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The Science of Sex Appeal: An Evolutionary Perspective

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Growing evidence shows that features we find attractive in members of the opposite sex signal important underlying dimensions of health and reproductive viability. It has been discovered that men with attractive faces have higher quality sperm, women with attractive bodies are more fertile, men and women with attractive voices lose their virginity sooner, men who spend more money than they earn have more sex partners, and lap dancers make more tips when they are in the fertile phase of their menstrual cycle. This paper highlights recent evidence showing that the way we perceive other people has been shaped by our evolutionary history. An evolutionary approach provides a powerful tool for understanding the consistency and diversity of mating preferences and behaviors across individuals and cultures.

Keywords: evolutionary psychology, facial attractiveness, body configuration, voice, menstrual cycle, muscularity, body fat, dishonest signals

A cursory glance at the women featured in popular men's magazines, such as *Maxim* or *Playboy*, suggests that men are attracted to young women with smooth skin, long soft hair, large eyes, slender bodies, long legs, curved hips, large pronounced breasts, rounded buttocks, and flat stomachs (Spitzer, Henderson, & Zivian, 1999; Voracek & Fisher, 2002). In contrast, a reader glancing through *Cosmopolitan* would conclude that women are attracted to tall athletic men with moderately muscular arms and legs, broad shoulders, little body fat, square and powerful-looking jaws, and toned abdominal muscles (e.g., Frederick, Fessler, & Haselton, 2005). Notably, however, some body types are rarely represented. Women's magazines almost never feature men who are very short, elderly, and fat, with wrinkly skin, open sores and wounds, and mouths with stained and missing teeth.

The pressure to be attractive can leave many people feeling dissatisfied with their appearance (Peplau et al., 2009; Frederick, Forbes, Grigorian, & Jarcho, 2007), and across cultures and history, men and women have devised a wide variety of techniques to enhance their attractiveness (Etcoff, 1999). Corsets give women the appearance of narrower waists relative to their hips and modern gyms allow men to enhance their muscularity and shoulder width. Cosmetic surgery enables women to create the appearance of youthful faces, large shapely symmetrical breasts, narrow waists larger buttocks, and more symmetrical faces. Human growth hormone and steroids enable people to grow taller and stronger. Cosmetics, such as make-up, enable people to cover blotches, wrinkles, and imperfections in the skin.

Why do so many people spend so much time, effort, and money on their appearance? Why do we find some people more attractive than others? If beauty is only skin deep, why should it matter how people look? What follows is a review of the science of sex appeal, targeting recent findings that illustrate the conceptual and heuristic value of an evolutionary perspective.[1] We first briefly outline how evolution shapes the way we process information about other people, and then focus on why we find certain faces, body types, and voices appealing. We show how an evolutionary perspective enables us to understand and predict ways that women's preferences for some of these traits shift across the menstrual cycle. We conclude with a discussion of how individuals have developed cultural and technological innovations to enhance certain aspects of their appearance.

The Impact of Evolution

It is important to understand that we do not experience the world or other people directly. Rather, our experience is a byproduct of sensory input acting on the nervous system. Our sensory receptors are evolved neurological mechanisms that convert mechanical, chemical, thermal, or electromagnetic energy into nerve impulses. These nerve impulses in turn activate evolved parts of the brain that translate these impulses into experience.

The age-old question, "if a tree fell over in the woods and no one was there to hear it, would it make a noise?" has a clear and definitive answer from a neurobiological perspective. No doubt a felled tree would produce intense air borne vibrations, but in order to be "heard" or to make a "noise" these vibrations would have to impinge on an ear and trigger nerve impulses that activate relevant

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[1] In biological terms, traits that are more typical of women are considered "feminine" whereas traits that are more typical of males are considered "masculine." For example, testosterone "masculinizes" men's faces by making their jaws squarer, and estrogen "feminizes" women's faces by making their jaws more rounded.

parts of the auditory cortex. Although we take sound for granted, sound is not an inherent feature of the world. Sounds only exist in your head.

Why is sugar sweet? Contrary to the impression it creates when placed on your tongue, sweet is not an inherent property of sugar. Just like sound, the experience of sweet is an evolved property of the nervous system (Barash, 1979). Sugar is a good source of calories. Organisms that developed receptors and neurological mechanisms that enabled them to experience foods containing sugar as sweet/pleasant had an adaptive advantage in being able to identify and preferentially exploit food sources that were rich in calories. For similar reasons, if vultures, hyenas, and other carrion eaters could talk, they would be the first to tell you that foul odor is not an inherent property of rotting flesh.

Why is being kicked in the groin an excruciatingly painful experience for men? Unlike women whose gonads are embedded deep inside the body, testicles migrate down through the body cavity during embryonic development and usually wind up outside the body in a thin, unprotected scrotal sack. As a consequence, descended testicles are inherently more vulnerable than ovaries. Males with descended testicles were selected during the course of evolution to develop receptors and neural mechanisms that mediate the experience of pain in response to testicular insults, which in turn prompts each successive generation of males to 1) learn to avoid situations that put the testicles at risk, and 2) refrain from engaging in behaviors that might endanger the testicles. In other words, men have evolved to behave in ways that maintain the integrity of the testicles and this effect is mediated in part by heightened sensitivity to testicular pain (Gallup, Finn, & Sammis, 2009).

