women belonging to the low motivation morph would only need to have sexual receptivity during the fertile window of rare fertile cycles (as they were pregnant most of the times) in order to conceive at each possible opportunity. Thus, a woman may be predisposed to experience desire only on a couple of days preceding ovulation in her most fertile cycles, and low sexual in other instances. In a post-industrial context,

these women will face difficulties in relationships with their male partners who will demand more frequent sexual intercourse than they are willing to supply. This friction is likely to lead many women and couples to the door of a psychologist or other sexual functioning expert, and to the low sexual motivation being classified as a dysfunction (e.g., in the DSM). But what appears to be a dysfunction today, is simply a sexually functioning mechanism working as it should in the environment where it evolved.

Overall, the balancing selection model suggests that there are two distinct female morphs, namely a low and a high sexual motivation. The ancestral neutrality model suggests that a mismatch between ancestral and modern conditions would result in the low motivation morph not to be able to deal effectively with the demands of the modern free mate choice context.

At this point a distinction needs to be made between state-like and trait-like effects. In the balancing selection model, the difference in the sexual motivation of women constitutes a trait-like effect; that is, women's differences in desire are relatively permanent states. Nonetheless, there is evidence for state-like shifts in sexual motivation within women. Some of these occur at a within-cycle level with shifts in hormones, and some are more life-stage related, such as a tendency for libido to be higher earlier in relationships, but then to decline as relationship length increases (Roney 2015).

Accordingly, it is likely that some of what is diagnosed as sexual dysfunction may be an effect of mechanisms that adaptively shift motivation from courtship and mate acquisition to other adaptive problems such as parenting. This argument is compatible with the balancing selection hypothesis, as the sexual motivation of each morph can change based on the state that a woman is. For instance, the libido of low-sexual desire and high-sexual desire women may decrease in the case a child is born, to enable the diversion of resources from mating effort to parenting effort.

Polygenic Mutation and Ancestral Neutrality

Polygenic mutation on its own is unlikely to be responsible for the high prevalence of sexual dysfunctions, as evolutionary forces remove fitness impairing mutations from the gene pool, preventing them from reaching high frequencies, and consequently, disorders attributed to such mutations affect only a very small part of the population (Keller and Miller 2006). Similarly, ancestral neutrality is also unlikely to be the sole factor as a low sexual motivation may not have been particularly impairing in ancestral times, but it was certainly not fitness neutral to allow for the high frequency of alleles that predispose for it. A combination of the two however, can potentially account for the more extreme cases of sexual motivation.

More specifically, how quickly selection removes harmful mutations is proportional to the fitness costs of the mutation, represented by the selection coefficient (s) against the mutation (Keller and Miller 2006). If (s) is reproductively lethal ($s=1$), the mutation will exist in only one body before it is eliminated from the population. Nevertheless, if (s) is small, the mutation may pass through many bodies before it is removed from the population. The result of this balance between mutation rate (m) and selection coefficient (s) is usually a low equilibrium frequency (p) of mutant alleles that have not yet been removed from the population by selection (Keller and Miller 2006).

Genetic mutations are likely to push the level of sexual motivation above or below what was optimal in ancestral societies. For instance, a very high sexual desire could

cause friction with a woman's parents, lower her mate value, and place her health and marriage at risk. That is, a woman would be more likely to be in conflict with her parents who would strive to control her sexuality, to have many premarital relationships acquiring a bad reputation and lowering her value as a prospective wife, to contract sexual transmitted diseases, and to engage in extramarital relationships increasing the likelihood of divorce. These mutations would then be selected out of the gene pool, but this would require some time. Having very low sexual motivation impairs the fitness of women less than does very high sexual motivation. This is because, given that spouses are provided by parents, and given that husbands can force sex on their wives, very low sexual motivation will have smaller negative impact on the fitness of a woman than very high sexual motivation. Accordingly: ($s_{high\_motivation} > s_{low\_motivation}$) so ($p_{high\_motivation} < p_{low\_motivation}$), meaning that in ancestral times selection forces would remove mutations that cause very high sexual motivation in women much faster than mutations that caused very low sexual motivation.

