SEXUAL DIMORPHISM IN FACES ACROSS DEVELOPMENT THROUGH EARLY ADULTHOOD : PERCEPTIONS, ATTRIBUTIONS AND STABILITY

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Sexual Dimorphism in Faces Across Development Through Early Adulthood: Perceptions, Attributions and Stability

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This thesis was submitted for the degree of Doctor of Philosophy in September 2005

I, Robin Elisabeth Cornwell, hereby certify that this thesis, which is approximately 50,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I was admitted as a research student in September, 2001 and as a candidate for the degree of Doctor of Philosophy in August, 2005; the higher study for which this is a record was carried out in the University of St Andrews between 2001 and 2005.

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So many people have been instrumental toward the completion of this thesis, that this small acknowledgment is a trifle compared to my teeming gratitude and indebtedness to each of them. I feel especially fortunate to have been tutored by David Perrett, the best supervisor any postgraduate could imagine. His intellectual curiosity, energy, generosity, kindness, support, knowledge, and occasional prodding have made this journey not only possible, but exceptionally rewarding.

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This thesis is dedicated to my brother Michael whose courage never faltered, and whose humour and determination have always sustained me. You are deeply missed.

Note to the reader:

Throughout all of the experimental chapters in this thesis, I have used the term 'we' as opposed to 'I'. The work herein is unequivocally my work in terms of analyses, hypotheses and conclusions; however, in an environment such as the Perception Lab, there is a great deal of collaboration such as running subjects, collecting photos, setting up software for experiments, pooling of questions, and exchange of ideas that should be acknowledged. Additionally, many of the experiments I describe herein were run as a part of a larger group of experiments, thus taking advantage of pooling participants for maximum efficiency. It is also necessary to note that throughout my post-graduate career, my supervisor David Perrett has of course played a significant role both in the concepts and design of the experiments described herein, as well as his invaluable advise throughout the writing process (not to mention occasional subtle and not-so-subtle nudges). Therefore, the term 'we' is not only more in keeping with intellectual honesty, for me it is far more comfortable.

Table of Content

Abstract

In this thesis, I use a Darwinian approach to explore the role of sexual-dimorphism in human behaviour across development and into early adulthood, and its impact on adult mating-strategies.

In Studies 1-2, I explore the importance of heredity and developmental stability of facial characteristics in light of theories of sexual selection. Using family photos, judgements of faces of parents and offspring revealed that facial sexual-dimorphism is passed on from father to son and mother to daughter, while inheritance of attractiveness is apparent only in daughters. I also examine the stability of facial appearance across development (infancy, childhood, young-adult), and find that sexual-dimorphism remains stable for both sexes, while attractiveness is stable only in females.

Feminine characteristics are perceived as attractive in infant faces, and feminine characteristics have been perceived as looking more neotenous. In light of these data, I develop a theory for increased preferences for neoteny in human infants (Chapter 4).

In studies 3-4, I examine the developmental milestones, puberty and first sexual intercourse in relationship to adult mate-choice strategies. Women who experience first coitus early prefer increased facial-masculinity in potential mates. In men, both early coitus and early puberty relate to increased preferences for facial-femininity in potential mates.

In study 5, I look at attributions of peri-pubertal children (aged 11 – 12 years) to peer faces manipulated on sexually-dimorphic features. Children's attractiveness judgements show evidence of adult-like preferences, with boys preferring feminine

girls' faces and girls preferring feminised boys' faces. Both girls and boys attribute the negative stereotype of bullying to more masculinised boys' faces.

Study 6 concerns the relationship between two modalities of sexual-dimorphism, pheromones and facial characteristics. Adults indicate preferences from a continuum of sexually-dimorphic face-shapes, in addition to rating sex-specific pheromones on pleasantness. Individuals who prefer sex-typical facial characteristics in opposite-sex faces also judged the sex-typical pheromone as more pleasant.

Introduction

Charles Darwin (1859; 1871) proposed two general theories to explain speciation and characteristics in plants and animals: natural and sexual selection. Whereas natural selection is used to explain the general laws behind the evolution of the complexity and speciation seen in organisms, sexual selection can explain the presence of sexual dimorphism within a species. Sexual selection is based on competition for reproductive access to the opposite sex and choice. Darwin proposed two key aspects to sexual selection, the first is that males will compete through male-male combat and/or threat displays in order to secure access to females; and second, that due to female fancy for particular male traits, such traits could become exaggerated in later generations. The first key component to sexual selection theory explains male traits such as large antlers, increased body size, and aggressiveness. The second component can explain the amazing array of male plumage, bright colouration, elaborate vocalisations, and captivating displays directed at any female willing to watch.

Since the synthesis of Darwin's seminal theories and genetics to explain the laws of inheritance, natural and social scientists have examined the behaviour of most known living (and many formerly living) organisms within the framework of the laws of evolution. One of the key contributions to the theoretical underpinnings of sexual selection came from R.A. Fisher (1958) who noted that for discriminating taste in mate selection to have evolved, it holds that the acceptance of one mate can result in the exclusion of another; and, while there is a loss incurred through rejecting a prospective mate, it is smaller than the possible gain of finding a superior mate. In other words, for sexual selection to occur, there must be variation in fitness that can be passed on from parent to child, and it pays for individuals to be 'choosey' and seek out prospective mates who possess these traits (Chapter 2).

Humans are not immune to the scrutiny of scientists, and perhaps, as we tend to be most curious about our own behaviour, Darwinian selection has helped to elucidate human behaviour, and in particular may help to demystify the differences between men and women. The stuff of poets, playwrights, and country western singers reflect the evolutionary history of our ancestors, particularly the different problems our fore-mothers and fore-fathers faced in the struggle for existence and reproduction. Our ancestors made the right choice when it came to mating, else you and I would not be here. Their preferences remain with us, and within this thesis we explore why some of those choices were beneficial.

The differences between men and women range across physical, behavioural and cognitive. By assessing these differences within the framework of sexual selection and the theories that it has spawned, we can explain why they exist and in understanding them perhaps we can quell the battle of the sexes – or at least bring it down to friendly banter. Although it has been said again and again, it cannot be overstressed that just because a particular behaviour has been selected for over the course of human evolution does not make the behaviour acceptable or excusable. There are no value judgements to be had.

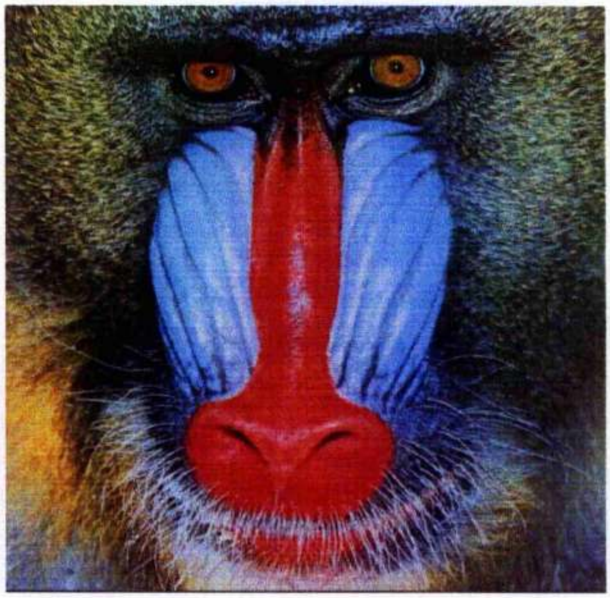
There are number of sexually dimorphic traits in humans (face, voice, odour – Chapter 8) and while many of them shall be discussed herein, the focus will be toward sexually dimorphic facial features. Theories of sexual selection all rely on one very important factor, that traits are inherited from parent to offspring; however, the method of inheritance – through mother, father or both – can help us understand an aspect of mate choice. Knowing whether or not the facial features women find attractive in men are passed on to offspring, and which sex, can help us understand the selection pressures that shaped her preferences.

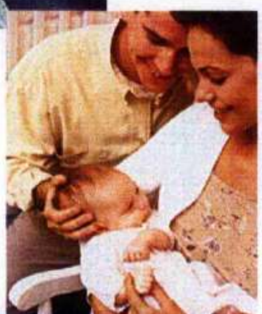
The development of sexually dimorphic features are influenced by our biology, that is our hormones and genes. By examining the proximate mechanisms, that is the direct influence of biological factors, of how traits develop, we can better understand why some features are attractive to the opposite sex, and why individuals vary on what they find attractive in a partner. Our biology impacts on our physical development (and subsequent decline), from the time in our mother's womb and throughout the remainder of our lives. One developmental milestone, puberty, is of particular interest because it is a time when we begin our transition from childhood to sexual maturity. It is reasonable to suggest that this particular period would be significant in terms of our attitudes and preferences. We go through tremendous physical changes, influenced greatly by hormones. Our brains too go through many changes and particularly in the frontal lobe area, which is necessary for social function, abstract thinking, and planning. Is it any wonder that adolescence is a time for exploring new social roles and beginning to understand one's own sexuality, attractiveness, and social status among peers. How and when do mate preferences emerge? (Chapter 7) How might these interactions between biology and environment influence later adult choices? (Chapter 5-6)

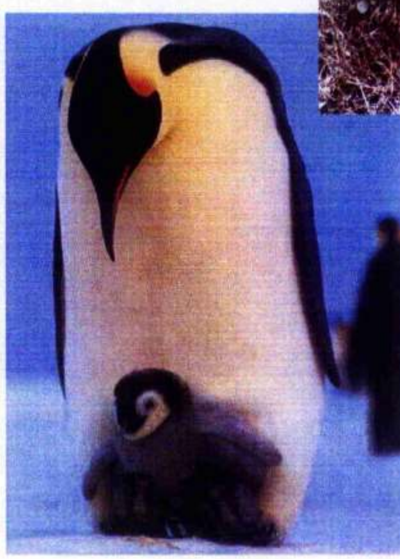
The studies to follow will explore these and other questions about the effects of development on adult sexual behaviour. Out of these studies, more questions will arise – but it is a beginning, and an exciting one at that.

I have often said religion and hormones ruin everything. I could write for days and miles on either subject and keep myself completely entertained.

Notes from the Loo







1 Literature Review

This thesis concerns the differences between the sexes evident in human facial characteristics, and how these sexually dimorphic characteristics affect mate choice. Thus, it is relevant to review the many factors affecting sexual dimorphism, including genetic and hormonal influences as well as environmental.

1.1 Hormones and their relevancy to the study of human behaviour

There are three propositions regarding the influence of hormones that are relevant to the study of human behaviour: Firstly, that prenatal hormones are linked to the anatomical and brain function differences between the sexes; secondly, that fluctuations of hormones can influence behaviour as well as physical maturation during development; and thirdly, that we can and do make assessments of others based on the physical attributes that have been influenced by hormones.

1.1.1 Hormones

Some of the earliest work in the area of hormones and behaviour was pioneered by scientists such as C.R. Moore, Frank Beach, Symour Levine, Geoffrey Harris, Claude Fotier, Luciano Martni, Charles Sayer, and David de Wied. The work of these scientists and others have increased our understanding of the importance of biology when considering animal behaviour, including that of humans. Since the initial work in endocrinology and behaviour, much has been revealed through both non-human and human research, and most scientists accept the general concept that hormones play an important role in sexual differentiation in animals, including both reproductive and non-reproductive behaviours (e.g. Arnold & Gorski 1984; Breedlove 1994; e.g. Collaer & Hines 1995; Goy & McEwen 1980; Jost et al. 1973; MacLusky & Naftolin 1981).

Animal models have been extensively used to explore the role of hormones in human behaviour. The sex chromosomes in all mammals determine whether the organism develops testes or ovaries, and it is these gonads which then secrete the sex hormones, including androgens such as dihydrotestosterone and testosterone and oestrogens such as oestradiol and progesterone, that set into motion phenotypic sex differentiation – a process that begins early during neonatal development. Androgens are produced in higher quantities by the male testis, while higher levels of oestrogens are produced by the female ovaries – hence androgens are often referred to as a male hormones and oestrogens and progesterones as female; however, both males and females produce the full complement of gonadal hormones.

