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The evolution of human sexuality

Randy Thornhill and Steve W. Gangestad

The study of human sexuality from the darwinian perspective is in an explosive phase. Recent research is diverse; for instance, the dynamics of heterosexual relationships, the role of honest advertisement in attractiveness, the role of fluctuating asymmetry in sexual competition, and sexual conflict over fertilization, seen in sperm competition adaptations of men and possible cryptic sire-choice adaptation of women. Also, recent research reveals that the sexual selection that designed human secondary sexual traits was functional rather than strictly fisherian.

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The evolution of human sexuality is receiving considerable attention from biologists, psychologists and anthropologists. Pioneers in the 1970s and 1980s demonstrated the scientific promise of applying modern darwinism, with its emphasis on genic and individual selection and adaptation, to a wide range of human activities[1–4], including human sexuality[5]. The current inspiration and motivation to study human sexuality stems from these earlier successes, and to a significant extent from the recent focus on human psychological adaptations, which has generated the discipline of darwinian or evolutionary psychology (EP)[6] (Box 1).

Evolutionary psychology emphasizes that universal mental adaptations will sometimes be sex-specific in design because males and females, consistently throughout human evolutionary history, faced sex-specific adaptive problems in the domain of sexual matters[5,12,13]. A vast body of empirical evidence, based on studies of heterosexuals' interests, behavior and motivations, now demonstrates that men's and women's sexual psyches show the sex-specific design[5,13–15] predicted by sexual selection and related theory[16]. Men are more eager and indiscriminate than women in mating decisions. Women value resources and status of potential mates more, and physical attractiveness and youth of a potential mate less, than men do. A potential mate's personality is generally more important to women than to men, particularly in traits associated with male willingness to invest[17]. Men, as predicted, become discriminating of mates when they will invest. For example, for long-term romantic relationships, both men and women value highly and equally intelligence of a mate, but women's standard for intelligence is significantly higher than men's in short-term, sexual relations (e.g. one-night stands)[18].

Although the sexes predictably use some similar mate attraction tactics, certain tactics that heterosexual men and women use to spark sexually dimorphic mate preference priorities differ[19]. For example, men display resources, status and athleticism more than women do. Women display attractiveness and sexual restraint more than men do. These sex differences in mate attraction tactics are reflected also in tactics of (1) mate retention behaviors, (2) derogation of sexual competitors, and (3) deceptions used in sexual competition[13].

Fantasies function to motivate individuals to achieve social goals that typically promoted the reproductive success of human ancestors[5]. They reveal our evolved preferences more clearly than actual behavior does, because behavior is necessarily constrained by many real-life exigencies. Thus, each sex's distinct sexual nature pertaining to mating decisions is acutely revealed by studies of sex differences in sexual fantasies. Men's fantasies have more explicit sexual content, partner variety and sexual content alone, whereas women's fantasies have more implicit sexual content, non-sexual content, affection, commitment, tenderness and emotionality[20].

Homosexuality has received considerable attention because such sexual behavior is not constrained by the opposite sex, and therefore provides a good test-case for differences in sexual psyches[5]. Homosexual and heterosexual men have the same motivation for non-committal sex and high partner number, but homosexual men score higher in the number of actual brief sexual liaisons and partners in a lifetime. Homosexual and heterosexual women, however, score the same (and much lower than men) in

Box 1. Evolutionary psychology

Evolutionary psychology (EP) is modern adaptationism[7] applied to the mind. An adaptation is a phenotypic feature that is functionally designed by past darwinian selection. Selection favors special-purpose designs because they can best solve the environmental problems (such as finding a mate who is most likely to assist one's reproduction) that generate selection. Accordingly, human psychological adaptations are viewed as special-purpose in function and thus designed to process specific information (so-called ancestral cues) that resulted in maximization of individual reproductive success in human evolutionary history, especially in the past few million years during which the species-specific psychological features of humans evolved. An important principle in EP is that there is a human nature: the human brain is composed of a large number of psychological adaptations that are virtually identical across people everywhere. Evolutionary psychology does not deny that local psychological adaptation, comparable to local adaptation in external physical features, may exist across human populations. Nor does it deny that alternative strategies (genetically distinct phenotypes) evolved by frequency-dependent selection may exist within human populations[8,9]. The major focus, however, is on universal human mental rules that give rise in different environmental settings to the variation in emotions and behavior that have been documented across cultures and recorded in the ethnographic record[6,10]. For a highly readable introduction to EP, see Robert Wright's excellent recent book[11].

motivation for non-committal sex and in lifetime sexual partner number[21].

