The Evolution of Human Physical Attractiveness

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Key Words

Abstract

Everywhere the issue has been examined, people make discriminations about others' physical attractiveness. Can human standards of physical attractiveness be understood through the lens of evolutionary biology? In the past decade, this question has guided much theoretical and empirical work. In this paper, we (a) outline the basic adaptationist approach that has guided the bulk of this work, (b) describe evolutionary models of signaling that have been applied to understand human physical attractiveness, and (c) discuss and evaluate specific lines of empirical research attempting to address the selective history of human standards of physical attractiveness. We also discuss ways evolutionary scientists have attempted to understand variability in standards of attractiveness across cultures as well as the ways current literature speaks to body modification in modern Western cultures. Though much work has been done, many fundamental questions remain unanswered.

Contents

INTRODUCTION

Intensive study of human physical attractiveness in the social sciences was prompted by a serendipitous finding by Hatfield and colleagues in 1966. These researchers randomly paired college men and women for a blind date. In return, participants filled out personality and interest measures, background questionnaires, and a survey following the date. A key question was whether they were interested in a subsequent date with their partner. None of the researchers' own hypotheses were supported. Rather, only one variable—added as an afterthought—reliably predicted interest: their partners' physical attractiveness.

Research over the past four decades has demonstrated profound and broad-reaching implications of physical attractiveness for people's lives. As might be expected, attractive people have greater choice in mating markets and hence are able to secure consensually more desired partners. But attractive people are treated differently from others more generally, leading them to have better jobs, higher incomes, and more friends than others—indeed, achieve more desirable outcomes in most spheres of life people consider important (e.g., Langlois et al. 2000).

Physical attractiveness matters to mate choice not only among U.S. college students. Buss (1989) surveyed people from 37 cultures around the world about mate preferences. The U.S. samples rated the importance of physical attractiveness only slightly above average for the cultures. In traditional groups as well, e.g., the Ache of Paraguay (Jones & Hill 1993), the Shiwiar of Equador (Sugiyama 2004), the Machigenka of Peru (Yu & Shepard 1998), and the Hadza of Tanzania (Wetsman & Marlowe 1999), individuals have reliable standards of attractiveness. Indeed, a recent meta-analysis concluded that people in different cultures generally agree on who is attractive (Langlois et al. 2000). Physical attractiveness appears to have important implications in traditional cultures too; attractive Ache women, for instance, have greater reproductive success (Hill & Hurtado 1996).

Symons's (1979) *Evolution of Human Sexuality* offered the first intensive analysis of physical attraction as an outcome of natural selection. It inspired Buss's (1989) survey and spawned research on features considered

attractive cross-culturally (e.g., Jones & Hill 1993, Cunningham et al. 1995). Research guided by evolutionary thinking steadily intensified over the past 15 years. Since 1990, nearly 300 articles with the keywords "physical (or facial) attractiveness" as well as "selection" or "evolution" in their titles or abstracts have appeared in scientific journals. Those published in the five years since 2000 outnumber those appearing in all of the 1990s (and, indeed, will probably soon outnumber those published in all of the twentieth century!).

We first discuss the adaptationist framework that has guided evolutionary analyses of attractiveness, with emphasis on biological signaling theory. We then review recent research in light of this framework and conclude with key issues for future research.

METATHEORY AND THEORY

The Adaptationist Framework: Basic Concepts

As a research strategy, adaptationism seeks to identify adaptations and elucidate the selection pressures that forged them in an organism's evolutionary past. In its current form, it crystallized in the 1960s and 1970s [heavily influenced by the writings of George Williams (1966)] and now dominates the study of animal behavior in biology (e.g., Krebs & Davies 1993, 1997). It also guides most evolutionary work on human attractiveness. We review briefly some basic concepts and tools. (For a more extensive discussion, see also Andrews et al. 2002.)

Traits. Biologists use the term trait to refer to aspects of organisms' phenotypes. A liberal definition allows a trait to be any aspect of the phenotype that can be discriminated on the basis of any criterion—its causes, effects, appearance, etc.—and includes dispositional traits (e.g., the disposition to develop calluses with friction; the disposition to choose mates with particular qualities).

Adaptation. The word adaptation has two meanings in evolutionary biology (Gould & Vrba 1982). It is the process by which natural selection modifies the phenotype and generates traits whose effects facilitate the propagation of certain genes over others, thereby causing evolution. It also refers to the end-products of that process—i.e., the traits that have been constructed by a process of phenotypic modification by natural selection for a particular gene-propagating effect. An effect refers to the way, or ways, in which an aspect of the phenotype interacts with the environment (e.g., Williams 1992). At least one effect of an adaptation is beneficial in an evolutionary sense; this effect is referred to as the adaptation's function. A function is an effect that caused the trait to evolve—that is, an effect that enhanced the reproductive success of the trait's bearers over others lacking the trait. Crudely put, the primary function of eyes is seeing; the primary function of wings is flight.

Byproducts. A small minority of traits qualifies as adaptations. Byproducts (or spandrels; Gould & Lewontin 1979) evolved merely because they were linked with other traits that had beneficial effects and hence were carried along with selection for adaptations. For example, vertebrate animals evolved skeletal systems of calcium phosphate (perhaps ancestrally for the function of storing calcium, but modified for the function of structural rigidity necessary for locomotion; e.g., Ruben & Bennett 1987). Calcium phosphate is white and hence so too are bones. The whiteness of bones, however, is not an adaptation. It is a byproduct of selection for other properties of calcium phosphate.

Energetic trade-offs. Organisms can be thought of as entities that capture energy from the environment (e.g., through foraging, hunting, or cultivating) and allocate it to reproduction and survival-enhancing activities. Energy does not come for free. Were individuals able to expend unlimited energy at no

cost, in principle they could evolve to grow and develop so rapidly they could begin reproducing immediately after birth, massively produce offspring, and preserve themselves such that they never age. In biological reality, however, individuals are constrained by finite energy "budgets" (themselves earned through energy and time expenditures). Allocation of finite energy and time budgets entails tradeoffs and hence forces decisions about the relative value of possible ways to spend. Individuals should be expected to evolve adaptations that lead them to allocate their budgets in ways that enhance their fitness. Hence, for example, selection does not favor ever-increasing clutch sizes in birds. Rather, selection presumably favors strategies of producing and raising offspring that maximize the overall reproductive success of offspring through an optimal balance of offspring number and quality, as constrained by energy and time budgets (see, e.g., Seger & Stubblefield 1996, Kaplan & Gangestad 2005). As we emphasize later, a key notion in the study of attractiveness is that the amount of effort that individuals can dedicate to a biological signal found attractive by the other sex is constrained by their energy budgets.