The adrenal glands, which sit above the kidneys, are involved in the release of over 50 hormones, and other glands such as the thyroid, pancreas, kidneys, and pineal glands also release hormones into the blood stream. The release of hormones via these various glands is thought to be under the control of the pituitary gland, which is part of the hypothalamic-pituitary-adrenal (HPA) axis. The pituitary is then controlled by the hypothalamus.

The complexity of the interactions between the brain, the various glands, and the environment cannot be overstated (see Breedlove 1994). While non-human animal studies have allowed researchers to manipulate levels of particular hormones, the interactions between cause and effect remain uncertain. With humans, identifying cause and effect is especially perplexing, and much of what we understand has been through studies of individuals with particular disorders (such as congenital adrenal hyperplasia or Kallmann's syndrome), or through congenital birth-defects due to hormone supplements or various pharmaceuticals introduced to the foetus through the mother. Research in both human and non-human animals has led researchers to accept that the organising effects of hormones on brain and body depend on the timing and levels during pre- and post-natal development.

Genetic and environmental influences are also important factors when considering the effects of hormones on behaviour (Arnold 1996; De Vries et al. 2002; Insel & Shapiro 1992; Temple et al. 2003; Vamvakopoulos & Chrousos 1993). For example, Young and Wang (2004) showed that oxytocin, arginine vasopressin, and dopamine were critical for the formation of pair-bonds among prairie voles (*Microtus ochrogaster*), a monogamous and highly social species. However, the activation of receptors depended on conditional learning (e.g. association with an opposite sex partner) for activation. A closely related species to the monogamous prairie voles is the montane vole (*Microtus montanus*), which is highly polygamous and asocial (Insel & Hulihan 1995; Insel & Shapiro 1992; Insel et al. 1994). While genetically very similar, the two species show different patterns of oxytocin and vasopressin receptors, and it has been suggested that the observed differences are due to minor genetic differences (Young & Wang 2004). The patterns of vasopressin receptor distribution in the brain of the monogamous prairie voles differ from those of the polygamous montane vole. Both pharmacological and genetic manipulation of these patterns can alter the species-typical pair-bond behaviour. Reward circuitry and dopamine are also implicated in the process of pair-bonding (Lim et al. 2004). There may also be sex-differences in that vasopressin is critical for the formation of male bonds with a female partner, whilst oxytocin aids in the formation of female bonds with a male partner (Insel & Hulihan 1995). The gene thought to be responsible for the difference in pair-bonding behaviour is the V_{1a}, which is responsible for coding for the vasopressin receptors. Young and his colleagues (1999) created transgenic mice to determine if the V_{1a} gene played a role in social affiliations. After injecting the transgenic and non-transgenic mice with arginine vasopressin, the transgenic mice showed increased levels of affiliation. When arginine vasopressin was injected into the monogamous prairie vole and the polygamous montane vole, social affiliation only increased in the prairie voles with little or no effects on the social behaviour of the montane voles, suggesting the importance of the V_{1a}-receptors. It should be noted that social behaviours are complex, and a number of other factors, including corticosterone, oestrogens, and environmental factors, have been found to contribute to the behaviour of these little voles (for review see Aragona & Wang 2004)

1.1.2 Foetal hormones

At conception, dependent upon whether we received an X or Y chromosome from our fathers, we were set on a trajectory that forever shaped our lives. In humans, 7 or 8 weeks into our embryologic development, gonads begin to produce high levels of androgens, which have been found to influence neural development (Cohen-Bendahan et al. 2005; Collaer & Hines 1995). Among these androgens, testosterone is particularly high and is thought to masculinise the brain through the stimulation of receptors, as well as reduce feminine-typical development (Goy & McEwen 1980; Hines et al. 2002). The initial testosterone surge appears to occur between gestation weeks 7 and 24, which is then followed by a release of testosterone between 1 and 6 months post-natally (Smail et al. 1981).

Steroid hormones are not responsible for the differentiation of the primitive gonadal ridge into testes and ovaries, rather, in mammals[1] it is under the direction of the sex determining gene, more specifically the SRY gene (Y-chromosomal) (Jost et al. 1973; McElreavey et al. 1995). This gene triggers a cascade of events, including the transcription of the high mobility group (HMG) box genes, initiating the development of a male foetus. In the absence of the SRY gene, the HMG-box genes default to produce a female foetus (Koopman 1999).

Between gestation weeks 7 and 8, depending on the level of testosterone and other androgens, the gonads begin to develop and secrete sex-hormones, thus affecting the development of either male or female genitalia (Grumbach et al. 2002). For example, high levels of testosterone will result in the development of a penis and scrotum, and the development of the clitoris, labia majora, and vagina result when only low (or none) levels of testosterone are present (Jost et al. 1973). When intermediate levels of testosterone are present during this critical phase of physical development, the foetus will develop 'ambiguous genitalia', such as a small penis or enlarged clitoris (Cohen-Bendahan et al. 2005).

1.1.3 Sexual differentiation

The relationship between genes and hormones leading to sex-differentiation is not entirely clear. Genes can affect the sensitivity or number of receptors to particular hormones, while in turn hormones can affect the phenotypic expression of the genes (Arnold 1996). Additionally, environment, both pre- and post-natal, can alter both the

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[1] The role of hormones and genetics, particularly the SRY-gene in determination of sex-differentiation in reptiles and birds is beyond the scope of this paper.

expression of the genes and the level and timing of hormones. Neural regions are also sex differentiated through direct action of hormones (Collaer & Hines 1995). Sex-differentiation in the brain, *organisational* effects, can lead to effects later in life as *activational* hormones are released (Pheonix et al. 1959). It has been useful to differentiate between early effects (organisational) as permanent and the late effects (activational) as transitory, subject to the ebbs and flows of hormone fluctuation. However it should be noted that these distinctions are *not* absolute (Arnold & Breedlove 1985; Arnold & Gorski 1984). Organising effects, as mediated by the gonadal hormones, are generally those associated with the masculinisation and feminisation of the brain, along with either the defeminisation or demasculinisation of the brain, respectively (Collaer & Hines 1995).

Testosterone has been found to regulate cell development, either by promoting or suppressing apoptosis (programmed cell death) or through creating or reducing synapses, and it is via these two mechanism by which testosterone masculinises the central nervous system (Morris et al. 2004). These changes to the central nervous system are often permanent, however, sex-typical behaviours may or may not be manifest dependent on whether activational hormones are present (Collaer & Hines 1995). The acceptance that hormones during critical periods of development impacts on both reproductive and non-reproductive behaviours in non-human animals is not controversial; however, when discussing humans, the effects of hormones on behaviour is much more contentious.

The role of the ovarian hormones in the sexing of the brain is more conflicted and less well understood. Evidence suggests that oestrogen can both feminise and demasculinise the brain as well as genitalia in mammals (Arnold 1996; Fitch &

Denenberg 1998; Hines et al. 1987). However, ovarian hormones may also play a role in masculinisation, and their effect appears to be dependent upon their timing (Collaer & Hines 1995). The effects of oestrogen on reproductive functioning has also been examined, and prenatal oestrogens were found to affect the development of female reproductive functioning, however it apparently did not affect sex-typical reproductive behaviours in rats (i.e. mounting and receptivity) (Matuszczyk 2003).

Three models of how hormones affect sex-differentiation have emerged: The passive feminine model, the gradient model, and the active feminisation model. The passive feminine model, the most widely accepted (Collaer & Hines 1995), suggests that testicular hormones are responsible for the masculinisation and defeminisation of the organism (e.g. Goy & McEwen 1980; e.g. MacLusky & Naftolin 1981). The gradient model (Döhler et al. 1982; Hines et al. 1987) suggests female-typical hormones, particularly oestrogen, also contribute to the masculinisation and defeminisation of the organism. The active feminisation model (Toran-Allerand 1984) suggests that the ovarian hormones act to increase feminisation and demasculinisation of the individual. It is beyond the scope of this review to evaluate the evidence in support or opposition to these three models, however for a full review please see Collear and Hines (1995).

1.1.4 Hormones and behaviour

In non-human animals, prenatal hormones as well as early environmental factors can have lasting effects on sex-specific behaviours (Breedlove 1994). Sex-typical behaviours such as reproductive behaviour (mounting and lordosis) (Goy & McEwen 1980; MacLusky & Naftolin 1981; Pheonix et al. 1959), play behaviour (Goy et al. 1988; Pedersen et al. 1990; Ward & Stehm 1991), aggression (Goy &

McEwen 1980), and spatial (maze) performance (Williams & Meck 1991) can be influenced through manipulation of gonadal hormones.

One of the earliest studies on the effects of prenatal hormones was carried out by Phoenix and his colleagues (1959) who found that endogenous prenatal hormones were critical for adult sexual behaviours in the female guinea pig. In other words, organisational effects of prenatal hormones were capable of structuring adult behaviour patterns. Many other studies along these lines were to follow, and prenatal hormones were found to affect not only adult sexual (reproductive behaviours), but non-reproductive behaviours as well (Arnold & Breedlove 1985; Arnold & Gorski 1984; Berenbaum 1999; Berenbaum & Hines 1992; Berenbaum & Resnick 1997; Clotfelter et al. 2004; Cohen-Bendahan et al. 2005; Delemarre-van de Waal et al. 2002; Goy et al. 1988; Goy & McEwen 1980; Williams & Meck 1991).

Female rats treated neonatally with testosterone displayed male-typical sexual behaviours, but only if treated with testosterone again in adulthood (Goy & McEwen 1980). This finding suggests that while organisational hormones prepare the brain, activational hormones are still necessary to trigger behaviour.

The hormones responsible for masculinisation and feminisation of the brain, while they may interact, work discrete processes and timing of critical periods differ. For example, Beach (1975) manipulated pre- and perinatal testosterone levels in female dogs. Bitches were injected with testosterone during the second-trimester of gestation (prenatal), and a portion of these female pups were also administered testosterone within 72 hours post-partum (neonatal). He found that only those females who received the neonatal testosterone injections displayed equally both female- and male-typical urination stances, while those females who received only the prenatal testosterone nearly always displayed female-typical urination patterns. Of perhaps more interest were the effects on adult sexual behaviours. Pre-natally androgenized females were mounted by males (42%) less often than controls (60%), and pre- and post-natally androgenised females were mounted far less often (1%). Injections of testosterone in the masculinised adult-females led to male-typical mounting and thrusting behaviour, which was not seen in control females or andronised females that did not receive testosterone injections in adulthood. Beach interpreted his findings as evidence for parallel but discrete processes of masculinisation and defeminisation. In their 1972 paper, Beach et al write: *Masculinization* of females refers to the induction of anatomical, physiological, or behavioural characters or traits which normally are well developed in males but lacking or poorly developed in females. *Defeminization* signifies partial or complete inhibition of traits normally well developed in females but absent or weakly developed in males.

The mechanisms by which masculinisation of the brain and body is achieved have slowly been elucidated over the past few decades. We now understand that the testes secrete an antimullerian hormone, a protein that suppresses the development of the female reproductive tract, and testosterone, which promotes the development of the male reproductive tract including external genitalia (Morris et al. 2004). Testosterone is thought to account for nearly all the sex differences in the neural structure and behaviour found in vertebrates (Morris et al. 2004); however, in many instances testosterone must first metabolise into other hormones such as dihydrotestosterone and oestradiol before it can become an active agent (MacLusky & Naftolin 1981).

In rhesus monkeys (*Macaca mulatta*), manipulation of prenatal androgen during gestation produced more male-typical behaviours; however, the type of behaviour affected depended on the timing, either early or late, of the manipulation. Early timing produced females displaying more male-typical behaviours of mother-mounting, peer-mounting, and less mother-grooming than those females exposed to androgens later during gestation. Later exposed females engaged in more male-like rough-and-tumble play, however they displayed more female-typical mother-grooming behaviour and not more male-like mother-mounting or peer-mounting behaviours. The authors concluded that aspects of male-juvenile behaviours are 'independently regulated by the organizing actions of androgen and have separable critical periods' (Goy et al. 1988).

