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FEMALE PERCEPTION OF TESTOSTERONIZED MALE FACIAL IMAGES: EVIDENCE OF A CO-EVOLUTIONARY TRADEOFF RESPONSIVE TO CONDITIONS FOR BOTH COMPETITION AND COOPERATION

BY

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DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

Biology

The University of New Mexico
Albuquerque, New Mexico

August, 2010

DEDICATION

For both of my sons, who sacrificed more than anyone for this pursuit. I hope that they may appreciate someday the mollifying effect that a compete-cooperate theory has on gender differences.

ACKNOWLEDGMENTS

For this dissertation to be completed during my allotted time as a PhD student of Biology at the University of New Mexico, much had to be personally overcome. Because of my frequently dire circumstances, the support of each person mentioned here (and others too numerous to name) has been critical to my PhD completion. As I began my dissertation research in absolute independence, along the way I have ultimately been humbled by the truth that ‘no one can do it alone’.

A career in biology is something I first remember dreaming of as a 15 year old, before I became enamored with physiological psychology at the college level, eventually discovering Evolutionary Psychology through Victor S. Johnston at New Mexico State University. Victor enabled me to be the first in my class to graduate with a master’s degree in Experimental Research in Psychology, and although I was invited to the PhD program at NMSU, I left for the lure of a new interdisciplinary Neuroscience program at the University of Arizona. Before a year was up, my husband made the decision to move out of state to pursue medical school at Marshall University, where I chose to follow, working there with Bev Delidow on the biochemical effects of prolactin on brain tissue. My first son was born and I began the prerequisites for the Biomedical Sciences PhD program at Marshall University. When my husband graduated with his M.D., he pursued his residency with UNM at my urging, knowing that world class evolutionists were in tenure there, and UNM is where I took my final undergraduate science class in preparation to apply for the PhD program in Biology. At the same time, I initiated research with a NASA grant that continued for three years, some of which has become the body of this dissertation.

The research I set up was made possible by the support of Paul Watson and Randy Thornhill, who eventually invited me into the PhD program in Biology at UNM. Randy Thornhill provided a clarity of focus in evolutionary science to which I had not yet been exposed. Paul Watson gave me the opportunity to work with a non-human system, Sierra Dome spiders at Flathead Lake Biological Station, and influenced my thinking about consciousness and the social nature of beings, all along serving as a staunch personal supporter through hard times. Working with a non-human species freed my thinking about evolutionary principles in a way that I had not before experienced, profoundly honing my capacity to think outside the box. Eric (Ric) Charnov has been my mainstay throughout my time at UNM, and eventually invited me to become his only student during his final years before retirement. Ric paved the way many times over in removing obstacles during my own final years at UNM. Ric and I have had many interesting talks about humans from a behavioral ecology standpoint, although Ric will still insist that he doesn’t “do humans”. Astrid Kodric-Brown’s training in behavioral ecology, her straight thinking about honest signaling and communication systems, and enthusiasm for my human work continues to be a support. Joe Alcock’s brilliant teaching in evolutionary medicine, generosity and guidance through a co-authored publication process has been integral to the directions I hope to pursue in the future. Angela Bryan’s expertise in health psychology was greatly appreciated, and her timely advice and support has been above and beyond the usual outside committee member.

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FEMALE PERCEPTION OF TESTOSTERONIZED MALE FACIAL IMAGES: EVIDENCE OF A CO-EVOLUTIONARY TRADEOFF RESPONSIVE TO CONDITIONS FOR BOTH COMPETITION AND COOPERATION

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ABSTRACT & OVERVIEW

Theorists and researchers who examine the evolutionary ecology of mating dynamics consider two primary forces, intrasexual and intersexual, as important pressures of selection. Bilateral symmetry and, more controversially, hormone markers in many species, impart information that has been found to influence some aspects of intersexual selection. Both symmetry, as a sign of developmental stability, and hormone markers (i.e., testosteronized traits as cues of immunocompetence) have been classically treated as signals of genetic fitness (Moller & Swaddle, 1997; Hamilton & Zuk, 1982), although neither are consistently shown to correlate with increased mating success. Indeed, results between studies on either trait independently are famously incompatible, but all agree that both of these physical cues result from indirect selection for high genetic quality of offspring. However, there is a growing body of research that has characterized testosterone as key to the calibration of mating and parental efforts, two forms of direct selection. Hence, as with any complete model of mating dynamics, the theory quickly finds itself appealing to both indirect and direct forces of selection. This dissertation is the first study that simultaneously considers the effects of both, using the two cues of testosterone and symmetry.

The studies that comprise this dissertation are designed to discover whether symmetry and testosteronized traits communicate the same (e.g., genetic integrity) or different (e.g., behavioral propensity) information or perhaps some mix of content under variant conditions. *Homo Sapiens,* an altricial species with a biparental mating system, is the chosen species of focus. These studies yield a new organizing framework for a theory of social systems that encompass but are not exclusive to mating systems.

Focusing on the nature of the human mating system, this dissertation was a study of female preferences, including behavioral associations with hormone markers, specifically physical cues in the face that reflected 1200 experimental gradations of gender-typical ratios of testosterone to estrogen. As well, experimental stimuli were presented that systematically varied in level of both

testosteronize and symmetry. Finally, detailed questionnaires were administered to gather information about the personal traits of all female participants viewing the experimental stimuli. For some studies, this included calculation of the risk of conception for each female's ovulatory cycle.

Results of the hormone marker studies indicate that females (1) associate extremely testosteronized faces with physical and behavioral traits well-designed for both physical and social competition, (2) significantly associate a lack of testosteronization with pro-sociality, (3) exhibit a tiny but strongly statistically significant shift ($p < .0001$) toward a more testosteronized male when choosing the most *attractive* face during high risk of conception, (4) appear to be maximizing a tradeoff within a compete-cooperate continuum when choosing their most *attractive* faces, and (5) choose an *attractive* male as a function of personal psychometrics and hormonal state.

As expected, another finding (6) showed that symmetry is significantly and consistently preferred by females for attractiveness across all combinations of testosterone and symmetry, while testosterone preferences vary widely and in conjunction with traits of the female viewers. (7) Most pertinent to revision of mating theory, this is the first study to independently test for effects of testosterone and symmetry, and their interaction. Speaking to the large and confusing literature, testosteronization is only preferred for attractiveness when combined with symmetry. That is, symmetry and testosteronization appear to convey separate information that significantly interacts to yield a powerful combination cue. Only when high symmetry and mild-to-moderate levels of testosterone occur together is the male considered attractive, probably because this is the strongest cue of somatic condition as expected from immunocompetence theory (Zahavi, 1975; Hamilton & Zuk, 1982) and maintenance of developmental stability (Thornhill, 1980). It would appear that symmetry may be a more pure marker of genetic integrity while testosteronization cues competitive ability beyond immunocompetence, that varies as a function of female condition.

In sum, these findings are consistent with the assumption that what the male is perceived to offer in both direct behavioral and indirect genetic form as reflected by current condition, is bartered for by the female with her own behavioral and genetic traits, and her condition. In caveat, genetic competence and behavioral predictors cannot be treated wholly separate as purely indirect or direct selection, respectively, since both have heritable components. Kokko et al. (2002) developed a working mathematical model that replaces a Fisherian runaway-good genes dichotomy with a sexual selection continuum, carrying "cheap" choice at one end and costly choice at the other. As long as variation in males continues, female preferences evolve as a response to the genetic correlation between level of male display and breeding value to the female. In this way, female choice is self-reinforcing, allowing for preferences and "sexiness" of sons to build-up genetic correlations (Lande, 1981) at the cheap end of choice, while mounting costliness of traits eventually halts runaway at the opposite end of the continuum. Regarding the results of this dissertation, the same continuum could be used with condition dictating under-developed testosterone and asymmetry for individuals in poor energetic state and only those in good condition or perhaps of highest genetic integrity affording high levels of testosterone while maintaining symmetry. In this way, displays would be an honest indication of traits desirable for offspring.

Another continuum developed in this dissertation involves a novel theoretical framework described as a compete-cooperate continuum, defined as follows. At the compete end of the continuum are those traits specific to individual challenges, whether it be intrasexual competition with conspecifics over resources or mate access, or competition in attracting the opposite sex. In contrast, traits for cooperation are defined as those traits for joining in purpose with one or more conspecifics, such as in parenting effort or group coalitions that may or may not engage in inter-group competition. There is much evidence from the fields of evolutionary development and neuroendocrinology that the social environment of the mother during fetal and infant stages as well as during childhood influence the setpoints for investment of testosterone-driven competitive traits (Kuzawa, 2009), with cooperation as the default, less expensive state.

Re-interpreting evidence at the broad level of bi-directional selection in a compete-cooperate continuum lends insight to understanding highly social species, particularly in the area of mating dynamics but extending to same-sex coalitions, lengthy juvenile periods and variation in life span. These dissertation findings appeal for a revision to theories of mating systems as co-evolution with general social challenges during life history. Many knowns have been established in the area of overall sociality. (1) Intrasexual conflict in the classic view is solvable by selection for traits that can deal with both same-sex antagonism and same-sex coalition (Ladd et al, 2008). (2) Intersexual conflict is expected to exist to some extent but is not addressed directly by this dissertation (Morrow, Stewart, Rice, 2008). (3) Finally, it is expected that both intrasexual and intersexual pressures select for cooperation in social alliances. In this dissertation, findings support special attention to those of high genetic integrity as capable allies. *Specifically, a basis for symmetry as a cue of developmental stability and a signal of genetic fitness is supported, and when symmetry is combined with mild to moderate levels of testosterone the two are significant to female choice, especially for short-term matings at high risk of conception, probably as a signal of current condition reflecting immunocompetence in the current environment.*

Much progress in the understanding of mating systems has been made by asking whether overall “genetic quality” is being used in mating decisions. However, in purest hypothetical form, generic “good genes” *per se* are expected to have small influence, expressly in altricial species, since traits that serve the opposite sex in a more explicit and specific manner will subsume any presumption of nonspecific generic quality. While all traits under selection must have some heritable component, it is not expected that all traits will be selected for simultaneously, under the same directional selection pressures. A more precise approach to traits reflecting genetic fitness is to consider the domain of selection. In this dissertation, developmental stability and immunocompetence were handled as reflections of somatic effort, having both genetic and condition related components that result from indirect selection (Kokko, 2002). Given this, testosteronization was treated primarily as a result of direct selection in the area of reproductive effort, afforded only when immunocompetence is high enough and developmental stability has been maintained as it trades off with another area, that of somatic effort. Lastly, it is integral to life history theory that both somatic effort and reproductive effort are sensitive to the changing social domain and are expected to tradeoff in a manner that maximizes lifetime reproductive success. In this dissertation, it was found that females exposed *in utero* to high androgens in the blood of their mothers who were in uncertain social environments behave differently than those females who have not been exposed *in utero*.

Considered altogether, these factors lead me to propose a general compete-cooperate tradeoff theory of social systems, encompassing mating systems and probably cross species communication (Navara, 2009). There is gaining evidence that testosterone (via inhibin, its controlling factor) directs mating and parenting effort (Gray, 2006). Testosterone, especially in conjunction with low cortisol, is associated with increased aggressive behavior with conspecifics, mates and offspring (Daly & Wilson, 1988) while lower testosterone (especially in concert with elevated prolactin and oxytocin, and lowered vasopressin) is found in pair bonded males, fathers and group coalitions (Kuzawa, 2004; Gray, 2009; Mehta et al., 2009) and is sensitive to changes in cortisol that result from social challenges but not physical challenges (Flinn, 2005).

The existence of individual challenges (i.e., social competition) in tradeoff with alignment-seeking with positive fitness correlates through cooperation (i.e., group formation, mate bonding, offspring care) are two basic economic problems that an adult in any social species must solve. A compete-cooperate spectrum provides a more focused theoretical framework that may unify and illuminate the current profusion of pertinent studies across many disciplines (i.e., development, psychology, psychiatry, policy-making, biology, anthropology, neurology, endocrinology, immunology, computational mathematics, and so on).

In conclusion, the novel aspect of the theoretical framework developed by this dissertation arises largely from the perceived cues of both competition and cooperation in the human, backed by large areas of literature from diverse scientific fields and across many species, particularly mammals. A preference for cooperation is viewed as a result of both intersexual and intrasexual preferences that are in a direct continuum with contrasting design selecting primarily for male physical competitive capacities. Furthermore, this competition-cooperation continuum may even be the greater evolutionary force in species where female parental care is vulnerable to exploitation (Trivers & Willard, 1973). Females of such species will prize males who signal cooperation in addition to genetic integrity and the physical capacity to protect. A preference for those individuals signaling good somatic condition (e.g., reflected by developmentally stability either alone or in conjunction with immunocompetence) is also supported by these data. What an individual has to offer in the way of cooperation, competitive abilities, and somatic condition is as important as those same qualities in the perceiver. This dissertation does not ignore or discount theories of “good genes”, but makes explicit when and what components of “good genes” may be of priority.

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1) **Introduction**

Behavioral ecologists contend that natural selection modifies animal behavior to favor efficient solutions to the problems animals face in their environmental niches. The ultimate evolutionary causes of decision-making can be revealed, in part, by cost-benefit analyses of organisms in their environments (Glimcher, 2002). From the evolutionary perspective, the question is *why* an organism has come to evolve a repertoire of expected responses to its physical environment. Generally speaking, a response must be filtered first through the sensory systems, given meaning by the brain and assigned an output of positive or negative affect, with this manner of proximate mechanisms resulting in approach or avoid behavior. A growing body of literature from a number of evolutionary psychology laboratories around the globe has begun to suggest that proximal and ultimate approaches are beginning to fuse (Gray, 2010; Perret, 2004; Ellison, 2007; Campbell, 2009) as demonstrated by the growing number of developmental scientists that pull from evolutionary biology, behavioral genetics, endocrinology, neurology, anthropology, psychiatry and medicine (Baron-Cohen 2002, 2003; Belsky & Draper 1981; Crespi, 2008; Flinn, 2005; Haig 2009; Hirshleifer ; Kuzawa 2009).

The main tenet of the stepchild field of evolutionary psychology posits that it is possible to define humans by the economic problems they face. Human problems involve tradeoffs from assorted domains that can be unified by but one common currency, the ultimate currency of genetic propagation. Li (2010) found that the sexes differ in what they are less willing to tradeoff. Physical attractiveness was a necessity to men, status and resources were necessities to women, and kindness and intelligence were necessities to both. The presumption is that decisions made today were efficient for one gender or the other in an environment that lasted for some significant period during human evolution, and may or may not be found successful in the modern setting. That all human decision-making can eventually be imparted to reproductive success is a tenet that has received considerable skepticism, from some human social scientists and some biologists who study non-human species. An application of evolutionary theory to humans is the subject of this dissertation.

This dissertation focuses on the physiology and implied social conditions under which pro sociality or competition among conspecifics have evolved, as part of the most intensive and socially complex relation of all, mateships. The experimental questions revolve around whether males may exhibit directly selected behavioral traits that carry a competitive function and that trade off with traits that function in cooperation, separate from indirectly selected traits cuing genetic integrity. Female preferences for both indirectly and directly selected male traits and the traits of the females themselves are studied for insight into the function of social strategies as they may have served in the natural environment of evolutionary adaptation.

From birth to puberty, female and male physical bodies are virtually identical. The farther from the pre-pubertal androgynous state the body develops, the more physiological expense must be spent. Therefore, the more expensive traits built largely by either estrogen dominance in females or testosterone dominance in males are a graded cue reflecting long-term summation of condition swings in the individual over time.

Due to anisogamy and slower gamete production in the female, males typically show the most interest in sexual willingness (i.e., sexual cooperation) of females and will compete greatly for access to females (Bateman, 1948). That is, anisogamy is presumed to set up a wide competitive range in males. It follows that a more developed cooperative repertoire may exist in females, doubly selected for in altricial species who may require social collaboration to meet the needs of offspring. Additional pressure for social cooperation comes from the fact that primates are an outlier in growth rate, growing at about 40% of that observed in other mammals of the same body size (Charnov, 2004). Therefore *Homo sapiens* have a high resource burden due to an unusually lengthy juvenile period. Men have been observed to hunt in order to attract mates and to gain allies, while females were observed gathering from controllable resources, maintaining autonomy yet accepting provisions from any who will share (Hawkes, 2004). Male-male competition and its role in mate selection has been well established, while any role for male cooperation in mate selection has been reasoned as a subject negligible (Trivers, 1972). This dissertation explicitly tests for female interest in male cooperation in the presence of cues of competition as well as genetic integrity and immunocompetence. Reasoning stems from the fact that atriciality is associated with high social interdependency, and mateships are not expected to escape social pressures for cooperation.