All of these examples are linked by a common theme. When there were recurrent adaptive problems, organisms that evolved solutions to these problems had genes that became better represented in future generations. Evolutionary psychologists hypothesize that many such evolved systems exist and that these systems respond flexibly in response to changing environmental inputs, ecologies, and internal states (e.g., Barrett & Kurzban, 2006; Pinker, 2002). Many of these systems serve clear adaptive functions, such as entering puberty earlier or later depending on whether ecological conditions are harsh or stable, rapidly acquiring fears of snakes and dangerous predators, generating language for the purposes of communication, seeking out food when calorie stores run low, and recognizing who is a kin member and discouraging incest with close genetic relatives (for an overarching summary see Buss, 2005).

What follows is a representative review of sex appeal designed to target recent findings that illustrate the value of an evolutionary perspective.

Attractive Faces

Many people think facial attractiveness is a byproduct of experience and cultural influences. According to this view attractive faces and sex appeal are learned social constructions (see DeLamater & Hyde, 1998). Are attractive features simply a byproduct of how people are educated and raised?

Our perception of faces often prevails in spite of our experience. Growing evidence shows that how people rate faces is largely independent of their gender, culture, ethnic group status, sexual orientation, and age (see Thornhill & Gangestad, 1999). There is a high degree of cross-cultural consensus about which faces are attractive. Not only do Caucasians rate Asian faces much the same way Asians do, but the same is true for the way Asians rate Caucasian faces (Cunningham Roberts, Barbee, Druen, & Wu, 1995; for a meta-analysis see Langlois et al., 2000). Even neonates without the benefit of prior experience or socialization spend more time looking at photos of faces that adults find attractive (Ramsey, Langlois, Hoss, Rubenstein, & Griffin, 2004).

Recent discoveries show surprising links between faces and underlying differences in health, vitality, and fertility. By sampling photographs taken from old high school yearbooks and matching them with obituary records, Henderson and Anglin (2003) discovered that both men and women with faces that contemporary college students rated as being attractive lived longer. Researchers are currently attempting to isolate the degree to which facial attractiveness is linked to health, which aspects of health it relates to, and how consistent the link is (Weeden & Sabini, 2005; Rhodes, 2006; Thornhill & Gangestad, 2006).

Faces also contain cues to fertility. Soler et al. (2003) took facial photos and semen samples from male college students. The semen samples were assayed for sperm count, sperm motility, and sperm morphology to generate a composite index of sperm quality. A number of women who did not know these men were asked to rate the photos for attractiveness. The researchers discovered that how the women rated the men's faces were correlated with the semen assay results. Men with faces that women found attractive tended to have significantly more fertile, higher quality sperm. There are several intriguing explanations for this pattern. Attractive men may garner more interest from women, which may boost their testosterone and sperm production, or men who are generally more robust and healthy overall may have more attractive faces and enhanced ability to produce sperm.

Even intelligence and semen quality may be related. In an archival sample of 425 Army veterans, Arden, Gottfredson, Miller, & Pierce (2009) found small, but significant positive correlations between general intelligence and several important parameters of sperm quality: sperm concentration, sperm count, and sperm motility. It turns out that people with attractive faces also tend to have higher IQ scores (Zebrowitz, Hall, Murphy, & Rhodes, 2002).

The way men rate facial attractiveness in women predicts estrogen levels and female reproductive health (Law-Smith et al., 2006). Faces can contain cues to underlying genetic resistance to disease. The Major Histocompatibility Complex is an important set of genes that help code for the development of the immune system. Being heterozygous at this loci—that is, having copies of different alleles (genes) rather than having multiple copies of the same alleles—provides resistance to a wider variety of potential parasites and threats to the immune system. Consistent with an evolutionary perspective, men who are heterozygotic at the Major Histocompatibility Complex are judged by women as being more attractive (Roberts et al., 2005). Both men and women with attractive faces also show fewer subtle morphological deviations from bilateral symmetry, which is a ubiquitous measure of health and fitness (Grammer & Thornhill, 1994).

A person's face even conveys information about their body and their behavior. Given the potential dangers of failing to detect a physically powerful rival, Sell et al. (2009) reasoned that individuals would be able to accurately gauge a person's strength based

on their facial features. Consistent with this hypothesis, they found that participants could judge the measured physical strength of Bolivian horticulturists, Andean pastoralists, and U.S. college students, just by seeing their faces.

This research extends the findings of Shoup and Gallup (2008) who found that men's faces were cues to their body morphology, grip strength, and sexual history. Using facial photos of male college students that were cropped at the neck, those with faces that women rated as attractive had more pronounced wedge shaped torsos (broad shoulders and narrow hips), a masculine[1] feature many women prefer. In addition, these same males had stronger grip strength scores (see also Fink, Neave, & Seydel, 2007; Sell et al., 2009), and more sex partners. Paralleling these findings, Brewer, Archer, & Manning (2007) report that women with attractive faces tend to have more accentuated hour glass figures (narrow waists and broad hips), a feminine feature men prefer.