Timing is not the only important element influencing the organisational effects of testosterone, the level of testosterone also affects the degree of masculinisation (Goy & McEwen 1980). Many species, such as rodents (mice, rats, voles, hamsters, ferrets, and gerbils), sheep, and swine display higher degrees of male-typical behaviours when adjacent to male siblings during gestation, including aggressive behaviours and mating behaviours (Ryan & Vandenbergh 2002). Human twins have also been studied, and there is some evidence that opposite-sex dizygotic twins are affected by the hormones released by their womb-mate. Females with male twins tend to show higher measures of sensation seeking and disinhibition compared to females with same-sex twins, while males with opposite-sex twins did not show any significant differences from males with same-sex twins (Resnick et al. 1993). However, other studies suggest the effects of co-twin male hormones on female reproduction is weak or non-existent (Loehlin & Martin 1998).

1.1.5 Humans and hormones

The role of hormones in human sexual dimorphism, particularly its role on behaviour, is far more controversial and at times contentious than the non-human animal models. While it is agreed upon that, like other animals, during gestation . humans are subject to the effects of hormones for physical sex-differences (e.g. sex-typical genital development), the range and influence of hormones on human behaviour are disputed. During normal development males will produce higher levels of testosterone during gestation (approx. weeks 8-27) and again during the first 6 months post-natally (Smail et al. 1981). However, before reviewing some of the growing evidence of the role hormones play in human sex-differences it is important to caution against what Breedlove (1994) termed as a 'false dichotomy.' He suggests that while hormones do play a role in the sexual-differentiation of the human nervous system, psychological and purely biological influences cannot be separated. Further he advocates that the entanglement of environmental and biological influences makes it difficult to classify any relationship between hormones and behaviour as purely biological. Moreover, it is unlikely that effects of hormones are unalterable. With this in mind we can, however, explore the potential effects of hormones on behaviour and in particular how they can underpin many of the sex-typical differences observed in the population.

The most profitable areas to assess the possible influence of hormones on behaviour are those differences between males and females that are reliably evident in the population at large. These include: sexual orientation, core sexual identity, childhood play, aggression, hand preferences, hemispheric specialization, specific cognitive abilities, and learning disabilities (see Collaer & Hines 1995 for full review). Much of the evidence for the effects of hormones on behaviour have come from studies of individuals with genetic disorders. Congenital adrenal hyperplasia (CAH) has been studied extensively in women. This disorder is due to elevated levels of prenatal testosterone causing the foetal adrenal glands to over-produce androgens (Collaer & Hines 1995; Pang 1997). Physically, females with this condition have slightly masculinised genitalia, and it has been speculated that the exposure to testosterone could also masculinise the brain (Berenbaum & Hines 1992; Dittmann et al. 1990; Hines et al. 2004; Paterski et al. 2005). Indeed, CAH girls show increased preferences for male-typical toys and activities (Berenbaum 1999; Berenbaum & Hines 1992), and these behaviours held true even when parents encouraged female-typical play behaviours (Paterski et al. 2005). Additionally, CAH women were less likely to indicate a desire for offspring and were more likely to indicate an interest in having a career in comparison to non-affected women (Dittmann et al. 1990). These effects could not be explained by other psychosocial factors such as sex of sibling, degree of genital masculinisation, or demographic factors (Dittmann et al. 1990). Females with CAH also indicate more male-typical responses to aggression scales (Berenbaum & Resnick 1997). These findings have led researchers to hypothesise that prenatal androgens can affect behaviour and psychological factors as well as physical appearance.

It is held that androgens are crucial for the masculinsation and defeminisation of genetic males, thus reduced levels of androgens should affect normal male development. In non-human animals studies, androgens manipulated through castration or chemical methods to block testosterone result in both physical and behavioural changes toward feminisation (Goy & McEwen 1980). In humans, individuals with reduced androgenisation due to genetic disorders have helped to elucidate the role of hormones for normal male development.

1.1.5.1Males and congenital idiopathic hypogonadotropic hypogonadism (IHH)

The most common form of IHH is Kallmann's syndrome (an X-linked genetic disorder). This condition is a failure of synaptic contact between the forebrain and the olfactory nerves. Anosmia is a result of this disorder as is the production of less than normal levels of gonadal hormones due to a deficiency of the pituitary gonadotropins or their hypothalamic releasing factor (Quinton et al. 1996). Male infants with the disorder generally have fully intact male genitalia, thus appearing 'normal'. However, the normal release of gonadal hormones throughout development is affected, and the release of gonadal hormones at the 6-month post-natal surge and the pubertal surge are completely suppressed. Males with IHH indicate male-typical sexual orientation and core-sexual identity (self-perception of gender), yet apparently low sex drives (Collaer & Hines 1995). It has been suggested that males with IHH are born with male-typical genitalia due to testicular sensitivity to maternal hormones rather than gonadal hormones (Heir & Crowley 1982). That IHH males are generally male-typical in terms of sexual orientation and identity suggests that prenatal androgens play a critical role.

Males born with the disorder of genetic androgen insensitivity (AIS), who are completely insensitive to androgens appear phenotypically female[2], and are

[2] There are six known phenotypic forms of androgen insensitivity, however for the purposes of this thesis we shall discuss only the complete form that results in males developing a fully female body

generally raised as females. At puberty, the testes (located in the abdomen) of AIS males begin to release testosterone, some of which is converted to oestrogen. This then triggers breast development and the distribution of fat deposits as are normal for pubescent girls (although onset of puberty generally follows male-typical timing). For the most part, these individuals are satisfied with the female core-identity and sexual orientation (e.g. they consider themselves female and prefer male partners). This genetic disorder highlights the importance of both the organising effects of hormones on sexual behaviour, as well as its effects on physical development.

1.1.6 Hormones and bone growth

In many animals, including humans, skeletal size is sexually dimorphic, with males for the most part being somewhat larger than females (Alexander et al. 1979). Gonadal steroids actively regulate skeletal growth by stimulating the growth hormones and through direct receptors in the bone (Weisman et al. 1993). Testosterone has been found to stimulate the effects of growth hormones in boys (Martin et al. 1968) and is responsible for the sexual dimorphism seen in facial structure (Enlow 1990), while oestrogen may actually suppress some forms of skeletal growth (Grumbach 2000; Jones 1996). Oestrogen plays an important role during pubertal growth as it stimulates the development of cartilage (chondrogenesis), thus increasing linear growth (Grumbach 2000). Additionally oestrogen is responsible for skeletal maturation and the closure of the long bone (epiphyseal) growth plate

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except for lack of uterus, shallow vagina, testes in the abdomen, and minimal androgenic hair at puberty.

(Grumbach 2000). A complete understanding of the role of hormones in skeletal growth is still unresolved; however, evidence strongly suggests that adult skeletal structure is influenced by both prenatal and childhood androgen and oestrogen activity (Martin & Nguyen 2004) (for review see Bland 2000).

1.1.7 Hormones and digit length

The pre-natal exposure of testosterone and oestrogen relate to the sexually-dimorphic difference found in the ratio between the length of the second to fourth digit (2D:4D). Men's mean ratio is lower than women's mean ratio (e.g. in men the 4^{th} digit tends to be longer than the 2^{nd}, and in women the 2^{nd} and 4^{th} digits tend to be equal in length) (Manning et al. 2000; Manning et al. 2002; Manning et al. 2003; Manning et al. 1998). It has been hypothesized that this difference emerges very early in the developmental process, approximately by week 14 *in utero*. Low 2D:4D ratios thus ought to be indicative of high levels of prenatal testosterone and low levels of prenatal oestrogen, whilst high 2D:4D ratios result from low levels of prenatal testosterone and high levels of prenatal oestrogen. Support for this comes from Lutchmaya and colleagues (2004) who found that testosterone levels during foetal development, as assayed from amniotic fluids, were later negatively correlated with 2D:4D digit ratios measured when the children were 2 years of age. This relationship is likely due to the production of testosterone from the foetal gonadal and adrenal glands.

The 2D:4D ratio then can be used as post-hoc assessment of the level of prenatal sex-hormones during the critical period of brain organisation and sexual differentiation (Manning et al. 1998). Thus, 2D:4D can be used to compare with other measures of sexual dimorphism to gauge whether or not pre-natal hormones are a possible factor in any differences found.

For example, Manning et al (1998) found that sperm count was negatively related to 2D:4D ratios, thus high prenatal testosterone exposure could relate to later reproductive potential in males. In the same study they found that oestrogen in women was positively correlated with 2D:4D ratios, and as oestrogen has been associated with female fecundity (Baird et al. 1999; Lipson & Ellison 1996; Stewart et al. 1993), the 2D:4D correlations suggest that prenatal hormones may play a role in adult female reproductive potential. In another study (Manning et al. 2004), testosterone levels in adult men with testicular dysfunction were negatively associated with 2D:4D.

Athletic prowess, mental rotation scores (Manning & Taylor 2001), and musical abilities (Sluming & Manning 2000) have also been negatively correlated with 2D:4D ratios in adult males, suggesting that prenatal androgens are associated with male performance and competitive success. In another study, men's attractiveness and frequency of courting displays were also associated with low 2D:4D suggesting further evidence for the organisational effects of prenatal hormones on both physical development and adult sexual behaviour (Roney & Maestripieri 2004).

1.1.8 Hormones and pubertal growth

Puberty marks the major transition period from childhood into adulthood beginning with the activation of the hypothalamic-pituitary-gonadal axis and ends when adult body composition and reproductive capability has been fully attained

(Marshall & Tanner 1986). It is also during this period of growth, the secondary sexual characteristics emerge.

The onset of puberty is marked by what is often referred to as 'takeoff', when growth acceleration begins. Prior to takeoff, boys are taller than girls (150.60 SD 6.98 and 141.79 SD 7.60 respectively), and growth patterns in the year of onset of puberty are sex-dependent with boys beginning their pubertal growth later (USA) (10.45 yrs SD 1.47) compared to girls (USA) (9.25 yrs SD 1.15) (Abbassi 1998). The pattern for take off to be sex-dependent is also seen among British and European boys and girls (12.05 yrs SD 0.85; 10.30 yrs SD 0.95, respectively). The peak growth velocity is also reached later in boys than girls (USA: boys 13.57 SD 1.11, girls 11.49 SD 1.17; British & European: boys 13.91 SD 00.84, girls 11.89 SD 0.90) (Abbassi 1998). One of the greater sex differences is that boys gain greater height on average than girls (USA: boys 33.00 cm, girls 25.00 cm; British & European: boys 27.56 cm, girls 25.25 cm) (Abbassi 1998). Boys and girls also differ in terms of when they reach final adult height, with boys around 17 years of age and girls averaging at about 14 years of age (Hammill et al. 1977). Pubertal growth accounts for 17% - 18% of full adult height in males, and 17% in females, thus the average height difference in boys compared to girls has been attributed to the additional childhood (prepubescent) growth period, during which boys gain on average 10 – 11 cm in height (Abbassi 1998).

1.2 Sexual dimorphism

Sexual dimorphism refers to differences in characteristics found between males and females of the same species. Physical differences can be either primary sexual characteristics, referring to the reproductive organs, or secondary sexual characteristics, which refer to sex-typical characteristics that are not necessary for reproduction, however they relate to reproductive success. Behaviour and cognition can also be characterized as sexually dimorphic, for example lordosis in females and mounting in males (behaviour), and spatial rotation tasks (cognitive) (e.g. Linn & Petersen 1985; e.g. Maccoby & Jacklin 1974).

Charles Darwin took great notice of the differences between the sexes across a number of taxa, and he developed his theory of sexual selection to explain his observations (1871). He speculated that those traits exclusive to males that could not be explained by natural selection evolved through competition for mates. He writes:

> We are, however, here concerned only with that kind of selection, which I have called sexual selection. This depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction (Darwin 1871 p. 256).