Cost-benefit modeling. Adaptationists often use quantitative optimization models to try to understand how selection operates on phenotypes, given trade-offs (e.g., Seger & Stubblefield 1996, Winterhalder & Smith 2000). A model has one or more actors (e.g., two or more individuals engaging in social interaction, etc.) expressing the phenotypes that the theoretician is trying to understand. The payoffs of the model are expressed in a currency, such as actual fitness units or some correlate of fitness (e.g., units of energy). The decision set is the suite of phenotypic or behavioral options available for pursuing payoffs, and selective constraints delineate how these options translate into costs and benefits (typically dictated by constraints of energy and time budgets). The optimal phenotypic or behavioral option is the

one that maximizes net benefits under the constraints. Complexities can be taken into account. For instance, optimal strategies may be contingent on the condition or phenotype of the individual (conditional or phenotype-limited optima). Hence, as we'll see, an important theme of biological signaling theory is that the optimal intensity of a signal may vary as a function of individuals' own condition. (See Parker & Maynard Smith 1990).

The special design criterion for identifying adaptations. Evolutionary biologists are interested in understanding adaptation. Because adaptations don't come with labels, however, their identification requires inference. The major criterion used is special design (e.g., Williams 1966; Thornhill 1990, 1997). A feature exhibits special design if it proficiently performs a specific function; and moreover, it is difficult to imagine any alternative evolutionary process that would have led to the feature or its details other than selection for that function. For instance, eyes are good for seeing and it's difficult to imagine an evolutionary process that would have led to many of their details other than selection for their optical properties, that is, for seeing. Evidence for design is not only evidence that adaptation has been at work; it's evidence that the organism has been shaped by particular selection pressures. Just as wings and eyes are telltale signs of historical selection for flight and seeing, respectively, certain psychological features of modern humans (e.g., patterns of attraction to mates and their features) may be telltale signs that particular selection pressures shaped the minds of ancestral humans (e.g., selection for a signaling system due to particular benefits associated with the signal).

Attractiveness and beauty as an outcome of adaptation. Individuals find other individuals attractive as a result of the latter possessing specific favored traits. Obviously, however, attractiveness reflects traits in

perceivers as well: Perceivers have traits leading them to find some features more attractive than others. Adaptationist researchers have typically adopted the working hypothesis that perceiver traits are adaptations—evolved as a result of their having benefits for perceivers—or, as the title of an article by Symons proclaims, "Beauty is in the adaptations of the beholder" (1995).

Generally speaking, tendencies to be attracted to particular traits in individuals of the opposite sex are presumed to have benefited their bearers because individuals' own reproductive success (or that of their offspring) is affected (or, more precisely, was affected ancestrally) by qualities of the individuals with whom they mate. In broad terms, evolutionary biologists delineate two types of benefits that mates provide: first, genetic benefits to offspring—i.e., endow offspring with superior ability to survive; second, material benefits to the perceiver such as food, care for offspring, physical protection for self or offspring, or avoidance of disease. Individuals disposed to mate with others who enhanced their own fitness would have, *ceteris paribus*, out-reproduced those not so disposed. Hence, selection may have favored dispositions to be attracted to mates who possessed qualities that signal (or ancestrally signaled) delivery of benefits. Adaptationist researchers typically adopt a working hypothesis that many of people's tendencies to find specific features attractive are outcomes of this kind of historical selection (though see our discussion of alternative, sensory bias models below).

Once individuals of one sex prefer particular qualities, the preferences exert selection pressures on the preferred traits. Individuals who possess preferred traits, by virtue of their enhanced ability to exercise choice in a mating market, have greater reproductive success. Selection hence leads individuals to expend energy and time to display favored traits. As Charles Darwin himself recognized (1871), such selection can in theory lead to the evolution of extravagant ornaments, even those

detrimental to an animal's viability, provided they gave a sufficient advantage in the realm of mating. In turn, selection may come to exert pressures on perceivers' greater ability to discern truly favored traits. Preferences and the traits they prefer coevolve.

Sexual Selection and Signaling Theory

Physical traits individuals are selected to find attractive may be thought of as signals of underlying qualities. The coevolution of preferences and preferred traits, then, can be thought of as the evolution of a signaling system, which entails that one sex (signalers) possess signals and the other sex (receivers) possess psychological (cognitive and motivational) capacities to perceive and act upon (e.g., be attracted to) those signals. (In a given species, both sexes may evolve preferences and hence be receivers in signaling systems, of course.) Signals of underlying quality or condition have received the greatest attention from biological signaling theorists. Quality or condition refers to an individual's ability to successfully interact with the environment to acquire and effectively expend energetic resources (e.g., Rowe & Houle 1996). Superior condition has been associated with the concept of health (e.g., Grammer et al. 2003). The concept of health it implies, however, is much broader than simply the absence of disease; it implies greater phenotypic fitness or resourcefulness. Indeed, as discussed below, in particular circumstances individuals of superior condition may even be more prone to disease than others. The term health, then, is generally a poor stand-in for biologists' notion of condition.

Individuals in superior condition may make better mates for a variety of reasons: fitter genes to pass on to offspring (e.g., a relative absence of mildly harmful mutations; Houle 1992); greater ability to provide material benefits such as protection or food; greater fertility and ability to reproduce (e.g., more viable sperm in the case of males or greater ability to

conceive and carry offspring through gestation and lactation in the case of females); and a relative absence of disease. General models of signals of quality do not speak to the precise nature of the benefits associated with choosing a mate of superior quality, though researchers are often interested in determining these benefits.

A signaling system may be said to be at equilibrium when neither the signaling sex nor the receiving sex benefits from a change (i.e., in signal sent or preference exercised) given that the other retains its strategy. For a signal to be a valid indicator of one's quality at equilibrium, a reliable relation between the signaler's quality and the signal strength must persist. Zahavi (1975) introduced the idea that it is the very costliness of a trait that ensures its honesty. He specifically proposed that animals may signal that they are of superior quality with a "handicap"—a feature that imposes a cost on the individual. Zahavi did not provide an optimization model of this process; his argument was a verbal one. The basic intuitive notion is that individuals who can afford a large handicap must be more viable than individuals who have smaller handicapping traits. Big signalers can afford to "waste" some of their viability and still have residual viability greater than that of small signalers, and this fact presumably renders the handicapping trait an "honest" signal of viability. (In this context, a "bigger" signal need not be larger. Rather, the term indicates greater cost for individuals, on average, to produce. The cost itself may be due to the signal's size, its complexity, or any other characteristic requiring effort to produce. Costs can also be mediated socially, for some signals let competitors know that their bearers should be tested through competition.)

Grafen (1990) was the first to quantitatively model handicapping. He assumed that all individuals, regardless of quality, obtain the same fitness benefits from a particular level of a signal (however, see Getty 1998). The signal can evolve to display quality, according to this model, when the fitness costs (in the currency of mortality) associated with developing and maintaining a particular level of the signal are less for individuals of higher quality than for individuals of lower quality. In that instance, the size of the handicap that maximizes net fitness (benefits minus costs) is larger for individuals of higher quality than for individuals of lower quality. The signal "honestly" conveys fitness, then, simply because it is not in the interest of individuals of lower quality to "cheat" and develop a larger signal; the viability costs they would suffer exceed the fertility benefits they would derive from the increased signal size.