A recent study by Jokela (2009) based on an archival sample of high school yearbook photos and follow-up surveys from over 10,000 people who graduated in 1957, shows that attractiveness is, in fact, related to reproductive success. More often than not people with more attractive faces have more children. Thus, the reason there is good consensus as to which faces are attractive is because faces contain embedded features that are honest biological signals of reproductive fitness. As a consequence, the human nervous system has been shaped by natural selection in ways that prompt us to experience the faces of reproductively viable people as more attractive. Why? Evolution is not about survival, it is about the perpetuation of genes. People who mated preferentially with individuals with attractive faces had a better chance of leaving healthier, more reproductively viable descendants. As a consequence, their genes became better represented in subsequent generations. Attractiveness is not an inherent feature of a person's face. Just like foods that taste good, attractive faces are an evolved property of the human nervous system.

Faces also vary in other domains. Some people have mature faces others have likable faces, trustworthy faces, or faces that convey a sense of power and leadership. Without revealing the source or identity of the pictures, Rule and Ambady (2008) asked college students to rate photographs of the chief executive officers of the 25 highest and 25 lowest ranking companies listed in the Fortune 500. Ratings of power (competence, dominance, and facial maturity) and global ratings of leadership were both significantly related to corporate profitability, each accounting for about 10% of the differences in company profits. For multibillion dollar corporations this translates into earning differences of hundreds of millions of dollars on an annual basis.

Body Configuration

Attractiveness is also influenced by what is going on below the neck. There are reliable sex differences in body configuration (technically, sexually dimorphic differences). Women tend to have narrower waists and broader hips that often create the impression of an hour-glass figure, whereas men tend to have broader shoulders and narrower hips that lead to wedge shaped torsos. These sex differences in body configuration begin to emerge during puberty, and can be easily measured and converted into waist-to-hip ratios (WHRs) and shoulder-to-hip ratios (SHRs).

Waist-to-Hip Ratios

Women with low WHRs (narrow waists and broad hips) are consistently rated by men in many cultures as more attractive, with optimal WHRs being about .7 (Singh, 1993). Large samples of *Playboy* models (Tovee et al., 1997) and female film stars (Voracek & Fisher, 2006) both converge on this value, with each showing average WHRs of about .68. In a recent study, men who were born blind or developed blindness later in life were presented with mannequins varying in WHR. Even those who were born blind preferred the shape of the low WHR, indicating that visual input is not necessary to develop or maintain this preference (Karremans, Frankenhuis, & Arons, 2010).

Platek and Singh (2010) have uncovered neurobiological evidence for the effects of female body configuration on interpersonal attraction. Their research was based on a unique sample of before and after photos of women who underwent cosmetic reconfiguration surgery. By using patients who had fat transplanted from other body parts to accentuate their WHRs, it was possible to make before and after comparisons while holding body mass constant. Using functional MRI to compare and contrast the way men responded to pre- and postsurgical images of these women, the authors found compelling evidence for unique activation of neural reward centers in men's brains when they saw the postsurgical images. In another study using these images, Singh, Dixson, Jessop, Morgan, & Dixson (2010) discovered that men found these surgically altered bodies with lower WHRs more attractive using community samples in such diverse areas as Cameroon, Indonesia, and Samoa.

Why Do People Find Women With Hour Glass Figures Attractive?

By now it should come as no surprise that women with low WHRs are more reproductively viable. They ovulate more often (Jasienska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004), have more regular menstrual cycles (Van Hoof et al., 2000), and are more likely to conceive as a result of artificial insemination (Zaadstra et al., 1993) and in vitro fertilization (Wass, Waldenstrom, Rossner, & Hellberg, 1997). Women with low WHRs are also healthier. They have a lower risk of heart disease, stroke, diabetes, gall bladder disease, kidney disease, and various cancers (see Singh & Singh, 2006).

An hour glass figure serves as an important reproductive signal in other ways (Hughes & Gallup, 2003). The configuration of a woman's waist relative to her hips is an indication of whether she is pregnant. The abdominal enlargement that occurs as pregnancy progresses leads to the loss of an hour glass figure. Since impregnation produces hormonal changes that preclude reimpregnation, genes being carried by men that mated preferentially or exclusively with pregnant women would not have been well represented in subsequent generations. Broad hips are also indicative of underlying pelvic skeletal morphology that enables women to undergo relatively unencumbered childbirth. Caesarian sections were not an option during human evolutionary history. Women who were unable to deliver their babies perished, along with their babies, effectively eliminating their genes and those of their mate's from the gene pool.

Evidence also shows that the configuration of a woman's waist relative to her hips may be an index of the availability of special fat stores (Lassek & Gaulin, 2008). Lower body fat on women's hips and buttocks can be distinguished from upper body fat by the presence of more gluteofemoral fat consisting of unique long-chain polyunsaturated fatty acids that are important for neurological development. Using WHRs to index the ratio of upper to lower body fat as a means of estimating the availability of these "brain building" resources, Lassek and Gaulin found that women with more gluteofemoral fat (i.e., lower WHRs) had significantly higher cognitive test scores, and so did their children. Although hardly conclusive it is interesting that people who were breast fed as infants tend to have higher IQ scores (Mortensen, Michaelsen, Sanders, & Reinisch, 2002), an ostensible benefit of the presence of these fatty acids in mother's milk.