The competition for mates is generally categorised as intrasexual, the competition between two members of the same sex, and intersexual, refers to the competition to attract the opposite sex. Intrasexual competition can be quite violent, such as rutting behaviour in bighorn rams or stag elks, and the most violent of these clashes occur when it is a winner take all situation – and the losers are left as genetic dead ends. Examples of intrasexual competition include the grand display of the peacock's tail, or the elaborate nests of the male Bowerbird. The competition in this arena is no less fierce in terms of the stakes, for in some cases, such as peacocks, winners secure a high number of mates while the losers secure few or none.

Both forms of competition can lead to the exaggeration of traits in either one sex, dimorphism, or both sexes, monomorphism. An example of a monomorphic trait is found in the crested auklet (*Aethia cristatell*), where both males and females exhibit ornaments of elongated forward-curving feathers on their foreheads during the breeding season (Jones & Hunter 1999). The early Darwinists, including Darwin himself, focused on male exaggerated traits, such as the ornamentation displayed by the bird of paradise or the great antlers of the red deer stags. Today, scientists understand that competition for mates is not an exclusive domain of males, and desire to attract the best males has shaped the sexually-dimorphic traits of females (Amundsen 2000; Amundsen & Forsgren 2003; Amundsen et al. 1997; Hill 1993; Jawor et al. 2004; Langmore 1998). For example in two-spotted gobies (*Gobiusculus flavescens*), males show mate-choice preferences for females with bright yellow-orange bellies over females with drab bellies (Amundsen & Forsgren 2001). Female intersexual competition is also evident in species such as the spotted hyena (*Crocuta crocuta*) (East et al. 1993; Glickman et al. 1992). In this review, the focus will be on sexual dimorphism, when sexes differ on particular traits.

1.2.1 Why study sexual-dimorphism?

The sex-differences observed within a species give us an insight into their evolved mating strategies (polygynous, monogamous, polyandrous, or promiscuous), as well as the type of parenting behaviours that have evolved (maternal care, paternal care, or bi-parental). In non-human animals, we use this information to speculate about patterns of evolution, genetic variation, niche specialisation, and the relationship between biology and behaviour. And armed with this cornucopia of information, scientists make predictions of how changes of environment, hormones, and now genes will alter behaviour, cognition, or anatomy. But then there is always the tantalising question: how does this relate to humans?

Humans too are sexually dimorphic on a variety of characteristics, behavioural, cognitive, and physical. But it isn't just the differences between men and women that intrigue us, the variation of sexually dimorphic traits within the same sex is perhaps even more fascinating. After all, if all peahens adore showy peacock tails, why don't all peacocks have the same showy tail? This is the crux of sexual selection and the host of theories that have arisen out of it.

An in-depth review of the theories of sexual selection opens the chapter '*Sexy Sons, Sexy Daughters*'; however, a brief review here is warranted.

1.2.2 Fisher's 'runaway selection'

Fisher's 'runaway selection' (Fisher 1915) is often employed to explain exaggerated male traits, as in the peacock's tale. If females have a preference for a particular male trait, independent of whether or not that trait confers any benefits, then males possessing that trait will gain a reproductive advantage over those males not possessing the trait. The gene[3] for that trait will then increase in the next generation. The other essential factor is the heritability of the preference for the male trait along the female line (continuing the desire for that trait into the next generation) leading to a 'runaway' process resulting in an exaggerated trait. A more detailed review of the Fisherian run-away process is discussed in the Chapter *Sexy Sons, Sexy Daughters*; however, one more point should be made at this juncture concerning the very basic premise of this sexual strategy.

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[3] Please note that using the term 'gene' does not necessarily refer to only one gene, but is a euphemism for a collection of genes.

Males and females often have differentiated reproductive potential; and, generally it is the male who can potentially produce vastly more offspring than females (Trivers 1972b). This is because a female, most often, is constrained by the number of offspring she can produce independent of the number of mates she can obtain, whereas male reproductive success is most often positively related to the number of mates he can attract. It can therefore be a sound strategy for females to seek out sexual partners who possess heritable traits that most females prefer for the simple reason that her sons have the potential to out-reproduce all of her daughters. Selecting mates with the genes that could propel her sons to greater success could be a wise female mate-choice strategy. The degree of exaggeration of these traits is kept in check by natural selection, for example when it begins to negatively affect reproductive success due to reduced survival rates. More on this topic shall be discussed in the *Sexy Sons, Sexy Daughters* chapter.

1.2.3 'Good genes' theory

The 'Good genes' (Andersson 1994; Trivers 1972b; Zahavi 1975) theory suggests that preference for a trait is established when the trait signals genetic benefits that can be passed on from parent to offspring. An important aspect of this theory is that the sex which has the most to lose (usually females, as previously noted) by selecting an inferior mate directs the evolution of the exaggerated trait in the opposite sex – but only if it the trait chosen is an honest signal of genetic quality.

It best serves those individuals who possess superior genes to signal their quality to potential mates in order to secure either as many mates as possible or the best quality mate available. Individuals who can best accurately assess signals of genetic quality will out reproduce individuals who are less accurate. Additionally, if the ability to accurately assess signals of genetic quality is heritable, then the genes responsible will continue to increase within the population, thus a coevolutionary-process leads to 'honest signals' of good genes and the preference for them (Ryan & Keddy-Hector 1992).

Signals of genetic or phenotypic quality that increase the reproductive success of the opposite sex will come under selective pressure due to mate choice (Grafen 1990; Johnstone 1995; Zahavi 1975; Zahavi 1977). But what really are we talking about when we say that individuals are looking for a few 'good genes'? Good genes can offer direct benefits, indirect benefits, or a bit of both.

Direct benefits refers to those which can directly offer advantages to the recipient. For ease of explanation, let's assume it is the female who is the recipient. Examples of direct benefits would include nuptial gifts, access to better territory, paternal care, fertilization ability, and decreased risk of contracting disease or parasites (see Johnstone 1995 for review).

Indirect benefits improve the potential fitness of offspring. In other words, the female does not gain an advantage that affects her ability to reproduce, but rather the advantages go to the reproductive fitness of her offspring. Such signals would include heritable genes for better parasite resistance, viability of offspring (e.g. weight at birth), and longevity. Some support for the good genes theories comes from observations of lekking behaviours (Johnstone 1995; Kirkpatrick & Ryan 1991). In lekking species, males contribute nothing to offspring care, nor provide the females with nuptial gifts or better territories. It appears that the only possible benefit to be gained, from the female's vantage, are superior genes, which are advertised through costly male displays (Johnstone 1995). While the evidence is very strong, the possibility that females are not seeking a direct benefit cannot be ruled out. Selecting a mate can be costly due to increased energy expenditures, chance of predation, or increased exposure to parasites and disease (Pruett-Jones & Pruett-Jones 1990). Another possible factor to explain female choice, is that they might choose the male with the most vigorous display as a way of minimising her risk to infection (Kirkpatrick & Ryan 1991; Reynolds & Gross 1993). Gibson and Höglund (1992) suggest that females imitate the choice of other females in order to reduce the costs of seeking a mate. In the case of the lek, a Fisherian run-away selection cannot be ruled out.

Better evidence in support of the good genes theory comes from female extra-pair copulations in socially monogamous[4] species (Johnstone 1995). Females who seek extra-pair copulations can gain no other benefit than genetic ones; and, evidence from cross-fostering experiments lend support to this theory. Norris found that the viability of male offspring was linked to paternal plumage colouration, a trait females use in mate choice; and, that the plumage trait was associated with attractiveness from their father (1993). *Poecilia reticulate* is a species of guppy subject to high predation, and females show a mating preference for males with larger total combined areas of orange, red, and yellow pigmentation independent of body size (Evans et al. 2004a). The newly-born offspring of the more attractive guppies, those with larger areas of pigmentation, showed greater ability to evade capture, suggesting an indirect benefit via female mate choice preferences (Evans et al. 2004b).

[4] Socially monogamous species refers to individuals who form pair-bonds and invest in offspring via parental care

1.2.4 'Immunocompetence' principal

Folstad and Karter's (1992) immunocompetence handicap principal is an extension of the good genes theory. They proposed that testosterone, which is often necessary for exaggerated traits in males, suppresses the immune system, thus only the healthiest males can both sustain compromised immunity and the exaggerated trait. Females that have inherited the preference for the trait will receive indirect benefits by passing on the genes coding for a superior immune system. Thus, both the trait and the preference will increase in subsequent generations. There have been criticism of this hypothesis, which is discussed in more detail in *Sexy Sons, Sexy Daughters*.

1.2.5 The problem of parenting

As noted above, the good genes theory takes into consideration the role of parental investment. The sex that invests the most into producing offspring will be the choosier sex (Trivers 1972b). This, for the most part are females, especially in mammals due to the length of gestation and lactation. In some species, the only part the male plays in reproduction is insemination; and employing runaway selection and good genes theories, we would predict that the females, being the choosier sex, would be looking for indirect benefits from the male genotype (see above for other considerations). More specifically, she would either choose males who signalled superior immunocompetence in the case of good genes theory, or, as predicted by runaway selection, she should choose an exaggerated male trait that is irresistible to other females so as to produce sons who are also irresistible.

In many cases, which is often seen in birds (Lack 1968), but only in a small number of mammals (Kleiman 1977), parental care is taken on by both parents. Even in bi-parental care species, females often remain the most investing sex, but males too are investing and incur costs for their devotion. In order to invest in offspring, males must sacrifice other mating opportunities. In a lekking species, where males do not invest in offspring, they expend their energy mating with numerous females, who make no further demands on them. When paternal investment occurs within a species, females place more demands on the male, and responding to this males must demonstrate their ability to invest in any resulting offspring. The signals for high-paternal investment will vary. In species where extra-pair copulations are rare or non-existent, those males that females find more attractive will invest more in their offspring than less attractive males. Evidence in support of this is found with brightly ornamented male Kestrals (*Falco tinnunculus*) (Palokangas et al. 1994). Where female extra-pair copulations are more likely to occur, then those males females consider attractive will invest less in offspring – as is seen in zebra finches (*Poephila guttata*) (Burley 1986). The reasoning is that in species where extra-pair copulations are more common, females will seek out males with good genes and find a less attractive male to raise her offspring.

Bi-parental care species pair-bond, at least for one breeding season and often for several seasons or throughout life. Such pairs are described as monogamous or socially monogamous, but this does not exclude the possibility of either sex seeking out extra-pair copulations. In bi-parental care species (this will be discussed in more detail in the chapter *Sexy sons, Sexy daughters*), both sexes should look for signals of quality, since both males as well as females pay dearly for choosing an inferior partner. Pair-bonded species, such as the great crested grebe (Huxley 1914), often continue to signal during the duration of the bond. It has also been speculated that displays after initial courting serve different purposes than the displays during initial courting (e.g. Wachtmeister 2001; Wachtmeister 2000).

Humans are bi-parental care species (Marlowe 2000), and human offspring, as most any parent would attest to, require high investment. One could reasonably argue that humans are by far one of the most costly offspring to raise in terms of time and energy. Women are considered the most investing sex, at least in terms of time spent with offspring, not to mention the cost of pregnancy in terms of physical health and the risk of childbirth. Men also invest in offspring, not only in time spent with offspring, but in terms of resources. Men also invest both time and resources directly in their long-term mate (Marlowe 2003), thereby incurring not only loss of resources but loss of potential mating opportunities with other women.

What have the economics of mate selection have to do with sexual dimorphism in humans? A simple answer is most everything. If we take into consideration that some of the evolutionary pressures facing our ancestors differed for males and females, we can begin to understand the reasons for the extant sexually-dimorphic characteristics, behavioural, cognitive, and physical, in humans.