Recent developments in honest signaling theory have furthered and revised our understanding of it. Despite the intuitive appeal, systems of mate choice via signals of condition need not imply that the biggest signals are sent by the most viable individuals. For signals to be reliable, higher quality individuals need only higher efficiency, i.e., a greater fitness return from a marginal increase in signal investment (Getty 2002). Modeling has shown that individuals of highest quality may have the same, higher, or lower viability than small signalers at equilibrium, depending on specific parameters of the system. A key parameter is the expense paid by receivers for preferring those with big signals over others, most notably, the cost of search time. Individuals with strong preferences for a signal of a certain size may delay mating and hence lose valuable time reproducing. A preference may be very cheap in some species—e.g., lekking species in which males collectively gather and display to females, who can assess relative quality without sacrificing search time. In such species, a few males who "win" the display contest may garner nearly all the matings, which in turn boosts the intensity with which males capable of sending strong signals will do so, sometimes beyond the point at which high quality males have reduced their viability to that of their lower quality rivals. Oddly, then, quality and mortality can actually become positively correlated in a population, with the highest quality individuals dying, on average,

at younger ages than lower quality individuals (Kokko et al. 2002). When females pay relatively high costs for their preference in relation to its benefits, the system will not drive signal intensity to be as great (i.e., signals themselves will be less costly at equilibrium) and, furthermore, individuals of highest quality are unlikely to invest in signals to the extent that they actually have lower viability than individuals of lower quality. Similarly, the association between quality and parasite load (disease-level) can be positive, negative, or negligible, depending on the system (Getty 2002).

Are Honest Signaling Systems of Quality Ubiquitous?

A model that does not assume an association between signal intensity and quality is the sensory bias model (e.g., Kirkpatrick & Ryan 1991). In this model, one sex has a bias to prefer individuals of particular qualities because that bias has advantages in realms other than mating. For instance, redness may be preferred in features of mates because redness signals ripeness of fruit and a sensory bias to be attracted to redness spills over into domains other than food selection. (Here, the bias applied to mates is a byproduct of an adaptation for food choice.) Fisher (1930) famously described a process whereby a small initial preference ultimately leads to extreme traits and preferences through "runaway" selection. If a particular trait in one sex is preferred in mates due to sensory bias in the other sex, then genes disposing stronger preference for the trait could spread because they become linked with genes predisposing the preferred trait. In essence, genes for strong preference "piggyback" on the success of the preferred trait, leading to stronger and stronger preferences and more and more extreme traits.

A distinct variant of a sensory bias model is the "chase-away" model (Holland & Rice 1998). It assumes that individuals of the choosing sex with a sensory bias nonadaptively

applied to mate choice pay a cost for it (e.g., increased search time) and, hence, have lower reproductive success than those who are "resistant" to the bias. This purportedly leads to selection for more intense signals in the other sex, ones than overcome the resistance of a greater proportion of choosers, which in turn leads to selection for a higher threshold of resistance. Over time, the chase-away process results in extreme manifestations of the trait.

Kokko et al. (2003) recently argued that runaway or chase-away processes due to small initial sensory biases are unreasonable models of signaling equilibria. In each case, the signal that evolves is presumed to become increasingly costly. As costs increase, individuals of highest quality will be able to produce the signal more efficiently than others—precisely the condition in which a signal comes to honestly convey quality. Inevitably, then, signals initially preferred merely due to sensory bias should become correlated with quality through runaway or chase-away processes. Rather than conceptualizing sensory bias or chase-away models as competitors of honest signaling models, then, Kokko et al. (2003) argues that sensory bias may be the starting point of a process that leads to honest signaling. Such biases may explain how preferences for seemingly arbitrary traits—ones prior to the evolution of the signaling system were probably not associated with quality (e.g., a tail brighter or larger than average)—can get off the ground, such that these traits ultimately become correlated with quality.

Honest signals of quality need not initially be uncorrelated with quality, however. Features may covary with quality prior to being signals because individuals of higher quality pay lower marginal costs for them—e.g., in some species, larger individuals or those better able to intrasexually compete may possess higher quality. Preferences for these traits (or natural correlates of them) may then evolve, which further intensifies them by increasing the benefit of investing in the development of these traits. As we discuss later, a number of features preferred by humans may well have

correlated with quality prior to their evolution as signals.

Genetic versus Direct Benefits

Again, honest signaling of quality can evolve through either benefits that directly enhance reproductive success (e.g., food, protection, lack of contagious disease) or genetic benefits passed on to offspring. In some instances, both may account for the preference. For instance, males in a multi-male primate group better able to protect offspring than others and hence providing direct benefits to choosers may well possess genes associated with quality as well.

In mating systems in which males and females form socially monogamous (or mildly polygynous) pairs and males invest heavily in offspring (e.g., many bird species), direct benefits and indirect benefits may covary negatively. This should particularly be true when females are not sexually monogamous and offspring are frequently sired by "extrapair" males (also true of many bird species; e.g., Petrie & Kempanears 1998). In such cases, males of superior condition may optimize their allocation of effort by investing less in offspring and more in efforts to secure extra-pair matings (as they may succeed more often than males of lower quality). Where direct and indirect benefits correlate negatively, either can be stronger; females may have a preference for males offering less direct benefit or less indirect benefit. Moreover, female preferences may vary depending on whether they are selecting a social partner or an extrapair mate. In collared flycatchers on the island of Gotland, for instance, females have no clear preference for males having a relatively large forehead patch, an honest signal of quality (Qvarnström 1999). When choosing extrapair partners, however, females clearly prefer large-patched males. In theory, direct and genetic benefits of social partners negatively covary and cancel out. (Males with larger patches feed offspring less.) Extra-pair partners, however, provide no direct benefits and, hence,

choice is based only on males' ability to provide genetic benefits.

Multiple Signals

In many species, mate choosers attend to multiple signals, sometimes transmitted through different sensory channels (e.g., both olfactory and visual cues). One possible explanation is error in signal transmission; multiple signals of the same quality evolve because each adds incremental information that others do not (e.g., each signal or its perception is not perfectly correlated with quality; Grafen & Johnstone 1993). Alternatively, such mixing might be explained through a combination of constrained transmission time and a need to convey abundant information (Endler 1993). As a parallel, one might imagine the use of both hand gestures and oral instructions in giving directions to a driver stopped at a red light. A third explanation is that signals carry information about different qualities altogether.

Mutual Mate Choice

In many species, sexual selection on signals is much greater in one sex than the others. In mammalian species, females are typically a limiting reproductive resource and, hence, males compete through intrasexual competition and through signaling for females. Selection on female signaling is much weaker, as males may seldom turn down sexual opportunities with females. In species in which both males and females invest substantially in offspring, however, mutual mate choice may evolve (e.g., Kokko & Johnstone 2001), whereby both sexes are selected to display desired mate qualities. Although the extent to which human male assistance to offspring has historically functioned to increase offspring quality or, alternatively, to increase access to mates is hotly debated (e.g., Kaplan et al. 2000, Hawkes et al. 2001), in any case mutual mate choice appears to characterize human cultures. Both men and women discriminate

the desirability of potential mates, partly on the basis of physical qualities.

FEATURES ASSOCIATED WITH ATTRACTIVENESS: WHAT DO THEY SIGNAL?

Researchers have focused attention on three facial features found attractive across many cultures: sexual dimorphism, averageness, and symmetry. In addition, researchers have examined the effect of several nonfacial bodily features on attractiveness, most notably, female waist-to-hip ratio and male body type.