Human sexual tactics are condition-dependent

In addition to a sex-specific human nature comprising many functionally specialized adaptations, EP emphasizes that environmental conditions cause feelings, preferences, other mental states and overt behavior by virtue of this human nature. Psychological adaptations are information-processing mechanisms and thus react to the cues experienced in the current environment. How environmental contexts affect psychological states and behavior is not capricious because the underlying psychology is the product of historical selection. Men's selectivity in long-term mate choice, mentioned above, is one example.

With the concept of human nature and the importance of context in affecting human nature, EP seeks to understand the patterning of human group differences and within-group individual differences. Thus, an individual human's sexual expression and repertoire is viewed as importantly tied to its sex-specific, species-typical sexual psychology, the immediate ancestral cues (Box 1) faced by the individual, and the ancestral cues encountered during ontogeny. For example, the pursuit of short-term versus long-term romantic relationships by women[22] depends upon whether a woman perceives that men in the environment will invest and commit in relationships[23]. Compared with women who perceive that they are in an environment in which men will invest, women who perceive that they are in an environment where men are not likely to invest, act and dress in a more sexually provocative manner, and use copulation to attract desirable men. This variation can be understood as a facultative response of an evolved female sexual psychology designed for an output of sexual restraint (thus giving cues of paternity reliability) when investing males may be accessible, and less sexual restraint (to access material benefits) when each male can or will invest little[23] (Box 2).

Another example of human sexual nature giving variable but theoretically predictable outputs is female copulatory orgasm. The female copulatory orgasm increases sperm retention and is hypothesized to be an adaptation that biases retention in favor of preferred sires[28]. Women and their mates report more female copulatory orgasms, especially those that promote greatest sperm retention (simultaneous with or after the male's orgasm[28]), when the man has relatively low fluctuating asymmetry (Box 3). The exact ancestral cues affecting women's sexual response during copulation are not yet identified, but the correlation of orgasm and male symmetry would suggest that they may include male behaviors or morphological features associated with male body symmetry.

Adaptation and current adaptiveness

The functional design of an adaptation reveals the type of historical selection that made the adaptation[7]. Identifying and characterizing the design of human psychological adaptations is the means by which the selective forces that produced the human mind can be identified. Evolutionary psychology does not emphasize the importance of current adaptiveness, that is, current reproductive success associated with outputs of psychological adaptations, because current adaptiveness is not a criterion by which adaptation can be identified[7]. Considerable debate has arisen recently about the value of current adaptiveness in the study of human evolutionary history[36]. Evolutionary psychology focuses on evolved phenotypic design and thus on historical selection rather than current selection. Nonetheless, studies of current selection are useful in research on human evolutionary history when they assist thinking about adaptation[37] (Box 4).

The relationship between status and sex partner number in Canadian heterosexual men[39] shows how the absence of current adaptiveness can illuminate evolutionarily novel circumstances. Male status is positively correlated with offspring number in traditional societies and throughout the record of written history[1,13,40], but there is no correlation among Canadian men. However, men's status predicts positively the number of sexual partners men report having had in the previous year, as well as their reported number of current copulatory partners. Women do not show either correlation. This sex difference is understandable if men's brains have design for converting status into partner number, and women's brains lack the adaptation. In the modern West, evolutionarily novel circumstances have eliminated

Box 2. Darwinian developmental psychology

The proximate construction of psychological adaptations is through an ontogeny of genetic and environmental causes. The latter include learning experiences, but learning itself must be understood in terms of functionally specific psychological adaptations. Darwinian developmental psychologists are discovering the ancestral juvenile learning cues that shape adult sexuality. The cues that were predictive of stable circumstances are expected to have long-term effects on an individual's behavior giving rise to stable personality features. For example, father absence during a girl's development appears to prompt speeded development to adulthood and early sexual activity[24,25]. In human evolutionary history, father absence may have been reliably correlated with reduced investment[26] and, under such circumstances, women may profitably use sex to gain the lost paternal resources and protection.