2) Do female perceivers agree on behavioral propensities associated with level of facial testosteronization?

Abstract

Research examining androgen levels and behavior across species finds that variants of testosterone are more prominent in males than females and are associated with “bold”, dominant or aggressive behavior (squid, Sinn et al. 2010; many fish, Brown et al., 2007; 2009; birds, Laidre & Vehrencamp, 2008; and mammals, Archer, 2006; Carre et al. 2006, Hermans et al., 2008; Josephs et al., 2003, 2006; Johnson et al., 2007; Mazur & Booth, 1998; Mehta et al., 2008; van Honk et al., 1999, 2001; Wirth & Schultheiss, 2007). Females demonstrate mate preferences that appear to be responsive to behaviors and secondary sexual traits associated with testosterone (Folstad & Karter 1978; Mazur & Booth, 1998 (West Point Cadet Study); Perret, 1994; Zahavi, 1975, handicap principle).

The first study of this dissertation was designed to determine whether human females agree upon the level of testosteronization the believe to be associated with 8 different male functional types that have been studied by other laboratories -- specifically, *dominant, intelligent, good father, healthy, attractive, masculine*, *average* and *androgynous* faces. Female choices were measured used a morphing face (1200 gradations) that was designed to systematically modify an extreme male into an extreme female configuration, with the extreme male exhibiting the highest level of testosteronization. Females could stop the face at any point during its morph with a finely tuned sliding bar control. Females exhibit tight agreement on a four functional male face types: *dominant; masculine; attractive/healthy*, and *good parent*,/*intelligent*/*average*. These face

choices reflect female function in adaptive mate decisions that attend to testosteronization in a systematic way. Specifically, perceived competitiveness and cooperativeness tradeoff in opposition to each other, with competitiveness positively associated and cooperation negatively associated with testosterone.

Background

The large advantage of studying humans is that a researcher can gather a rich verbal report of individual perception, thoughts, intentions, past behavior, and forecasts of behavior. The primary argument, especially for biologists, against using humans to find mating patterns is that societal and familial culture may overshadow or masquerade as evolutionary design and the results may or may not extrapolate to other species. The answer to this criticism is straightforward. (1) The purported small number of humans that may have created an artificial culture that is counter to naturally selected adaptations cannot be found (Alcock, 2001), (2) nor would humans consume a culture that was not within the realm of adaptive desires for which there is a cognitive design to understand and appreciate. That said, being a highly social species, human opinion and behavior are expected to be subject to influence by peers, whether peers are real or imagined. For all data in this dissertation, great efforts were made to make the experimental subjects feel comfortable enough with confidentiality to reveal true behaviors and perceptions. This experiment purposely limited each subject to react to simple stimuli in a private setting wherein the subject believed there was no chance of her responses becoming known to her immediate social group.

In a fraction of a second, the human brain is able to ascertain the physical traits of another person’s face and place a value on them (Johnston & Oliver-Rodriguez, 1997; Oliver-Rodriguez, Guan, & Johnston, 1999). This remarkable feat appears to track fitness indicators that promise function to the perceiver (Thornhill, 2003) generating an emotional response. The current experiment attempts to examine how inferred behavior is associated with level of testosterone.

Most studies of human mating behavior focus on the perception of attractiveness. Indeed, this was the aim of Perrett, May, and Yoshikawa (1994), who demonstrated that faces that are higher in level of “masculinization” are perceived higher in age and dominance, while emotionality, honesty, cooperativeness and parenting ability followed lower masculinity.

Are masculinization and testosteronization the same effect? Most likely, given that an extensive study initiated by the military for purposes of fitting facial equipment was done by Tanner (1978) that recorded variance and averages for most human anthropometric measurements. These measurements confirm the assumption that biological maleness is in the opposite direction to biological femaleness. The majority of consistent male-female differences are the result of bone-growth, which depends upon complex interactions between androgens, estrogens, and growth hormone (Tanner, 1978; Grumbach, 2000). It is well established that pubertal long-bone growth (especially brow ridges and lower jaw) are stimulated by androgens that form testosterone (Tanner, 1978; Marieb, 2008). At puberty in the female, estrogen fuses growth plates and terminates long-bone growth. Individuals vary in overall level of these sex steroidal hormones as well as their ratio of androgens to estrogen. These levels change in a dynamic fashion that is not yet thoroughly understood, often covarying with adrenal hormones, external events, age, and developmental experiences (Kuzawa, 2009).

Johnston and Franklin (1993) found that an attractive female face displays hormone markers (low testosterone / high estrogen) that serve as reliable indicators of fecundity, a finding that was confirmed by others (Perret 1994, 1998; Langlois, 1990; Cunningham, 1986, 1990). In contrast to the research on female facial attractiveness, studies of hormone markers on male facial attractiveness have produced divergent results. For example, although a number of experimenters have demonstrated that women favor a ‘‘masculinized’’ male face possessing a large jaw, prominent brow ridges, and cheekbones (Grammer & Thornhill, 1994; Scheib, Gangestad, & Thornhill, 1999), other studies have reported that both British and Japanese females prefer a more ‘‘feminized’’ male face with a shorter than average lower jaw (Perrett, et al., 1998; Penton-Voak, et al.,1999). Still others have found that a mixture of mature features (large lower jaw, prominent cheekbones and thick eyebrows) and neotenous features (large eyes and small nose) is the most desirable configuration of male faces (Cunningham, Barbee, & Pike, 1990).

Scheib and colleagues (1999) found that attractiveness of male faces as rated by females was correlated with longer lower jaw and prominent cheekbones. Keating (1985) also found that the shape of the lower jaw was an important attribute of male facial attractiveness. Sheib examined the effects of eye-size, lip fullness, brow thickness, and jaw shape, on both dominance and attractiveness ratings. The combination of masculine features (square jaw, narrow eyes, thick eyebrows, and thin lips) enhanced the dominance ratings of male faces, but only a subset of these attributes (square jaw and thin lips) resulted in significantly higher attractiveness ratings. It appears that some high testosterone markers (square jaw), and low estrogen markers (thin lips) influence both the dominance and attractiveness of male faces, but dominance and attractiveness are not identical attributes. Given this disparity, the current study attempts to clarify the role of hormone markers in the perception of behavioral propensities and attractiveness of male facial images.

Some of the discrepancy in findings among male attractiveness studies may be a consequence of differences in the participant populations. Opportunity for female autonomy varies with culture and may effect female preferences. In unstable social environments, females may prefer testosteronization as a cue of dominance (Wirth & Schultheiss, 2006) with chance of protection.

The present study examined how a variety of different facial types representative of having some direct behavioral function serve the female (i.e., *dominant, good father, intelligent*, etc.). If accurate forecasting of behavioral propensities (verified as real by Penton-voak et al., 2006) in a potential mate was important for female reproductive success during human evolutionary history, it is predicted that modern female brains will tightly agree on the functional value of each face type.

METHOD

Participants

The participants were 42 female volunteers between 18 and 35 years of age (M= 22). These women were recruited from the undergraduate population in New Mexico (USA). Participation in the experiment was limited to volunteers who stated that they were (1) heterosexual, (2) not currently pregnant or breast feeding a child and (3) not currently taking any steroid medications or birth control pills. All participants signed an informed consent document indicating that they were volunteering for an experiment on facial preferences that would be conducted over two experimental sessions. They were also informed that they would be asked to provide relevant personal information, all such data would be confidential, and they could withdraw from the experiment at any time.

Apparatus

In 1999, NASA PURSUE program at UNM granted the author funds to cover two semesters of 15 hours/week of minimum wage salary for herself and one other undergraduate student, as well as minimal copying and office supplies in order to perform the pilot studies that led to the experiments comprising this dissertation. The set of experimental stimuli used for the study discussed in this chapter involved use of UNM undergraduate photographs taken by Randy Thornhill laboratory group. The author scanned these photographs into the computer, standardizing size by interpupil distance, which varies little between individuals (Tanner, 1978), straightened head tilt according to methods of Gangestad & Thornhill in prior work, and then used Morph 2.5 software to create black and white facial images for the *average* male and *average* female. Morph 2.5 rendered all the facial images between the average male and average female. As well, the highly feminine female evolved from previous work was used as an anchor point to extend the female end of the morphing continuum beyond the average (Johnston & Franklin, 1993).

After running the pilot studies and developing the accompanying questionnaires (Appendix A), the author then collaborated with V.S. Johnston to ‘evolve’ an extreme male face using a program that employed the genetic algorithm (Holland, 1975). This program (patented by Johnston as “FacePrints”) codes binary strings of 1‘s and 0‘s to represent facial features, while tracking the ratings associated with such features so that similar features are more represented in new ‘generations’ of faces. The version of the genetic algorithm that drove this program also employed such evolutionary concepts as crossover (occurring in sexual recombination) and a mutation rate set at a low biologically relevant level (less than 1%). Human facial raters using the FacePrints program acted in the place of selection to ‘evolve’ their idea of an attractive face, or in this case, an extremely masculine male face.

The ‘evolved’ extreme male acted as an endpoint allowing morphing software to create facial images at points between the extreme and the computed average. The final experimental tool was a color 1200-frame QuickTime movie that gradually morphs from an extremely masculine male facial image into an extremely feminine facial image (see Figure 1). In sum, there were 1200 distinct faces that varied in hormonal markers from which a user could choose by employing a sliging bar control that could be stopped at any point.

Details of the Creation of the Final Morphing Movie *(optional to the reader)*

The final movie was created in four steps. First, sixteen random male and sixteen random female facial images were separately morphed to produce a composite average male and a composite average female image; after fusing about 6-7 faces no further changes in the average traits could be visually detected so 16 appeared to be an ample number to create the average anthropometrics and was verified as average by known measurements taken by Tanner (1978). The male photographs were college students between 18 to 26 years of age at the University of New Mexico, USA. The female pictures were digital photographs of females from California, USA archived on a purchasable CD-ROM photographed by the professional photographer and Japanese artist Akira Gomi (1998), ranging in age from 18 to 30. All of the photographs were taken under constant light conditions and showed faces with neutral expression and with no apparent make-up, facial hair, or adornments (e.g., earrings). Prior to morphing, all pictures were standardized to the same orientation using the procedure described by Rikowski and Grammer (1999). Using the ‘‘Facial Explorer’’ program (Grammer, Fieder, & Fink, 1998), the composite average male and the composite average female image were produced in a single step. [For details on the morphing algorithm itself, see Wolberg (1990), Beier & Neely (1992), Gomes, Darsa, Costa, & Velho (1999)].

Next, extreme endpoints of the morphing movie were needed. The features and proportions of a perceived masculine and a perceived feminine face were ‘‘evolved’’ using the FacePrints software program (Johnston, 1994). The details of this program have been described elsewhere (Johnston & Franklin, 1993). In short, FacePrints employs a genetic algorithm that allows participants to search a multidimensional face-space of more than 34 billion possibilities and find their most masculine or most feminine facial image. Together with the average male and female faces, these extreme masculine and feminine faces defined the features and proportions of the four key data points needed to construct a movie that slowly morphed a highly masculine male face to a highly feminine female face. However, in order to conceal from the present subjects the locations of the extreme masculine and extreme feminine faces that were created by earlier subjects using ‘FacePrints’, both ends of the movie were extrapolated using a five second caricature. That is, the average male to masculine male difference was extrapolated to produce an extremely masculine male facial image and caricaturing the average female to feminine-female difference produced an extremely feminine face. In the final step, all faces were fitted with the same androgynous hairstyle and the movie clips were combined into a single QuickTime movie using Adobe PremiereTM. Manipulating the movie permitted systematic modification of the major features and proportions that differentiate human male from female faces following pubertal surge in hormones (Farkas, 1981). A user could move back and forward through the movie using both a slider control and single frame buttons.

Facial symmetry measures were obtained following the procedure developed by Grammer and Thornhill (1994). Based on the inter-correlations between naive users, this procedure has been shown to produce a highly reliable index of bilateral symmetry (Grammer & Thornhill, 1994; Rikowski & Grammer, 1999). Twelve standard landmarks were identified on the average and extreme male and female images were used in the morph movie. These landmarks included the innermost and the outermost corners of the eyes and the leftmost and the rightmost edges of the nose. The points for measuring the cheekbones were defined as the leftmost and the rightmost pixels of the face on a horizontal line directly beneath the eyes. The x-coordinates of the jaw and mouth were identified as points on a horizontal line passing through the corners of the mouth. The ‘‘Facial Explorer’’ program (Grammer et al., 1998) then measured the midpoints of the six resulting horizontal lines and computed an index of horizontal symmetry by summing the x-axis differences between the midpoints. This analysis revealed that (1) the average male face was very symmetrical (FA = 16) and (2) symmetry decreased systematically toward the extreme masculine end of the movie (FA = 16.5) as a programming artifact controlled by collaborator Bernard Fink (Vienna). In this way, the effect of symmetry was removed so that only the effect of masculinization would predominate the extreme end of the movie. Interestingly, these male facial stimuli are consistent with the immunocompetence theory of testosteronization (Hamilton & Zuk, 1982). That is, immunocompetence is harder to maintain, along with bilateral symmetry, with increasing sexual dimorphism.

Procedure

The identical procedure and questionnaires that were developed under the NASA grant for two semesters by the author were then utilized for another set of female subjects using the new movie. Each woman viewed the morph movie and was told how to use the slider and single step controls to find the male or female facial image that was closest to a specified target face, such as an *androgynous* face. The female participant was then required to use these controls to find the facial image that most closely resembled a set of target faces. The targets were, an average-male face (AvM), an average-female face (AvF), an *attractive*-male face (AtM), an *attractive*-female face (AtF), a *dominant*-looking-male face (DoM), a *dominant*-looking-female face (DoF), a *healthy*-looking-male face (HtM), a *healthy*-looking-female face (HtF), a *masculine*-looking-male face (MaM), a *feminine*-looking-female face (FmF), an *intelligent*-looking-male face (ItM), an *intelligent*-looking-female face (ItF), a *good-father*-male face (GfM), a *good-mother*-female face (GmF), and an *androgynous* face (Andr). In each case, a descriptive phrase was used to clarify the desired target face. For example, an *average* face was described as "a typical male (female) on the street", a *dominant* face as that of a male (female) who was "more likely to give than take orders", an *androgynous* face as "a face that could be either male or female", and an *attractive* face as "the male (female) that you like best from this range of possibilities and may or may not reflect the opinions of others". [See the actual questionnaire as part of the experimental materials exhibited in Appendix A.] The order of these target faces was counterbalanced among participants on their questionnaires to avoid any potential effect of order itself.

As each target face was located, the corresponding movie frame number was noted. When complete, the eight faces that had been chosen by the participant were displayed again in a random order. While each face was visible, the participant was asked to rate the face on 20 different attributes, using a 7-point Likert scale for each rating. These attributes were: physically attractive, sexually exciting, protective, intelligent, coercive, sensitive, impulsive, selfish, trustworthy, good parent, dominant, healthy, masculine, wealthy, volatile, threatening, cooperative, manipulative, helpful, and controlling.

After the face experiment, each participant was given a questionnaire on personal items. Participants also received a debriefing statement.

RESULTS

For all participants, the selected mean frame number, over sessions, was computed for each target face shown in Table 1, ranging from zero to 1200 with zero as the extreme male and 1200 ending in the extreme female. Table 1 describes for male faces the means as follow: DoM (43), MaM (115), AtM (284), HtM (275), GfM (341), ItM (385), AvM (394), Andr (699). The *attractive* male face was significantly more masculine than the *average* male face (t = 4.39 (28); p < .0001) and significantly different from all other target faces with the exception of the *healthy* male face (t = 0.64 (28); p = .74). A similar analysis of the female target faces revealed the following mean frame numbers: Andr (699), AvF (925), GmF (959), ItF (995), HtF (1021), FmF (1053), AtF (1074), DoF (1195). In agreement with prior studies, the *attractive*-female face was significantly more feminized than the *average*-female face (t (28) = 6.93, p < .0001), and differed from all others except the *feminine*-female face (t (28) = 1.17, p = .88). That is, what the females chose as a “*feminine* face” was the same as what they chose as an “*attractive* female face”. This finding on the female face was of academic interest because it confirmed by research what most lay people already suspect about female faces, and showed a similar pattern in level of hormonization to male faces.

