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Mate choice decisions: the role of facial beauty

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For most people, facial beauty appears to play a prominent role in choosing a mate. Evidence from research on facial attractiveness indicates that physical beauty is a sexually selected trait mediated, in part, by pubertal facial hormone markers that signal important biological information about the displayer. Such signals would be ineffective if they did not elicit appropriate cognitive and/or emotional responses in members of the opposite sex. In this article, I argue that the effectiveness of these hormonal displays varies with perceivers' brains, which have been organized by the degree of steroid hormone exposure in the uterus, and activated by varying levels of circulating steroids following puberty. I further propose that the methodology used for examining mate choice decisions has general applicability for determining how cognitive and emotional evaluations enter into decision processes.

Introduction

For most human beings, mate selection is a complex real-world decision that is of paramount concern for their future happiness. Such decisions inevitably involve emotional and cognitive assessment of prospective mates, and the ability to integrate these evaluations into the decision process. Given the importance of our final judgment, it is curious that an apparently trivial and ephemeral quality, beauty, appears to play such a prominent role in the decision process. In this article, I examine evidence for the biological importance of facial beauty and its influence on mate choice decisions. Based on these findings, I argue that physical attraction arises from an interaction between a perceiver's brain and a perceived face, both of which have been modified, in a complementary manner, by the actions of steroid hormones. Finally, I propose that this analysis might shed light on how affect and cognition work together in real-world decision processes.

Women's facial attractiveness

In the early 1990s, Langlois and colleagues [1] provided theoretical and empirical support for the hypothesis that the average female face in a population is the most attractive. However, investigators have noted that the overlay averaging procedure used in these studies could blur facial details, increase symmetry, and change proportions [2,3], all factors that could enhance attractiveness. To avoid such potential problems, Johnston and Franklin [4] developed a computer program that allows individuals to 'evolve' their most attractive facial composite. This approach found that evolved attractive female faces are (i) judged to be about 25 years of age, but (ii) possess features and proportions that are systematically different from an average face of that age. Specifically, the lower jaw region is smaller and the lips are fuller than those of the average (Figure 1).

Using a different methodology, Perrett *et al.* [5] independently verified most of these findings and Cunningham *et al.* [6] showed that female faces with small narrow chins, large eyes and fuller lower lips are rated highest in beauty across many different cultures. It appears that the average face within any population might be judged attractive, but the most attractive face differs from the average in a systematic manner. The significance of these differences appears to lie in their hormonal origin.

Boys and girls enter puberty with very similar proportions of muscle, fat and bone but exit puberty as reproductive adults with completely different body shapes and compositions [7]. This metamorphosis is primarily a function of steroid hormones. Under the influence of high estrogen levels, a young woman gains about 35 pounds of fat, changing the shape of her breasts, hips, thighs and lips. By contrast, a young man acquires about one and half times as much muscle and bone mass, controlled by the complex action of androgens (and aromatized androgens) acting both directly and indirectly (via release of growth hormone) on bone and muscle tissues [8,9]. As a result, the average adult male has a longer and broader lower jaw than that of a female, and brow ridge growth results in more sunken narrow eyes.

From this hormonal perspective, attractive female faces are displaying physical features indicative of higher levels of pubertal estrogens (full lips) and lower levels of androgen exposure (short narrow lower jaw and large eyes) than average females. This combination of hormones also appears to be responsible for the female body shape that has been found to be most attractive in industrialized societies and predictive of high fecundity [10]. (The atypical preferences found in some non-industrial societies are believed to be a consequence of imminent threats such as famine or high parasite load [10,11]). In the absence of contraception, female fertility reaches its maximum in the mid-twenties (which is the estimated age of evolved attractive composites), declines by about 20% in

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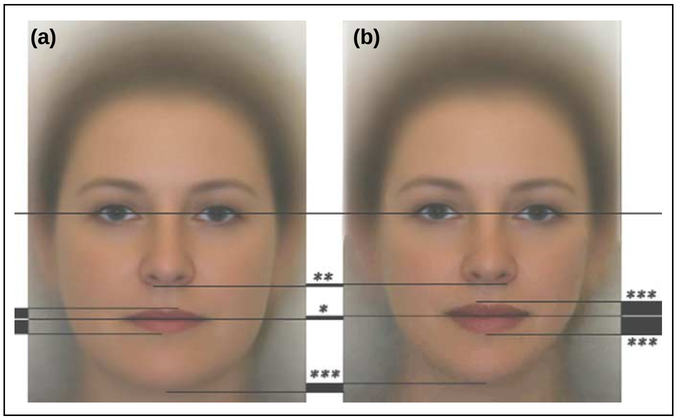

Figure 1. Differences between average and attractive female faces. An average female face **(a)** and an attractive face **(b)** generated by modifying only the lower jaw and lips of the average face, using the program of Johnston and Franklin [4]. Note that the eyes seem larger and the cheekbones appear higher in the modified face. $* = p < 0.05$; $** = p < 0.01$; $*** = p < 0.001$.

the mid-thirties, and then falls precipitously by a further 60% during the forties [12]. The thinning of a female's lips parallels these steep declines in fertility and, in the modern world, it is not uncommon for females to use lipstick or collagen injections for maintaining or enhancing their facial attractiveness.