Finally, it is important to acknowledge that preferences for WHR do not always center on .70 across history and all cultures (e.g., see Sugiyama, 2004; Swami, Jones, Einon, & Furnham, 2009). For example, a recent analysis of Reuben's paintings shows that women on average had a WHR of .78, not .70 (e.g., Swami, Gray, & Furnham, 2007). One possible solution to this conundrum suggested by Cashdan (2009) is that in harsh ecological conditions, women with higher WHRs might be preferred because the testosterone levels needed to create higher WHR enable women to better compete for and obtain resources and status. In harsh ecological conditions, body types that indicate an ability to obtain scarce resources may be valued more highly than body types that indicate slightly better fertility.

Body Fat

Make no mistake about it, fat is highly adaptive. Because food was not always plentiful in the ancestral environment, the capacity to store energy in the form of body fat enabled organisms to take advantage of periods where food was plentiful in order to bridges times when it was scarce (i.e., periods of feast or famine). Despite the preoccupation many women in the Western world have with maintaining a slender figure, there is growing evidence that generalized stores of body fact are critically related to female reproductive function. Research reviewed by Rose Frisch (2008) has shown that the onset of puberty in girls is largely independent of age and requires reaching a point where approximately one sixth (17%) of their body weight is represented by body fat. This appears to be the reason overweight little girls often begin menstruating sooner. But it is not until body fat stores reach about one quarter of a woman's body weight that they actually become fertile. This may be one of the reasons why overweight (but not obese) women go through menopause later than their normal weight counterparts. Extreme weight loss due to exercise and/or starvation and the resulting depletion of body fat often leads to infertility in women, as in the case of anorexia nervosa. Adequate stores of body fat may be particularly valuable to women during pregnancy and lactation because these conditions can increase caloric demands by 10% to 15%, respectively (Dufour & Sauther, 2002).

Perhaps one of the biggest mysteries in evolutionary psychology is the preference for thinness in industrialized societies. A recent cross-cultural study of 41 sites across 10 world regions found that thinness was preferred in all industrialized countries studied, and reported exposure to Western media only explained a small percentage of the variation in preferences. In contrast, women with relatively high levels of body fat were rated most attractive in rural nonindustrialized sites, such as rural Malaysia (Swami et al., 2010).

Following Ford and Beach's (1951) ethnography documenting widespread preferences for plumpness in 81% of nonindustrialized societies, decades of research has documented cross-cultural, temporal, and individual differences in attitudes toward obesity and body weight. In less socioeconomically developed societies where resources are not as plentiful, plumpness is linked with psychological traits of fertility, sexuality, and attractiveness. In many of these societies, extreme weight gain is culturally acceptable for women, particularly in the period preceding marriage. In parts of Africa and the South Pacific adolescents from elite families reside in "milking huts," where they are fed high-fat diets in order to become properly plump in preparation for marriage (see Swami et al., 2010).

A recent paper illustrates the role of culture and context when it comes to body fat (Tovee, Swami, Furnham, & Mangalparsad, 2006). Traditionally, South African Zulus find heavier bodies more attractive, whereas Whites in the U.K. prefer thinner bodies. In their study of South African Zulus who moved to the U.K., they found that these Zulus adopted preferences that were much more similar to those of individuals living in the U.K. than in South Africa. These findings suggest that preferences for some traits, particularly body fat, are malleable based on changing social, financial, and ecological contexts.

Some body fat may be beneficial. Research at the Centers for Disease Control has shown that individuals who are overweight (BMI = 25–29), but not obese, actually have the lowest mortality rates (Flegal, Graubard, Williamson, & Gail, 2005). Although the exact nature of the link between body fat and health is controversial (Rigby, 2006; Campos, Saguy, Ernsberger, Oliver, & Gaesser, 2006), one thing is clear: the extreme thinness prized in many Western cultures is a recent phenomenon and not inherently healthier than being in the overweight category (for reviews see Campos, Saguy, Ernsberger, Oliver, & Gaesser, 2006; Flegal et al., 2005). In fact, being thin and emaciated carries a far greater risk of reproductive impairment for women than being overweight—but not obese (Frisch, 2008).

The other point to consider in the context of the contemporary aversion to body fat among women in the Western world is that obesity can be thought of as a pregnancy mimic. Because of the inevitable abdominal enlargement that accompanies pregnancy and obesity, each of these conditions involve the gradual loss of an hour glass figure. Moreover, just as pregnancy leads to hormonal changes that arrest fertility, the same is true for obesity (Frisch, 2008). Thus, under conditions nowadays in which food is plentiful, women's preoccupation with dieting and weight loss may be driven in no small part by an unconscious attempt to minimize any signs of appearing pregnant.

Breast Enlargement

The attraction that many men have to enlarged breasts may be a consequence of the connection between female body fat and reproduction. Breast enlargement beginning at puberty, that is independent of a woman's lactational status, is largely due to the localized accumulation of adipose tissue or fat in the breasts. Life

span developmental changes in the shape and configuration of the breasts are correlated with changes in a woman's capacity to ovulate, and as a consequence enlarged breasts may have evolved to compensate for the loss of ovulatory cues by signaling ample energy stores and ovulatory potential (Gallup, 1982). Indeed, recent evidence shows that women with large breasts actually have elevated levels of salivary estradiol and higher fertility (Jasienska et al., 2004). The value of breasts as a cue to fertility changes as women age and nurse children, which cause breasts to droop and become less firm. Research in the United States shows that women tend to become less satisfied with their breasts as they age, and the effects on men's satisfaction with their partner's breasts are reciprocal (Frederick, Peplau, & Lever, 2008).