Psychic sexually dimorphic design for social learning is the theoretical foundation for darwinian developmental sexual psychology. Boys are expected to have design for being interested in, learning and remembering cultural information that will promote their access to resources, status and mates when the boys grow up. Girls are expected to have design for being interested in learning and remembering cultural information that will yield effective parenting and effective use of their sexuality to secure benefits from the opposite sex. Parents and other teachers inculcate juveniles according to sex-specific learning adaptations[27]. Across traditional societies, boys are taught to be successful polygynists and girls are inculcated in sexual restraint before marriage and in other behaviors that can raise paternity confidence and improve mate choice. The degree of this inculcation in each sex across societies depends, in males, on the degree of sexual competition boys will face when they become men, and, in females, on the value of paternity behaviors in general in accessing and maintaining marriages with resource-providing men.

Box 3. Fluctuating asymmetry

Fluctuating asymmetry may be a reliable indicator of an individual's phenotypic and genetic quality. Fluctuating asymmetry is deviation from symmetry in bilateral morphological traits for which the signed differences have a mean of zero and are normally distributed in the population. Because the same genes control the development of the two sides of the body on such traits, their asymmetry is thought to result from developmental instability – the imprecise expression of developmental design owing to disruptions during development. Thus, fluctuating asymmetry increases with exposure to disruptive environmental insults, such as parasites and toxins, as well as genetic disruptions, such as mutations, inbreeding and directional selection[29–31]. Within-population differences in fluctuating asymmetry reflect variation in the extent to which individuals have had robust, well-canalized development, either because of variation in resistance to specific environmental disruptions (e.g. pathogens) or variation in exposure to specific environmental disruptions (e.g. mildly deleterious mutations). In a range of species, individuals' fluctuating asymmetry negatively predicts their fecundity, growth rate, survival and mating success[29–31]. Interestingly, fluctuating asymmetry possesses non-zero heritability[32], which may provide the genetic variation for sexual selection based on heritable viability[29–31].

Compared to men with high fluctuating asymmetry, men with low asymmetry have greater facial attractiveness, greater numbers of sex partners, more extra-pair copulations, are chosen as extra-pair copulatory partners more often, and begin sexual intercourse earlier in their life history[33,34]. Also, the mates of symmetrical men show the most reported copulatory orgasms[35].

the positive correlation between male rank and offspring number that exists in traditional societies and existed in recorded and evolutionary history. The male design manifests itself in the West but is non-adaptive, at least in terms of offspring number. The novel event involved in men's non-adaptive status pursuit is almost certainly the widespread use of modern contraception.

Studies of traditional societies can identify the functioning of human sexual adaptations in environments more similar to those in which humans evolved. In the West, there is evidence of a negative correlation between male body symmetry and male investment in romantic relationships[34]. Men with low fluctuating asymmetry invest less time in their romantic partnerships, deceive their partners more, and engage in more extra-pair copulations. However, such men are perceived by self and mate as protectors. Compared to men with high fluctuating asymmetry, those with low fluctuating asymmetry are heavier for their height and are more socially dominant, muscular and vigorous by their own and their partner's ratings. Women may be designed to trade-off certain forms of investment (e.g. time, sexual exclusivity) for others (protection). The importance of male protection to females and their offspring can be observed in the natural human environment[26]. The trade-off to get protection may also partially be the result of women's design for the evolutionary environment of sexual coercion and infanticide from non-pair-bonded males during warfare and between group raids[38].

Sperm competition and mate guarding

As predicted by sperm competition theory, ejaculate size delivered in copulation positively correlates with the proportion of time that a pair-bonded man and woman have spent apart since their most recent copulation. Testicle size shows the same pattern: men who generally spend less time with their mates have larger testicles than men who spend more time with their mates[28]. Time apart from the mate may be an ancestral cue that was processed by the aspect of male sexual psychology that affects differential allocation to testicles and differential release of semen, because it was probably correlated with the probability of insemination of the female mate by a sexual competitor (Box 5).

Sexual jealousy is a sexually dimorphic, psychological mate-guarding adaptation. Men's arousal in the context of sexual jealousy is cued by threats to paternity, that is, cues associated with loss of sexual exclusivity. Women's sexual jealousy is cued by threats of loss of a mate's emotional commitment and thus his investment[13].