Each of the participants selected eight male face types (including the *androgynous*) during each experimental session, and subsequently rated each of these faces on twenty different behavioral attribute scales. Averaged across sessions, this procedure yielded 232 male faces with mean ratings for all twenty attributes for each face. A Principal Components Analysis was performed on the correlation matrix between the 20 attribute ratings that participants had assigned to these faces. Three factors accounted for 75 percent of the variance: 46%, 22%, and 7% respectively. All three factors were rotated using the Varimax method. The rotated factor pattern indicated that the first factor was heavily loaded with negative attributes. In order of importance, these were: threatening, volatile, controlling, manipulative, coercive, selfish, dominant, and impulsive - all characteristics useful in social competition. Again in order of importance, F2 was loaded with the following positive attributes: helpful, cooperative, trustworthy, good father, wealthy, and intelligent - all characteristics of a desirable social partner. Finally, F3 factor-loadings were as follows: physically attractive, sexually exciting, masculine, healthy, and protective - all descriptions of a desirable mate.

DISCUSSION of RESULTS

The morph movie used in the current experiment proved a sensitive tool for examining facial preferences by providing participants who chose among 1200 facial images varying in degree of hormonization. Each chosen face type was recorded as an exact frame number from the movie, with zero at the most testosteronized end of the movie, 700 as the perceived *androgynous* zone, and 1200 at the most estrogenized end of the movie. These hormone markers reflect the real human maleness and femaleness that follows pubertal restructuring (Tanner, 1978; Grumbach, 2000). Indeed, there is much neuroendocrine evidence for brain and behavioral reorganization at puberty (Sisk & Zehr, 2005; Flinn, Gray & Campbell, 2009).

The question was whether females would agree in their perception of the behavioral propensities associated with the systematic variation in testosterone level exhibited by the morphing face. The task was for each female to choose from the 1200 gradations her own idea of which face matched a functional description of a male (i.e., father, dominant, intelligent, and so on). The distribution of choices by females for the average male were tightly centered around the known average male face for the movie. It is important that females are able to recognize and agree on the population average, as the average is verifiable. The chosen average movie face contained virtually identical proportions to the average male facial morphometrics taken by Tanner (1978). It is worth restating that the relative degree of testosteronization associated with a chosen face type was all that varied systematically in these faces. And, female subjects tightly agreed in their choices of any one functional male.

The *androgynous* face, the face agreed upon as appearing “neither male nor female”, is the face that this dissertation presumes is the least physiologically expensive to build (see Figure 2). Androgyny is the morph displaying the least anabolic effect of testosterone and/or estrogen. That is, before puberty there are little to no differences in morphometrics between boys and girls. If after puberty the face remained similar in proportions and features to the pre-pubertal face, little physiological investment has been made. It is under pubertal hormone direction that the bodies and faces of boys and girls undergo changes that result in the features of men and women. The longer and greater the hormonal influence, the more extreme the sexual dimorphism, with the most dimorphic traits being the traits requiring the highest physiological investment. There were functional face types chosen from the continuum between the *average* male and the *androgynous* male. Whatever function testosteronization may communicate about a male to a female, the zone where a male was still perceived as a male but more feminized than the average was ignored by these female subjects when tasked to choose for the 8 experimental face types. As an artifact of building background symmetry into the morph movie, the *androgynous* area contained slightly more symmetrical faces, yet the feminization level of these male faces still averted female choice despite any appeal that symmetry might have had otherwise. Perhaps the feminized male faces appeared too young (Perret, 1994).

Testosteronization controls those aspects of male physiology that are necessary for average male reproductive success, and *most different* from female reproductive success. Since male reproductive succes is most closely tied to successful mating opportunities across species, testosterone is most closely tied to behavior surrounding male-male competition and sexual interactions. Both males and females produce testosterone and estrogen, in different ratios. The daily demands of the primary environment of adaptation upon any human are more similar than not for each gender, while androgens form the biochemical predecessors to testosterone in both genders. A minor biochemical addition to testosterone results in the predecessor for estrogens. Therefore, a “testosteronized” effect on physiology comes from a ratio of both of these steroidal hormones in a proportion that is dominated by testosterone. An “estrogenized” effect on physiology comes from a ratio dominated by estrogen. Yet, both genders have pharmacological receptors for various forms of both estrogens and testosterones.

The data from this study clearly demonstrate that females do not generally carry a preference for extreme testosteronization. If female choice is not driving male traits to extreme levels of testosteronization, what selective pressures are? A more detailed examination of the specific features that are influenced by testosterone at puberty in humans elucidates.

Boys and girls enter puberty with almost identical proportions of muscle, fat, and bone, and nearly identical anthropometric proportions in the face, but they exit this critical phase of development as reproductive adults with significantly different body shapes and compositions. During puberty, a male’s body undergoes a pronounced adolescent growth spurt regulated by aromatized testosterone (Tanner, 1978) in the presence of growth hormone (Grumbach, 2000). By the end of puberty, men have about 1.5 times the skeletal and muscle mass of women, whereas women have stored twice as much body fat as men (Forbes, 1975), especially subcutaneous fat, primarily serving as physiological fuel stores in anticipation of successful pregnancy and lactation (Kaplowitz, 2008). Facial changes parallel these modifications to a male’s body. On average, men have more pronounced bony brow ridges, resulting in sunken eyes in addition to bushier eyebrows set closer to the eyes (Farkas, 1981). Both the nose and the mouth are wider in the male face, while the lower jaw is both wider and longer than that of an average female face (Farkas, 1981). All of these male characteristics appear to have little relevance in today’s world, but they would have been useful during his long ancestral history for arduous physical activity. The enlarged openings of the mouth and nostrils provide effective passageways for the rapid transport of air to and from the lungs. This enhanced airflow, together with the larger male vital capacity of his lungs (Marieb, 2008), is necessary for an adequate supply of oxygen to support the higher metabolic rate and hemoglobin level required for the efficient use of his larger muscle mass (Marieb, 2008).

While male attributes are clearly advantageous during physically strenuous demands. The adaptations around the eyes have been proposed by Zahavi (1975) as having a role in communication of intent. Brows drawn down or together, that shade gaze direction, appear aggressive and/or difficult to read by observers. Another prima facie argument is that a high degree of energy expenditure inevitably entails profuse sweating from the brow and other regions of the body to regulate body temperature. Large bushy eyebrows set close to the eye on protruding brow ridges provide an effective method for excluding sweat from the eye sockets and also offer protection from an overhead sun. Given these considerations, the male physique appears more adapted than the female's for both physical prowess and physical competition.

Physical traits are not the only traits rewired at puberty. Adolescents have immature frontal lobes, with less mylenization of neuronal axons, leaving the brain malleable to hormonal influence (Sisk, 2005). In this way, a behavioral repertoire is coaxed and developed as a male matures. Visible physical features reflect the invisible organization of the brain driving behavioral tendencies. Converging lines of evidence indicate that adolescence may be a sensitive period for steroid-dependent brain organization and that variation in the timing of interactions between the hormones of puberty and the adolescent brain leads to individual differences in adult behavior and risk of sex-biased psychopathologies (Zehr, 2006). For example, males with idiopathic hypogonadotropic hypogonadism whose hormonal replacement was delayed until their 20's did not successfully respond with the sex-typical body and "personality" changes (Zehr, 2006). The neural changes that take place during adolescence open a window of sensitivity to hormonal organization that remains open indefinitely until such hormone-dependent organization results in the gelling of neural circuits and a diminishment of neural plasticity from that point forward (Sisk, 2005). It is during this critical period, lasting several years or more, that the brain is especially susceptible to the influences of pubertal hormones.

Behavioral Predictors

Testosterone has been proposed as playing a primary role in the calibration of mating effort and parenting effort (Gray 2006, Kuzawa, 2009). Face choices by the present female subjects are expected to reflect intrasexual and intersexual selection as the hallmarks of every sexually producing species known (Ernst Mayr, 2001) with humans as no exception.

In these participants' face choices, the levels of testosteronization between the *average* male and the *androgynous* face and the *dominant* male and the *androgynous* face are vastly different. As Table 1 shows, the face chosen as *average*, is 305 frames in the more testosteronized direction than the *androgynous* male, while the chosen *dominant* male and *masculine* male, are respectively 656 and 584 frames away (Figure 3). It was unexpected that the *masculine* face would be less testosteronized than the perceived "*dominant*" male. The *dominant* male is almost wholly at the end of extremity, while the *average* male appears to split the difference between the least physiologically expensive traits and the most extreme traits where the *dominant* male exists. Yet to be *dominant*, a male must make far more physiological expenditure than that required simply to be *attractive* to a female. The finding that the *attractive* face sits at 110 frames farther in the more testosteronized direction than the *average* male face and 241 frames *less* testosteronized than the *dominant* male face. It is not surprising that the attractive male face is more testosteronized than average. But it is unexpected that attractiveness is conceptually closer to the average than to dominance in our females' minds. Only a more fit male can afford to build testosteronized traits, and would therefore be desirable to a female. Again, if female choice is not driving male traits to extreme testosteronization the most apparent alternative selective pressure is physical male-male competition. Social dominance may coincide, or not, with physical dominance (Bryan, 2010).

Support that females are choosing a level of testosteronization based on the associated behavioral traits is more defined by this dataset than any other to date to my knowledge. The first factor of the Principle Components Analysis that accounted for most of the variance, 46%, includes behaviors such as threatening, volatile, controlling, manipulative, coercive, selfish, dominant, and impulsive - all characteristics useful in social competition. The second factor that accounted for about half the variance of the first one (22%), reflects pro-sociality and perhaps parenting, but not individual rivalry.

Females will choose males based upon traits that increase their chances of being a successful mother. That is, a mother whose offspring reach reproductive age and have a maximum number of offspring (Charnov, 1982). Historically, a mother's certainty of her relatedness to her baby is virtually 100%. In contrast, a male does not birth his child and so has some degree of paternity certainty that is less than the female's. Therefore, what increases the chances of being a successful father will have to do more with the chance of becoming a father at all.

From an evolutionary perspective, femaleness and all things in the direction of the average female, ultimately have to do with both becoming a mother and mothering offspring to reproductive age. Becoming a mother is not technically difficult given the abundance of willing males available. But the ability to mother, to anticipate the needs of another who may or may not be able to clearly express needs or in a era that was preverbal (as was the case for much of hominid evolutionary history), is something that requires sophisticated neural wiring. A male with this skill in an altricial species would be appreciated as a mate by a female.

In the data from this study, the faces that females chose for the *average* male, the *intelligent* male and the *good father* were indiscernible from one another. It is plausible that selection by female choice forces a premium on both parenting and intelligence in males of biparental species, pushing the capacities of an average male to peak in these domains. Alternatively, some have argued that the neural integrity of an individual is the ultimate signal of genetic fitness (Geoffrey Miller, 2000). If this is so, one might expect female choice to canalize this trait in conjunction with other traits that combine to make a good mate. Why this is occurring in the average male and not a more extreme male suggests some manner of a costly tradeoff, although what that tradeoff may be for intelligence and extreme testosteronization is not readily apparent. As has already been suggested, one suite of traits associated with good parenting revolves around cooperation and the capacity to read another's 'mind,' that is, to predict the needs of another (Doherty, 2009). The other primary suite of behavior traits, associated with social competition parallels high physicality perhaps reflecting very early non-verbal hominid periods wherein competition took a physical form.

Intelligence would conceivably be useful in intrasexual competition as well as in non-physical forms of social competition appearing with language in *Homo Sapiens*. It is fascinating to entertain the possibilities that might draw intellectual capacity in a direction that is similar to parenting but dissimilar to intrasexual selection. What tradeoffs must exist in order for selection to be in antagonistic directions? For social competition alone, one would expect intelligence to peak in the same direction as the most competition-ready, extremely testosteronized males. Only parenting (mate choice) and general pro-sociality (by both intrasexual and intersexual choice) would appear to oppose the direction of extreme testosteronization. This order of evolution predicts that brain studies would find brain areas for physical competition in older areas of the brain, social competition in the outermost newer areas of the brain, and suppressive effects on physical competition in the newest outermost layer of the cortex. The behavioral traits associated with the second factor of the Principal Components Analysis were, in order or priority: helpful, cooperative, trustworthy, good father, wealthy, and intelligent - all characteristics of a desirable social partner. Perhaps the uncoupling of physicality and sociality was critical for honest signaling of prosociality during the selection process. If those who were not endowed with great muscularity became prosocial by necessity, one would still expect females to prefer those males who have a capacity to physically protect in addition to social cooperation, pulling female preferences and male traits to an extreme end. Why wouldn’t evolution have selected for both prosociality and physicality in the same direction? This study does not directly test for this, but it could be that the cost of empathy halted extreme, standalone prosociality. Overly empathetic individuals may not be able to execute ‘selfish gene’ (Dawkins, 1981) programs in a way that maximizes their own reproductive success as well as those with a more malleable conscious sense of selfish desires.

Alternatively, high intelligence appears to couple with high sociality and is likely a more easily evolved behavioral solution to both intersexual competition pulling traits in the same direction as intersexual attraction to prosociality and parenting cooperation. High intelligence will not easily couple with high physicality as bodily condition dictates heavily the capacity to build a big brain *and* maximal bone and muscle size. Indeed, brain and muscle nutrient flow and blood flow are in opposition to each other as a result of basic mammalian nervous physiology, the para-sympathetic and sympathetic nervous systems (Marieb, 2008). Nutrient availability and disease exposure may have directed this physiological constraint in design.

Genetic Competence

Any trait and trait plasticity is passed on through genes, therefore treating behavioral traits as if they were not part of the plastic design passed along from generation to generation can be misleading. Defining what is meant by male genetic competence quickly becomes obscured by the mix of female pressures upon the male (i.e., protection, nurturing/provisioning/genetic donation of offspring). This experiment was a study in female choice across functional domains, as represented by the face types), but when asked to simply choose the *attractive* male, the face chosen was the same as the *healthy* male. This finding is consistent with the large body of literature across many species that posits that male hormone markers serve as an index of immunocompetence, more fully explaining why females are attracted to such features (Folstad & Karter,1972; Zahavi, 1970; Hamilton & Zuk, 1982).

This dissertation takes a novel approach to immunocompetence by recognizing that, across species, immunocompetence may relate primarily to the first response of “general immunity” (i.e., as a less expensive, and *visible* defense against infection) as opposed to specific immunity (i.e., a very elaborate and expensive secondary immune response including antibody production). The latter is more poor in males than females.

When diverting energy to anabolic processes in the case of building up muscular soma under direction of testosterone, the immune system suffers in specific ways. A “handicap hypothesis” of immunocompetence (Hamilton & Zuk, 1982) contends that only those males in the highest health condition may afford the impact of high testosterone diversion of resources to musculature. Continued or inherently high expression of testosterone may result in a body with greater muscular bulk and strength, but if a male can not afford the anabolic expense of maintaining both immune function and the soma, he will be put into poor health condition, perhaps with damaged developmental stability as indicated by his lack of bilateral symmetry and/or disease symptoms. This is a clear example of a tradeoff between reproductive effort building the competitive and attractive shape of the male body at the cost of somatic effort, health and survival, in part due to immune function.

Preferences for Behavioral Propensities by Females from Different Environments

The current finding that women chose *attractive* male faces that were more masculinized than an *average* male face is consistent with published work in America (Mealey et al., 1999; Thornhill, & Gangestad, 1993) but not in other populations (Perret et al, 1994; 1998 in Scotland and Japan). That is, the *attractive* male face chosen by this sample of New Mexico women possesses more extreme testosterone markers, such as a longer, broader lower jaw, and more pronounced brow ridges and cheekbones than the average male face, while Scottish and Japanese samples preferred a face more feminine than average. The populations of study have differed between researchers. In New Mexico single parent households make up 40% of the population, while in Scotland and Japan, where a more feminized than average male was chosen as attractive, single parent households are at 10.5% (Scotland) and 1% (Japan). Single parent rearing of offspring may indicate instability of the social structure in a population wherein a female would be expected to be attuned to and prefer to be surrounded by good protectors.

In the female, reproductive effort and somatic effort are closely tied in the same direction to reproductive success (i.e., pregnancy, lactation, and child survival to adulthood). In the male, because of his lack of child bearing potential, reproductive effort consists only of attraction and competition. If the male is successful, somatic maintenance need not be afforded at all times.

The close relationship between attractiveness and perceived health is also evident in the analysis of female ratings of male faces for behavioral attributes. Based on their close correlation, a third factor of the Principle Components Analysis (accounting for 7% of the variance) grouped these traits in order of priority: physically attractive, sexually exciting, masculine, healthy and protectiveness. This third factor is referred to as “Attract” and in Figure 4 it is revealed that the relationship between health, attractiveness, and hormone markers, is not linear. Although the ‘‘Attract’’ scores initially increase with facial testosteronization, they reach a maximum value and then decline with further testosteronization, just at the point where females assign “protectiveness” and before the point where females begin associating the competitive traits listed in Factor 1 (the “compete” factor).