Shoulder-to-Hip Ratios

Broad shoulders and narrow hips in men are the sexually dimorphic counter point to an hour glass figure in women. Just as men rate females with narrow waists and broad hips as more appealing, women rate males with wedge shaped torsos as more attractive (Dijkstra & Buunk, 2001), and consistent with the thesis developed in this paper, SHRs signal various embedded dimensions of fitness. Men with broad shoulders and narrow hips (high SHRs) have higher testosterone levels (Kasperk et al., 1997). Body configuration is also related to physical prowess. Men with high SHRs tend to be stronger and more aggressive in high school (Gallup, White, & Gallup, 2007). Just as for women who have hour glass figures, Hughes, Dispenza, & Gallup (2004) found that men with more accentuated wedge shaped torsos began having sex at earlier ages and have more sex partners.

Muscularity

Frederick and Haselton (2007) proposed that women have an evolved propensity to attend to overall levels of male physical prowess. Muscularity requires extensive calories and testosterone to build and maintain. Because testosterone compromises immune function and increased muscle mass entails high energy demands, muscularity and other masculine features may function to signal superior health and immune system competence. The ability to build greater muscle mass is partially heritable, suggesting that advantages associated with muscularity can be passed onto offspring (see Frederick & Haselton, 2007). Looking across primate species, humans show an exaggerated sex difference in overall muscle mass and physical strength, suggesting that muscle mass provided an advantage to ancestral males in terms of hunting, acquiring resources, and in male-male competition (Lassek & Gaulin, 2009; Puts, 2010). Many men in the United States, Ukraine, and Ghana want to be more muscular, and male college students desire greater muscularity in order to be more attractive to women and more successful in competitions with males (Frederick & Buchanan, et al., 2007).

In support of the hypothesis that muscularity is attractive to women, Frederick and Haselton (2007) found that muscular male college students reported more sexual partners and short-term affairs, and that women's most recent short-term sexual partner was more muscular than their committed sex partner. Additionally, they introduced the "inverted-U hypothesis of masculinized traits," which states that women will experience less attraction to individuals with low levels of masculinity (because it is a cue of lower testosterone and dominance) and also very high levels (because high levels of testosterone can impair health, as well as produce unpredictable, volatile, aggressive behavior which may pose a risk to the woman herself).

One problem, however, is that much of the existing psychological research on male attractiveness is limited to Western contexts. To remedy this problem, Frederick, Swami, and the 56 members of the International Body Project (2010) examined preferences for muscularity in 41 community and college samples in sites across 26 countries. Participants rated a series of images of male bodies that varied systematically in muscularity or body fat. Patterns of preference for muscularity were significantly more prevalent than preference for body fat. In almost all of the testing sites, women preferred men who were more muscular than average and men wanted to be more muscular than average (in the few remaining sites, the effects were in this same direction but failed to reach statistical significance). In every culture without exception, there was a clear inverted-U association between muscularity and attractiveness: very low and very high levels of muscle mass were not preferred. Notably, however, there were significant cross-cultural differences in the degree of muscularity that women found attractive. Exposure to Western media, however, showed only weak relationships to these preferences in most settings. This research suggests that male muscularity may be an important cue of attractiveness, and that local ecological factors can shape the degree to which is it important.

Skin

The loss of body hair is a distinguishing feature that sets humans apart from other primates. There are any number of reasons why this may have happened. One possibility was the need to more effectively cool an ever expanding brain (Falk, 1990), so the surface area of the body could serve as a radiator to keep the brain from overheating. There may also have been selective pressure to eliminate body hair as a refuge for parasites (Pagel & Bodmer, 2003). Indeed, there is suggestive evidence that the incidence of infestation by human public lice has decreased along with the recent increase in pubic hair removal by women in some parts of the world (Armstrong & Wilson, 2006).[2] The widely acknowledged pleasant and even erotic properties of skin-to-skin contact made possible by the loss of body hair could likewise have reinforced the development and maintenance of long-term pair bonds between mates and between mothers and infants as well. Finally, exposing smooth unblemished skin may have become a signal or advertisement for health and reproductive viability.

Skin quality can be an important cue for health and genetic adaptations to resist infection (Symons, 1995; Sugiyama, 2005). The presence of blotches, open wounds and sores, and insects are visible signs of current disease and parasitic infection. Many diseases or parasites can produce yellowing of skin, and clear skin

[2] Pubic hair removal is a peculiar anomaly from an evolutionary perspective. There is reason to believe that human pubic hair evolved as a salient puberty signal and a means of preserving sex pheromones. Since effective body hair removal was not an option during most of human evolutionary history, men that mated preferentially with females who did not have pubic hair would have been pedophiles.

denotes an absence of communicable diseases. One can imagine the benefits of coming equipped with a system that inhibits sexual arousal when encountering people covered with infected boils that are oozing and bursting with puss, rather than learning this primarily through trial and error, associative learning, or socialization. The emotion of disgust may have evolved initially because it served as a motivational system that prompts people to avoid others that are teeming with potentially deadly parasites and bacteria (Fessler & Haley, 2006).