Physical attractiveness and attraction

Cross-cultural research has shown that although men place more value on physical attractiveness of a mate than women do, both sexes value it highly[13]. The aesthetic judgments of faces made by individuals of different cultures tend to agree, and children as young as two months show preferences similar to those of adults[41,42]. Facial secondary sexual traits, in addition to conveying sex and sexual maturity (Box 6), may be designed to advertise phenotypic and genetic quality[44].

Testosterone appears to be an immunosuppressor[45]. Estrogen may also negatively impact immunocompetence when at high titers[46]. Sex-hormone facilitated markers may honestly advertise immunocompetence because the high hormone titer needed to produce attractive features simultaneously handicap disease resistance accordingly, and thus can only be afforded by individuals of extraordinary immunocompetence[45]. This model applied to human facial secondary sexual traits suggests that (1) the facial hormone markers are conditionally expressed advertisements of phenotypic quality, and simultaneously (2) the view that attractiveness judgments based on these features arise from psychological adaptation designed to detect mate quality. Disease organisms seem to be important in human attractiveness. The value placed on physical attractiveness in choice of a long-term mate in each sex correlates positively with the prevalence of parasites across human societies[47].

Other evidence that physical attractiveness is not arbitrary has come to light. In both sexes, faces with high bilateral symmetry are more attractive than less symmetrical faces[48]. Interestingly, facial symmetry in each sex correlates with the sex-specific attractive expression of facial secondary sexual traits (e.g. symmetry positively correlates with chin size in men and negatively with chin size in women)[34]. Also, composite faces made from many individual photos are rated more attractive than the majority of the individual photos used to make the composites. This means that, at least for certain facial features (not the secondary sexual traits), being near the mean is associated with greater attractiveness. It has been suggested that facial averageness

Box 4. Coercive sexuality

Evolutionary psychology does not ask if men's sexual coercion in the West is adaptive currently. Instead, it seeks to determine if men's sexual coercion arises from psychological adaptation for rape *per se*, or, alternatively, arises as an incidental effect of psychological adaptation for coercing desired commodities other than sexual access. Only evidence that men process cues that specifically pertain to benefits and costs of sexual coercion in human evolutionary history and that high-benefit/low-cost conditions motivate men's interest and arousal in coercive sexual situations would identify rape-specific psychological adaptation.

Sexual coercion by men is common and thus cannot be explained as a pathology resulting from a selection-mutation balance. Also, its near universal occurrence cross-culturally indicates that it is not the product of high population density or other evolutionarily novel ontogenetic factors in the West. Circumstances in which rape is currently adaptive – if any – in traditional societies without contraception (for example, in the context of a pair-bonded man raping his unwilling mate who is seeking an alternative mate, or in the context of inseminating women in warfare) could help to identify the best experimental stimuli to use in laboratory studies that identify the visual and auditory cues accompanying sexual coercion that arouse men sexually[38].

Box 5. Women's extra-pair matings

Men's design for sperm competition indicates that female extra-pair mating with a male other than a pair-bond mate, such that fertilizable sperm from multiple males were simultaneously in the uterine tract, was a recurrent condition in human evolutionary history. Extra-pair copulations by women are not uncommon[28,34]. These copulations, in part, seem to be directed at men of high developmental stability[34]. Thus, women's extra-pair sex may have functioned in human evolutionary history to obtain genes associated with increased attractiveness and viability of offspring. That good genes of some sort may be pursued by extra-pair mating behavior of women is suggested by the fact that these copulations are over-represented at the fertile stage of the menstrual cycle and are associated with high sperm-retention orgasms[28].

As mentioned, copulatory orgasm is a means by which women can control paternity. Intercopulatory masturbatory orgasm is another female sexual trait that appears to be the outcome of selection on females in the coevolutionary race between males and females for control of fertilization during human evolutionary history. Masturbatory orgasm in women reduces sperm retention in subsequent copulation. Such orgasms are less likely before extra-pair matings than before in-pair matings[28].

marks phenotypic and genetic quality because averageness is likely to covary positively with heterozygosity[44].

The immunocompetence model may also hold for non-facial secondary sexual traits of men. For example, male body mass may honestly signal immunocompetence. Adult body mass is differentiated sexually, with males being larger. This is because of, in part, men's greater muscle mass, which arises at puberty as a result of testosterone. Male body mass in the non-contracepting Ache Indians positively correlates with number of offspring produced, apparently because heavier men are more attractive to women[49]. In the West, women rate male athletic builds more attractive than other male builds[34], and the mates of larger men tend to orgasm during copulation more frequently[35]. Men's mass and athleticism appear to signal men's developmental health, that is, low-fluctuating asymmetry, which may reflect immunocompetence. Thus, male body mass is correlated positively with male body symmetry[35,50], and men of high body-symmetry are more muscular and vigorous than men of low body-symmetry[34]. Men exhibiting developmental stability are more attractive to women (Box 3).