CONCLUSIONS

Females choose more testosterone as desirable, but only to a moderate point. Too much testosterone is avoided by the average female. This curvilinear relationship may result from multiple antagonistic selection forces. An examination of Figure 4 shows that the “Compete” factor (F1) increases while the “Cooperate” factor (F2) decreases at high levels of testosteronization. Clearly the women in this study perceived extremely pronounced testosterone facial markers to be associated with a host of negative traits (threatening, volatile, controlling, manipulative, coercive, unfriendly and selfish) in addition to *dominance*, defined as “someone more likely to give orders than to receive them”. The relationship between physical displays of testosterone and behavioral attributes is controversial (see review by Mazur & Booth, 1998). However, at least one rigorous study suggests that such relationships may be valid. Penton-Voak et al., (2006) found that self-reported personality measures of Scottish individuals and ratings of photos of these same individuals by others who did not know them agreed on the same personality measures.

Gonad-to-Gonad Resonance

It has been put forth that aesthetics are an emotive evaluation that is evoked by attributes most important in a hunter-gatherer era than in today’s environment (Johnston, 1999). Preferences in this study result from a positive emotion generated within the brains of women, in response to a complex configuration of visual cues displayed on the faces of males. Such features and proportions of interest in this study are “the promise of function” to the perceiver (Thornhill, 2003). Brain reorganization and facial restructuring that are the result of pubertal hormones (Zehr, 2005) may indicate fitness enhancing attributes that are, or were, of importance in mate choice. When viewed within this framework, facial preferences are not a trivial matter, but rather, the product of the co-evolution of fitness cues, in this case, markers built under direction of gonadal hormones, and fitness monitors (subjective feelings in the brain, such as a preference) that have, or had, important reproductive consequences for both males and females.

A Compete-Cooperate Spectrum

Aesthetic preference of human females can be viewed as an adaptive compromise between the cooperative attributes associated with less testosterone and the competitive attributes associated with more extreme testosteronization. The “Attract” factor (F3), peaks at that point where the Compete and Cooperate factors cross, suggesting that the most attractive face is the one that maximizes the compete and cooperate tradeoff. This is precisely the point where females perceive the competitive factors under the influence of the cooperative factors, and as having protective function.

Finally, females judging females need not be interpreted in any different perspective than has been discussed thus far. Signs of pressure from intrasexual competition are in the same direction as the male. That is, females chose the most estrogenized face as the most socially *dominant*. Similar to the order of male face choices, females chose the next most hormonized (estrogenized) faces as *feminine*, *attractive* and *healthy*. This subset of results suggests that female attractiveness lies in the same direction as male traits important for social dominance or capacity to win attention from the opposite sex, only without any selection pulling female traits in the opposing direction.

Recall that the reproductive value of the female is closely tied to her somatic condition, and so prized by the male may lend such a female social power (Arnfred, 2007; Blaffer-Hrdy, 1981, 1984, 1986, 1999; Schmalt, 2005; Liesen, 2008). Although, female somatic condition is not expected to be the only source of social power that a female may wield even in naturalistic settings (Hawkes, 2009; Voland, 2005). The remaining female faces chosen by females, the *average*, *intelligent* and *good mother* fell together in a group just as they did in the male. In keeping with interpretation for male faces, intelligence and parenting may be canalized to peak in the average female. The overall spread between chosen female face types, as represented by number of frames in the morphing movie, was narrower between the face chosen as the *average*-looking female and the most extreme female face, 270 frames of distance between the female faces as compared to 351 frames for the male faces. Academically, this comparison of females judging males versus female judging females is important for the proposition that multiple selection pressures have pulled male traits in divergent directions, while selection pressures on the female have been in similar directions.

FINAL SUMMARY

In the current study, participants (1) demonstrated agreement on the general behavioral propensities associated with degree of testosteronization, and (2) showed a tight agreement on the eight face types, and (3) of the chosen face types four groupings fell out, (a) *dominant*, (b) *masculine*, (c) *attractive*/*healthy*, and finally (d) the *average* male, which was not significantly different from the *intelligent* male or *good father*. Lastly, this population of females expressed a preference for male faces that were (3) more testosteronized than the average.

By imposing a binary interpretation on patterns in the data, a compete-cooperate spectrum can account for much. Male testosteronization appears to reflect a history of strong selection for traits that reflect competition. Female subjects perceive less testosteronized males as more cooperative. It is expected that a male viewing another male as a social partner would also value traits at the cooperation end of the spectrum. In this sense, intrasexual selection on the male pulls the testosteronized traits in the male in opposite directions, just as the female’s preferences also have a bi-directional effect on selection of male traits by valuing both ends of the spectrum. The most *attractive* face choices center around the point of intersection between perceived competition and perceived cooperation, where males appear both capable and willing to provide protection. Finally, the *healthy* face was not perceived as significantly different from the *attractive* face. Sorting out the value of testosteronization as a cue of health, or somatic condition, is the topic of the next chapter.

3) Bilateral symmetry but not level of testosteronization independently effects female preferences: support for developmental stability and questions regarding the concept of pure immunocompetence signaling.

Abstract

Research across species has found that females shift their preferences toward both higher bilateral symmetry (Thornhill, 1999) and greater testosteronization (Hamilton and Zuk, 1982; Grammer et al., 1994) at high risk of conception. Genetic quality is implied by symmetry as a sign of developmental stability, while in ‘handicap’ fashion testosteronized features may indicate an ability to afford more exaggerated dimorphism despite immunosuppression, and may covary with symmetry. Immunocompetence theory predicts that women will prefer more testosteronization especially during high risk of conception. Yet, some populations of study find attractive more masculinity than the average (American, Johnston et al., 2000) while others prefer less masculinized traits (Scotland & Japan, Penton-Voak et al., 1998). This last confusion of results indicates that masculinity may signal information that is sensitive to qualities of a population. The question of this study is simply, are symmetry and testosteronization conveying the same information, that is, purported genetic quality? Also, does testosteronization signal any information above and beyond genetic quality? To date, no study of any species has manipulated both variables simultaneously in an attractiveness or mate choice study.

Experiment 1 and Experiment 2, comprising this chapter, attempt to tease apart effects of symmetry and testosterone. Experiment 1 tests for shifts toward testosteronization in perceived attractiveness and health with rising risk of conception, while Experiment 2 uses experimental stimuli that systematically vary in degree of testosterone and symmetry designed to force females to choose between the two traits, again at differing level of conception risk.

Background

The ovulatory cycle of a woman in her non-contraceptive and also non-stressed state contains a brief, punctuated interval during which conception risk is high, bracketed before and after by longer phases of low conception risk. As well, in the pleistocene era without contraceptive use, women would have been pregnant or lactating during most of their reproductive years. Therefore, when not at high conception risk, women would be ascertaining potential mates for abilities beyond those for genetic contribution to her offspring, with an interaction expected between genetic integrity and non-genetic traits that directly affect the female’s reproductive success. The experiments of this chapter were designed to determine whether one or both of these domains is communicated by two specific markers, testosterone and bilateral symmetry.

In the preceding chapter of this dissertation and in other labs (Perret et al., 1994; Thornhill & Gangestad, 2006), there are hints that females associate level of testosteronization at times with competition and at times with health. Bilateral symmetry, as an indicator of health, has been constructed as a marker of genetic quality in hundreds of species from plants and sea creatures to insects, fish, reptiles, birds and mammals (Moller & Thornhill, 1998; Leung et al, 1996; Watson & Thornhill, 1994).

Penton-Voak, et al. (2000) have shown that females' preferences for male faces changed as a function of menstrual phase at the time of testing. Females tested during the nine days prior to ovulation (the high conception risk group) preferred a less feminized male face than females that were tested outside of this window (a low conception risk group). The authors interpret their findings as evidence for a conditional mate choice strategy whereby females in the high conception risk group are exhibiting a preference for male facial cues that signal adaptive heritable genetic characteristics, such as immunocompetence (a.k.a., "good genes").

However, these menstrual studies have not shown that the observed change in preference over the menstrual cycle is specific to attractive male faces. To explore the generality of the menstrual effect, Experiment 1 examined how different facial choices (*attractive, average, androgynous, healthy, intelligent, good father, masculine and dominant*) were, or were not, modified by the hormonal state of female viewers. Testosteronization of male faces was manipulated by the morphing movie of earlier studies (Johnston et al., 2000). It was predicted that the face chosen as the most *attractive* to female subjects would shift toward more testosteronization while all other functional face types would not. If so, specificity of the ovulatory effect on perception of male facial attractiveness will be demonstrated, thus providing strong evidence for sophisticated, adaptive function (Williams, 1966). The second study discussed in this chapter clarifies the separate information roles of symmetry and hormone markers.

Methods for Experiment 1

The participants were female volunteers between 18 and 35 years of age (M= 22) from the undergraduate population in New Mexico State University in Las Cruces (USA) and the Ludwig-Boltzmann-Institute for Urban Ethology in Vienna (Austria). Participation in the experiment was limited to volunteers who stated that they were (1) heterosexual, (2) not currently pregnant or breast feeding a child and (3) not currently taking any steroid medications or birth control pills. All participants signed an informed consent document indicating that they were volunteering for an experiment on facial preferences that would be conducted over two experimental sessions. They were also informed that they would be asked to provide relevant personal information, all such data would be confidential, and they could withdraw from the experiment at any time.

Apparatus for Experiment 1

The morph movie detailed in chapter 1 was used to gather this set of data. Relevant to this chapter, it should be noted again that an undetectable background level of symmetry was introduced into all the faces as they changed in degree of testosteronization by Bernard Fink in Vienna. This lent more realism to the facial images and also happened to bias the stimuli in the direction opposite to predictions, thereby a confirmation of predictions would carry all the more power.

Procedure for Experiment 1

During sessions one and two, the female viewed the morphing face and was taught how to use the slider and single step controls to find a male or female facial image that was closest to a specified target face, such as *attractive, average, healthy, intelligent, good parent, dominant, androgynous, and masculine / feminine*. In each case, a definition was used to clarify the named target face (see Appendix A).

After session two, each woman then completed a personal history form that included questions concerning the exact date of her last menses (first day of bleeding), the typical length of her menstrual cycle, regularity of her cycle, her age, her prior hormone use, and her pregnancy history. Finally, each participant was given a debriefing statement that explained the purpose of the experiment, and she was requested to telephone or e-mail the date of the onset of her next menses using an assigned identification number.

For each participant, the date of their last ovulation was computed using either their post-experimental menses report or the reported menses between their experimental sessions. Although the duration of the menstrual cycle varies among females, this variance is almost exclusively confined to the follicular (pre-ovulatory) phase. Thus, ovulation is almost exactly 14 days prior to the onset of the next menses, irrespective of the cycle length (Fluhmann, 1957; Matsumoto, Nogami, & Okhuri, 1962; Lein, 1979). In a 28-day cycle ovulation occurs on about the 14th day; but in a 34-day cycle ovulation occurs on about the 20th day (Katchadourian, 1980).

For Experiment 1, in the absence of direct hormone measures, this counting backwards procedure offered the most accurate method for determining the date of ovulation that was closest to these participant's test dates. Knowing the date of ovulation allowed each subject's menstrual state on the days of testing to be defined in terms of the number of days before or after ovulation (Jochle, 1973).

Predictions for Experiment 1

It is predicted that of all the various face types, only the face chosen as the most *attractive* from the 1200 frame (or rather, 1200 face) movie would shift at high risk of conception. The attractiveness shift is predicted to be in the testosteronized direction, more testosteronized than the face chosen as the most average male face.

Results for Experiment 1

For Experiment 1, analyses were performed to examine only those participants who had been tested during the time of highest conception risk. Based on the probability of conception over the menstrual cycle, the time of highest conception risk was defined as the nine days prior to ovulation (Barrett & Marshall, 1969), see Figure 5 (Jochle, 1973). Twenty-nine of the women had been tested within this high-risk window. A within subject analysis revealed that at high risk of conception women selected an *attractive* male face that was significantly more masculine than their choice outside of this high risk window (t (28) = 2.20, p = .02). Furthermore, no shifts in the subjects' choices were observed for any of the other target faces. These findings replicate and extend the menstrual shift effect (Johnston et al., 2000; Little et al., 2008; Penton-Voak et al., 1999). The observed shift in preference toward a more masculine male face was a change in preference from a mean frame number of 299 during the low-risk phase, to a more masculinized frame of 270 during the high risk phase; a total mean shift size of 29 frames in the 1200-frame morph movie.

For all 29 participants in Experiment 1, the selected mean frame number, over sessions, was computed for each target face for analyses. Zero refers to the frame number representing the beginning of the movie with the most extreme male face, while 1200 was the end of the movie with the most extreme female face. The *attractive* male face was significantly more masculine than the *average* male face for this NM population of women ($t = 4.39$ (28); $p < .0001$) and significantly different from every other target face with the exception of the *healthy* male face ($t = 0.64$ (28); $p = .74$). Table 2 displays the pattern of significance.

Discussion for Experiment 1

In agreement with prior studies done in the USA, (Mealey et al., 1999; Thornhill, & Gangestad, 1993), Experiment 1 results support the conclusion that New Mexico women prefer male faces that are more masculinized than an average male face when at high conception risk. That is, the *attractive* male face possesses more extreme testosterone markers, such as a longer, broader lower jaw, and more pronounced brow ridges and cheekbones than the *average* male face. The same hormone markers are also associated with good health. Specifically, when participants were required to select a *healthy* male face, their choice was not significantly different from the *attractive* male face. This finding suggests that women consider such testosterone markers to be an index of good health and that important health considerations may underlie their aesthetic preference.

Specificity of female preference is highly evident, as predicted from an adaptive framework. Only the *attractive* male face varied as a function of menstrual phase. The overall shift in preference was small, 29 face frames out of the 700 faces perceived as male, yet the shift washighly significant, at p < 0001. No other face type for both males and females: *androgynous, average, dominant, intelligent, good parent,* even *healthy* and *masculine/feminine* faces did not shift with conception risk. This implies that the function for which a female is choosing a face greatly guides her choices, and that the menstrual cycle effect is not a generalized perceptual bias.

That function underlies these female choices is best illustrated by the choices for a *healthy* male face. The mean of the choices for a *healthy* male was not significantly different from the mean of the choices for the most *attractive* face when a female is at low conception risk. Yet, when the same female made her choices at high conception risk, her concept of a *healthy* male remained at the same point, while her concept of the male that is most *attractive* to her at that moment became more testosteronized! Again, the importance of this is that a generalizable perceptual bias toward testosteronization across all functional types of males does not exist. Only an adaptive framework would predict a menstrual cycle shift with such specificity. This suggests that the neural mechanism responsible for generating such a preference is sensitive to circulating levels of hormones that direct female fertility. In support of the notion that hormones effect brain perception, Welling et al., (2008) find that blood circulating levels of testosterone in males predicts the strength of preference for estrogenization in females.

That the preference shift of Experiment 1 is restricted to the time of high conception risk indicates that the *attractive* face may involve factors that would only be most important during high risk of conception, when the male may donate his genetic material to the female for her future offspring. Indeed, immunocompetence theory argues that more testosteronized males are able to afford the associated immunosuppression only if their genetic integrity in other areas is robust enough in the current environment to withstand this testosteronization ‘handicap’. The handicap principle as put forth by Zahavi (1975) presumes no other function for testosterone in the context of female mate choice. In choosing her *attractive* male, female subjects from Experiment 1 who were at high conception risk appear to be, without conscious predilection, responding to testosteronization more strongly, implicating it as a real cue of genetic integrity.

Methods for Experiment 2

The participants were female volunteers from the undergraduate population at the University of New Mexico in Albuquerque (USA) and were treated in exactly the same way as Experiment 1 with two exceptions. (1) urinalysis was performed to confirm ovulation, and (2) new facial stimuli were created.

Apparatus for Experiment 2

Novel facial stimuli were created by this author's request to Ian Penton-Voak at the laboratory of Dave Perrett in Scotland with the study's purpose in mind. Original photographs of undergraduate men were manipulated to vary in three levels of symmetry and "masculinity". Original facial photographs were made more symmetric using software designed by the Perret lab for this purpose, and then less symmetric by caricaturing each original face against the more symmetric version. These three faces were then made 40 percent more feminized and 40 percent more masculinized in a linear fashion (see Figure 6). At greater than 40 percent masculinization, the faces gain random inhuman characteristics. Hence, because this technique moves facial masculinization in a linear fashion, and not according to an anchor point that evolved from the minds of volunteers (as was the case with experimental stimuli described earlier), the changes in masculinization are far more subtle than that of the dramatic range of the morphing movie used in Experiment 1.