This evidence suggests that female beauty depends upon specific highly visible hormonal markers that indicate high fecundity. In other female primates, fecundity signals such as labial swelling, chest blisters, or face reddening are quite common [13] and males who are attracted to such cues enjoy clear reproductive benefits. However, in contrast to the pronounced cyclical fecundity signals exhibited by non-human primates, a woman's physical beauty is continuously displayed throughout her entire reproductive years, although some subtle changes in attractiveness at ovulation have been observed [14]. This continuous display of attractiveness might be an adaptation to the large parental investment that arises from prolonged human infant immaturity. A continuously attractive woman can choose from a larger number of high quality males, secure a male's support for a long period of time, and replace him if necessary. Her choice, however, is influenced by the attractiveness of her male suitors.

Sexual selection

Beautiful songs, elaborate mating dances, and brightly colored iridescent tails, are some of the lures used by male animals to the entice members of the opposite sex. The effectiveness of these seductive signals has been evaluated by experimental 'plastic surgery'. For example, increasing the length of a widowbird's tail by adding additional feathers produces super-tailed males who enjoy more reproductive opportunities than their average-tailed competitors [15]. In the absence of human intervention, however, mating with attractive males appears to have real biological benefits. Petrie [16] has shown that peacocks with large tails have higher survival rates and perhaps more importantly, this enhanced survival is evident in his mate's offspring. From a peahen's perspective, it appears that a male's beauty is not just an empty promise. She can gain reproductive benefits by selecting males who exhibit these extraordinary secondary sexual characteristics. Of course all such elaborate testosterone driven displays require significant energy to produce and flaunt so they automatically attest to the physical health of a male suitor, but the demonstrated benefits to an attractive male's offspring suggests that there is more here than meets the eye.

The major threat to the health and welfare of all multicellular organisms is invasion by parasitic microorganisms like bacteria, viruses, protozoa and fungi. Given these circumstances, it would be beneficial for females to select males with excellent immune systems because their offspring would reap the benefits of his good genes. However, good immunocompetence genes are not directly visible but a male's secondary sexual traits might provide a female with an 'honest' signal of their presence. This arises because testosterone acts like a 'double-edged sword'. It is required for the expression of all secondary sexual traits, (songs, dances, ornamental displays, etc), but it is also a powerful immunosuppressant that reduces the effectiveness of a male's immune system [17,18]. A male's body must choose between the competing demands of parasite resistance and the display of secondary sexual characteristics, and only males with the best genetic resistance to parasites can afford the latter choice [18]. Elaborate testosterone dependent displays can serve as 'honest' proxies for good genes because they are simply beyond the means of males with lesser quality immune systems [19,20].

Men's facial attractiveness

There is some controversy concerning the appearance of an attractive male. Before reading about this debate, you can examine your own preferences by completing the experiment presented in Box 1.

Although there is still no complete explanation for the apparently contradictory findings discussed in Box 1, attempts to resolve the issue have uncovered several important variables that influence women's preferences [21–25]. Both the UK and US groups have found that women: (i) shift their preferences towards a more masculinized male face during the high-probability-of-conception phase of their menstrual cycle [22,23]; and (ii) select more masculinized male faces for short-term mates (STMs) than long-term mates (LTMs) [23–25]. These are the very circumstances when females would be most interested in males with 'good genes'.

The relationship between masculine secondary sexual traits and 'good genes' is supported by studies of fluctuating asymmetry (FA). FA is the measured deviation from perfect bilateral symmetry of those physical traits for which signed differences between the left and right sides have a mean of zero over the population [26]. Across many species [27] including humans [28] males with low FAs enjoy better health and more mating success than asymmetrical males. Asymmetries can arise as a result of parasites, toxins or other insults encountered during the course of development, so global body symmetry is believed to be a valid index of immunocompetence [29]. Although several studies have found that the facial attractiveness of males is correlated with their measured

Box 1. What do women want?