Facial Sexual Dimorphism

Men's and women's faces differ in a number of ways. On average, men's chins are longer and broader than women's. Development of the brow ridge renders men's eyes smaller (relative to total face size) and narrower than women's (e.g., Gangestad & Thornhill 2003a). Women's cheekbones are more gracile and their lips fuller. During adolescence, testosterone promotes growth of the lower face (see Swaddle & Reierson 2002). Estrogens may cap growth of bones during puberty, contributing to sexual dimorphism as well. Despite variation in facial proportions across human groups, sex differences exist wherever they have been examined (e.g., Jones & Hill 1993). We refer to the aggregate differences between men's and women's faces as facial masculinity versus femininity.

The attractiveness of female facial femininity. Facial femininity is attractive in women; highly attractive women's faces are more feminine than average (e.g., Johnston & Franklin 1993, Perrett et al. 1994). This finding has been replicated in a wide variety of human groups (e.g., United Kingdom, Japan, Russia), including traditional South American groups with little to no exposure to Western standards of beauty (e.g., Ache; Jones & Hill 1993). Men prefer female faces with relatively small chins, large eyes, high cheekbones, and full lips (e.g., Cunningham 1986).

Several theories explaining men's attraction to femininity have been offered.

Facial femininity reflects babyness, preferred due to sensory bias. An early theory is that feminine features such as large eyes and small chin reflect "babyness" (Cunningham 1986, Johnston & Franklin 1993, Jones 1995). People may be disposed to respond to babies with care and, hence, be attracted to baby-like features (Jones 1995). Ancestral females who exploited this preference may have been advantaged over those who didn't, driving the sexual dimorphism itself.

This theory encounters two major problems. First, some attractive feminine features are not baby-like. Babies have puffy, protruding cheeks (e.g., McArthur & Apatow 1984), whereas men find gracile, high cheekbones attractive in women's faces (e.g., Grammer & Atzwanger 1994). Second, as noted earlier, even a sensory bias model should expect that, as a trait is driven to be more extreme, some individuals should be better able to display it and, hence, it should become correlated with quality (Kokko et al. 2003).

Female facial femininity marks sex appropriateness. The view that attractive displays exaggerate species- or sex-typical traits to foster choice of a species- or sex-appropriate partner was prominent in the first half of the twentieth century (see, for a review, Cronin 1991). It might also expect women to particularly prefer highly masculine faces, which as we discuss below is not the case. Furthermore, once again, selection due to a bias favoring a trait uncorrelated with quality should ultimately result in covariation between the trait and quality.

Female facial femininity is a marker of reproductive value. Reproductive value (RV) is the expected residual reproductive success of an individual, generally based on age (Fisher

1930). RV is maximal when women reach reproductive age and diminishes thereafter. If men ancestrally mated serially with the same partners throughout their reproductive career (e.g., Kaplan et al. 2000), men may have maximized their fertility by selecting mates with maximal RV (Symons 1979). As women age, their facial proportions become less feminized, probably due to accumulated exposure to androgens (see Thornhill & Gangestad 1993). Men's preference for facial femininity, then, could reflect selection for age-based RV.

RV could account for selection and maintenance of a preference favoring facial femininity. Once again, however, women should have been selected to exaggerate and prolong the period of facial femininity, with some women better able to do so than others, ultimately leading facial femininity to be a cue of quality.

Facial femininity is a marker of female quality or condition. Female femininity may signal reproductive condition and ability to dedicate energy to offspring production. Women's production of estrogen and fertility status are designed to be sensitive to conditions that affect their ability to carry and lactate for offspring—their energy condition (total stored energy in fat), energy balance (residual energy consumed minus expended available for reproductive effort), and energy flux (total energetic output). Women have diminished ovarian function when they do not have fat stored for reproduction, do not reliably take in calories that surpass energy expenditure, or incur extreme (either very low or very high) energetic demands (e.g., Ellison 2001, 2003). Extreme instances result in amenorrhea, but normal variation affects the production of ovarian hormones, including estrodiol, and thereby ovarian function, such that female fecundity varies along a continuum. Energy balance and flux appear to have larger effects than energy status, at least in the United States (Lipson & Ellison 1996). Facial femininity does not change drastically with immediate circumstances, but it could index

women's accumulated history of energy balance and flux appropriate for reproduction.

The advantages of attraction to women with such a history (at least ancestrally) could be twofold. First, it could be a cue of direct benefits, as it could reflect lower disease incidence, better development due to favorable levels of parental investment, greater ability to forage effectively, etc., all affecting current reproductive capabilities. Second, such a history could be associated with genetic benefits to offspring. Women with more efficient metabolisms due to fewer mutations (and hence more favorable energy balance, controlling for energy intake) or genotypes more resistant to extant pathogens would produce genetically more fit offspring.

Evidence pertaining to whether women's facial femininity or attractiveness are associated with health is mixed. Hume & Montgomerie (2001) and Henderson & Anglin (2003) found associations between facial attractiveness and relative absence of past health problems and longevity, respectively (see also Langlois et al. 2000; compare Kalick et al. 1998). Rhodes et al. (2003) reported no association between rated female facial femininity (in adolescence) and actual health records, whereas Thornhill & Gangestad (2005) found facial femininity (measured from digitized photographs) to predict recent history of respiratory infections and antibiotic use. Body symmetry (aggregated across fingers, wrists, ears, elbows, etc.) measures developmental stability, a lack of perturbations during development due to infection, mutations, and other stresses. Koehler et al. (2004) reported that women with greater body symmetry are perceived to have more feminine faces; Gangestad & Thornhill (2003a) found no association. No study has examined facial femininity in relation to health in traditional societies exposed to ecological circumstances reasonably similar to ones encountered by ancestral societies, in which the childhood mortality rates due to disease may typically have been 30–50% (e.g., Hill & Hurtado 1996) and energy budgets

were constrained. Moreover, no one to our knowledge has explored associations between ovarian function and facial femininity. Although we suspect that preference for female facial femininity has been maintained because of this trait's historical association with both RV and fecundity, the latter link requires additional evidence.

Attractiveness in relation to male facial masculinity.   One might suspect that, just as men find feminine faces attractive, women might be attracted to masculine faces. In fact, no clear preference exists; studies have found a female preference for somewhat masculine faces (Keating 1985, Johnston et al. 2001), preference for feminine faces (e.g., Perrett et al. 1998, Penton-Voak et al. 1999), and no systematic preference either way (e.g., Cunningham et al. 1990, Jones & Hill 1993, Swaddle & Reierson 2002).