Procedure for Experiment 2

For Experiment 2, female undergraduates at the University of New Mexico agreed to attend three one-hour sessions to participate in the study for course credit. During session one, females completed a personal history form that included questions concerning the exact date of her last menses (first day of bleeding), the typical length of her menstrual cycle, regularity of her cycle, her age, her prior hormone use, and her pregnancy history. Calendars were then consulted to count out her reported average cycle length. Counting backward fourteen days from the predicted last day of her current cycle gave a predicted ovulation window for either her current cycle if she was in pre-ovulatory phase or for the next cycle if she was in post-ovulatory phase. A five-day window was determined to attempt to capture the 24 hour luteinizing hormone (LH) surge that precedes ovulation. Urinalysis for LH confirmed real ovulation and pinpointed peak conception risk using OvuSign detection kits with reported 99 percent accuracy. Once the dates for a subject's five-day ovulation window were predicted, the subject was instructed on use of the OvuSign urinalysis kit for each of the five days. The kits were taken home by subjects with detailed instructions for recording the reading of the urine stick. Sessions Two and Three were the experimental sessions, one of which occurred in the five-day high conception risk window and the other session at low conception risk. During the experimental sessions the facial stimuli were evaluated by subjects for attractiveness.

The use of this novel facial stimuli for Experiment 2 involved a different experimental design, a forced choice method. There are two issues that a forced choice paradigm addresses for this study. (1) The facial differences in symmetry and masculinity were subtle, (2) the task to determine attractiveness of what *nearly* appeared to be the same male nine times is not consistent with real world experience. A within-subjects design was used for detection of ovulation by hormonal measures. Nine versions of eight Scottish male undergraduates, varying in three levels each for symmetry and masculinity, totaling to 72 experimental faces. These high resolution faces were printed out at good quality (720dpi resolution) on photographic paper to create a "set" of nine versions of each individual male. The order of the sets for individual males was counterbalanced. The subjects were instructed to shuffle each set of any one male at the end of handling that set to avoid an order bias. The subject was asked to handle one set at a time, and to force a ranking from 1 to 9 for each face. Specifically, the subject placed every printed facial version of any one male (or one set) in one of 9 boxes in a row clearly marked as a ranking, 1 to 9. To be clear, the top of a rectangle read, from the leftmost rectangle, “1 least attractive”, then “2”, “3”... so on, until the rightmost rectangle read “9 most attractive”.

Predictions for Experiment 2

Because as Chapter 2 discusses, masculinity appears to signal the two ends of opposing selection forces in a compete-cooperate continuum that may be sensitive to female condition, and no such behavioral effect has been found for symmetry, it is predicted that symmetry will have a simple uni-directional main effect, while masculinity will not. A large range in sensitivity to masculinity in attractiveness ratings has been demonstrated by this lab priorly, therefore masculinity is expected to strongly covary with symmetry, and an interaction is predicted. For the same reasons, an independent uni-directional effect for masculinity is not predicted.

Results for Experiment 2

Many of the 130 subjects did not test positive for LH, due to the high irregularity of menses in this age group and poor recall of first day of the current menstrual cycle. Women were included in the final analysis if an LH surge was observed, yielding an N of 21 for Experiment 2. Due to the low number of participants included in the analysis, there was not enough power to detect an effect of conception risk. Although results were in the predicted direction: symmetry strongly increased with attractiveness ranking and masculinity was more flatly distributed over the nine attractiveness rankings, Figure 7a.

For the conception risk variable, only the distribution of counts for rankings of 9 are evaluated, again only for those females with high conception risk (CR) confirmed by urinalysis. Each male facial version was cross-classified according to level of symmetry (SYM) and masculinity (MASC), listed in the observed versus expected tables, in order consistent with the observed and expected count titles in Table 2b. The resulting chi-square is 10.076 with a p-value of 0.259. The distributions of counts for ranking 9 do not differ significantly across the two levels of the variable CR. Superficially, it appears that conception risk plays no role in determining facial preference based on level of symmetry and masculinity. Because the expected distribution of data was not significantly different from the observed distribution by chi square (Figure 7b), conception risk can be ignored and a second chi square was performed assuming a random distribution across the 9 facial versions.

The distributions of counts for the highest attractiveness ranking of 9 are basically the same, so another question can be asked. Are the participants assigning ranks at random? To answer this question, a chi-square test for goodness of fit was done, ignoring the variable CR and using the total N of 596 divided by 9 (levels of ranking), the number of combinations of symmetry and masculinity. The resulting chi-square is 179.027 with a highly significant p-value of 1.64^{E-34} (Figure 8). This means it can be said with great confidence that the participants are not assigning rank in a random manner, but are being influenced by symmetry and masculinity in the faces. Table 8 displays the distribution of counts for each of the nine combinations of symmetry and masculinity.

To analyze whether symmetry and masculinity are behaving in the same manner, a logistical regression was done on the two variables, varying in three levels. The main effect of masculinity is non-significant, near perfect to flat ($p = 0.404$), as predicted. Also as predicted, a uni-directional effect of higher attractiveness rankings with increased symmetry is highly significant ($p = 0.0001$).

Are the participants detecting the subtle changes in masculinity in these new stimuli? Two findings indicate that they are. (1) There is a significant interaction for symmetry and masculinity, $p = .0001$, indicating that masculinity in combination with symmetry communicates information regarding male attractiveness to a particular female. It is still possible that, in keeping with findings from Chapter 2, only moderate levels of masculinity in the faces are preferred in curvilinear manner. (2) After rating for attractiveness, subjects then were asked to pick out the face most likely to be a criminal, or untrustworthy. Their choices were overwhelmingly in the direction of asymmetrical, highly masculine males for such a face. If subjects could not detect masculinity changes in the faces, they would not have been able to agree that asymmetrical, highly masculine males appear somehow untrustworthy.

Summary of Results for Both Experiment 1 and Experiment 2 with Discussion

For Experiment 2, participants (1) expressed a preference for male faces that were more testosteronized than the average, (2) significantly shifted their preference toward a further testosteronized face during periods of high conception risk, illustrated by Figure 9, and (3) only the *attractive* face shifted; all other face types chosen by each female stayed the same. This is remarkable given that there were 1200 faces and these subjects were able to settle in statistically significant agreement on the same level of testosteronization for a particular functional type (i.e., *good father, intelligent*) as well as find a face type chosen during one session and again at the next session.

The strongest evidence for adaptation or function in female face choices comes from the observation that only the *attractive* face shifted, and in the predicted direction of further testosteronization during highest risk of conception. This appeared to support the assertion that hormone markers indicate genetic fitness, perhaps by advertisement of immunocompetence. The hormonal state of viewers, as determined by their ovulatory cycle point, modulates the intensity of preference evoked by testosteronization. Despite the confirmed specificity of preference for testosteronization, Experiment 1 leaves open the possibility that testosterone may communicate information that is different from general genetic fitness. This was the experimental question of Experiment 2.

Experiment 2 did not use the morphing face. Instead, completely novel stimuli were used that systematically varied within one individual male the level of his symmetry and masculinization. Females forced an attractiveness rank for every version of each individual male. As predicted, masculinity and symmetry interact to have a significant effect together on female perception of attractiveness. Also as predicted, symmetry yielded a massive uni-directional main effect, increasing with attractiveness rankings. On the other hand, masculinity as teased apart from symmetry separately, resulted in a nearly flat response curve across all attractiveness rankings from 1 to 9 (Figure 7a). This would be expected only if masculinity were communicating different information than symmetry -- especially if that information were bi-directional (traits for competition versus traits for cooperation) and evolve in response to changing female states.

In consideration of the communication value of hormone markers on a compete-cooperate continuum found in Chapter 2, one may expect that the individual traits and condition of a female could be driving her to differentially weigh cues of compete-cooperate behavioral propensities in tradeoff with immunocompetence. Wide variance in female circumstances, experience and somatic condition would explain choices across females that vary widely in preference for testosteronization. For example, if the female is in poor somatic condition for successful conception and pregnancy (Frisch, 2007), or in a volatile social setting (Flinn, 2006) perhaps she may weigh more heavily the compete-cooperate continuum over immunocompetence cues. Individual differences begin to be addressed by the final study of this dissertation, discussed in the next chapter.

4) Beauty is in both the eye of the beholder and what is beheld.

Abstract

An examination of individual differences revealed that women who scored low on a ‘‘masculinity’’ test (1) showed a larger menstrual shift, (2) had lower self-esteem, (3) differed in their choice of male faces for dominance and short-term mates, and (4) assigned different behavioral attributes to the faces they chose for short-term and long-term mates.

Background

Many recent studies have found that hormonal state influences perception. Particularly, facial perception is influenced by testosterone levels of the perceiver (Welling, et al. 2007). Both males and females who have either been given sublingual testosterone or simply vary naturally in levels of blood-circulating testosterone, have been found to have reduced activity in the amygdala fear centers in response to angry faces (Werth & Schultheiss, 2006; Van Honk & Schutter, 2007; Derntl, Windischberger et al., 2009). That is, by reducing fear, higher blood circulating testosterone enhances responsiveness to social threat in the neural circuitry of social aggression in humans (Hermans, Ramsey and van Honk, 2009). A higher circulating level of testosterone has been shown to reduce detection of facial anger in females (van Honk, 2007) and increase men’s preferences for estrogenized female faces (Welling et al., 2008). In addition, Pound et al., (2009) found that circulating testosterone levels rose in men with highly masculinized faces after a challenge task and but not in men with low facial masculinization. Important to the theory, Pound found that baseline testosterone levels were not associated with men's facial masculinity, but sensitivity (responsiveness) to testosterone was.

Raised salivary testosterone in females correlates with early copulatory behavior in humans and adult copulatory readiness across species (ref?). Roney & Simmons (2007) found that females preferred testosteronized physical features most strongly during the luteal (non-fertile phase) of their menstrual cycle and concluded that preference for testosterone followed estradiol peaks, but these researchers failed to control for experiential traits of the female perceivers.

Taken together, testosterone continues to be characterized as that hormone that may be most positively associated with the calibration of reproductive efforts in both males and females by heightening competitiveness and sexuality, or lessening these behaviors in its absence. The current study is a first look at female traits in association with their perception of faces. Specifically, female psychological masculinization, self-esteem and face preferences for short term and long term mates are examined. Self-esteem is presumed as a measure of perceived stability in the environment and/or perceived ability to negotiate the environment. Masculinization of females has been linked to *in utero* environment. Specifically, mothers who experience psychological or physical duress during pregnancy increase the exposure of the fetus to androgens, which in turn influence brain organization (Zehr, 2005).

Procedure

Each woman was evaluated during two experimental sessions that were two weeks apart. During both sessions, she viewed the morph movie and was taught how to use the slider and single step controls to find the male facial image that was closest to the same specified target faces detailed in Chapter 2 and Experiment 1 of Chapter 3. Each chosen face was rated on the same behavioral trait scale used in Chapter 2 of this dissertation.

After session one, each woman then completed a personal history form that included questions concerning the exact date of her last menses (first day of bleeding), the typical length of her menstrual cycle, regularity of her cycle, her age, her prior hormone use, and her pregnancy history.

During the last session, each returning woman was required to respond to the 60-item Bem sex-role inventory (BSRI), and the Rosenberg self esteem (SES) questionnaire (Bem, 1974; Rosenberg, 1965). Using a 7-point Likert scale for each rating, participants also evaluated the desirability of faces varying in testosteronization in the morphing movie as a short-term mate (STM) and a long-term mate (LTM).

Predictions

From a compete-cooperate theory of hormone markers, females who indicate high confidence in their own abilities to manage their environment, as indexed by high scores on the Rosenberg Self-Esteem Scale, may prefer less testosteronized males as they may perceive less need for a protector. From immunocompetence theory, females who report low self esteem may prefer more testosteronization for two reasons. If self esteem indicates the perception that the environment is unpredictable and/or the female may not be able to manage it alone, then (1) attention to cues for a protector may occur, and (2) if her own perceived mortality is at risk, the psychology associated with increased reproductive effort and heightened sexuality may pull attention to cues for high quality genes.

Measured psychological masculinity from the Bem scales is predicted to vary with the size of menstrual cycle shift. Non-pairbonded females were found by Penton-Voak et al. (1999) not to shift in preference toward masculine male faces, while pairbonded females did shift. Although the question was not asked by Penton-Voak, it is possible that the non-pairbonded females differed from the pairbonded females in psychological masculinity. Hence, the reason for including Bem scales in this study.

A mother in an unstable environment may cause neural sensitivity to testosterone and masculinization of her daughters through exposure to androgens in utero (Manning, Scutt, Wilson, & Lewis, 1998; Csatho, Osvath, Bicsak, Karadi, Manning, & Kallai, 2003; Wade, Shanley, & Imm, 2003; Neave, Laing, Fink, & Manning, 2003; Manning, & Taylor, 2001). Such masculinized daughters may exhibit preferences for highly testosteronized males as potential protectors in further concurrence with inter-generational unpredictability of environment. Psychologically feminine subjects may have lacked the exposure to androgens that indicate an unstable maternal social environment, and so may relax their preference toward testosteronization at all times except when they are at high conception risk, when cues of immunocompetence and good genes would take precedence. Furthermore, because masculinized females may be already be maximizing competitive ability in a mate, and weigh competitiveness more heavily than immunocompetence, a smaller menstrual cycle shift is expect for masculinized females. In contrast, because less masculinized females may avoid potentially more volatile, testosteronized males except when genetic quality becomes paramount, a larger menstrual cycle shift toward testosteronization is expected in these females.

Results

There was considerable variance in the size of the menstrual shift among the female participants. These individual differences were clarified by examining the size of the menstrual shift as a function of participants' scores on the Bem sex-role inventory. On this inventory, individuals are classified as androgynous if they scored above the median value of 4.9 on both the masculinity and femininity scales (Bem, 1974). When female participants were classified in this manner, the size of the menstrual shift was significantly larger for the non-androgynous women (56 frames) compared to the androgynous women (-5 frames); t (27) = 2.55, p = .017. A more detailed analysis revealed that the shift in preference toward a more masculine male during the high-risk days of the menstrual cycle was most closely related to a participant's score on the masculinity scale. That is, there was a significant inverse correlation between the size of participants' menstrual shifts and their score on the masculinity scale (r = -.40, p = .03). Also, the size of the menstrual shift was significantly different for participants classified as above or below the median on the masculinity scale (t (27) 2.79: p = .009). As predicted, the low masculinity group's average *attractive* male face changed from frame 298 to a more testosteronized face at lower frame number 245 (a 53 frame shift). A smaller shift occurred as predicted in the high masculinity group, but in an unexpected direction. The high masculinity group mean frame number for face choice changed from 299 to 315, sixteen frames in the feminized direction (see Figure 10). Participants in the high masculinity group, also scored higher on the Rosenberg self esteem questionnaire (t (27) = 2.12, p = .04).

Finally, irrespective of menstrual phase, high masculinity and low masculinity women differed on the facial frame selected to exemplify a *dominant* male; (t (27) = 2.46, p = .02. As predicted, the high masculinity group selected an extreme masculine face (frame 6!), whereas the low masculinity women perceived a much less testosteronized male face (frame 63) as depicting a *dominant* male, also as predicted. This supports the novel hypothesis posed here that high masculinity females may be attending to competitive ability in a social partner important for an unstable social environment.

Figure 10 shows third-order polynomial curves fit to the mean ratings of male faces with respect to their suitability as a short-term mate (STM) and as a long-term mate (LTM). These preference curves are plotted separately for the high masculinity and low masculinity groups. For the high masculinity participants, the LTM and STM rating curves are similar despite level of conception risk. In other words, there was no detectable menstrual cycle shift in perception. At both high and low masculinity scoring females, the preference rating initially increases with increasing masculinization, reaches a maximum value, and then declines with further masculinization as this female. Females may be avoiding extreme levels of testosteronization because they are perceived as the most volatile males, or perhaps other valued traits (e.g., cooperation; immunocompetence/genetic integrity) are reigning in a linear preference for testosterone. This same preference pattern is reflected in the LTM curve of the low masculinity participants, but the STM curve for this group shows a remarkably different pattern. In this case, the desirability of a male as a STM continues to increase with facial masculinization. That is, low masculinity women shift their preference toward a more masculine male face during the high-risk phase of their menstrual cycle, and prefer short-term mates to have extremely testosteronized male features, but not long-term mates. This pattern is consistent with the prediction that low masculinity females may be weighing more heavily the cues of immunocompetence or genetic quality over cues for a good protector.