Gangestad, Haselton, and Buss (2005) examined how parasite prevalence across cultures influences different mating preferences. If physical attractiveness is a cue to health and resistance to parasites, then high parasite prevalence should evoke a stronger preference for physical attractiveness when choosing a mate. Consistent with this prediction, physical attractiveness was ranked as more important in a mate in societies where parasites were more prevalent, even after controlling for a variety of other variables.

Skin quality can also provide an index to age and therefore fertility (Symons, 1995; Sugiyama, 2005). The capacity to produce offspring decreases as men and women age, and this capacity diminishes much more rapidly for women. Given the association between age and fertility, one would expect preferences for smooth, unwrinkled skin, and that this preference would be stronger for female bodies than for males. Evolutionary theory would suggest, however, that this preference would be balanced with other cues besides youth when choosing a partner, such as ability to obtain resources, parenting ability, and the social influence and status the person has, as well as one's own attractiveness and ability to attract mates (Pillsworth, 2008).

Voice Attractiveness

There are two approaches to the study of attractiveness. The one featured in this paper involves looking at different traits as evolved signals for important biological information. The other approach focuses on proximate rather than ultimate mechanisms, and attempts to identify particular features such as pitch that distinguish attractive from less attractive voices (e.g., Feinberg, Jones, Little, Burt, & Perrett, 2005), or bilateral symmetry that contributes to attractive faces (e.g., Rhodes, 2006).

Prior to the invention of artificial illumination, sound was our principle means of communication at night, and this was undoubtedly one of the reasons we developed spoken language based on sounds as opposed to sign language based on gestures (Gallup & Cameron, 1992). Talking on the telephone approximates what it used to be like to have a conversation at night because on the telephone you do not see the person you are speaking with. The evidence shows that just like a person's face, the sound of a person's voice functions as a medium for the transmission of biologically relevant information. When you answer the phone, even if you do not know who it is, as soon as the caller starts to speak you usually know 1) whether it is a male or a female, and 2) whether it is an adult or a child.

People who participate in much of the research described below are typically asked to speak into a microphone and simply count from 1 to 10 as their voice is recorded. This holds what they say constant and it keeps the content neutral. That way, when listeners are asked to rate these recordings they will not be responding to what subjects say, but rather to how they say it.

The Sound of Symmetry

The extent to which features on one side of the body match those on the other has been taken as evidence for the ability to resist minor insults and perturbations that occur during embryological development (Livshits & Kobyliansky, 1991). No one shows perfect bilateral symmetry, but there is growing evidence that as random deviations from bilateral symmetry increase, known as fluctuating asymmetry (FA), health and fertility are compromised (for a recent review see Gallup, Frederick, & Pipitone, 2008).

In the initial voice study on this topic seven representative features (e.g., finger length, wrist diameter) were measured on each side of the body and compared in a sample of male and female undergraduates (Hughes, Harrison, & Gallup, 2002). Each student's voice was also recorded as they counted from 1 to 10. When other students who did not know the speakers were asked to rate their voices, it was discovered that ratings of voice attractiveness were inversely proportional to the magnitude of fluctuating asymmetry. In other words, people with attractive voices tended to show fewer deviations from bilateral symmetry as an ostensible consequence of being better able to withstand prenatal and developmental insults/perturbations, as well as parasitic infections.

Just as attractive voices signal subtle, rarely noticed differences in fluctuating asymmetry that bear in important ways on health and fertility, the same is true of faces. People with faces that are more symmetrical are also rated as being more attractive (Perrett et al., 1999).

Voice, Body Configuration, and Sexual Behavior

In another study voice samples were taken from college students, their SHRs and WHRs were measured, and they were invited to complete an anonymous survey about their sexual behavior (Hughes, Dispenza, & Gallup, 2004). Men with attractive voices had more accentuated wedge shaped torsos (higher SHRs), and women with attractive voices likewise had more accentuated hour glass figures (lower WHRs). Both men and women with attractive voices also reported having sex at earlier ages, more sex partners, and were more likely to have engaged in sexual infidelity. Some of these effects were quite pronounced. Ratings of voice attractiveness accounted for almost 25% of the variance (i.e., individual differences) in number of sex partners among the female college students in this study. Who would have known that the mere sound of a person's voice would be related to their sexual behavior?

Voice and Fertility

Women's voices not only change with the onset of puberty, they also vary as a function of where they happen to be in their menstrual cycle. In a recent longitudinal study, multiple voice samples were taken from females at different points in their cycle (Pipitone & Gallup, 2008). Ratings of voice attractiveness peaked for samples collected during the ovulatory phase, which is the point of maximum fertility. On the other hand, there were no cycle dependent voice changes for women using hormonal contraceptives as they do not show the same hormonal fluctuations.

Apicella, Fienberg, and Marlowe (2007) found that voice was associated with self-reports of reproductive success among male hunter-gatherers, where men with lower pitch voices claimed to have more children. Although suggestive of a link between fertility and voice, without independent evidence of paternity it remains possible that men with more masculine voices merely think they have more children and/or they may be more prone to exaggerate claims of paternity. Puts (2005) has shown, however, that men with low pitch voices tend to be preferred as short-term mates when women are in the ovulatory phase of their menstrual cycle.