This would be particularly so in the later stages of human evolution (i.e., following the agropastoral revolution 10,000 years ago), where mating was more strongly regulated and where low sexual desire was even less consequential and high sexual desire even more consequential. In effect, it is expected that in the population today there will be a small number of women with a mutation load that predisposes them to abnormally low levels of sexual motivation and an even smaller number of women with an abnormally high level of sexual motivation that selection forces has not had sufficient time to eliminate.

A Model of Sexual Functioning

Overall, a model that accounts for the high prevalence of sexual dysfunction in women is proposed, which combines the three evolutionary models. In this model most of the variation in sexual functioning is accounted for by balancing selection with polygenic mutation, and ancestral neutrality also playing a role. On the basis of this model at least 10 predictions can be made.

Predictions Derived from the Model

(1) *The main prediction of the model is that there are two primary types or morphs of women: one with low sexual motivation and one with high sexual motivation*. This prediction is consistent with the epidemiological studies of sexual dysfunctions, which find that the majority of women have a high level of sexual motivation, but there is also a considerable proportion of women with low sexual motivation (Mercer et al. 2003; Laumann et al. 1999; Shifren et al. 2008; TrÆen and Stigun 2010).

(2) *Moreover, the low sexual motivation type is characterized by a low level of sexual functioning in several dimensions such as desire and orgasm, which predicts a high comorbidity in sexual dysfunctions*. Consistent with this prediction, studies find that female sexual arousal disorder is strongly associated with sexual desire and orgasmic disorders, and rarely appears as an independent clinical entity (Bancroft et al. 2001; Rosen and Leibum 1995). Segraves and Segraves (1991)

found that in a sample of 527 clinical cases from a sexology clinic, only eight women were exclusively diagnosed with sexual arousal disorder. Nobre et al. (2006) found that 43 % of women in clinical sample suffering from one sexual dysfunction also suffered from another (see also King et al. 2007). Hartmann et al. (2002), in another clinical sample, also found high comorbidity and concluded that "female sexual dysfunctions and low desire in particular are not discrete phase disorders, but rather a global inhibition of sexual response." A different study which aimed to identify genetic and environmental factors influencing sexual dysfunctions and which was based on a non-clinical sample concluded that female sexual dysfunctions are best seen as separate entities with some shared etiology (Witting et al. 2009).

(3) *A key prediction of the model is that there will be specific alleles predisposing for each sexual motivation type, and consequently the differences between women in terms of sexual functioning will, to a considerable extent, be accounted for by differences in their genetic make-up*. Consistent with this, Zion et al. (2006) found that individual allelic differences in the dopamine D4 receptor gene (DRD4) contribute to individual differences in human sexual behavior including desire, arousal and sexual function. Another study performed a genome-wide association study on 2.5 million single-nucleotide polymorphisms (SNPs) in 1104 female twins (25–81 years of age) in a population-based register and phenotypic data on lifelong sexual functioning (Burri et al. 2012b). Although no associations at conventional genome-wide level of significance were found, strongly suggestive associations were found. As these associations have been replicated in independent studies, this indicates that these are real associations and not spurious results (Burri et al. 2012a, b).

In the same vein, Burri et al. (2012a), using a sample of 1489 female twins found significant heritability for sexual desire, arousal, lubrication, orgasm, sexual satisfaction, and pain during intercourse. Furthermore, Dawood et al. (2005) in a sample of 3080 Australian women found a high heritability in the capacity of women to experience orgasm (see also Zietsch et al. 2011 and Dunn et al. 2005). Other studies also found substantially heritability in sexual behavior (Dunne et al. 1997; Mustanski et al. 2007; Witting et al. 2009).