To examine the relationship between these facial preferences and the behavioral traits assigned to face choices for LTM and STM, behavioral ratings were correlated with the F1, F2, and F3 factor scores of the same 8 different face types as detailed in chapter 2 of this dissertation. For high masculinity participants, their LTM and STM mean ratings were significantly correlated with both the Cooperate ($r = .57$, $p < .001$ and $r = .44$, $p < .001$, respectively) and Attract ($r = .62$, $p < .001$ and $r = .74$, $p < .001$, respectively) factors, but not the Compete factor. Similarly, the low masculinity group’s LTM ratings were significantly correlated with the Cooperate ($r = .41$, $p < .001$) and Attract ($r = .54$, $p < .001$) factors, but their STM ratings were correlated with the Compete factor ($r = .45$, $p < .001$) and not significantly correlated with the Cooperate factor ($r = -.08$). These relationships indicate that the attributes associated with desirable STMs are quite different between the high masculinity and low masculinity participants. This may reflect an emphasis on immunocompetence for low masculinity females and not competitive ability cued by testosteronization in the male faces.

Discussion

Experimental participants showing the largest menstrual shift in their *attractive* male preference were those scoring lowest in masculinity. The actual observed correlations between masculinity scores and the size of the shift indicate that this relationship is a continuum rather than a dichotomy. Although one may view the two ends of the continuum as representing two different reproductive strategies.

The high masculinity female chose STM and LTM faces that remained consistent and relatively stable across their menstrual cycle, with little shift in preference. The low masculinity participants shift their preference significantly toward a more masculinized male both for STMs and during the high conception risk phase of their cycle. That is, the low masculinity group may be most attuned to those cues for “good genes”. An opportunistic strategy to gain “good genes” offers a solution to what Cashdan (1996) describes as a woman’s conflict between finding a mate who will invest (LTM) and securing good genes for her offspring (STM); different males are preferred for different functions.

It could be added, that cues and neural wiring that ready a female for an unpredictable social clime would create a tradeoff different from the investor-genes tradeoff as it is described by Cashdan, who assumes a stable social clime. Although the low masculinity females in this sample did in fact behave according to Cashdan’s tradeoff. These low masculinity females are presumably more free of *in utero* exposure to androgens, with mothers who experienced social stability during pregnancy. In contrast, greater attention to the extremely testosteronized *dominant* males at the far end of the compete continuum would be important in unstable social climes wherein a competent competitor and potential protector may be most valued. The preference of a high masculinity female for an extremely testosteronized (competitive) male appears to override any other considerations, reducing their menstrual cycle shift in preferences to statistical non-significance.

It has also been suggested that long-term and short-term mating strategies arise as a function of the security of attachment to primary caregivers during childhood (Bowlby, 1969, 1973, 1980; Draper & Harpending, 1982). Girls, for example, who grow up without fathers, are more likely to mature earlier, exhibit ‘‘precocious’’ sexuality, have low self-esteem, and have difficulty forming long-term relationships (Chisholm, 1993; Jones et al 1972; Moffitt, Caspi & Belsky, 1992; Surbey, 1990; Draper & Harpending, 1982). Although the current research findings do not directly test these hypotheses, it is congruous that the short-term oriented females were lower in self-esteem and more sensitive to male dominance cues than those making evaluations for long-term mate-choice.

Some have proposed that the dichotomy in female tradeoffs between good genes/short-term strategies and material benefits/long-term strategies is false (Kokko et al., 2002). In practice, pleiotropic effects on mate choice from both natural and sexual selection forces may produce variation in a singular attractive signal. As Kokko states, the goal is to identify specific parameters (e.g., genetic correlations, intensity of selection for individual male traits, net fitness) to discover their magnitudes and to find general patterns to see if they are repeatable across taxa or ecological contexts. Over all four of the experimental studies discussed in this dissertation, it has become apparent that pleiotropic effects and multiple factors are influencing the perception of testosteronized traits. Testosteronization is clearly not a simple variable conveying one type of information. It can vary *in utero* and at puberty to serve organization and restructuring of the brain and body, and it may vary in daily blood circulating levels that are sensitive to social cues to calibrate reproductive efforts. The next Conclusions chapter draws from cross-discipline research to defend the working theoretical framework of this dissertation.

5) **Theoretical Conclusions**

This dissertation studied face preferences in *Homo Sapiens* in attempt to gain insight into the nature of mating dynamics in an altricial species. Two human traits of high research focus in *Homo sapiens* were explored, bilateral symmetry and hormone markers, specifically testosteronization. Both markers have conventionally been characterized by evolutionary scientists as conveying information about genetic quality in female mate choice. Yet, testosterone and not symmetry has been extensively studied in other fields for its effects on behavior, especially as related to the calibration of reproductive effort between mating and parenting domains (Gray, 2006). My experiments were designed to reconcile the large and at times divergent bodies of literature. From the literature and current data emerges a unifying theory, termed as the Compete-Cooperate theory of sociality.

Female reproductive success is more strongly correlated with her own survival and somatic condition than is male reproductive success. From the male's perspective, he must not only compete with other males for resources and mating access, but also be able to attract the female. Since, by definition, altricial species exhibit a long period of dependence during development, and this period of dependence for humans is distinctly exaggerated compared to other altricial species (Geary, 2000), there is a heightened need for the supporting resources for maternal and offspring survival. In a natural environment, much of a human female's lifespan would be spent in a non-fertile state, pregnant, lactating or possibly post-menopausal, and concerned primarily with nutritional acquisition, and to a less pervasive degree, physical safety. Selection would have favored those female hominids that were able to defray energetic costs and personal harm by forming social alliances.

Many researchers have focused on the nature of resource acquisition in modern men and women. My work is concerned more with the evolution of the social brain and the nature of social alliances than resource garnering behavior. Although resource variability and its effect on plastic behavioral strategies is acknowledged as having a central role during the evolutionary history of humans. As a biparental species, human male provisioning would have been important for reproductive success given the unusually lengthy period of dependency for offspring, relative to other species. Indeed, intrasexual competition over resources has been typified as a predominant characteristic of *Homo Sapiens*, and many other altricial species as well. In times of scarce resources, social volatility increases. Whatever the causative agent, social volatility in humans has shaped a brain sensitivity to this volatility that influences mating psychology. As well, this may begin with the psychological spectrum in developing girls and boys (Ellis, 2009 ;Flinn, 2006 ; Gray, 2009). Indeed, there is much neuroendocrine evidence for brain and behavioral reorganization at puberty (Sisk & Zehr, 2005; Flinn, Gray & Campbell, 2009; Penton-Voak, 2000) that suggests that female brains are more prone to social neuroses while male brains move more toward autism.

Gender biases in behavioral tendencies can be demonstrated from toddlerhood, persisting throughout adulthood (Crespi, 2005; Baron-Cohen, 2002). Given the high incidence of such biases that predispose each gender to its own particular log of dysfunctionalities in modern times, it is a paradox as to why natural selection favored such exquisite sensitivity of the stress response to social stimuli in the human child. Longitudinal anthropological study on the island of Dominica (Flinn, 2006) finds that the family environment, comprised of its positive fitness correlates, is a critical mediator of stressful events in a child's world, with stress events predisposing an individual to illness (i.e., viral illness).

Across taxa, empirical research is mounting on the effect of prior social experiences on the resulting biases in behavior such as "boldness" (Oosten, 2010). Studies in non-human species are increasingly pointing to the *social* clime for understanding set points in mating strategies, animal 'personality', immune function, in utero androgen levels, and so on. The challenges that are central to this pattern of sensitivity are essentially the same. Dependence on other conspecifics for aspects that are pertinent to one's reproductive success selects for individuals who are highly sensitive, perhaps even above a necessary threshold for decision-making, such that no subtlety of a social cue is missed.

Decision-making for any organism to maximize lifetime reproductive success involves direction of efforts between reproductive and somatic domains. Testosterone is classically depicted in its role as a toggle within reproductive effort, reallocating mating effort and parenting effort as conditions change. Parenting effort is treated here as a *cooperative* event, while mating effort is classically treated as a mix of access to mates competition over resources. Supporting evidence for these various efforts is laid out in a Compete-Cooperate Continuum detailed in Table 5.

As listed in Table 5, testosteronization results in physical changes, such as increases in muscular bulk, teeth protrusion, jaw size/strength, height (Tanner, 1978), bone density (Marieb, 2008), and hoodedness of brow, as well as decreased display of white in the eye (related to determination of gaze direction by onlookers, Zahavi, 1975). Taken as a whole, well-developed testosteronized traits are the traits of a competitor. The estrogenized traits are essentially the opposite of those of a physically daunting competitor, the more estrogenized (to a point), the more cooperative and nurturing the behavioral and physical response (i.e., estrogen has an inhibiting effect on most testosteronized traits and implicit to the storage of subcutaneous fat as a readily available fuel source, especially during pregnancy and/or lactation). Testosterone's relationship to reproductive effort has been well documented. Higher testosterone has been associated with sexual arousal and earlier coitus in both males and females (Alexander, 1990), as well as earlier onset of puberty as measured by menarche in females (Geary & Flinn, 2000) and first ejaculation in males (Geary, 2000). Testosterone's link to intrasexual competition is the stronger selective force on the male than the female due to competition over both resources and copulatory access, while females do not need to compete typically for copulatory access to males.

Interestingly, testosterone is not linked to a change in the first line of defense in immunity ("primary" immunity). Testosterone's classic immunosuppressive effects appear to be limited to "secondary" immunity or specific immunity, involving antibody production. In general, the more effort being diverted to reproductive efforts by testosterone, the shorter the overall lifespan and decrease in somatic maintenance, as indicated the average male as compared to the average female across species. In contrast, estrogen dominance over testosterone is associated with increased somatic maintenance, with this factor being more closely tied to female reproductive success than male reproductive success due to her carriage of offspring in the womb and its dependence on her for nutrition immediately after in altricial species. Increased somatic effort is associated with boosts to immunity, and increased lifespan. Table 5, lists the supporting literature for the compete-cooperate continuum. Under the reproductive-somatic effort tradeoff, parental effort is placed as somatic effort for females and not males due to the strong link between somatic condition and success of pregnancy and lactation (and rearing of offspring in any altricial species). In contrast, *lower* parenting effort is listed under reproductive effort in Table 5 as more closely associated with *higher* reproductive success in males (Trivers, 1972).

The next continuum in Table 5 parcels out the intrasexual and intersexual dynamics as related specifically to testosterone and competition, contrasting with those related to the absence of testosterone and cooperative behavior. Testosteronization is strongly linked to male-male intrasexual competition, with some evidence for this in female-female competition as well, in the context of access to resources and high value mates. Furthermore, intersexual selection factors associated with testosterone and competition result in the male's attraction of the female. That is, from research detailed in this dissertation, "dominance" (chapter 3), and "health" as advertisement of "good genes" via immunocompetence (chapter 2). Along the same line, female attraction of the male is primarily a result of her fecundity (Johnston & Franklin, 1993) and conceivably her fecundity may determine her social leverage or ‘dominance’ as well.

For traits supported by a lack of testosterone at the cooperative end of the spectrum for intersexual selection in Table 5, parenting capacity is listed as important for male attraction of the female. Directly extrapolating from anisogamy, females are most interested in male cooperation with regard to parenting, while males are more singularly interested in female cooperation with regard to sexual receptivity. Cooperation between the sexes is different from the perspective of each sex. Still falling under intersexual selection is “health” as a parasite-free somatic condition that a somatically-protective female will value. Same sex cooperation is expected to occur as well, that is, intrasexual selection for cooperation within a sex. Given so much advantage for selection of cooperative traits, it is curious why testosteronized traits did not become linked to cooperative behavior. In an alien species perhaps we could imagine this happening. If one is going to truly address the origins of social dynamics, then considering *when* cooperation happens is important.

Table 5 lists supporting research for a continuum in individual versus group-oriented efforts. Group efforts align with cooperative efforts while competitive traits parallel group behavior. There are explicit events where selection is in the direction of individual versus group dynamics that are pertinent to the Compete-Cooperate theory of sociality, and is rooted in mating dynamics. Under the Compete-Cooperate framework, parental cooperation can be treated as a simple ‘group’ effort with two members in the group, that may expand at times to include alliances with those outside the mateship when a parenting demand cannot be met, or individual interests motivate one of the parenting duo. In contrast to traits associated with cooperation in a group context, intersexual pressures may select for parental competency (i.e., food acquisition, social dominance, protection) at the level of the individual. Such competencies encourage independence away from social groups, and therefore this is placed under individual effort in Table 5.

In caveat, group effort is defined here as cooperation between two or more individuals for a common goal. This definition allows for inter-group competition wherein a display of coalitionary behavior occurs between members of one's own group and dominance or aggression is directed at out-group members. In this scenario, both cooperation and competition occur simultaneously, at the group level, while only competition in the form of self-preservation and independence occur at the individual level. This makes for interesting predictions that can be addressed by looking at non-theoretical research outside the area of biology.

It would be predicted that there exists psychological adaptations important to challenges at the individual level. Evidence for this comes from studies of facial processing in the brain. An impressive amount of functional magnetic resonance imaging research by van Honk (2005, 2006, 2008, 2009) has demonstrated that decreased sensitivity in the brain to angry faces is associated with blood circulating levels of testosteronization, in both males and females. It is argued that this phenomena encourages approach behavior during dominance challenges. In this same vein, Crespi (2005) and Baron-Cohen (2002) have organized and further inspired a growing body of research that associates marked reduction or even absence of emotionality with more system or object-oriented intelligence (including physical orientation, or spatial, tasks). Lowered emotive reasoning leads to a preference for greater autonomy, or *individualism*. At the other end of the Crespi-Baron-Cohen spectrum is greater emotional intelligence (at the expense of a lessened system intelligence) associated with empathy and presumably successful *group* behavior (i.e., better theory of mind, Baron-Cohen, 2002). It is not too great of a leap to make the statement that testosteronized brains excel in behaviors built for independent challenges while estrogenized brains demonstrate keen abilities that are attuned to group dynamics. Why one should be at the expense of the other is not apparent, unless a Compete-Cooperate theory of sociality is appealed.

Figure 10 is a hypothetical illustration of what is in the minds of female participants in the facial perception experiments of this dissertation. Lack testosteronization is perceived as a cue of probable cooperation and is in keeping with evidence that this is a valid perception (Penton-Voak et al., 2006; Manning et al., 1999). Judgment of photographs by outsiders matched self-reports on personality attributes including the potential for cooperative or competitive behavior. If more testosteronization is attractive to the average female, but only to a point at which it suddenly becomes aversive, the question becomes, what is tempering female preference? The answer lies in the fact that the threshold point for level of testosteronization changes with female condition and experience, as Chapter 4 only begins to address. Further research with other female traits (i.e., perceiver morphometrics, and family dynamics) may illuminate.

In conclusion, Figure 10 shows coarsely drawn hypothetical distributions of males and females, meant to pictorally represent the results of selection according to Compete-Cooperate social pressures. The figure shows competition in the form of individual challenges at the testosteronized end and cooperation or group-oriented behavior toward the estrogenized end. Data discussed in this dissertation has revealed that testosteronization is associated with a reduction in pro-social traits, increased individualistic tendencies and a readiness for one-on-one physical challenges while the absence of testosteronization is associated directly with pro-sociality and group acceptance. This spectrum is so broad that it reconciles diverse bodies of literature from areas such as behavioral ecology, neuroendocrinology, and anthropology, with future implications for psychiatry and medicine for understanding basic physiological and psychological function, and plasticity in the context of the modern world.

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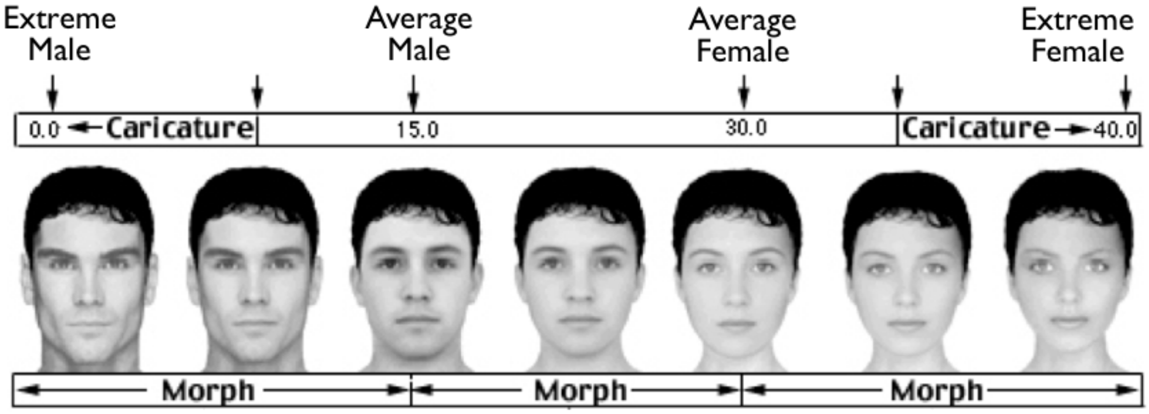
Figure 1: The making of the morph movie.