Given the foregoing, it should come as no surprise that men with attractive voices also have more attractive faces (Saxton, Caryl, & Roberts, 2006). But what is particularly interesting about this effect is that the relationship between attractive voices and attractive faces is dependent upon the maturational/hormonal status of the listener; the effect only holds when listeners are post-pubertal women (adolescent and adult females). Ratings of the same men's voices by prepubescent girls failed to predict independent ratings of the speaker's faces. Thus, both the perception as well as the production of voice would appear to be subject to hormonal influences.

Voice, Finger Digit Ratios, and Strength

Voices not only predict facial appearance and body configuration, they reveal other differences. In addition to attractiveness, voices can be rated along any number of dimensions (e.g., approachability, maturity, sexiness, intelligence, dominance). Hughes, Pastizzo, and Gallup (2008) found that women with voices rated as sounding more dominant could be distinguished from others based on their finger morphology. The length of the second digit or index finger relative to the fourth digit or ring finger (expressed in terms of finger digit ratios: 2D/4D) appears to be influenced by exposure to different levels of sex hormones during embryological development. People exposed to high levels of testosterone during prenatal life tend to have ring fingers that are longer than their index fingers (low 2D/4D), whereas exposure to high levels of estrogen has the opposite effect, producing high 2D/4D (Manning, 2002). Hughes et al. discovered that female college students with dominant sounding voices had significantly lower, more masculine finger digit ratios indicative of greater prenatal exposure to testosterone. Not unrelated to these findings, Sell et al. (2010) recently found that men's voices contain cues of physical strength.

To summarize, the sound of your voice conveys information about what happened to you during prenatal development. It also says something about your gender, your age, your body configuration, your hormonal statues, your strength, your sexual behavior, whether you are on birth control pills and if not, where you are in your menstrual cycle.

The fact that the human voice is such a rich source of reproductively relevant information can be used to make a distinction between "blind dates" and "deaf dates." A blind date is a date sight unseen. Whereas a deaf date would be a date sound unheard. The emerging evidence would suggest that before you agree to a blind date it might be prudent to have a telephone conversation with that person first. Indeed, the growing popularity of Internet dating may also make a telephone conversation an important element in the decision making process about dating a person you have never met.

The Menstrual Cycle

In many species when females ovulate they enter estrus, a period of heightened interest in or receptivity to sex. In such species, females often mate preferentially with males displaying costly traits linked to testosterone or dominance status (for a review see Thornhill & Gangestad, 2008). The evolutionary logic behind this preference is straightforward. When females are most likely to conceive, they have been selected to show increases in preferences for individuals with traits that are cues to underlying genetic benefits that can be passed on to offspring. Unlike chimpanzees, human females do not exhibit obvious changes where their genitals enlarge dramatically during estrus. Evolutionary psychologists, however, have tested whether there are other more subtle cues of ovulatory status, and whether women's preferences for traits associated with testosterone, status, and general robustness are strongest when they are in the ovulatory phase of their cycle.

One function of these shifts may be to motivate women to seek out a short-term sexual partner who can pass on advantageous traits to their offspring, particularly if their current long-term partner does not possess these traits. In a series of studies, researchers found that women with dating partners experience increased sexual desire for other men when ovulating, but this occurred primarily for women whose partners were relatively less attractive. In parallel, less attractive men were more likely to engage in loving and jealous mate guarding behaviors when their partners were ovulating, suggesting that they were responding to cues related to the women's fertility status (Pillsworth & Haselton, 2006; Haselton & Gangestad, 2006).

Changes in women's sexual motivations can have interesting effects on women's self-ornamentation. In one study, women were photographed when they came into the laboratory during the high and low fertility phases of their menstrual cycles. Independent judges, blind to the women's fertility status, rated their photos and indicated that women were trying to look more attractive when they were in their fertile phase. The effect was stronger the closer women were to the day of ovulation. One factor driving these results is that women in committed relationships are more likely to show more skin and to wear miniskirts when they are ovulating (Haselton, Mortezaie, Pillsworth, Bleske, & Frederick, 2007).

In a landmark study, Geoffrey Miller and his associates (Miller, Tybur, & Jordan, 2007) found that lap dancers made 80% more tips on average during the fertile phase of their menstrual cycle than when they were menstruating. Those that were normally cycling earned approximately $335 per 5-hour shift when ovulating, $260 in the luteal phase, and $185 when menstruating. Naturally cycling lap dancers also made more tips regardless of where they were in their cycle compared to those taking hormonal contraceptives. Moreover, while the lap dancers were aware of differences in the amount of money different dancers made, as well as day to day fluctuations in their own tips, none realized that their earnings were related to their menstrual cycle. Why did their income increase so dramatically when they were ovulating? The possibilities include that the women were more sexual, they had greater energy, and/or they had changing vocal, physical, and olfactory cues that men found more appealing during high fertility.

As Miller's study suggests, there is evidence that menstrual cycle variation in fertility can have important, albeit subtle effects on how women are perceived. Roberts et al. (2005) photographed women at different points during the menstrual cycle and discovered that their faces were rated more attractive when they were in the ovulatory phase. Likewise, women's WHRs become more accentuated (Kirchengast & Gartner, 2002), and breast asymmetries diminish (Manning, Scutt, Whitehouse, & Leinster, 1997) during ovulation. Female body odor (Singh & Bronstad, 2001) as well as vaginal odor samples (Doty, Ford, Preti, & Huggins, 1975) are also rated as being more pleasant and, as already noted, voice recordings taken during midcycle are more attractive (Pipitone & Gallup, 2008). Cycle dependent changes in attractiveness such as these likely functioned in the ancestral environment to synchronize insemination with ovulation as a means of increasing the chances of impregnation.