Male facial masculinity nonetheless covaries with certain desired male traits. Across a variety of cultures, men with masculine faces are perceived to be and probably are (Mueller & Mazur 1997) socially dominant (e.g., Keating et al. 1981, Mazur et al. 1984). Kung San bushmen with broad chins and robust bodies have relatively high reproductive success (Winkler & Kirchengast 1994). One argument is that testosterone promotes male mating effort, which partly involves male-male competition, and that men's condition affects the extent to which they can effectively dedicate effort to mating (in a way analogous to how women's condition affects their ability to dedicate effort to reproduction). Variation in condition therefore gives rise to variation in testosterone metabolism, which, during adolescence, causes variation in facial masculinity. Men with more masculine faces may be tested in male-male competition, a cost that may ensure its honesty as a signal of condition. Consistent with this interpretation, two studies have found associations between male facial masculinity and reported health (Rhodes et al. 2003, lower half of the distribution only; Thornhill & Gangestad (2005),

Zebrowitz & Rhodes 2004). Gangestad & Thornhill (2003a) found that men with masculine faces have greater body and facial symmetry, though Koehler et al. (2004) did not. Among childless men in a rural village in Dominica, body symmetry positively predicts testosterone levels (controlling for age; S.W. Gangestad, R. Thornhill, M.V. Flinn, L.K. Dane, R.G. Falcon, C.E. Garver-Apgar, M. Franklin & B.G. England, unpublished data). (Male facial masculinity may be weakly associated with current testosterone level; Penton-Voak & Chen 2004.) As male testosterone varies as a function of a variety of factors, including mating status and paternity (e.g., Burnham et al. 2003), however, facial masculinity may better index levels during adolescence and early adulthood. If adolescence is characterized by relatively intense male-male competition, facial masculinity may nonetheless reflect condition.

If male facial masculinity covaries with condition, as conjectured, why do women not consistently prefer masculine faces? Penton-Voak et al. (1999) speculated that women face a trade-off: Although more dominant and possibly more fit, masculine men may be less willing to invest exclusively in partners and help care for offspring. Hence, just as female collared flycatchers do not particularly prefer males with large forehead patches as social partners, women do not prefer more masculine men as mates. As this view expects, men with feminine faces are perceived to be warmer, more agreeable, and more honest than men with masculine faces (see Fink & Penton-Voak 2002).

According to this view, attraction to male masculinity should have been shaped by selection to be conditional—depend on conditions that affect (or ancestrally would have affected) the relative value of (possibly heritable) condition and paternal investment. Evidence suggests that it is.

Preference varies with phase of the ovulatory cycle. Women's mate preferences vary across their ovulatory cycles. When normally

ovulating (e.g., nonpill-using) women are close to ovulation (and hence fecund), they are particularly attracted to the scent of symmetrical men (Gangestad & Thornhill 1998, Thornhill & Gangestad 1999, Rikowski & Grammer 1999, Thornhill et al. 2003), deep, masculine male voices (Putz 2005), and more confident, intrasexually competitive male behavioral displays (Gangestad et al. 2004), particularly (where it has been examined; e.g., Gangestad et al. 2004) when they evaluate men as sexual partners (their "sexiness") rather than as long-term mates. Changes in preferences across the cycle may reflect female design to weigh signals of heritable condition more heavily when they are fertile, particularly when selecting a sex partner. Interestingly, then, the face that women most prefer when close to ovulation is more masculine than the face most preferred when they are in the luteal phase [Penton-Voak et al. 1999 (United Kingdom, Japan), Penton-Voak & Perrett 2000 (United Kingdom), Johnston et al. 2001 (United States, Austria)]. Furthermore, the effect is specific to female attraction to men as sex partners, not long-term social mates (Penton-Voak et al. 1999).

Preference varies as a function of relationship context. The face women find most attractive in short-term mates is more masculine than the face they find most attractive in long-term mates (Penton-Voak et al. 2003).

More attractive women have a stronger preference for masculine faces. Little et al. (2001) reasoned that, attractive women need not trade-off male condition and investment as markedly as must unattractive women; masculine men should be more likely to invest in relationships with attractive women. Hence, attractive women should more strongly prefer facial masculinity. Studies by Little et al. (2001; using self-reported attractiveness) and Penton-Voak et al. [2003; using others' ratings of facial attractiveness and

waist-to-hip ratios (see below)] support this hypothesis.

Preference for masculinity varies with culture. Penton-Voak et al. (2004) proposed that women's preference for masculinity should have been selected to be sensitive to cues of the relative value of condition (and genetic benefits) and investment of male mates in their local ecologies. In Jamaica, infectious disease is more prevalent (due to higher parasite loads and poorer medical care) and male parental investment less pronounced than in the United Kingdom. They predicted and found that Jamaican women show greater preference for facial masculinity than do British women.

Findings that women's preferences for facial masculinity are conditional constitute provisional design evidence that women's attraction to male faces have been shaped by how male condition and parental investment have traded-off.

Facial Averageness

In 1990, Langlois & Roggman published a highly influential study. They digitized photographs of faces, then created composites of sex-specific sets of them. Raters of both sexes found the "averaged" faces to be attractive, consistent with earlier speculation by Symons (1979) and suggestive findings by Galton (1878). The finding has been replicated many times (e.g., Wehr et al. 2001), including in China and Japan (e.g., Rhodes et al. 2001a) and in the Ache (Jones & Hill 1993). This preference is not merely due to the fact that composite faces are symmetrical and have unblemished skin; people find average face shape and morphology attractive (e.g., O'Toole et al. 1999, Rhodes et al. 1999, Valentine et al. 2004). As discussed above, some faces are more attractive than average faces. Nonetheless, extreme departures from average on even sexually dimorphic traits are not attractive.

Two main hypotheses may explain preference for averageness.

A generalized sensory bias favors prototypes.
Organisms may show preference for stimuli that are readily processed (e.g., Enquist & Arak 1994). People may build up cognitive prototypes of distinct categories of stimuli, representations consisting of average features, which are useful for discriminating new instances of the category. Stimuli that match a prototype well may then be preferred. Halberstadt & Rhodes (2000, 2003) found that people indeed find averaged instances not only of faces, but also of dogs, fish, birds, wristwatches, and automobiles, attractive. Although familiarity of the stimuli could account for preferences for average wristwatches and automobiles, it could not explain preferences for dogs, fish, or birds. They proposed that people have a preference for averageness per se, independent of familiarity, when judging the attractiveness of living organisms, which may reflect a preference for signals of quality.

Averageness reflects quality. Departures from average may reflect the effects of genetic mutation, chromosomal abnormality, nongenetic congenital deformation, disease, or other factors affecting quality. Zebrowitz & Rhodes (2004) found that facial averageness predicted pubertal intelligence and adolescent health (the latter for women), but only in the lower half of the distribution. They therefore proposed that averageness (and other purported indicators of condition, such as facial masculinity) discriminates average from "bad" genes (or poor condition) but not from "good" genes. In fact, however, this effect may not be robust, as the regression slopes for high and low averageness groups did not significantly differ. Moreover, a plausible alternative is that prediction at the high end of averageness is compromised because some nonaverage features indicative of good condition (e.g., sexually dimorphic features) are preferred. Aggregates of different signals may discriminate condition along a continuum, a possibility to be explored in future research.