Given the central role of hormones in both the displays of male animals and the configuration of attractive female faces, several groups of experimenters have devised methods for systematically manipulating the hormone markers on male faces. One group, based in the UK, developed a method for 'masculinizing' or 'feminizing' male faces by applying caricaturing or warping transforms that exaggerate or reduce facial masculinity based on the differences between an average male and an average female face [22,23]. Using this methodology, they found that both Japanese and UK women expressed a consistent preference for male faces that were more feminized than the average male. A group of US investigators [24,25] manipulated masculinity by morphing an average male face towards an average female face (feminizing) or towards a male face that was rated high in perceived masculinity (masculinizing). In contrast to the UK findings, US females expressed a consistent preference for male faces that were more masculinized that the average male.

The discrepancy between the UK and US findings might have arisen from real cultural differences or from methodological differences. For example, the average male face used in the US studies was developed from a sample of only 16 randomly selected male faces. It is possible that this 'average' face is actually more feminized than the 'average' face used by the UK group. If so, the observed masculinized male preference of US participants might actually be feminized with respect to the UK average face. It is also possible that the UK group's linear extrapolation of female to male differences (caricaturing) to produce masculinized male faces does not capture the real-world hormonal interactions of androgens, estrogens and growth hormone, that underlie facial masculinity.

The four male faces shown in Figure I are designed to evaluate three theories of facial attractiveness. **(b)** is an average male face generated by a simultaneous morph of 117 randomly selected male faces. Votes for this face support the 'average-is attractive' hypothesis. Face **(a)** is the average face warped 20% of the distance towards an average female face. This 'feminized' face is similar to that found to be attractive by UK experimenters. Faces **(c)** and **(d)** are the average male face morphed 20% and 50% of the distance towards a very masculine male face. The 'masculinized' face (d) is similar to that found to be attractive in US studies.

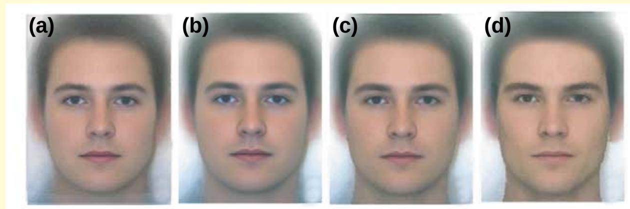

Figure I. Which face is most attractive? (see text for descriptions of how they were created). You can record your vote at http://www.faceprints.us

symmetry [30], Scheib *et al.* [31] have demonstrated that this relationship persists even when judging pictures of one side of a male's face; a situation where cues to bilateral symmetry are absent. These authors concluded that facial masculinity serves as a proxy for bilateral symmetry. A follow-up study [32] demonstrated a significant positive correlation between facial masculinity and body symmetry so it appears that, just like a peacock's tail, the testosterone markers on a human male's face might be attractive because they serve as 'honest' signals of good genetic quality.

The beholder's brain

Women and men agree on the appearance of attractive male and female faces, but electrophysiological and fMRI studies indicate that only attractive faces of the opposite sex evoke an emotional response in the brain of heterosexual observers [33,34]. Such brain sex differences are presumably a consequence of the organizational effects of early androgen exposure. According to the standard model of sexual differentiation of the mammalian brain, the 'default' sex is female and maleness is a consequence of gonadal androgens that de-feminize and masculinize the developing embryo [35]. In humans, studies of androgen insensitivity [36], congenital adrenal hyperplasia [37], idiopathic hypogonadotropic hypogonadism [38], Turner's syndrome [39], and homosexuality [40] are all consistent with this model. The 'default' sex (female) is normally attracted to male features in adulthood but following early exposure to androgens there is a remarkable reversal in preference; the vast majority of the resulting sex (male) is now attracted to female features. Scarbrough and Johnston [25] proposed that smaller variations in androgen exposure might account for some of the differences in mate preference within heterosexual males and females.

Women's mate preferences

To evaluate this hypothesis, Scarbrough and Johnston examined the mate choices of heterosexual females as a function of their '2D:4D' digit ratio (index finger length divided by ring finger length), a sexually dimorphic trait (it is lower in males than females) that is a putative index of androgen exposure in the uterus [41]. They found that compared with high 2D:4D females, low 2D:4D females were psychologically de-feminized (measured by the Bem Sex Role Inventory [42]), physiologically de-feminized (measured by menstrual regularity), bonded poorly to their fathers (measured using a parental bonding instrument [43]), reported shorter intimate relationships with males, and preferred a more masculine male face around ovulation. Although all women had a preference for a masculinized STM who was not significantly different from their attractive male choice, only low 2D:4D women desired similar masculine attributes in their LTMs.