1.2.6 Sexually dimorphic features in humans

As previously noted, females are, on average, slightly smaller than males, and this is true for both height and body mass (Alexander et al. 1979). Digit length ratio (2D:4D), discussed earlier, is also sexually dimorphic. Other features include: waist-to-hip ratio, breast development, external genitalia (e.g. penis and scrotum), vocal cords and voice, skin colour and texture, and facial characteristics, such as size of eyes, chin shape, nose, and mouth. This is far from an exhaustive list. As previously discussed, hormone levels are also sexually dimorphic, as is brain differentiation.

These play a role in the observable sexually-dimorphic features mentioned above, as well as cognitive and behavioural differences.

1.2.7 Body shape: Waist-to-hip and chest-to-waist

Men and women's body shape differ, with men being on average broader across the shoulders than are women and the waist and hips are nearly the same circumference, whereas a woman's waist is generally narrower than her hips. It is precisely this difference, the ratio of waist-to-hip, that Devendra Singh has suggested as a cue to fecundity, health, and youthfulness (Singh 1993a; Singh 1993b). Singh argues that because the fat distribution is guided by gonadal hormones, with testosterone directing fat deposits on the abdominal region, while oestrogen inhibits abdominal deposits and instead directs deposits onto the thighs and buttocks, body shape signals reproductive health and fecundity (Singh 1993a; Singh 1993b; Singh 1994b). Indeed, there is evidence that low waist-to-hip ratios relate to fecundity (Wass et al. 1997; Zaadstra et al. 1993) and to higher levels of oestrogen and progesterone (Jasienska et al. 2004).

There is substantial evidence that men (as well as women) prefer low waist-to-hip ratios in women (Furnham et al. 2001; Furnham et al. 1997; Henss 2000; Singh 1993a; Singh 1993b; Singh 1994a; Singh 1994b; Streeter & McBurney 2003). There is, however, some contention about the role of waist-to-hip ratio coming from evidence suggesting body mass could be a more important component of shape attractiveness (Tovée & Cornelissen 2001; Tovée et al. 2002; Tovée et al. 1999; Tovée et al. 1998). Although the debate continues over whether waist-to-hip ratio or body mass is the signal men find more important in their judgments of women, both appear to signal aspects of attractiveness (Tovée et al. 2002).

Women have preferences too when it comes to body shapes of potential mates. Men with an inverted triangle shape (chest-to-waist ratio), wide at the shoulders and narrow waist, are more attractive to women (Maisey et al. 1999a) than men whose shoulders and waist widths vary less – or when waist is larger than chest. This preference reflects the body shape differences between men, with an inverted triangular shape, and women, with a more hourglass shape (Campbell 1989). Both men and women will work to enhance these body-shape differences through physical exercise (Mealey 1997), which suggests that at some level men and women are aware that the 'right' body shape can increase attractiveness. It is thought that the breadth of the chest (which corresponds to shoulder width) signals physical strength (Maisey et al. 1999a). Male strength would have been useful both for male-male competition as well as mate-guarding.

1.2.8 Skin texture and colour

Charles Darwin (1871) hypothesised that skin colour in humans was due to sexual rather than natural selection. He noted that among African races, the tint of women's skin differed from those of men. Skin colour differences between men and women were noted by many early ethnographers (see Frost 1988 for review). More recently, it has been suggested that natural selection would have favoured darker pigmentation as our ancestors lost most of their body hair, independent of latitude (Aoki 2002). Preferences for lighter skin in mate choice would have (in a classical Fisherian selection process) increased the tendency toward lighter skin; and, in higher latitudes where dark pigmentation was no longer under strong natural selection pressures, lightness in skin colouration would continue to increase within the population (*ibid*). Others, however, argue that lighter skin pigmentation found in the peoples of higher latitudes would have been necessary for the production of vitamin D, and that natural selection would have brought to a balance the need to protect against ultra-violet radiation and its destructive photolysis of compounds such as B vitamin folate and the need to produce vitamin D despite reduced sunlight, particularly during the autumn and winter seasons (Chaplin 2004; Jablonski 2004; Jablonski & Chaplin 2000). The argument from natural selection does not necessarily exclude the influence of sexual selection for the sexual dimorphism of skin colouration.

There is growing evidence for the role of sexual selection in skin colour. Van den Berghe and Frost (1986) reviewed studies in which spectrophotometry measures were used to examine skin reflectance, that is light not absorbed by skin pigmentation. Thirty-two groups from every major inhabited area worldwide were assessed for skin pigmentation, and in all but two studies post-pubescent females were found to be lighter than post-pubescent males. The two studies showing opposite effects were noted for design flaws.

In a study by Hill et al. (1995), sex discrimination was more accurate using cues of skin colour than those of face shape. In another study, statistically accurate sex discrimination was based on red/green ratio, with men having a higher ratio than women; while pre-pubescent targets were at chance (Tarr et al. 2001). Manning and Caswell (2004) suggest that adult and foetal oestrogen influence skin colouration. Indeed Law Smith et al. (in prep-a) found that skin colouration was related to oestrogen levels, and that males preferred colouration signalling higher levels of oestrogen. Such evidence suggests that aspects of skin colouration could be an honest signal to reproductive health.

1.2.9 Pheromones

Karlson and Luscher (1959) defined pheromones as "airborne chemical signals produced by an individual of a species that trigger a neuroendocrine response or control behavior, endocrine state, or development in another member of the same species." The compounds were originally employed in animal husbandry, thus research was limited to non-human animals. This all changed when Brooksbank and Haslewood (1961) discovered that human urine contained the same steroid pheromones (16-androstenes) similar to ones found in boar testes. This discovery spurred research into whether or not pheromones played any role in human behaviour, and soon it was found that the androstenes steroids differed between men and women, in that men's urine contained significantly higher levels (Cleveland & Savard 1964). One oestrogen based (female) putative pheromone, estratetrenol, has been found in the urine of pregnant women in the third trimester (Thysen et al. 1968). For convenience, I will refer to the androgen-based pheromones as 'male', because they are more abundant in males due to the higher androgens, and the oestrogen-based pheromone as 'female', again because females produce higher levels of oestrogen. It must be noted, however, that both sexes can produce the full complement of human pheromones.

1.2.9.1 To be or not to be a VNO, that is the question

Before moving on to some of the studies concerning human behaviour and pheromones, a brief overview of the status of the human vomeronasal organ (VNO) is needed, especially since there is currently a debate as to whether or not humans even possess a functioning one, which is important to assess considering that the VNO is critical to the processing of pheromones in terrestrial vertebrates

(Grosser et al. 2000; Keverne 1983). The VNO has been found to exist in normal human embryos (Boehm & Gasser 1993; Smith & Bhatnagar 2000); however, there is evidence that due to loss of receptor cells it loses its functionality and is no longer on parity with other mammals (Smith & Bhatnagar 2000). In adults, it appears that the VNO structure, while it exists, the presence of the neuronal cells is missing (Bhatnagar & Smith 2001). That these neuronal cells are apparent early during neonatal development but then wane is without precedent in mammals (Bhatnagar & Smith 2001), and the epithelium lining is unlike any other species (Moran et al. 1991; Stensaas et al. 1991). Yet, in a study by Monti-Bloch and Grosser (1991), steroids, including androstadienones and estratetraenyl, elicited electrovomeronasogram responses, whereas conventional odours did not. This provides evidence for a chemosensory response. We have then a dilemma, without a homologous animal model, it is difficult to understand the processes associated with human pheromones and human behaviour. If it is not chemosensory, as Bhatnaga and Smith (2001) suggest, then the question remains as to the mechanisms by which humans respond to pheromonal signals. But if it is chemosensory as Monti-Bloch and Grosser (1991) have indicated, then the question still remains as to how the pheromone signals are directed to the brain. It is beyond the scope of this review to debate the functioning of the human VNO. For a full assessment of the debate see Michael Meredith's review article (2001).

One of the earliest studies concerning the possible influence of human pheromones on physiology was conducted by Martha McClintock (1971). She found that menstrual synchrony can occur when women reside together, and while she did not demonstrate the mechanism by which women came into synchrony, subsequent studies have revealed that axillary odours as a factor (Petri et al. 1987; Stern & McClintock 1998).

Grammer (1993) found that attitudes toward olfactory cues produced by a male pheromone (5-α-androst-16en-3α-on) was mediated by the timing of the menstrual cycle, with women who were in the most fertile phase of their cycle finding the odour less unappealing than women in the less-fertile phase of their cycle. This finding indicates a possible hormonal component affecting women's reproductive-related judgments.

Strong evidence for sexually dimorphic effects to male and female pheromones has also been found for two steroid compounds, α4,16-androstadien-3-one and 1,3,5(10)16-estratetraen-3-ol, in cerebral activations using regional cerebral blood flow (rCBF) and positron emission tomography (PET) measures (Savic et al. 2001a). In this study, 12 men and 12 women were each exposed to one of three conditions: androstenone, estratetraen, and a no-odour condition. None of the subjects were anosmic to androstenone and women were in their second to third week of cycling during testing (however control for pill use is not evident). In women, the androstenone produced activation in the anterior-ventral hypothalamus, but not in the olfactory regions (amygdala, piriform, orbitofrontal, and insular cortex); however, in the estratetraen condition, these olfactory regions became active while the anterior-ventral hypothalamus did not. The activations were converse in males, with activation in the anterior-ventral hypothalamus during exposure to estratetraen, while the olfactory region was activated during the androstenone condition. In comparison to the no-odour condition, sex-differentiated activations were also found. Women in the androstenone conditioned exhibited clusters of activation in the hypothalamus, and the right amygdala + piriform cortex, anterior cingulate, and right lingual gyrus, while men in the estratetraen condition showed clusters of activation in the hypothalamus and in the right and left amygdala + piriform + insular cortex and in anterior cingulate. These sex-differentiated brain activations provide further evidence that in humans, chemosensory signals may play a role in human sexual interactions. More recently, Savic and her colleagues (2005) found in both homosexual males and heterosexual females hypothalamic activation in response to α4,16-androstadien-3-one were similar, this is suggestive of prenatal effects of brain organising hormones.

Smelling human pheromones has also been found to influence perceptions of masculinity. When smelling a male-typical pheromone (5-α-androstenst-16-en-3-one), men perceived men's faces as more masculine looking (Kovács et al. 2004), providing evidence that individuals use a number of signals to assess mate quality. In the chapter, *Concordant preferences for opposite-sex signals?*, the concept of multiple modalities of signaling is expanded.

1.2.10 Acoustic signals

Acoustic signalling can be found among a number of species, and it relates information regarding size, dominance, and condition (for review see Johnstone 1995). Intensity and frequency of acoustic displays, because they are costly to perform, can signal quality and condition; whereas repertoire and complexity of song can signal parental care or survivability (as these signals will take additional time to learn and/or require extended parental care to acquire) (*ibid*).

Signalling can also be used to deter male-male combat. In the toad species, *Bufo bufo*, males mate with females by hoping on to their backs and clinging to them until they lay their eggs. Males are often seen wrestling to gain position on the backs of the hapless females (Davies & Halliday 1978). These male-male scuffles generally go in favour of the larger male; but, the disputes over females can be avoided when males advertise their size through acoustic signals, this is because the larger the male – the deeper the croak (*ibid*). Davies and Halliday noted that whenever there was a potential dispute, that is when one male was mounted and another approached, only the mounted male croaked, thus signalling his size. To test the role of the acoustic signals in avoiding male-male conflict, they collected various sized male toads, 24 medium, 12 small, and 12 large. The small and large toads were all paired with females, whilst the medium sized toads were divided into 12 'paired' toads and 12 'attacker' toads. All of the paired toads were rendered 'croakless' through the use of tape. All the attacker toads were in two experimental conditions, one where they heard the croaks of a large male (deep croak) and the other where they heard the croak of a small male (high-pitched croak). In the deep-croak condition, the attacker toad was less likely to try to unseat his rival male, independent on the actual size of the paired male; however, in the high-pitched croak condition the attacker male was much more likely to attempt to usurp the smaller or medium paired-male's position, but attempts were rare if the paired toad was larger.