Facial Symmetry

Bilateral asymmetry on features that, on average within a population, are symmetrical may reflect perturbations occurring during development due to mutations, pathogens, toxins, and other stresses (e.g., Møller 1999). Manipulations of symmetry of signals in some (but not all) other species affect attractiveness (see Møller & Thornhill 1998). Grammer & Thornhill (1994) found facial asymmetry to negatively predict attractiveness. Manipulations of symmetry generally enhance attractiveness [Rhodes et al. 1998, 1999, 2001a (including samples from China and Japan); Perrett et al. 1999; Koehler et al. 2002; compare Noor & Evans 2003]. [Studies manipulating symmetry by pairing left- or right-face mirror images, which look strange, have not found this effect. See Møller & Thornhill (1998).]

Two empirical questions arise. The first is the size of the effect of symmetry on normal variation of attractiveness. Whereas female femininity and facial averageness reliably account for moderate amounts of variation in attractiveness, symmetry does not: Grammer & Thornhill (1994), Baudouin & Tiberghein (2004), Jones et al. (2004), Hume & Montgomerie (2001), and Scheib et al. (1999) report positive findings, whereas Rikowski & Grammer (1999), R. Thornhill & S.W. Gangestad (unpublished data), Rhodes et al. (2001b), Shackelford & Larsen (1997), Simmons et al. (2004), and Koehler et al. (2004) found null or mixed results. The correlation in most populations is probably in a predicted direction but weak ($r < 0.2$).

A second question concerns the extent to which facial symmetry per se generates its association with attractiveness. Scheib et al. (1999) found that both facial and body asymmetry predict male facial attractiveness. But facial symmetry predicted just as well the attractiveness of half-faces, which possess

minimal cues of symmetry (see also Penton-Voak et al. 2001). Jaw size and prominent cheekbones (the first a masculine trait, the second not; see also Gangestad & Thornhill 2003a; compare Koehler et al. 2004) covaried with symmetry and was able to account for its association with attractiveness. Men with symmetrical faces may have healthier looking skin as well (Jones et al. 2004).

Perhaps ironically, it is not clear that facial symmetry should be used as a cue of condition. Single trait asymmetries are very weak indicators of underlying variation in developmental instability, with <10% of their variation owing to it (Gangestad & Thornhill 1999, 2003b). Only by aggregating asymmetries of multiple traits can researchers develop reasonably valid measures. Facial symmetry reflects symmetry on multiple traits. Because the traits are developmentally linked, however, it is unclear how much nonredundant information about developmental stability individual facial features contain. Researchers have found near-zero to modest correlations between facial asymmetry and broad composites of body asymmetry (Rikowski & Grammer 1999, Scheib et al. 1999, Gangestad & Thornhill 2003a, Koehler et al. 2004). Quite possibly, facial symmetry weakly taps developmental stability. [Indeed, facial masculinity/femininity could possibly be a better measure of it; Gangestad & Thornhill (2003a).]

Enquist & Johnstone (1997) proposed that symmetry preferences may be a byproduct of generalization effects when individuals are exposed to asymmetrical variants of an object (e.g., faces) that are symmetrical on average. Jansson et al. (2002) demonstrated that chickens repeatedly exposed to asymmetrical novel stimuli (around a symmetric mean) came to prefer symmetrical stimuli to which they had not previously been exposed. Little & Jones (2003) demonstrated a greater symmetry preference for faces in normal orientation than for inverted faces, which can be explained by generalization (as people rarely see inverted faces). They also showed a preference for symmetry even in familiar faces, which a prototype (though not a mere familiarity) account may explain. Simmons et al. (2004) found that, although faces are characterized by directional asymmetries (mean L > R or R > L differences in the population), these asymmetries do not affect attractiveness; rather, deviations around them (atypical asymmetries) do, a finding also consistent with either the perceptual bias account or the symmetry-marks-quality explanation.

One finding favoring the symmetry-marks-quality explanation is that, just as attractive women have relatively strong masculinity preferences, they have strong symmetry preferences (Little et al. 2001). At the same time, Koehler et al. (2002) found no evidence that normally ovulating women particularly prefer symmetrical faces—as they prefer masculine faces—when near ovulation. Zebrowitz & Rhodes (2004) found an association of facial symmetry with childhood intelligence but not health. In sum, we do not yet know the extent to which it drives attractiveness judgments and, to the extent that it does, what explains the preference.

Female Body Form

In 1993, Singh proposed that, although preferences with respect to female body weights vary cross-culturally, men universally prefer women with a low waist-to-hip ratio (WHR). Women have lower WHRs than do men, largely due to the fact that women tend to store fat in the hips as well as breasts, which is selectively available for gestation and lactation. It now appears that, across a wide variety of cultures (though see below), men do prefer a lower-than-average WHR (most preferred typically being about 0.7, compared to a mean in most populations of about 0.75–.80; e.g., Singh 1993, 1994a,b; Singh & Luis 1995; compare Tassinary & Hansen 1998, but see Streeter & McBurney 2003).

The primary benefit of this preference may ancestrally have been the same as a benefit of

a preference for feminine faces: Low WHRs reflect a history of energy balance and flux that promotes allocation of energy into reproductive effort. The proximate mechanism may involve estrogens. Indeed, Jasienska et al. (2004) found that, within a Polish population, women with lower WHRs and larger breasts have greater fecundity than other women, as assessed through precise measurements of estrodial (E2) and progesterone. Quite possibly, reproductive women's tendency to store fat on the hips and breasts evolved as adaptations for creating a low center of gravity appropriate for carrying fetuses and babies and putting fat where it can readily be converted for lactation, respectively (e.g., Pawlowski & Grabarczyk 2003). As a correlate of fecundity, however, it may have coevolved as a signal of quality, with mating benefits possibly leading to some exaggeration and display.

If facial femininity and attractive body shapes signal overlapping qualities, one might expect them to covary across women. Penton-Voak et al. (2003) reported a significant, modest correlation between facial attractiveness and WHR in a U.K. sample ($r = -.28$). By contrast, Thornhill & Grammer (1999) found a near-zero correlation ($r = 0.013$), despite correlations between attractiveness of distinct bodily features (e.g., face and back attractiveness). Similarly, R. Thornhill & S.W. Gangestad (unpublished data) found little correlation (or curvilinear relationship) of female WHR with measured facial masculinity ($r = -.07$) or facial attractiveness ($r = -.11$). Body shape and facial femininity contain largely nonredundant information; future research should address their distinct sources of influence.

The universality of a preference for low WHRs has been challenged. Men in two foraging or traditional societies have been claimed to largely disregard WHR and generally prefer women viewed as relatively heavy: the Matsigenka of Peru (Yu & Shepard 1998) and the Hadza of Tanzania (Wetsman & Marlowe 1999). Sugiyama (2004) found a similar preference for large body size in the Shi-

wiar of Ecuador. There, as in other foraging societies studied, however, women have higher WHRs (close to 0.9 on average) than do women in Western populations. Using a sample of figures with variation typical of the Shiwiar and controlling for weight, Sugiyama found that Shiwiar men do prefer smaller WHRs. In foraging societies, female body weight may be a positive predictor of fecundity (e.g., Hill & Hurtado 1996) and obesity may rarely be a health problem (e.g., Brown & Konner 1987). Hence, men may use energy status (stored body fat) as a cue of fecundity and ability to lactate effectively. In Western cultures, energy status appears to be weakly associated with fecundity (Ellison 2003) and hence men weight more heavily indicators of energy balance and flux (e.g., WHR). At the same time, they may prefer women of moderate body mass index (BMI), argued to be a powerful predictor of female body attractiveness in Western samples (e.g., Tovee et al. 1999, 2002).