It has to be said that heritability is not sufficient for proving the distinct morphs argument. In particular, we would expect that one or more genes should be found which have fairly large directional effects on sexual motivation for the balancing selection position to be better supported. Consistent with this, Burri et al. (2012b) estimate regression slopes in numbers of standard deviation units per each additional copy of the effect alleles that they have identified which ranged from 0.232 to −0.421. These suggest that the presence of a specific allele can have a considerable effect on the sexual functioning of woman. Nevertheless, more research is required to replicate these findings, and identify additional genes and their respective effects on sexual functioning.

(4) *A further prediction of the model is that the sexual functioning of women will be relatively stable during their reproductive years*. For instance, women with alleles that predispose them to low sexual motivation will experience, on average, a low sexual motivation for most of their reproductive years. Consistent with this, in a sample of 4366 Australian women, Smith et al. (2012) found that 68 % of the

participants who experienced one or more sexual difficulties at recruitment, reported having had at least one difficulty again at their 12-month follow-up. Another study of 474 Danish women assessed sexual desire in three 5 year intervals and found that 70 % of the participants experienced no change in sexual functioning (Koster and Garde 1993). Similar results were obtained in a study of Swedish women (Hällström and Samuelsson 1990).

In the same vein, one Danish study asked participants to indicate how their level of sexual desire has changed over the last 5 years (Eplov et al. 2007). Approximately half the women in the age category 25–66 indicated that their sexual desire remained unchanged, while the other half indicated a moderate increase or decrease, with less than 7 % of women indicating a considerable change in their sexual desire. For the 16–24 age group, sexual desire was much more variable, with only 19.6 % of women reporting their sexual desire to have remained unchanged and more than 60 % reporting a moderate or high increase in sexual desire; a finding that reflects the onset of puberty.

In this model, the differences in sexual functioning between women are predominantly due to genetic predispositions that have been optimized by selection forces in ancestral environments.

(5) *Accordingly, differences in sexual functioning (*i.e.*, low and high levels of sexual motivation) will not be limited to one culture, but will characterize most if not all human cultures*. Consistent with this, Laumann et al. (2005) found a high prevalence of sexual dysfunction in women in 29 countries. Different prevalence studies in different countries using different measures have also found a high prevalence of sexual dysfunctions (e.g., Abdo et al. 2004; Goshtasebi et al. 2009; TrÆen and Stigun 2010).

(6) *Moreover, the model predicts that very low and very high sexual motivation types will be rare*. Accordingly, Zietsch et al. (2011) found that almost one fourth of women in their sample reported experiencing orgasm rarely, but only 15 % reported never experiencing orgasm. Similarly, more than one third of women reported experiencing orgasm frequently and very frequently, but less than 5 % reported experiencing orgasm always (see also Lloyd 2005). Moreover, a Danish study, in the age category of 16–44, found that approximately half the women in the sample reported having sexual desire occasionally or rarely, but only 1.5 % reported never having sexual desire (Eplov et al. 2007).

(7) *It is further predicted that the distribution of sexual functioning is left-skewed, as evolutionary forces working on women were stronger on the right end (*i.e.*, very strong sexual motivation) than on the left end of the distribution (*i.e.*, very low sexual motivation)*. Consistent with this, Zietsch et al. (2011) in their study of orgasm found that the frequency of "never" to be higher than the frequency of "always." Similarly, Dawood et al. (2005) found that during sexual intercourse 13.7 % of women in their sample never experienced orgasm, but only 5.3 % experienced always. Unfortunately most prevalence studies do not examine the right tail of the distribution of female functioning (Kaplan and Kruger 2010). Thus, further research needs to test this prediction by examining and comparing the tails of the distribution of different aspects of female sexual functioning.