In humans, men and women differ in the acoustic properties of the voice, and individuals are able to discern the sex of a person using only the cues from vowel sounds (Childers & Wu 1991). Men, on average, have lower fundamental and formant frequencies than women (Whiteside 1998a; Whiteside 1998b), and this has been attributed, in part, to the thickness and the size of the vocal folds (Fant 1960; Lieberman 1984; Schön Ybarra 1995), which is attributed to higher levels of testosterone (Beckford et al. 1985; Hollien 1960). Simply put, the thicker the vocal folds, the deeper the voice.

Sarah Collins found that women judged closely spaced, low-frequency harmonics in male voices (deeper voices) as more attractive (2000), however, she points out that women incorrectly associate this vocal characteristic with larger body size and more chest hair, when in fact they are unrelated. When the fundamental frequency of male voices are manipulated, women indicate stronger preferences for lowered frequencies over higher frequencies, suggesting that deeper male voices could signal sexual maturity (Feinberg et al. 2005). Women's voices are also an apparent signal of quality, and men's judgments of women's facial and vocal attractiveness are positively related (Collins & Missing 2003). Men judged women with relatively higher formants and fundamental frequency as being more attractive, and women with higher fundamental frequency as younger. As further evidence, more feminine facio-metric properties of female faces were found to positively relate to a more feminine (high) female pitch of voice (Feinberg et al. in press). In the same study, when averaged-composite faces were made of two groups of women with high-pitched and low-pitched voices, men preferred the composite face image of the high-pitched group. Additionally, the individual faces of those women with higher-pitched voices were preferred over the individual faces of women with lower-pitched voices. These above noted findings indicate a relationship between hormonal profiles and sexually-dimorphic signals; and, these signals are used by both sexes to make judgments concerning members of the opposite sex. It is also evident that men and women use multiple signals, face and voice, to assess mate quality. The use of multiple modalities for mate evaluation will be discussed later in Chapter 8, concerning the concordance between pheromones and face-sexual-dimorphism.

1.2.11 Sexual dimorphism and the face

From nearly the moment we are born, we humans are fascinated by faces. Evidence suggests that human infants are born with a representation of the human face (Gorren et al. 1975; Johnson et al. 1991). In a classic study, human neonates of the ripe old age of 9 minutes, responded (eye and head following) significantly greater to accurate representations of face patterns than to either scrambled faces or a blank stimuli (Gorren et al. 1975). The authors suggest this finding is indicative of an unlearned response that has evolved in humans. There is even evidence that young neonates show a preference for more attractive faces (Langlois et al. 1991; Langlois et al. 1987; Slater et al. 2000; Slater et al. 1998). Neonates also imitate adult facial gestures, that is mouth opening and tongue protrusions (Meltzoff & Moore 1977; Meltzoff & Moore 1983); and, apparently so do the neonates of our closest cousins, chimpanzees (*Pan troglodytes*) (Myowa-Yamakoshi et al. 2004). It has also been made clear that specialised structures in the brain code and respond to faces and facial features in non-human primates (Perrett et al. 1982) and in humans (Kanwisher et al. 1999). We come into this world prepared to learn about faces (Slater & Kirby 1998).

The human face plays a powerful role in inter-personal relationships, and people gain cues of the emotional states of others through interpretation of facial expressions (e.g. Ekman & Friesen 1971; Izard 1971). Given that the face is so important to humans, it stands to reason that facial-signals of mate-quality would exist. And they do.

Epigamic features of the face include eyes, chin, nose, and face-shape. In a study conducted by Oliver-Rodríguez and his colleagues (1999), men and women were asked to rate specific facial features of adult male and female images for attractiveness. They found that open eyes in female faces were rated as significantly more attractive than narrow eyes, however the same was not found for male faces. Full lips were more attractive than narrow lips for both sexes, however the effect was much stronger in female than in male faces. Short facial proportions (relative jaw length) were also found more attractive in female as compared to male faces. The feature found to differ most between men and women's faces was the chin; and, broad chins were preferred in male faces, whilst narrow, fine chins were rated as more attractive in female faces. Using anthropometric methods (Farkas 1981; Farkas 1994), several differences have been found between the mean measures of men's compared to women's faces; and, on average men's features tend to be larger (Cunningham et al. 1990).

The facial characteristics more typical of females includes fuller-lips, gracile chins, larger eyes, smaller nose, and over all more delicate features, whilst male-typical features include heavier brow, square jaw, and thinner lips. Male- and female-typical facial features are thought to be mediated by the sex-hormones, with differences between average male and female faces becoming more exaggerated during pubertal growth (Enlow 1990; Jones 1995). As with other sexually-dimorphic features, facial features are thought to signal particular traits that the opposite-sex zero in on to make mate-selection decisions. This is covered in more detail in chapters, *Sexy Sons, Sexy Daughters* and *Age of First Sex.*

What is central to this thesis, is that we use face-shape-characteristics to make judgments related to mate-choice (Cornwell et al. 2004; Little et al. 2001a; Little et al. 2002; Perrett et al. 1998; Perrett et al. 2002). By manipulating female face-shape to appear more 'feminine', men's ratings of attractiveness increase (Cornwell et al. 2004; Fauss 1988; Jones 1996; McArthur & Berry 1983; Perrett et al. 1998; Perrett et al. 1994; Rhodes et al. 2003; Riedl 1990). With women's preferences of men's faces, the relationship between masculinity and attractiveness is less predictable. Some studies indicate that women prefer more masculinised male faces (Grammer & Thornhill 1994; Penton-Voak et al. 2001; Scheib et al. 1999), while others indicate a preference for more feminised male faces (Cunningham et al. 1990; Ishi et al. 2004; Penton-Voak et al. 2003; Penton-Voak et al. 1999; Perrett et al. 1998; Rhodes et al. 2003; Swaddle & Reierson 2002). The difference in preference judgements within women have been attributed to individual differences, including menstrual cycle (Penton-Voak et al. 1999), partnership status (Little et al. 2002), age of parents (Perrett et al. 2002), waist-to-hip ratio (Penton-Voak et al. 2003), and self-perceived attractiveness (Little et al. 2001a). Other factors, including father-absence and relationship with father, also contribute to individual preferences for male facial masculinity (Boothroyd 2004c).

It has been proposed that in males, masculine facial characteristics are signals of superior immunocompetence (e.g. Thornhill & Gangestad 1999a). Evidence for the role of testosterone and suppressed immunocompetence is, however, mixed (see chapter *Sexy Sons, Sexy Daughters* for review). It has also been suggested that masculinity traits confer negative personality attributes such as dishonesty and coldness (Paunonen et al. 1999; Perrett et al. 1998) as well as dominance (Paunonen et al. 1999). Increase in eye size was also positively related to judgments of facial femininity and 'babyface-ness', and increased eye size was positively associated with personality traits of honesty, nurturance, empathy, agreeableness, and neuroticism for both male and female faces (Paunonen et al. 1999).

Men show a strong preference for feminine facial characteristics in adult females (Cornwell et al. 2004; Jones 1996; Perrett et al. 1998; Thornhill & Gangestad 1999). The important components of female facial attractiveness include neotenous facial proportions and features, and it has been suggested that these carry cues for youthfulness, thus good reproductive potential (Fauss 1988; Jones 1996; McArthur & Berry 1983; Riedl 1990). Female facial characteristics are related to oestrogen (Jones 1996; Law Smith et al. in prep-b), thus providing beneficial cues to reproductive quality (Thornhill & Gangestad 1999a). Feminine and neotenous facial features are associated with personality traits such as warmth (Perrett et al. 1998), naiveté, honesty, kindness (Berry & McArthur 1985) and being more child-like (Berry & McArthur 1985; Berry & Zebrowitz McArthur 1986; Eagly et al. 1991; Zebrowitz & Montepare 1992).

When assessing facial characteristics for possible mate-choice, the cues individuals use to make judgments will convey not only mate-quality in terms of immunocompetence and reproductive health, but information about personality traits. The later is particularly important to consider when assessing judgments of facial attractiveness since humans invest in pair-bonds and bi-parental care, and personality traits are important to both mate selection and lasting pair-bonds (Botwin et al. 1997; Penton-Voak & Perrett 2001).

1.3 Mating strategies and parental investment

In this section, the relationship between parental investment and mating systems will be reviewed. The degree of sexual dimorphism is related to mating systems and reproductive strategies. For example, there is a relationship between the degree of sexual dimorphism and the greater the difference in male body size to female body size, the more likelihood the species will be polygynous (Alexander et al. 1979). Examining human body size dimorphism, Alexander concluded that humans are mildly polygynous. Polygynous males are less likely to invest more than genes in their progeny, and females take on all of the post-conception care. Considering that parental investment can range from minimal (genes only) to over 20 years investment (as is the case for the parents of many undergraduates), mating strategies should reflect the quality and quantity necessary for raising healthy, fecund, and attractive offspring. The definition of parental investment used herein comes from Trivers' (1972b, p. 139) :

> Any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring.

Individuals will make tradeoffs whenever they invest in reproduction. Males for example have limited sperm production capacity, no matter how virile they are, thus even lekking species must choose between investing more sperm with some females via multiple copulations or sperm quantity while limiting sperm with other females or eschewing them altogether (Dosen & Montgomerie 2004; Werner & Lotem 2003). On the other end of the parental investment extreme are species like the monogamous pair-bonded California house mouse, *Peromyscus califonicus*, where neither males nor females engage in extra-pair copulations and both invest all their reproductive efforts into their joint offspring (Dudley 1974; Gubernick & Alberts 1987).

1.3.1 r and K strategies

The distinguished American ecologist Robert MacArthur (1962) incorporated aspects of R.A. Fisher and J.B.S. Haldane's theorems to account for varying degrees of inbreeding and effects of population density in terms of fitness. From this, as well as later work (MacArthur & Wilson 1967), arose '*r* and *K* selection' theories. The names come from two parameters of standard population dynamic theory. '*K*-strategists' are said to live close to *K*, the carrying capacity of the environment; '*r*-strategists' are said to maximize *r*, the intrinsic rate of increase of the population.

The general premise is that organisms must adapt to their environment to maximise their fitness, and environments vary in stability. In unstable environments, the best strategy would be to produce large numbers of offspring, many of which will die but a few are likely to survive. In stable environments, the better strategy is to have fewer offspring, but invest more in each, so that offspring survival chances are increased. Thus, '*r*-selected species' are short-lived, reproduce rapidly, take advantage of open niches, and are prone to boom or bust populations depending on the vagaries of the environment. They are often called 'weeds'. '*K* selection' refers to species that are longer-lived, reproduce slower, and are more immune to environmental swings. At the '*r*' extreme of the continuum, the organism will be small, energy required to produce one offspring is low, many offspring are produced, offspring reach sexual maturity quickly, life expectancy is short, individuals reproduce once, and survivorship expectancy for offspring is very low, but a few will survive to reproduce. *K* strategists are larger, the energy to produce one offspring is high, few offspring are produced, life expectancy is long, individuals can reproduce multiple times, sexual maturity is slow to arrive, and survival of offspring should be fairly high – with most offspring living a full maximum life-span. Species can lie at any point along the continuum between these two extremes.

Humans seem to lie near the *K* end of the continuum, if we go by our long lives, slow maturation, few offspring, and good offspring survival rates (Mace 2000). But some scientists have suggested that even within a species there is variation of strategy, and have employed the ideas of *r* and *K* strategies to characterize human mating strategies, reproduction, and parental investment (Belsky et al. 1991; Bereczkei & Csanaky 2001; Draper & Harpending 1982; MacDonald 1997). The idea is that in unstable environments, humans may opt to increase their rate of reproduction, investing less in each individual offspring, and that offspring will reach sexual maturity earlier and begin their own reproduction earlier than humans raised in stable environments. Unstable environments during development could affect reproductive strategies including mate choice. Indeed, girls who experienced longer duration of father absence (e.g. fathers left earlier) were more likely to engage in sexual intercourse earlier than girls whose fathers left later or not at all (Ellis et al. 2003). Quinlan (2003) looked at retrospective data for 10,847 U.S. women to examine the effects of divorce and separation of parents, including any effects related to the age of the child when divorce or separation took place. He found that when women's parents divorced or separated early during her childhood (before birth up until 5 years of age) the women were more likely to reach menarche earlier, engage in sexual intercourse earlier, become pregnant earlier, and whose marriage was shorter in duration when compared to women whose parents' separation occurred later or not at all. Additionally he found, if parents divorced or separated during the women's adolescence, these women were likely to have more sexual partners than women whose parents did not separate or divorce.