Non-facial human secondary sexual features in women appear to honestly signal phenotypic quality, and higher quality expressions are judged to be more attractive. The sexual dimorphism in waist-to-hip ratio in humans arises at puberty and is apparently facilitated by sex hormones. Waist-to-hip ratio in women correlates negatively with estrogen, age, fertility and health, and positively with age. Low waist-to-hip ratios (0.6–0.7) are maximally attractive in women; low ratios also correspond with absence of pregnancy and mulliparity[51]. Adult female breasts develop at puberty under the influence of estrogen. Women with symmetrical breasts report higher age-independent fertility (number of children) and breast-size symmetry positively affects attractiveness[52].

Current knowledge of human physical attractiveness leads to the conclusion that the sexual selection responsible for designing many of the secondary sexual traits was not fisherian, that is, male and female winners of sexual competition in human evolutionary history were not arbitrarily attractive. Human attractiveness, instead, covaries with functionality. Attractive faces of both sexes signal developmental stability and reflect secondary sexual traits requiring high titers of sex-specific hormones that may connote immunocompetence. The adult male body is attractive when reflecting testosterone effects and athleticism, which covary with developmental health. The adult female body is attractive when it shows developmental stability in breasts and high reproductive potential in low waist-to-hip ratio.

It has been suggested that an evolved preference for symmetry in mates may be an incidental by-product of a pre-existing sensory bias evolved in contexts other than selecting mates of high phenotypic quality (e.g. object recognition or perception in general)[53]. This view has not received support from studies of humans, which indicates that a preference for symmetry would be associated with tangible benefits.

Box 6. Facial secondary sexual traits

Certain human facial features are secondary sexual traits, arising or increasing in size at sexual maturity under the proximate influence of androgens and estrogens. Both sexes have both hormones, but the ratio at puberty is sex-specific. Relatively high testosterone leads to growth of lower face and jaw, cheekbones and brow ridges, and projection of the central face between the brow and bottom of the nose. Relatively high estrogen at puberty prevents this growth, but yields increased lip size. These features distinguish young men's and women's faces[12]. As estrogen declines with female age, testosterone masculinizes the female face. Thus, a highly estrogenized female face marks youth and thus high fertility[12]. Abundant evidence indicates that small lower jaw, and lower face in general, is attractive in women's faces[12,42], By contrast, a large lower jaw is rated as dominant and attractive in the male face[12]. The dominance rating of adult men's faces correlates positively with their amount of previous sexual experience and with testosterone level during puberty[43].

Future directions

At this time, results are equally consistent with secondary sexual traits functioning as markers of ability to provide material benefits and markers of good genes for offspring viability. One promising avenue for looking at the role of viability genes may involve women's and men's adaptations that have arisen from the coevolutionary race between males and females to control fertilization. If women's cryptic female choice adaptations (e.g. copulatory orgasm) select sires with markers of high viability (e.g. low fluctuating asymmetry, major histocompatibility profiles adaptive against common diseases), it would be difficult to explain this form of *sire* choice in terms of sexual selection for good providers or effective sperm competitors, or mere preference of fertile over infertile sperm. Also, if female orgasm adjusts fertilization potential of ejaculates of a female's different mates (by influencing their proximity to fertilization sites[28]) and the males have the same ejaculate quality but differ in viability markers, the case for cryptic female choice of viability genes would be strengthened.

Research on diversity and similarity across cultures and within cultures through time is critical for further understanding of the design of human sexuality. Detailed studies of traditional societies are needed to determine the expression of human sexual nature under conditions that are closer to the human evolutionary environment. Although studies reported in the Human Relations Area Files are not nearly as in-depth as those carried out by human behavioral ecologists[2,37,49], the data in the files are useful for testing many cross-cultural questions about human sexuality[1,27], especially given that Galton's problem, that is, the lack of independence between cultures, has been solved[54]. Darwinian historians have demonstrated the value of darwinism for understanding human sexual behavior across time within cultures[1,40].

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