A 40-second quicktime movie was made by morphing to fill in the differences between the average male and female (composites from photos), then morphing to extreme endpoints for the male and female (evolved with FacePrints software), and finally caricaturing in a non-linear fashion to exaggerate the differences between the average male and female.



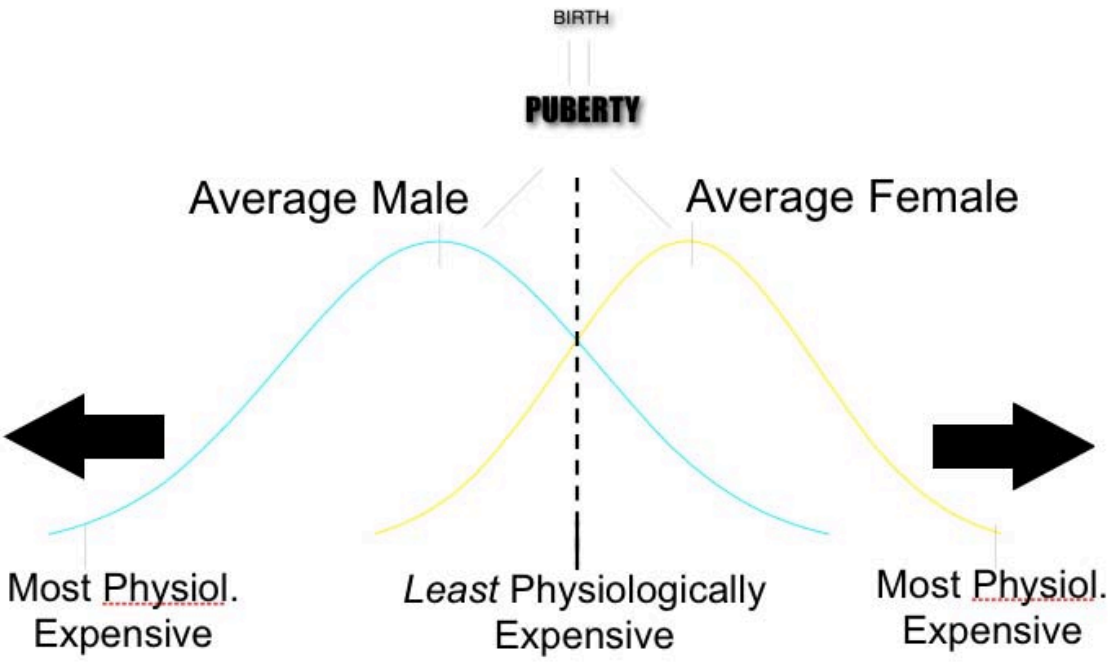


Figure 2: Physiological expense of secondary sexual traits.

At birth, the anthropometric differences between males and females is insignificant. At puberty, hormonal restructuring directs changes in features that result in the divergent, but overlapping, distributions of morphometric traits between males and females (Tanner, 1978). Depicted here are hypothetical distributions for males and females.

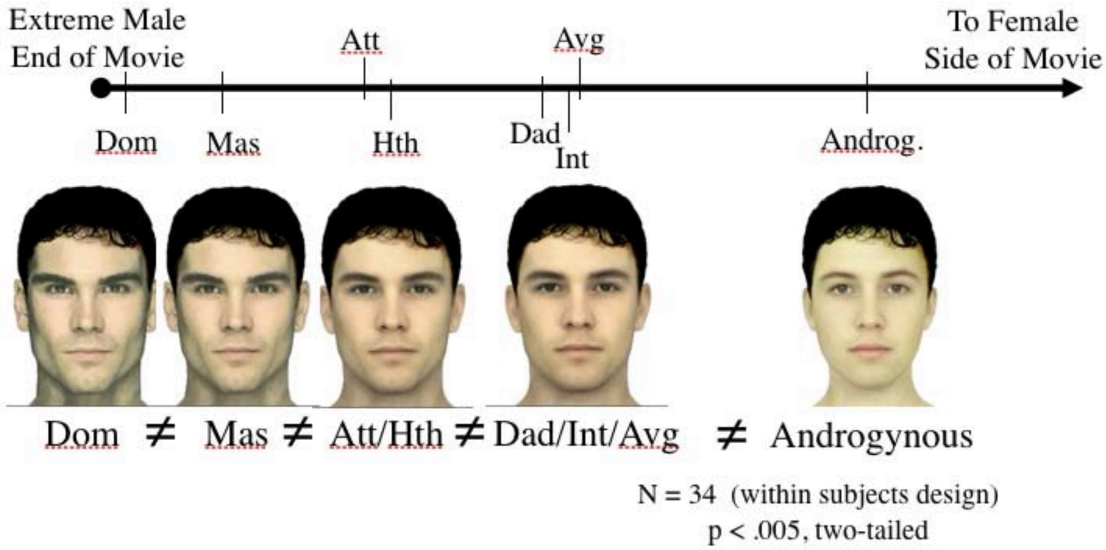


Figure 3: Results of face choices from the morph movie.

The dominant male is the most extremely testosteronized face choice and its mean is significantly different from every other face type. The masculine male is the next most testosteronized, and is significantly different from every other face type. The mean face choice for the attractive male and health male were not significantly different from each other but were from other face types. The face choices for good parent, intelligent and average male were not significantly different from each other but were from other face types. The androgynous male was located in between the sides of the movie that were perceived as appearing male or female, and was significantly different than all other face types.

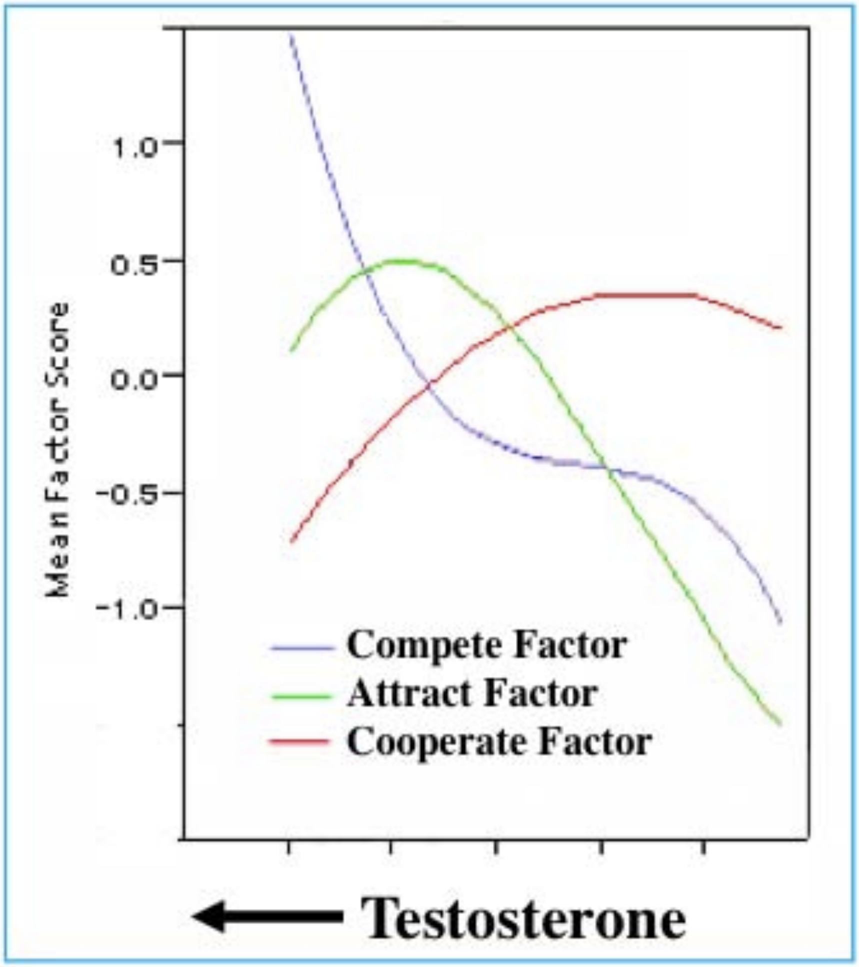
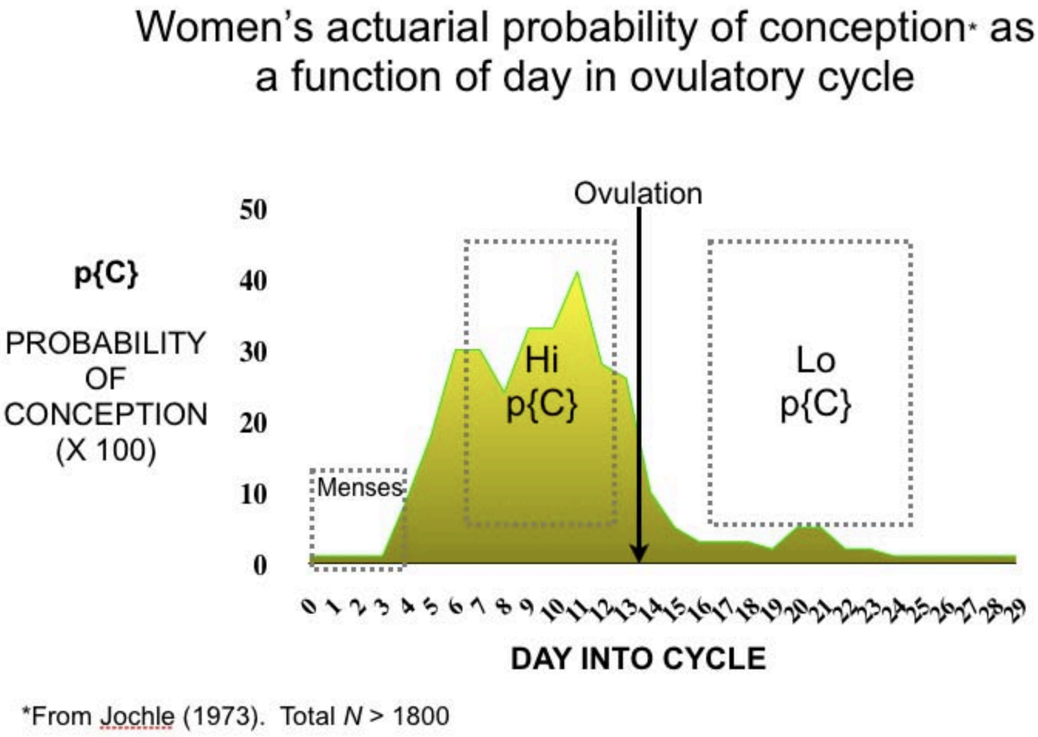


Figure 4: Compete-Cooperate-Attract tradeoff curves

Third order polynomial curves fitted to the mean factor scores of all three factors (Compete, Cooperate and Attract) over the first 700 frames (masculine images) of the morph movie. The peak of the Attract factor is above the point of dissection where Compete and Cooperate cross.


Women's actuarial probability of conception* as a function of day in ovulatory cycle

*From Jochle (1973). Total *N* > 1800

Figure 5: Women's probability of conception across day in ovulatory cycle.

Menses, the first 4-5 days of the cycle was avoided for data collection. A high risk of conception window (Hi p{C}) was chosen for days 5-9. A low risk of conception window was defined as days 16-25.

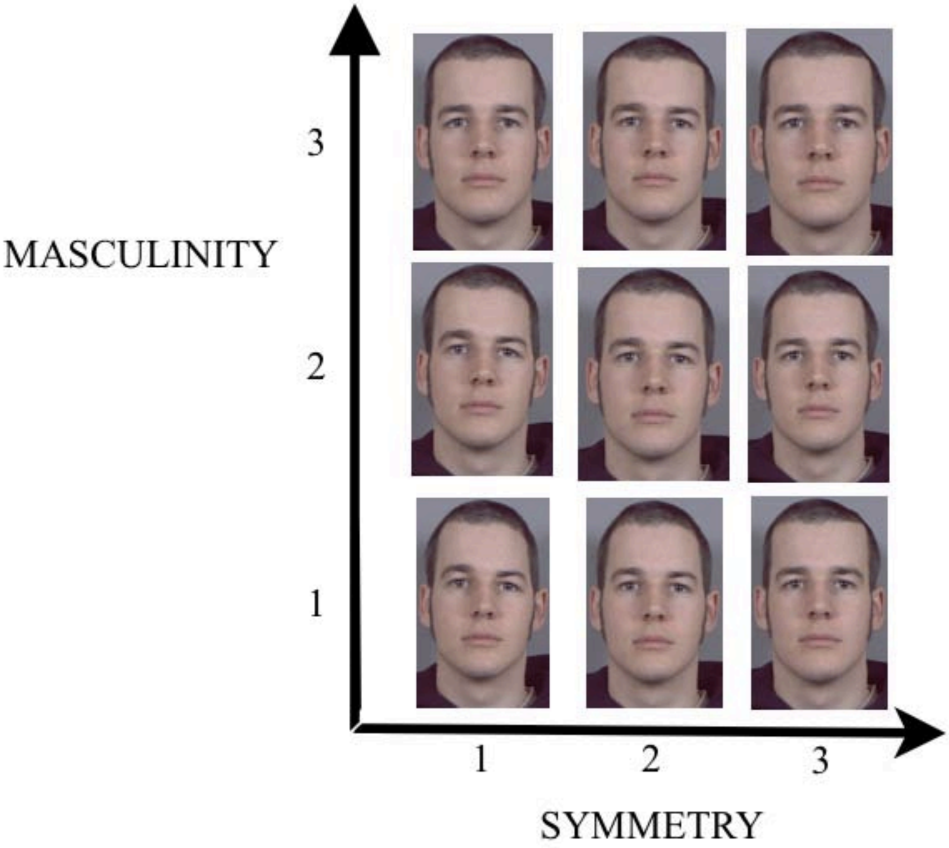


Figure 6: Novel stimuli, symmetry vs. masculinity.

On the y-axis is increasing masculinity. On the x-axis is increasing symmetry. The original male face is center. Experimental faces did not vary in size as occurred during the creation of the figure here. Experimental facial photos were 7 inches by 10 inches and relative face size was standardized in relative face size by inter-pupil distance, a feature that varies little in the population (Tanner, 1978).

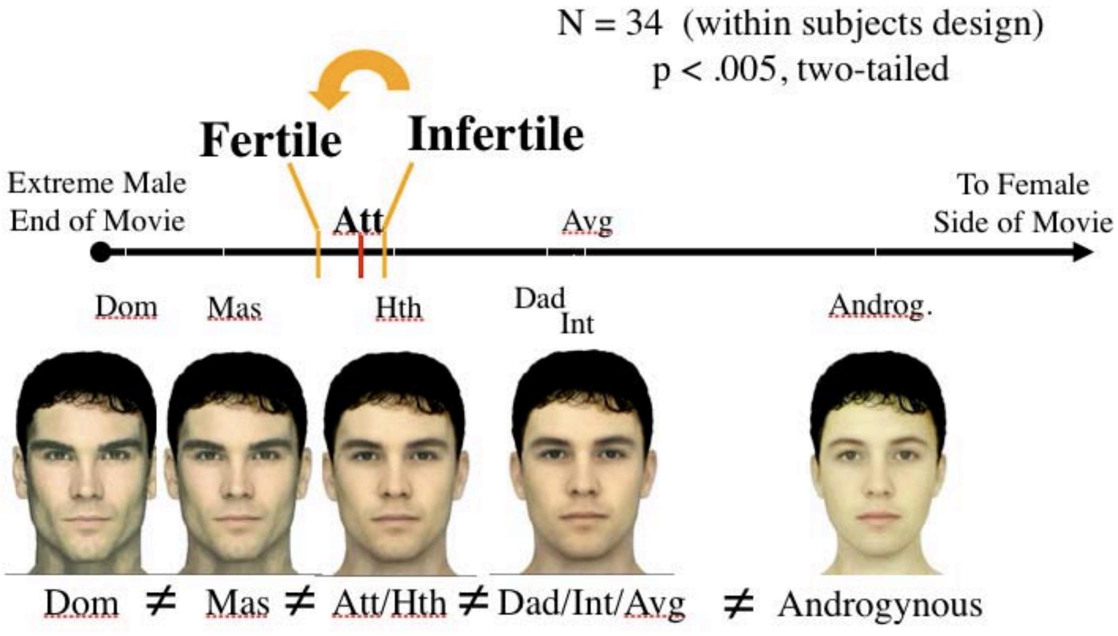


Figure 7: Fertility shift in perception toward testosteronization.