The original work by MacArthur was not intended to explain mating strategies, but to account for varying degrees of inbreeding and effects of population density in terms of fitness. Certainly, it was not developed to explain individual differences of mate choice within a species. Considering home environment during human development is important, as many factors can affect adult behaviours such as attachment to parents, parenting styles, siblings, extended family, moving house, illness, and home and community environments (e.g. violence). Whether these factors can be fitted into '*r* and *K*' selection is perhaps debatable. In the next section, hypotheses specific to mating strategies are explored.

1.3.2 Mating strategies

In this section, we will consider how distribution of essential resources contribute to the ability of one sex to monopolise reproduction of the other sex as proposed by Gordon Orians (1969). A key concept from his work is the *polygyny threshold model*, wherein female choice and male resource control combine to predict when polygyny will occur within a population. In an excellent review article, Emlen and Oring (1977) expand upon Orians' original work, and stress the importance of one sex being able "...to control the access of others to potential mates" (p. 215). Further they outline the types of ecological and environmental factors in relationship to how particular types of mating strategies will occur within a population. They also suggest along the same lines as Orians, that there will be a bias toward polygynous mating strategies because females are most often the limiting sex in terms of reproductive potential. In short, polygamy should be the most prevalent mating system except where constraints prove too costly and reproductive potential is greatly reduced. Factors friendly to polygamy include: one sex is more likely to assume the majority of parental care, parental care is minimal, and food resources are abundant (allowing for one parent to adequately care for self and young) (p. 216). A key point they make is that the opportunity for 'emancipation' (e.g. males abandoning females) on its own does not necessarily lead to abandonment, it is only a strategic advantage when the abandoning sex has the potential for additional mating opportunities. For example, if all the females within a population were to become sexually receptive at once and for a limited length of time, making it impossible for males to mate sequentially, then male abandonment holds no substantial advantage. Thus, it could be a better strategy for males to remain with the female and invest in her and her young. However, if within a population female oestrus is asynchronous or occurs over a longer period of time, males can gain an advantage by deserting females and seeking out other mating opportunities. The more asynchronous the receptivity of one sex, the more likely the other sex will take advantage by mating with multiple partners (usually this results in polygyny) (*ibid*).

Distribution of resources also will be important in determining mating strategy. Uniformly spaced resources lend little opportunity to monopolise them, thus reproductive fitness might favour bi-parental care. If resources vary in density and/or are stable over time, then territoriality can occur; and, those individuals who control areas of desired resources will be able to attract multiple mates (Emlen & Oring 1977). Another influence of resource distribution combined with the risk of predation is that it can lead females to aggregate, giving a few males the opportunity to monopolise sexual access, usually through fierce male-male competition (*ibid*).

While all factors that contribute to various types of mating strategies have not been discussed above (see Emlen & Oring 1977 for full review), a point that must be stressed is that one factor on its own will not determine which mating strategy will emerge within the population.

Figure 1.1: An ecological classification of mating systems (Emlen & Oring 1977)

Monogamy: Neither sex has the opportunity of monopolising additional members of the opposite sex. Fitness often maximised through shared parental care.

Polygyny: Individual males frequently control or gain access to multiple females

Resource defense polygyny: Males control access to female directly, usually by virtue of female gregariousness.

Male dominance polygyny: Mates or critical resources are not economically monopolizable. Males aggregate during the breeding season and females select mates from these aggregations.

Explosive breeding assemblages: Both sexes converge for a short-lived, highly synchronized mating period. The operational sex ratio is close to unity and sexual selection is minimal

Leks: Females are less synchronized and males remain sexually active for the duration of the females' breeding period. Males compete directly for dominant status or position within stable assemblages. Variance in reproductive success and skew in operational sex ratio reach extremes.

Rapid multiple clutch polygamy: Both sexes have substantial but relatively equal opportunity for increasing fitness through multiple breedings in rapid succession. Males and females each incubate separate clutches of eggs.

Polyandry: Individual females frequently control or gain access to multiple males.

Resource defense polyandry: Females control access to males indirectly, by monopolizing critical resources

Female access polyandry: Females do not defend resources essential to males, but through interactions among themselves, may limit access to males. Among phalaropes, both sexes converge repeatedly at ephemeral feeding areas where courtship and mating occur. The mating system most closely resembles an explosive breeding assemblage in which the operational sex ratio may become skewed with an excess of females

Another pattern of mating strategy, not mentioned above, is promiscuity. Males and females both mate with multiple partners, however, there are no male-female pair-bonds (Clutton-Brock 1989). The issue of pair-bonding is essential, for monogamous species often engage in extra-pair copulations (both males and females), but are not labelled as a promiscuous mating strategy or social organisation.

1.3.3 Parental investment

As noted above, Trivers' (1972b) seminal paper considering the evolution of mating strategies in light of the differential investment in offspring between the sexes. This theory has proven to be extremely useful in explaining differences in mate choice preferences and sexual strategies. There is often a huge discrepancy between the reproductive potential of males and females; and, for the most part, the female is limited in the number of offspring she can produce while males can ostensibly produce thousands of offspring or more. Let's acknowledge that in some species, such as pipefish, the sex roles are reversed, but for ease of reading for the rest of this section we will assume that the female is the limiting sex. Because the sex ratio within a population is approximately equal, if some males impregnate more than one female, other males will find themselves without a mate. This sets up the potential for some males to take advantage of multiple mating opportunities, while females are unlikely to gain direct benefits in terms of fecundity by mating with multiple males. But the whole purpose of mating is to reproduce offspring who are themselves successful at reproduction. Offspring who never reach reproductive age or never reproduce because of poor condition result in an irretrievable loss of resources for both parents. Each sex must consider the cost of investment in offspring against the potential loss of future offspring. In mammals, females gain little from multiple matings, thus a female is better served by investing in her offspring rather than pursing new mates. By contrast, males can greatly increase their actual reproduction by mating with numerous females, the cost of lost mating opportunities usually outweighs the advantages of extended investment in offspring. Males are much better off, generally, in expending all their energies to pursuing mates.

Since females will invest the most energy into offspring, they will be a limiting resource to the males and become a very valuable commodity. The argument then goes that males should be more aggressive in their pursuit of multiple mates and not particularly discriminating, while females, who stand to incur greater losses if offspring fail to thrive, should be much choosier when it comes to mating.

In the same paper, Trivers writes "At any point in time the individual whose cumulative investment is exceeded by his partner's is theoretically tempted to desert." He explains that gamete size, the female's being larger, predisposes females to continuing to invest because her initial investment is larger compared to the male's investment and argues that past investment should bear upon future investment. This aspect of the theory has been criticised because it incorrectly assesses why the quantity of previous investment is important (Dawkins & Carlisle 1976). The reluctance or temptation to desert should be based on future investment costs, not what has already been spent. A parent must weigh the cost of future investment against the cost of investment to rear another offspring to the same age (*ibid*). Maynard Smith (1977) carried this idea further, using mathematical models to assess evolutionarily stable strategies of parental care based on future mating opportunities and population sex ratios (also see Maynard Smith & Price 1973). Thus, parent abandonment should be weighed against future costs, not past.

In species where males only contribute sperm, they can afford to be practically indiscriminate while females choose the best possible genes. In bi-parental care species, where both males and females pair-bond in order to jointly invest in offspring, both sexes risk significant losses if they choose the wrong mate. However, as has been previously noted, there is a pressure for males to be polygynous – if only in the most opportunistic ways. Any energy expended by the male to pursue extra-pair copulations outside the pair-bond will result in loss of energy expended on his mate and her offspring.

1.3.4 Human mating strategies and parental care

Mating strategy and parental care are interrelated, and as previously noted humans tend toward bi-parental care and long-term investment in offspring. So where does this put us in terms of mating strategy? Anthropological data suggest that humans tend toward polygyny. By looking at different human societies, we find that 82% allow polygyny, 17% prohibit polygyny, and less than 1% allow polyandry (Murdoch 1967). Yet, most marriages across all societies are monogamous. Frank Marlowe (2000), using published ethnographic data, evaluated mating strategies and parental investment based on ecological and environmental factors. He suggests that when males are able to amass resources, to the exclusion of other males, polygyny is more likely to exist, and polygyny would be associated with less paternal investment in offspring. Data are supportive of this hypothesis, and societies of horticulturalists had both higher rates of polygynous marriages and lower rates of paternal investment. Interestingly enough as well, women in horticultural societies also reported more extra-pair copulations than within non-horticultural societies (*ibid*).

1.3.4.1 Evidence for mild polygyny in humans

Evidence for mild polygyny in humans, according to Harvey and Pagel (1991), comes from comparative studies of testes size across various taxa. The argument is, that in species where males control harems, such as elephant seals and gorillas, energy should be expended on physical features that aid in male-male competition; and, as males monopolise females in harems, there is no need to waste precious resources on features that aid in sperm competition – e.g. large testes in comparison to body mass. In species with a promiscuous mating strategy, such as bonobos and chimpanzees where males and females both mate with multiple partners, male-male physical competition is less fierce[5] while sperm competition becomes more important, thus more energy should be placed into making larger testes rather than larger body mass to exclude other males from access to females.

By considering the relationship of body mass to testis size in primates using logarithmic scales, Harcourt and his colleagues (1981) provide convincing evidence for humans being mildly polygynous. Chimpanzees and bonobos have relatively bigger testis in relation to their body mass, where as gorillas testis to body size ratio goes in the opposite direction. In *Figure 1.2*, primate species are plotted out on a graph with the X axis representing body mass (log scale) and the Y axis representing testes mass (log scale). The solid dots represent species that

[5] This is not to say that male-male competition does not exist, only that as opposed to winner-take-all male-male competition, promiscuous species are less likely to fight with intent to harm for access to females.

engage in a promiscuous mating strategy, with females and males mating with multiple mates. The open dots are those species more likely to engage in polygyny, and the + is where human males plot out on the graph. In relationship to the other primates, we are closest to orang utans, and over all we appear to be more like the polygynous primates than promiscuous ones.

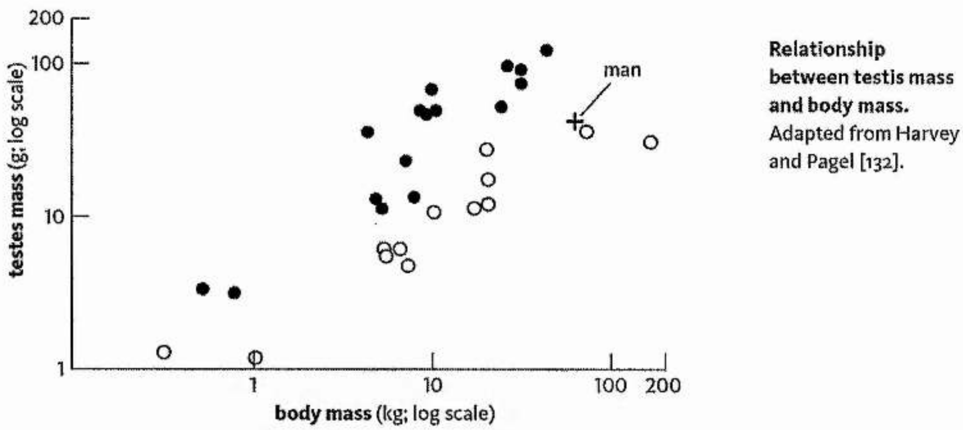


Figure 1.2: Relationship between testis mass and body size (Harvey & Pagel 1991)

1.4 Recapitulation

The theories that have been covered in this brief review are applicable to all living organisms. But this thesis concerns the role of facial sexual dimorphism in humans, not voles or peacocks. In the following experimental chapters, the theories discussed above will be employed to explain more specific behaviours in humans. The usefulness of each theory to explain human behaviour is limited. For example, Trivers' theory of parental investment can help us understand why men tend to be less discriminating than women when it comes to sexual partners, and why women are more likely to seek long-term rather that short-term relationships. But the theory cannot tell us how women will assess men's mate-potential qualities, or why certain facial features signal particular traits. For this, we need to keep in mind the theories such as runaway selection, good genes, and the immunocompetence principal.