A key unanswered question is whether and, if so, how selection has shaped adaptations for male preference for female body shapes or sizes to be conditional and depend on local ecological factors that affect predictors of female fecundity. Sugiyama (2004) has proposed that men do have specialized adaptations for preferring women of high fecundity (see also Marlowe & Wetsman 2001), which have been shaped to be sensitive to local conditions, but the nature of such conditional inputs (e.g., food scarcity, distribution of body types, etc.) remains poorly understood. Cultural transmission processes (e.g., Boyd & Richerson 1985) may also play important roles, but these are not well understood either.

Male Physique

Scant research has addressed female preferences for male body features. Dixson et al. (2003) found that women in both Britain and Sri Lanka prefer lean, muscular (mesomorphic) body types most, followed by average and then skinny body types; heavy

WHR: waist-to-hip ratio

BMI: body mass index

(endomorphic) body types are least preferred. Women also prefer men with broad shoulders, relative to waist or hip size (i.e., a "V-shaped" torso; see also Horvath 1981, Franzoi & Herzog 1987, Lindner et al. 1995, Mehrabian & Blum 1997, Hughes & Gallup 2003), average WHRs (Singh 1995), and possibly chest hair (Dixson et al. 2003). To date, these preferences have been studied in few cultures.

A number of potential benefits could explain these preferences: physical protection, nutritional resources, and positive externalities of male status, as well as indirect genetic benefits to offspring. Women particularly prefer muscularity in men as short-term (as opposed to long-term) partners (e.g., Buss & Schmitt 1993), and normally ovulating women may be particularly attracted to muscular men as short-term partners when near ovulation (Gangestad 2004), effects consistent with muscularity functioning partly as an indicator of genetic benefits (Frederick & Haselton 2004). Naturally, however, direct benefits cannot be ruled out.

One question left begging to be asked is why women prefer masculine body traits (fostered by testosterone, which promotes muscle growth; see Ellison 2003) but do not systematically prefer masculine facial features. Possibly, though sharing some influences, body and facial masculinity do not signal precisely the same traits. Future research should examine the independent influences on these traits to address why female preferences for them apparently differ.

BODY MODIFICATION

To the extent that one can produce the signals that have been recurrently associated with high mate quality throughout the history of our species, he or she will activate, in potential mates, their psychological adaptations for choosing suitable mates. These adaptations are vulnerable to deception, and humans have found innumerable ways of modifying their bodies to just this effect. A wide range of methods, from the quotidian (diet and exercise) to the absurd (e.g., buttock implants), may be understood as techniques of enhancing the strength of mate value signals. Men and women alike report using various techniques of appearance enhancement for attracting and/or retaining mates (Buss & Shackelford 1997). Practically every inch of the body surface provides some indication of age, health, strength, and fertility. Although age, per se, may not be an important aspect of quality, age cues are also cues to health and fertility status. Substantial cross-cultural variation in the size of the sex difference notwithstanding, men throughout the world are more concerned with women's physical attractiveness than vice versa, and women who look relatively young are consistently rated as attractive (Buss 1989, Jones 1995).

Among the ways people's faces reliably change with age are decreases in the visible area of the eyes and the red area of the lips and an increase in the size of the nose (Jones 1995). Duncan & Collison (2003) report that extracts from the toxic *Atropa belladonna* (deadly night shade) were first used for pupillary dilation to enhance eye appearance over 2000 years ago. Today botulinum toxin is used for a number of cosmetic purposes, including lifting the eyelids. Blepharoplasty (eyelid surgery) is the third most popular cosmetic surgery in the United States (Meisler et al. 2000). Slightly less popular, but nonetheless routine, procedures include rhinoplasty and collagen lip injections. To some extent, a more youthful facial appearance can be achieved through makeup, but over a million cosmetic surgeries were performed in the United States alone in 1998, and the number is expected to rise in the coming decades (Meisler et al. 2000).

The color, luster, and volume of hair all indicate age and health. The hair of younger women is judged to be of higher quality than that of older women, and it is primarily younger women who choose to wear their hair long (Hinsz et al. 2001). Hair growth tonics of varying efficacy have for hundreds of years been successfully marketed to men concerned

with hair loss. Laser follicular stimulation and countless dietary supplements are purported to reverse or slow hair loss. Hair implants (plugs), toupees, strategic combing, and in a sense, shaving, are also popular ways to cover the problem. For those men and women who have no shortage of hair, but are unhappy with its appearance, the number of products to clean, condition, or color the hair defies a thorough cataloguing.

Tiggemann & Kenyon (1998) describe a youthful feminine look as including a slim body, high taut breasts, and smooth hairless skin. Dieting, exercise programs, weight loss surgeries and medications, breast augmentation and reduction surgeries, liposuction, electrolysis, and shaving can be variously mixed and matched to achieve such an appearance. Removal of body hair by women in many societies is so widespread as to go unnoticed, except by its omission. A survey of female Australian students (Tiggemann & Kenyon 1998) showed that over 99% of female college students in the sample had shaved their leg or underarm hair at some point, and about 92% of the full sample, including high school students, regularly shave their leg and/or underarm hair. The number one reason given by college students was, "It makes me feel attractive," and of high school students, "Body hair is ugly." This is a historically novel position, at least among people of European descent (as most of this sample was), but clearly the idea has gained great popularity.

By the year 2000, more than million women in the United States had either silicone or saline breast implants, but riskier forms of breast implants have been documented from the eighteenth century and primitive brassieres from as early as 5000 years ago (Sarwer et al. 2000). Sarwer et al. estimate the average age of breast augmentation patients to be 31 years and conclude that the weight of the evidence supports improvements in "body image, quality of life, and (a reduction in) depressive symptoms" following cosmetic surgery. Although the ideal breast size varies by culture and period, the authors declare that "large breast size has been more or less in vogue since antiquity" (Sarwer et al. 2000).

Body sculpting, not weight reduction, is the primary purpose of liposuction (Meisler et al. 2000). Corsets, girdles, and other sculpting undergarments have been used to give the appearance of a slender waist (but not hips) for hundreds of years. These facts are consistent with Singh's (1994b) evidence that a low waist-to-hip ratio is a better predictor of women's attractiveness than is thinness. Interestingly, however, in a U.S. sample, thinness itself is so highly valued that 24% of women and 17% of men "would surrender three years of their lives to be thinner" (Alam & Dover 2001).

Breast augmentation patients, compared to controls, report greater health and greater investment in fitness and health, and also report higher rates of having been teased about their appearance in adolescence (Sarwer et al. 2003). A recent review of the psychological and psychosocial results of cosmetic surgery procedures (Honigman et al. 2004) found high satisfaction among recipients of breast reduction and augmentation procedures vis-à-vis self-esteem, confidence, attractiveness, and body image, but something of a mixed bag among recipients of facial surgeries. A number of these people reported being shocked by their new appearance and feeling a loss of identity, an understandable outcome for anyone suddenly confronted with a new face (attractive or otherwise) in the mirror.