It has been shown that women who prefer masculinized LTMs also like the odor of 4,16-androstadien-3-ol, a putative male pheromone [44,45]. Furthermore, women with low 2D:4D digit ratios also score high on the Sociosexual Orientation Inventory [46], a measure of their willingness to engage in uncommitted sexual activity [47], and they might also have an impaired resistance to parasites [48]. Taken together, these findings indicate that low 2D:4D women are more attracted to a male's secondary sexual characteristics (facial androgen markers and male pheromones), prefer such 'good genes' males as mates (STM, LTM, and at ovulation), but don't bond well (low paternal bonding, short relationships, and promiscuity), perhaps as a consequence of their emotional structure (de-feminized). By contrast, high 2D:4D females are stereotypically female, bond well to males, are sexually reserved, and seek less masculinized males for LTMs, or when there is a high probability of conception.

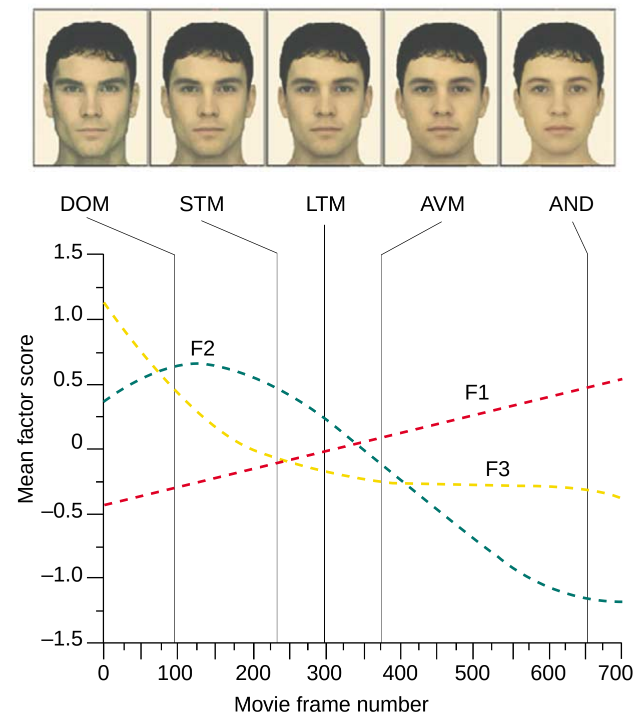

Figure 2. Mate selection and personality traits. Using a movie that morphs a very masculine male face (frame 1 of 700) into an androgynous face, the facial pictures and vertical lines indicate the mean location of participants' dominant male (DOM), short-term mate (STM), long-term mate (LTM), average male (AVM) and androgynous face (AND) selections, with respect to experimentally assigned personality traits. F1 ('Friend' factor) is composed of positive attributes such as sensitive, helpful and trustworthy. F3 ('Enemy' factor) consists of undesirable attributes like selfish, controlling and threatening. The 'Lover' factor (F2) includes sexually exciting, supportive and healthy. The STM selection appears to be the best 'good-genes' choice (Lover factor), while avoiding the negative traits associated with high degrees of masculinity (Enemy factor). The LTM selection appears to trade off some 'good genes' attributes in favor of those required for a good friend and good father (included in F1).

These two mate-choice strategies are best viewed as the extremes of a 'good genes' to 'good dad' continuum, with most females falling somewhere in between. A choice for 'good genes' directly benefits offspring through the inheritance of immunocompetence genes, whereas a 'good dad' choice offers indirect benefits to offspring in the form of paternal care and/or physical and psychological resources (see Figure 2).

The finding that STM and attractive faces are statistically identical suggests that STM selections are primarily based on affective 'good genes' considerations. By contrast, the additional cognitive inference of 'good dad' traits appears to influence LTM decisions. However, as noted above, this preference for 'good dad' traits varies with increasing digit ratio, feminization and bonding, hence implicating hormonal and affective factors in the evaluation. This observation provides additional support for Trafimow's hypothesis [49] that cognitive evaluations depend on the affect (feeling) attached to such cognitions because affect serves as the common currency for integrating emotional and cognitive appraisals into the decision process. Indeed, examining how 2D:4D digit ratio and steroid hormone levels influence the effects of other cognitive factors involved in mate choice, or other decisions, offers a general methodology for revealing how emotional and cognitive processes might be integrated into decision processes.

Conclusions

There is now considerable evidence that (i) pubertal hormone markers influence the attractiveness of male and female faces. I am proposing, however, that the emotional impact of such sexually selected signals depends on the beholder's brain that has also been (ii) organized by hormonal events early in development, and (iii) activated by circulating hormones following puberty. For the most part, I have constructed and supported this model of attraction on the basis of experimental research on facial beauty, but I am also proposing that this hormone-mediated model of sexual selection is applicable to all sexually selected traits, and the list of these might be very large indeed [50].

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