The above figure is identical to Figure 3, only the shift in preference toward testosteronization at high risk of conception is added. Note that the *healthy* male, which was not significantly differently than the *attractive* male when females were infertile, did not shift when females were fertile. None of the other face choices shifted with perception, only the *attractive* face, providing strong evidence for specificity of design.

Figure 8. Face choices in low masculinity group.

From left to right in order of increasing testosteronization; the perceived *average* male face (frame 394) and the *attractive* male face when conception risk is low (frame 298), and when conception risk is high (frame 245).

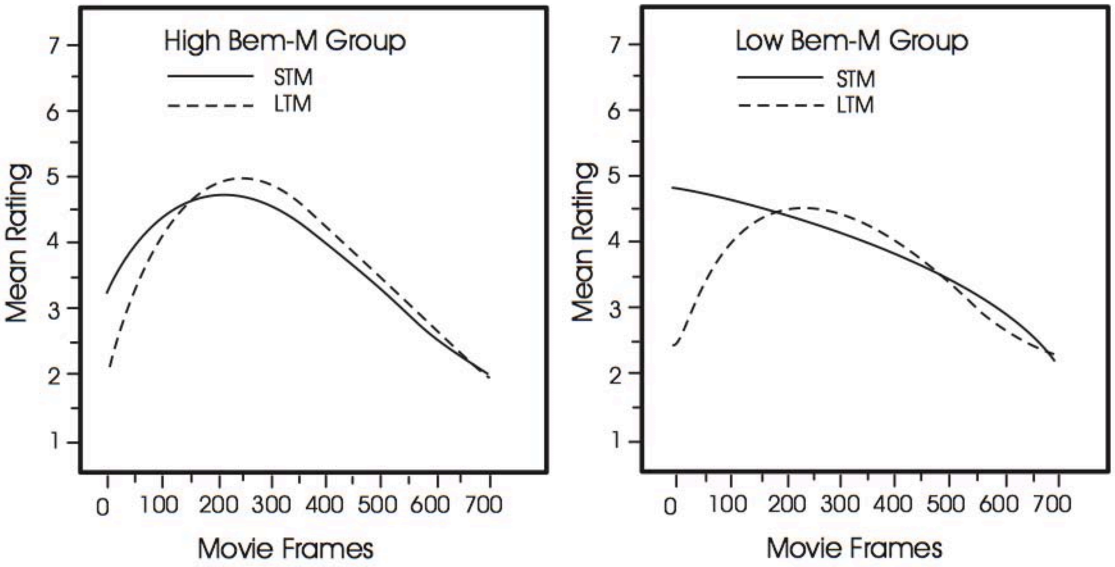
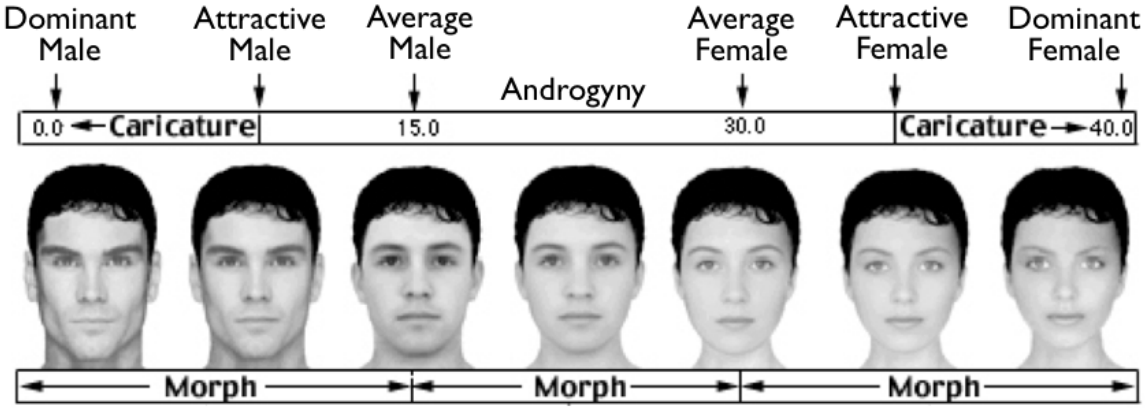


Figure 9. STM and LTM for low and high masculinity females.

Mean ratings of faces for desirability as a short-term mate (STM) and a long-term mate (LTM), for participants who scored high (High Bem-M Group) or low (Low Bem-M Group) on the Bem masculinity scale. Low masculinity females differ in that their preferences for testosteronized males where STM did not follow the other curvilinear patterns.



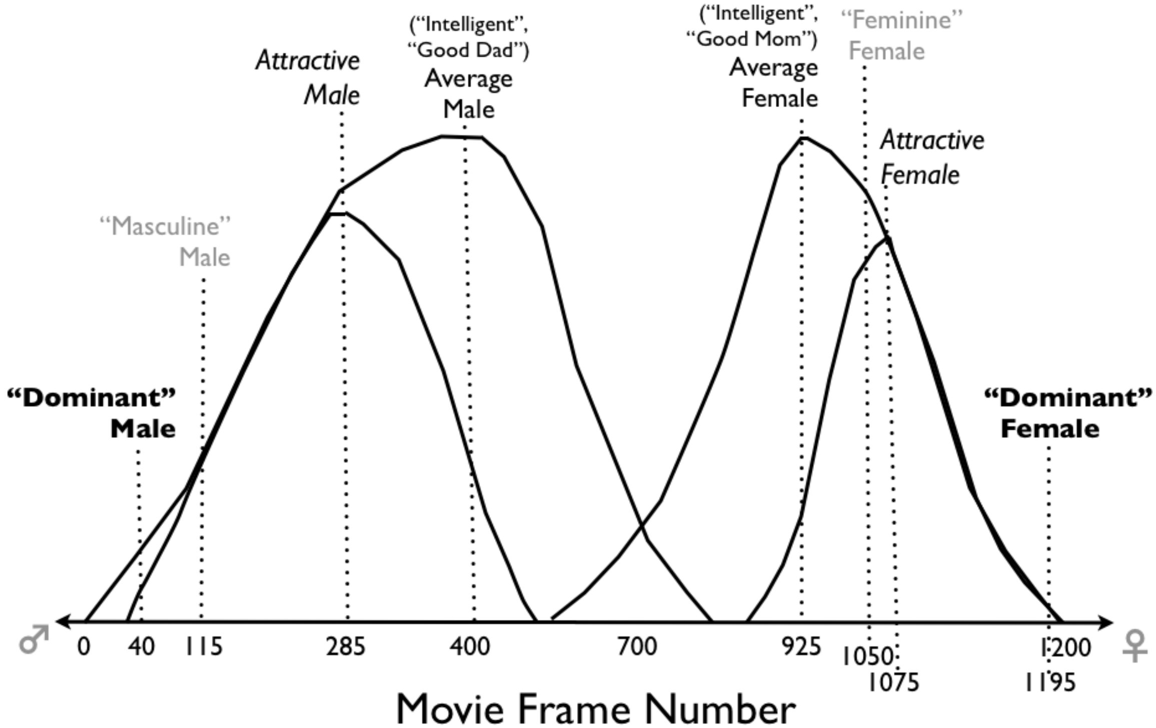


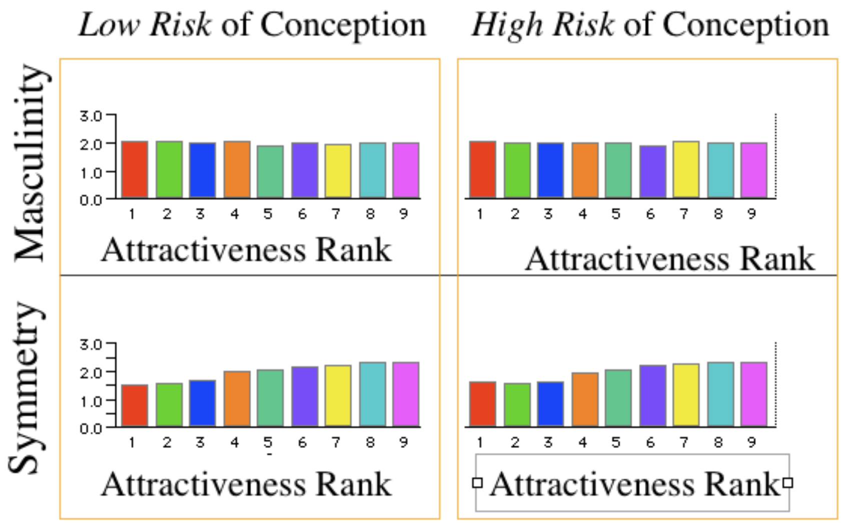
Figure 10. Hypothetical distributions of males and females on a Compete-Cooperate continuum.

At the testosteronized (male) end are the physical and behavioral traits for competition. Cooperation or group-oriented behavioral and physical traits are in the other direction of the continuum. The creation of these relative functional point comes from the choices made by female subjects in the facial perception experiments of this dissertation.

Frame Number	Dom	Mas/ Fem	Att	Hth	Avg	Int	Dad/ Mom	Andr
Male	43	115	284	275	394	385	341	699
Female	1195	1053	1074	1021	925	995	959	699

Table 1: Patterns in Means for Morph Movie Face Choices.

Shown here, are the means for each chosen face type. They are similar in pattern whether judging male faces or female faces. Extreme testosteronization begins at 0 and moves to the androgynous face mean at 699, and then through higher numbers for female face means with 1200 being the most estrogenized female face. More dominant (Dom) faces are the most extremely hormonized faces for both the male and female faces. The masculine (Mas) / feminine (Fem) faces were next in the extreme male continuum. Next came the attractive (Att) and healthy (Hth) face for both male and female faces. The average (Avg), intelligent (Int) and good parent (Dad/Mom) were not significantly different from one another.



*Of > 130 subjects, 80 completed all 3 one hour sessions.
Of these 80, 32 reported unpredictable cycling and were not tested for LH.
Of the 48 remaining, only 21 actually cycled as predicted with a detected LH surge. Hence, the number of subjects represented by the above histograms is 21.

Table 2a: No Effect of Conception Risk on Forced Choice Rankings.

Distribution counts for each attractiveness rank are shown separated by low and high risk of conception. Higher symmetry is preferred overall, but not significantly different between low and high risk of conception. Masculinity preferences are diffuse, as predicted from a Compete-Cooperate continuum that presumes a female's own traits and condition will drive her preference for level of masculinity.

OBSERVED COUNTS (SYM first & MASC second)

	1&1	1&2	1&3	2&1	2&2	2&3	3&1	3&2	3&3	TOTAL
CR=0	15	3	12	40	61	33	34	55	45	298
CR=1	6	9	14	42	59	43	37	54	34	298
TOTAL	21	12	26	82	120	76	71	109	79	596

EXPECTED COUNTS (SYM & MASC)

	1&1	1&2	1&3	2&1	2&2	2&3	3&1	3&2	3&3	TOTAL
CR=0	10.5	6	13	41	60	38	35.5	54.5	39.5	298
CR=1	10.5	6	13	41	60	38	35.5	54.5	39.5	298
TOTAL	21	12	26	82	120	76	71	109	79	596

Table 2b. No Effect of Conception Risk, Chi Square Counts.

Each of the nine boxes represents the nine rankings for attractiveness for each set of one male. Symmetry (sym) and masculinity (masc) are denoted by level as 1, 2, or 3 for each version of one male's face.

	(SYM & MASC)									
	1&1	**1&2**	**1&3**	**2&1**	**2&2**	**2&3**	**3&1**	**3&2**	**3&3**	**TOTAL**
observed	21	12	26	82	120	76	71	109	79	596
uniform	66.222	66.222	66.222	66.222	66.222	66.222	66.222	66.222	66.222	596

Table 3. Means Used in Goodness of Fit for Forced Choice Face Rankings.

A uniform distribution is used for the expected and chi square was performed to see if subjects were assigning ranks randomly, they were not (p-value of 1.64$^{E-34)}$. Each of the nine boxes represents the nine rankings for attractiveness for each set of one male. Symmetry (sym) and masculinity (masc) are referred to as level 1, 2, or 3 for each facial combination of symmetry and masculinity denoted respectively.

Male Faces	**Dominant**	**Masc /Fem**	**Attractive**	**Healthy**	**Average**	**Intelligent**	**Good Parent**	**Andr**
Dominant	-	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different
Masc /Fem	Significantly Different	-	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different
Attractive	Significantly Different	Significantly Different	-	**NOT Significantly Different**	Significantly Different	Significantly Different	Significantly Different	Significantly Different
Healthy	Significantly Different	Significantly Different	**NOT Significantly Different**	-	Significantly Different	Significantly Different	Significantly Different	Significantly Different
Average	Significantly Different	Significantly Different	Significantly Different	Significantly	-	Significantly Different	Significantly Different	Significantly Different
Intelligent	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	-	Significantly Different	Significantly Different
Good Parent	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	-	Significantly Different
Andr	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	Significantly Different	-

Table 4. Patterns of Significance for Morph Movie Face Choices.

All face types were significantly different from every other target face with the exception of the *attractive* and *healthy* male face (t = 0.64 (28); p = .74).

Continuum:	Compete	Cooperate
Testosteronization vs Estrogenization of Physical Features	TESTOSTERONIZATION: ↑Muscular bulk ↑Teeth protrusion ↑Jaw size/strength ↑Height ↑Bone density ↑Hair ↑Brow hooding ↓Eye whites ↓Subcutaneous Fat ↓2nd digit:4th digit ratio	ESTROGENIZATION: ↓Muscular bulk ↓Teeth protrusion ↓Jaw size/strength ↓Height ↓Bone density ↓Hair ↓Brow hooding ↑Eye whites ↑Subcutaneous Fat ↑2nd digit:4th digit ratio
Reproductive Effort vs Somatic Effort (reproductive success, RS)	↑REPRODUCTIVE EFFORT(♂>♀): ↑T early coitus♀♂ ↑T ↑sexual arousal♀♂ ↑T early menarche♀ ↑T early first ejaculation♂ ↓2° immunity♂ NO CHANGE1° immunity♂ ↓2° immunity♀(pregnancy) ↑1° immunity♀(pregnancy) ↓lifespan♂♀ ↑intrasexual competition ♂>♀ ↑mate acquisition♂>♀ ↑mating effort =↑RS♂>♀ ↓parental effort =↑RS,♂>♀	↑SOMATIC EFFORT (SE) (♀>♂): ↑SE = ↑parental effort♀ (lactation, pregnancy, rearing) ↑somatic effort =↑RS ♀>♂ ↑2° immunity♀ ↑1° immunity♂(♀pregnancy) ↑lifespan♀>♂ ↑parental effort =↑RS♀>♂
Direction of Intrasexual Selection vs Intersexual Selection	INTRASEXUAL ♂-♂,♀-♀ resource competition ♂-♂,♀-♀ mate competition INTERSEXUAL ♂attract♀(dominant♂, health/genes) ♀attract♂(fertile, dominant♀)	INTERSEXUAL ♀attract♂ (receptive periods) ♂attract♀(parenting, health/ genes) INTRASEXUAL ♂-♂,♀-♀ cooperation
Individual Effort vs Group Effort	INDIVIDUAL EFFORT: ♂-♂ competition for resources ♂-♂ competition for mating access ♂attract♀(dominant♂, health/genes) ♀attract♂(dominant♀, fecundity) ♀♂attract♂♀(independent parent) ↓Sensitivity to social cues (faces) ↑Autistic spectrum (system intelligence)	GROUP EFFORT: ♂-♂,♀-♀,♀-♂ cooperators group coalitions (kin; goal-oriented) intergroup competition ↑survival♀♂(hi risk environments) ♀♂attract♂♀(willing/cooperative) ↑Theory of mind♀>♂ (emotional intelligence) ↑Psychotic (emotional) spectrum

Table 5: The Compete-Cooperate Continuum: Summary of Evidence.

Hormonal restructuring of physical features at puberty reflects divergent tradeoffs between reproductive effort and somatic effort in males versus females. These physical traits are aligned under the compete-cooperate continuum with the direction of selection for intrasexual selection and intersexual selection, all organized within a broad compete-cooperate spectrum that views individual effort as competition and group effort as cooperation in altricial species, particularly biparental, not strictly monogamous ones. [Note: fecundity, health, and good ‘genes’ may each be viewed as indicators of somatic effort or condition. The primary goal of group effort is to improve condition (implicit to survival) in unstable social environments.