CURRENT AND FUTURE DIRECTIONS

Tremendous progress toward an understanding of human physical beauty has been made over the past decade and a half. Prior to that time, the literature offered at best rudimentary understandings of the extent of cross-cultural agreement on physical attractiveness (as well as precise domains of variable beauty standards) or of the impact of specific physical features. Much of our current understanding is owing to evolutionary thinking,

as many lines of research were motivated by hypotheses derived from explicit selectionist theory.

Despite this progress, the next 15 years may produce even greater gains. Key questions beg to be answered. Fundamental issues remain unresolved. Some have yet to be seriously addressed. We discuss five crucial topics for future research.

The Precise Benefits Generating Preferences

We have stressed this topic throughout our discussion. Though researchers have surely not ignored it, in few instances can we draw firm conclusions. Questions remain about the signal value of facial averageness, symmetry, male muscularity, and even sexually dimorphic facial features. Very little is known about the underlying fitness correlates of preferred traits in traditional settings (e.g., do estrodial profiles covary with facial femininity?). In most cases, even less is known about the precise proximate mechanisms that generate them and the factors to which they are sensitive (e.g., does mutation load or pathogen resistance affect facial averageness, symmetry, or the development of sexually dimorphic features?). Both issues are relevant to design arguments pinpointing the ultimate causes of signaling systems (e.g., Kokko et al. 2003). From an evolutionary perspective, this topic is a fundamental one. Fortunately, adaptationist theory offers a rich array of hypotheses about potential benefits to generate fruitful research programs.

The Overlapping and Independent Contributions of Preferred Features

Both men and women are attracted to arrays of features. Different features may signal the same underlying beneficial trait ("quality"; e.g., Thornhill & Grammer 1999), each an imperfect indicator of it (Fink & Penton-Voak 2002). Alternatively, multiple preferences may have evolved because different traits signal different preferred qualities (or resulted from unique sensory biases). Although the former view might suggest that all preferred features should covary, in fact positive, negative, or zero correlations between multiple indicators of the same trait may evolve (Kokko et al. 2003). As with the previous question, answers to this question may require an understanding of the precise fitness correlates and underlying developmental and proximate influences of preferred traits.

The Integration of Different Signals

Whether different features signal the same quality or different underlying qualities, the question of how individuals have been shaped to integrate them arises. Do sexually dimorphic features, averageness, and facial symmetry affect attractiveness additively or multiplicatively—and if the latter, in what manner? Dixson et al. (2003) found that if a male is heavy (endomorphic), variations in WHR or shoulder-to-waist ratio have little impact on his attractiveness; he is seen as relatively unattractive regardless. Among muscular men, however, variations in WHR and shoulder-to-waist ratio considerably affect attractiveness, as the ideal male body type is a restricted mesomorphic type. More generally, however, we have little grasp of these interactions and even less appreciation of how signal integration may have been shaped by selective forces.

The Conditional Nature of Preferences

As noted repeatedly throughout this chapter, preferences may be shaped by selection to be conditional: to depend on particular circumstances that modulate the value of attraction to specific features. This theme is one that has driven a number of recent research programs and should continue to do so. At least four types of condition-dependent preferences have been conjectured.

Calibration of preferences to local ecological and socio-ecological conditions. Despite substantial cross-cultural convergence with respect to standards of beauty such as female facial femininity and averageness, some preferences vary cross-culturally (e.g., female preferences for male facial masculinity, male preferences for female body fat). Do these variations reflect adaptations sensitive to specific ecological inputs that ancestrally affected the value of particular features (e.g., disease prevalence in relation to male facial masculinity; food scarcity in relation to female body mass)? To what to extent are these variations nonadaptive and maintained through cultural transmission processes?

Calibration of preferences to individual variations within culture. Different individuals may differentially benefit from pursuing particular individuals as mates. Just as Little et al. (2001) proposed that attractive women should have a stronger preference for facial masculinity, Johnston et al. (2001) argued that sex-typed, feminine women should particularly favor male masculinity and Brase & Walker (2004) hypothesized that attractive men should particularly value women with low, attractive WHRs. More generally, Scheyd (2004) proposed and found evidence that men's own attractiveness affects their weighting of features that are consensually considered attractive; in three different samples (including one from a rural village in Dominica, West Indies), unattractive men, relative to attractive men, were less drawn to those women found to be most attractive overall. Researchers have also speculated that men differentially disposed to long-term and short-term mating should be differentially attracted to signals of RV (youth) and current fecundity, respectively. Nonetheless, individual differences in weighting or integration of signals affecting attractiveness have barely been addressed. Adaptationist theories clearly speak to them, however; individual differences may be a key testing ground of adaptationist hypotheses about special design.

Preferences vary as a function of relationship context. What may be most attractive in a long-term mate may not be what is most attractive in a short-term mate. Researchers have explored and found differences in standards of attraction across relationship contexts. Most work to date, however, has used self-report measures of preferences (e.g., Buss & Schmitt 1993). None has been done in traditional societies.

Preferences vary as a function of individual circumstances. Until the late 1990s, no one reading the literature would have suspected that women's standards of attraction change across their ovulatory cycles. Owing to specific adaptationist hypotheses, we now know that they change in many ways. What other immediate life circumstances (e.g., pregnancy, mating status, parental status, etc.) affect standards of attraction in ways predicted by adaptationist hypotheses?

The Moderating Effect of "Non-Physical" (or Nonstatic) Features

Attractiveness research often assumes, at least implicitly, that people's attractiveness is judged on the basis of static cues, independent of other information about them. Except in attractiveness research and the print media, however, people's attractiveness is rarely if ever judged on the basis of static representations (photographs). And in traditional human societies, people typically have much information about others to whom they may or may not be attracted. Riggio et al. (1991) found that, although static facial attractiveness strongly predicts attractiveness in a situation in which observers see faces dynamically change, dynamic features also have important effects. And information garnered as a result of repeated interaction with others can change perceptions of individuals' physical

attractiveness, favorably or unfavorably (Kniffin & Wilson 2004). Adaptationist theories may speak to these effects (e.g., see Gangestad et al. 2004, for evidence that women's attraction to dynamic information changes across their cycles).

SUMMARY

We have presented a more-than-skin-deep look at the evolution of physical attractiveness. To summarize in one chapter a signaling system constructed by the mating choices of billions of our ancestors is a challenging task. Nonetheless, we have endeavored to explain how these choices have shaped the preferences and choices of present-day humans. We have presented our perspective on the nature of signaling systems generally and argued that the display and perception of human physical attractiveness form one such system. The details of this particular system are only now coming to light, but the importance of sexual dimorphism and averageness in attractiveness, and of one's own attractiveness or ovulatory state in judging it, are but a few examples of the broad range of fascinating work currently coming out of the field.

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Contents

Linguistics and Communicative Practices

International Anthropology and Regional Studies

Sociocultural Anthropology

Theme 1: Race and Racism

Theme 2: Indigenous Peoples

Indexes

Errata

An online log of corrections to *Annual Review of Anthropology* chapters
may be found at http://anthro.annualreviews.org/errata.shtml