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Human sexual selection

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Sexual selection favors traits that aid in competition over mates. Widespread monogamous mating, biparental care, moderate body size sexual dimorphism, and low canine tooth dimorphism suggest modest sexual selection operating over human evolution, but other evidence indicates that sexual selection has actually been comparatively strong. Ancestral men probably competed for mates mainly by excluding competitors by force or threat, and women probably competed primarily by attracting mates. These and other forms of sexual selection shaped human anatomy and psychology, including some psychological sex differences.

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Introduction

Recent reviews suggest that human psychological sex differences are typically small [1,2]. For example, Hyde's [2] 'gender similarities hypothesis' states that 'men and women, as well as boys and girls, are more alike than they are different'. Of course, males and females belong to the same species, so we should naturally expect similarity on many dimensions. But the hypothesis that males and females are more alike than different lacks predictive power about where sex differences are likely to lie, and about the direction and magnitude of these differences. Sexual selection theory offers this resolution.

Sexual selection is the type of natural selection that favors traits that aid in obtaining mates. It tends to be strongest where potential mates differ greatly in quality, and especially where members of one sex can monopolize multiple mates, leaving many unmated same-sex competitors [3]. When reproductive success hinges on winning mates, sexual selection may favor even those traits that harm survival if they compensate by boosting mating success. Here, I review evidence, focusing on recent findings, regarding the strength and forms of sexual selection operating over human evolution and consider how sexual selection has shaped human psychology, including psychological sex differences.

The strength of human sexual selection

Some evidence suggests that sexual selection has been relatively weak in humans. Although sexual dimorphisms in anatomy and behavior may arise from other selective forces, the presence of sexually dimorphic ornamentation, weaponry, courtship displays, or intrasexual competition indicates a history of sexual selection [3]. However, men's 15–20% greater body mass than women's is comparable to primate species with a modest degree of mating competition among males, and humans lack the canine tooth dimorphism characteristic of many primates with intense male competition for mates [4]. Moreover, humans exhibit biparental care and social monogamy, which tend to occur in species with low levels of male mating competition [5]. Concealed ovulation also hinders men's ability to monopolize women during the fertile phase of their cycles [6].

Yet, it would be misleading to characterize human sexual selection from these observations alone. To start, sexual selection can operate similarly on both sexes, so the magnitudes of sexual dimorphisms may underestimate the intensity of past sexual selection. More importantly, humans are in fact highly sexually dimorphic along dimensions associated with sexual selection. Humans exhibit modest body mass dimorphism only because of another dimorphism: women are 40% more adipose than men, perhaps for gestating and nursing highly encephalized offspring. So far as we know, other primates are not highly dimorphic in adiposity [7]. When we consider aspects of size that are more directly comparable to nonhuman primates, we find that men have about 40% more fat free mass and 60% more muscle mass than women [8]. Human postcranial skeletal dimorphism is also consistent with a primate species in which males are 45–50% heavier than females [9]. These sexual dimorphisms are outside the range of primates with low levels of male mating competition [10].

Humans are also highly sexually dimorphic in several other traits that appear to have been shaped by sexual selection, including facial shape, facial and body hair, and vocal characteristics such as pitch [4,8,11–13,14•]. And although humans lack pronounced canine size dimorphism, humans employ handheld weapons [4] and fists [14•] rather than teeth in combat. Manufactured weapons are sexually dimorphic insofar as men are their primary

producers and users [4] and are far more effective than teeth; even technologically unsophisticated societies produce weapons capable of dispatching the fiercest animals.

With regard to our mating system, most marriages are monogamous in all societies, but the strength of sexual selection depends not on the modal mating outcome but on the variance. Sexual selection tends to be strongest where reproductive variance is greatest, and where reproductive differences depend most strongly on mating success. In traditional societies, men's reproductive variances are approximately 2–4 times those of women, though these values vary across societies [15] and over time, suggesting that sex differences in the strength of sexual selection are also variable. Notably, transitions to stratified state-level societies pushed harem sizes and male reproductive disparities to extremes exceeding those found in gorillas and even elephant seals in some cases [16].

Humans deviate from perfect monogamy for several reasons, including polygamous marriage, serial monogamy, and infidelity. Polygynous marriage occurs in about 83% of human societies, and men are likelier to reproduce with a new spouse after divorce, making even societies with exclusively monogamous marriage effectively polygynous in terms of mating and reproduction [17]. Humans are unlike most primates with a multi-male social structure, in which males compete for estrous females. Rather, (mostly) concealed ovulation necessitates male competition to monopolize women throughout the cycle [6,18], producing a social structure in which individual males are mated to one or more females embedded within a larger multi-male, multi-female group. As in hamadryas baboons [19], men's proprietariness over their mates helps maintain these embedded harems [17].

Across species, sexual selection predominates in the sex that invests less in offspring and exhibits greater reproductive variance [3]. In humans and other mammals, this sex is males. The more investing sex — usually females — tends to be choosier about mates, and variation in male mate quality favors female traits such as mate preferences that act as filters on which males successfully mate. Women exhibit preferences for male traits thought to reflect mate quality [20,21••,22] and may possess other mate filters, perhaps including orgasm as a mechanism for selective sperm retention [23].

Men are unusual among male mammals in the degree to which they invest in mates and offspring through providing resources, protection, and paternal care. Because time and energy available for reproduction are finite, such investment generally detracts from mating competition. Sexual selection may nonetheless have operated potently among ancestral men due to variance in men's quantity of mates through polygynous marriage, serial monogamy, and extramarital affairs, and in the quality of their partners. Men's allocation of reproductive effort between investment and mating competition appears to track their own competitiveness for mates [24,25], as well as opportunities to invest in current mates and existing offspring — and to be mediated by testosterone [26].

Benefits conferred by men often cannot be shared among women; male investment in one offspring is unavailable to others, and male–male competition and female proprietariness limit men's ability to distribute genetic benefits widely. Variation in male quality thus engenders female mating competition. Women indeed appear to have evolved traits that increase their access to mates. Women's body fat distribution in particular seems suboptimal energetically and biomechanically but effective at attracting mates. Deposition of fat on the breasts, hips, and buttocks is universally attractive to men, although the precise amount and relative distributions of adiposity preferred vary across societies and time [27–29].

In sum, sexual selection has probably been weaker in women than in men, but stronger than in most female primates. Sexual selection has probably been somewhat stronger among men than among many — perhaps most — male primates, but weaker than in the most sexually dimorphic primates, such as gorillas, orangutans, and Hamadryas baboons.

Mechanisms of human sexual selection

Sexual selection can operate through multiple mechanisms, including contests, mate choice, scrambles, sexual coercion, and sperm competition (Table 1). Each of these mechanisms of sexual selection has probably played a role over human evolution, but contest competition — the use of force or threat of force to exclude same-sex competitors from mates — has probably been particularly important in men. By contrast, female mating competition probably mainly took the form of mate choice, which favors sexual ornaments and other traits for attracting mates.

Table 1

Mechanisms of sexual selection probably operating over human evolution.

Mechanism	Description
Contests	•Exclusion of same-sex competitors through force or threat of force
Mate choice	•Preferences or other traits that enhance the odds of copulation and/or conception with mates having particular characteristics
Scrambles	•Competition to locate fertile mates
Sexual coercion	•Use of force or threat against a potential mate, at a cost to her or him, that increases the odds of copulating with the potential mate and/or decreases the potential mate's odds of mating with a competitor
Sperm competition	•Competition within a single female between the sperm of multiple males