(8) *If there are two morphs of women, one with low and another with high sexual motivation, then sexual functioning in women needs to follow a bimodal*

distribution, with one peak being at a lower sexual motivation and the other peak at a higher or, what is presently considered, normal motivation. Consistent with this, Zietsch et al. (2011) found that orgasm rates during intercourse, and other forms of sex, followed a bimodal distribution which peaks at "rarely" and "almost always." Similar results were obtained by Dawood et al. (2005) in a different study of orgasmic functioning in women. Prevalence studies of other aspects of sexual functioning do not report the shape of distributions, or they use scales (e.g., a three-point scale) which do not give an adequate picture of the distribution. Thus, future studies need to examine more thoroughly the shape of the distribution of sexual functioning.

(9) *In this model, low sexual motivation reflects variation in sexual functioning rather than a dysfunction of specific mechanisms, which predicts that most women who experience low sexual motivation will not find it to be particularly distressing*. In accordance with this, Shifren et al. (2008), in a sample of 31,581 American women, estimated a prevalence of sexual dysfunction of about 40 %, but they also found that sexual problems associated with personal distress were much less common, reported in about 12 % of women. Another study, based on reported symptoms and behavior, found that 38 % of women had at least one sexual dysfunction, however, only 18 % of women perceived that they had a problem and only 6 % regarded this problem as moderate or severe (King et al. 2007). In the same vein, other epidemiological studies have found that only a small proportion of women reporting sexual problems consider them personally distressing (Bancroft et al. 2003; Öberg and Fugl-Meyer 2005). It has to be said at this point that, because younger women are less likely to have solved the problem of reproduction than older ones, they are also more likely to experience more distress from facing such dysfunctions, which appears to be so (Both et al. 2010; Brotto 2010).

(10) *Last but not least, it is predicted that in post-industrial societies the prevalence of these dysfunctions is in decline*. That is, the equilibrium frequency of low sexual motivation in such a context is much smaller than the actual frequency, which reflects ancestral selection pressures. Consequently, alleles that predispose for low sexual motivation will be under negative selection since women with low sexual motivation will suffer fitness cost in a context where mate choice is not regulated. This prediction remains to be tested by future research.

Conclusion

To conclude, there has been considerable research on sexual functioning, providing pieces of the puzzle over the high prevalence of sexual dysfunction in women; this paper employed an evolutionary framework in order to put these pieces together in an attempt to address the question why selection has favored considerable variation in the sexual functioning in women.

Women's sexual functioning is a complicated phenomenon and there are many factors that contribute to it. For instance, poor nutrition, high level of stress, health problems, and relationship problems are likely to have a negative impact on sexual motivation. Cultural factors may also have an effect. For instance, in Middle Eastern

cultures where women do not choose their mates, they may be less sexually aroused by their partners and will thus report greater sexual dysfunction. Cultural differences in the social acceptability of female sexual interest, pleasure, and arousal, further contribute to cultural differences in women's reporting. These factors are likely to interact with a predisposition for low sexual motivation amplifying the negative consequences for women. For instance, a relationship problem may be more difficult to overcome in the presence than in the absence of a sexual dysfunction.

This paper does not claim to provide a full account of the various factors and their complex interactions which contribute to the sexual functioning of women. It aims, however, to provide an evolutionary insight, namely that the mechanisms involved in this domain, have been shaped by selection forces in a context where the female sexuality was controlled, resulting in considerable variation in sexual functioning, some of which is not optimal for a setting where the female sexuality is less constrained.

Overall, by incorporating evidence from the anthropological and historical records, the argument was made that in an ancestral context there were fitness advantages for women who had low sexual motivation and for women who had high sexual motivation, and consequently, balancing selection had favored both female morphs in the population. The considerable discrepancy in the way of life between ancestral pre-industrial and modern post-industrial societies has resulted in low sexual motivation being considered dysfunctional in the latter. Future research needs to advance this hypothesis further and to explore its implications in the treatment of sexual dysfunctions. Future research needs also to examine whether low sexual motivation actually decreases or how much it decreases women's fitness in a post-industrial context.

Acknowledgments The author would like to thank Maria Hadjimarkou for her feedback during the preparation of this manuscript. The author would also like to thank James Roney and two anonymous reviewers for their constructive feedback which enabled the improvement of this work.

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