Kissing

Kissing between romantic partners occurs in over 90% of human societies (Eibl-Eibesfeldt, 1970) and appears to be part of an evolved human courtship strategy (Hughes, Harrison, & Gallup, 2007). Using a large questionnaire administered to over 1,000 college students, Hughes et al. (2007) found evidence for some interesting but not altogether unexpected sex differences in kissing. Women, for example, placed more emphasis on kissing in romantic relationships than did men. Women are not only more reliant on kissing as a mate assessment device, but they continue to use kissing in long term relationships to update and monitor the status of the relationship with their partner. Men, on the other hand, often use kissing as means to an end (e.g., trying to gain sexual favors), and as a way of attempting reconciliation.

While both sexes rate kissing as a highly romantic act, women view kissing as more important at all stages of the relationship than do men. Not only do females place more emphasis on kissing, they are more likely to insist on kissing before a sexual encounter, and more prone to emphasize the importance of kissing during as well as after sex. Many females would not consider having sex with someone they never kissed. By comparison, most males in this survey indicated they would be happy to have sex without kissing, and men were far more likely than women to agree to have sex with someone who was not a good kisser. Kissing may also be a relationship barometer. There is evidence for couples in committed relationships that the amount of reported kissing is related to relationship satisfaction (Gulledge, Gulledge, & Stahmann, 2003).

Another function of kissing may be to assess a potential partner's health. Dental disease, lesions of the mouth, inability to chew food, and poor teeth would have been a significant handicap. Oral health may indicate heritable differences in susceptibility to periodontal disease and environmental stresses (Symons, 1995; Sugiyama, 2005). Even common haliotisis, which stems from bacterial growth in the mouth, may be a cue for an inability to resist pathogens.

At the moment of a kiss there is a very rich and complicated exchange of visual, tactile, postural, and chemical information based on olfactory and gustatory cues. Hughes, Harrison, & Gallup (2007) discovered that the majority of both male and female college students reported having found themselves attracted to someone on one or more occasions, only to discover that after they kissed them for the first time they were no longer interested. Thus, there is reason to suspect the existence of unconscious, hard-wired mechanisms that are triggered at the moment of a kiss which may function to assess the health, genetic compatibility, and reproductive viability of a prospective mate.

Honest Versus Dishonest Signals

Honest signals are those that reflect a person's reproductive potential. Because men with attractive faces have higher quality sperm and women with facial wrinkles are less likely to conceive, faces are honest signals since they are correlated (positively in the former case and negatively in the latter) with a person's capacity to reproduce. In contrast, dishonest signals often improve your appearance but leave your reproductive potential unaffected. Whereas foods that taste sweet are usually a significant source of calories, saccharine is the equivalent of a face lift. Artificial sweeteners improve the flavor of food, but leave its nutritional value unaffected. Cosmetic surgery may improve your appearance, but your reproductive capacity remains unchanged. According to this analysis, the effectiveness of all appearance enhancement techniques ought to be dependent upon the extent to which they make you look more reproductively viable.

Cosmetics, such as make-up, enable people to cover blotches, wrinkles, and imperfections in the skin. The tagline for the cosmetics company Maybelline reads "Maybe she's born with it . . . maybe it's Maybelline," suggesting that the people at Maybelline are implicitly aware that their product can be used to mask biological cues.

A study by Kruger (2008) provides a compelling example of dishonest signals in a different domain. Kruger found that men who spend rather than save, and especially those who spend more money than they make have significantly more sex partners than those who are more frugal. Nowadays with the advent of easy credit, men can use conspicuous spending to exaggerate their earnings. When it comes to the use of dishonest signals in the arena of reproductive competition, "Mastercard" has become an analog to "Maybelline."

In theory, the existence of dishonest signals would be expected to create selective pressure for adaptations that enable people to detect and avoid instances of reproductive deception. As a case in point, dishonest courtship, or feigning good intentions for purposes of gaining sexual favors is a common male sexual strategy; for example, "I love you, so let's go to bed." Consistent with this analysis, commitment skepticism is common among women (Geher, 2009), particularly without further evidence of sincerity (Haselton, Buss, Oubaid, & Angleitner, 2005).

Concluding Remarks

Tasty foods, attractive faces, sultry voices, and sexy bodies are all evolved features of the human nervous system. Clearly one of the most effective means of piggybacking one's genes into subsequent generations is to pair them with someone who is reproductively viable. The reason "first impressions count" is because many of the features of interpersonal attraction are related to important underlying dimensions of fitness.

Although beauty is still in the eye of the beholder, we now know that the eye of the beholder has been shaped by the evolutionary history of the species.

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Correction to Annetta (2010)

In the article, "The "I's" Have It: A Framework for Serious Educational Game Design" by Leonard A. Annetta (*Review of General Psychology*, 2010, Vol. 14, No. 2, pp. 105-112), the final acceptance date was incorrect. The final acceptance date should be January 15, 2010.

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