Because individuals vary, there is a need to signal one's quality to both potential mates as well as potential rivals as well as being able to accurately read the signals carried by others. Throughout our evolutionary history, particular features originally carved out by natural selection have been co-opted through sexual selection to signal aspects of quality. Hormones and genes play an essential role in shaping these features, whether they be physical or behavioural. Environment too plays a critical role in shaping individual quality, as it affects gene expression as well as hormone levels.

Understanding any aspect of human behaviour is complex, and while it is the goal of every scientist to make things as simple as possible, making explanations too simple is of no use. Evolutionary theories allow us to build a framework by which to understand specific aspects of individual mating strategies. For example why do some women prefer men with more masculine facial features while others fall for the less masculine looking ones? (Chapter 8) Or why would rate of development affect adult mate preferences? (Chapters 5 and 6) The following empirical chapters will consider these and other questions at length, and attempt to gather up all the threads from higher level theories to specific hypotheses to actual data.

2 Sexy sons and sexy daughters: The influence of parent's characteristics on offspring

2.1 Introduction

In order to unravel the complexities of behaviour, we rely on theoretical models to help us organise and understand it. Increasingly, the lens of Darwinian selection has been applied to human behaviour; and, in particular comparative psychology, biology, and behavioural ecology are helping to elucidate the complexities of human mate choice. Darwin's (1871) prescient theory of sexual selection, that male characteristics are shaped and selected by female preferences, lay dormant for some time after its initial publication. Eventually it gave rise to Fisher's (1915; 1930) 'run-away' hypothesis (later dubbed the 'sexy-son hypothesis'), which argued that female preference for a male trait could lead to exaggeration of that trait over successive generations. It took another 40 years before Darwin's theory of sexual selection gained greater prominence with the work of Trivers' (1972b) parental investment theory (good genes), Zaharvi (1975) and Grafen's (1990) handicap principle, and Hamilton & Zuk's (1982) theory of heritable fitness. While these theories are not necessarily at odds (Kokko 2001), their validity and nuances continue to be debated. Scientists use both modelling as well as observations of mating systems across a wide variety of taxa, including humans, to ascertain these theories' strengths and weaknesses. Despite the debates, one thing remains unequivocal: in order for any theory on sexual selection to be viable, inheritance is necessary.

2.1.1 Fisher's Runaway Process

Fisher (1915) proposed three evolutionary stages as an indirect form of sexual selection to account for the exaggerated male ornamentation such as the plumage of the peacock's tail or the brilliant facial coloration of the mandrill baboon. The first stage, he argued, is that if a trait favoured by natural selection was also favourably assessed by the opposite sex, the advantage of the existing trait would increase as a result of this sexual selection. In the second stage, the trait no longer owes its advantage to natural selection, indeed Fisher posited that natural selection may have 'turned against it', but due to the increased sexual preference for it, the trait becomes exaggerated within the population and continues to do so as long as its advantage under sexual selection is retained. The third stage occurs when equilibrium is reached and natural selection and sexual selection are in balance, which Fisher pointed out was likely true in most all present day species. As a further comment to his three stage theory of runaway selection, Fisher argued that the equilibrium reached for one particular trait (or 'point' as he referred to it) would be broken as other traits became of interest and importance to the opposite sex.

The theory of 'runaway selection' is most often used to explain exaggerated male ornamentation, and that any female preference for a heritable male trait would generate non-random mating within a population. Thus both the preference and the preferred trait could co-evolve resulting in a 'runaway process'. That is, as both the preference and the trait increase within the population, an exaggeration of the trait results. Females for example gain an indirect benefit by producing sons who are more likely to be preferred by other females as mates; however, the female does not gain direct benefits such as increased fecundity or survival. Indeed, preference for certain male traits can go so far as to be deleterious to fitness of female offspring (Fedorka & Mousseau 2004) and for offspring in general, as exaggerated ornamentation is unlikely to be the optimal state that natural selection on its own would produce (Arnold 1983). Given there is often a differential reproductive potential between males and females (e.g., males can produce much higher numbers of offspring), females can increase their own reproductive success by choosing 'sexy mates' who provide the genes enabling her to produce 'sexy sons'. These 'sexy sons' are then chosen by a higher number of females as mates, thus leading to a potentially greater number of grand-offspring from one son than from a number of daughters. The amplification, or ratcheting-up, of the male ornamentation continues until it is checked by natural selection when it impedes the survival of the male to the point it no longer offers benefits to the female. This theory has found support across a number of species (Brooks 2000; Etges 1996; Jones et al. 1998; Wedell & Tregenza 1999). Although Fisher expressly discussed his theory in the light of human evolution and mate choice, less has been done to examine its usefulness in explaining sexual dimorphism in humans.

As noted, a critical feature of the Fisherian process is the genetic establishment of a preference for a featured ornamentation. The preferred ornament does not need to confer any benefits or signal quality, its only requirement is that the preference for the trait is heritable within one sex, and the preferred trait is passed on within the opposite sex. Once established within the population – the system is self-sustained.

Fisherian runaway selection has been largely used to explain male ornamentation and mating displays. However, the process is not exclusive to males, Fisher noted that in many species, especially those who share in parenting duties and who establish monogamous pair-bonds, traits and the preferences for them could be found in both sexes – thus producing similar ornamentation and/or mating displays in both males and females of the species. Lande (1980) posits that female ornamentation is a product of correlated response, that is similar ornamentation in females is the unavoidable, non-adaptive result of shared genomes and selection on male ornamentation. Natural selection would act more strongly on females to subdue sexual ornamentation since loss of cryptic patterns and camouflage would increase predation on both females and their young. Additionally, high androgen and low oestrogen, producing the masculine characteristics, could impact negatively on female fertility. Lande argues that these selection pressures explain the sexual dimorphism often seen in ornamentation, and this argument has received some support (Lande & Arnold 1985; Muma & Weatherhead 1989; Wolf et al. 2004), However, there is more convincing support for the alternative hypothesis that female ornamentation is a product of sexual selection and female-female competition (Amundsen 2000; Amundsen & Forsgren 2003; Amundsen et al. 1997; Hill 1993; Jawor & Breitwisch 2003; Jawor et al. 2004; Langmore 1998). Jawor et al (2004) found that multiple ornamentation (e.g. plumage colour, bill colour, crest length, and face mask) in female cardinals (*Cardinalis cardinalis*), a bi-parental care species, provided honest signals to condition and maternal behaviours. Interestingly, Jawor and her colleagues also found that while males and females may produce similar ornaments, they do not necessarily signal the same information about condition. Fisherian processes, then, can be responsible for exaggerated ornamentation in both males and females. Monomorphism, that is similar physical traits or behavioural characteristics found in both sexes, can therefore be a product of runaway selection that can occur in species wherein males invest little in offspring; however, one would expect that in bi-parental care species monomorphism would be more likely due to the higher investment of resources devoted to one mate, thus each sex should be equally or near-equally choosey.

In humans, as a bi-parental care species, we should expect that both males and females are choosey when selecting long-term mates. From this we can assert that humans have evolved preferences for particular features and behavioural characteristics (independent of whether these traits or behaviours confer benefits), and these preferences have increased the frequency of the preferred features and behavioural characteristics in the population. It also goes that if a feature or characteristic selected is under the rubric of sexual selection we should find evidence of inheritance of the trait. How the trait is passed down, that is whether it is inherited through the maternal or the paternal line, will help us understand the role, if any, of Fisherian sexual selection in human evolution.

2.1.2 'Good genes' theory

'Good genes' theory (Andersson 1994; Trivers 1972b; Zahavi 1975) suggests that sexually-dimorphic characteristics signal genetic superiority; and females being, for the most part the choosier sex, will have evolved preferences for signals conveying these advantages. These preferences are, however, mitigated by the amount of paternal investment desired by the female and offered by the male. Females then must make trade-offs, weighing the benefits of 'good genes' (e.g. immunocompetence, parasite resistance), which she can pass on to her offspring and gain indirect benefits, against the direct and indirect benefits gained through male parenting skills and ability to provide resources for her and her offspring. Applied to humans, researchers have suggested that masculine characteristics in males signal good genes (Fink & Penton-Voak 2002; Gangestad & Simpson 2000) but simultaneously signal lower paternal investment, likelihood of abandonment, and other negative personality traits (Perrett et al. 1998). The principal reason for a woman to choose a masculine partner signalling good genes is to pass them on to her offspring. Therefore, the inheritance of these good genes (masculinity) should be manifest in offspring, at least by the time the offspring reach reproductive age. We suggest that qualities such as parenting behaviour and generosity are also related to phenotypic signals; and as with good immunocompetence, the genes for these behavioural characteristics are heritable. Whether such signals manifest themselves in facial characteristics, as extended phenotypes (signalling of kindness toward children or generosity towards others) or both, they should play a role in mate selection especially in long-term relationships. We submit that genes controlling the expression of such characteristics could be referred to as 'good genes'(e.g. Wade & Shuster 2002; Wolf et al. 1999; e.g. Wolf et al. 1997); however, in the literature we find the label of 'good genes' overwhelmingly applies only to those genes responsible for superior immunocompetence.

The immunocompetence handicap principle, as posited by Folstad & Karter (1992) took the good genes hypothesis yet another step by suggesting a type of feed-back loop wherein only those males healthy and vigorous enough to withstand the deleterious effects of testosterone would be capable of displaying exaggerated sexually-dimorphic characteristics. Thus, testosterone acts as a 'double-edged sword' by increasing the expression of sexually-dimorphic traits while suppressing the immune system. In other words, less than healthy males would produce lower levels of testosterone if their immunocompetence was inadequate to handle its deleterious effects, while healthy males would produce higher levels. This process would ensure honest signalling. The theory is not without criticism, for example not all sexually-dimorphic traits and behavioural characteristics are dependent on testosterone levels (Kimball & Ligon 1999; Owen-Ashley et al. 2004). Additionally, the production of some testosterone regulated traits occur at a time when circulating levels of testosterone are low and, as such, immunocompetence is not compromised to the point where the trait reflects an honest signal (Hillgarth & Wingfield 1997). Another criticism has been that the role of testosterone in suppressing immunocompetence is equivocal in both the mammalian and avian literature (Owen-Ashley et al. 2004). While, there has been some evidence that testosterone suppresses the immune system (Kurtz & Sauer 1999; Møller et al. 1999), it has also been found to enhance T-cell activity (Tanriverdi et al. 2003). The immunocompetence handicap theory has met with other contradictory findings (Duckworth et al. 2001), and the function and signalling of the feedback loop remains unclear (Getty 2002; Roberts et al. 2004).

The good genes hypothesis suggests that the more investing sex, usually females, are choosing the best genes, e.g. superior immunocompetence, for all their offspring independent of the sex of their offspring. Signals of immunocompetence should manifest themselves early on in offspring in the form of symmetry. During the development of the foetus and thereafter, low fluctuating asymmetry is thought to be a product of developmental stability, which is influenced by the ability to ward off various maladies such as high parasite load, infection, and other environmental stressors (Badyaev et al. 2000; Møller 1995; Møller 1996; Palmer & Strobeck 1986;

Parsons 1990). If male offspring of genetically-fit fathers are expected to inherit more masculine characteristics, what can we predict for female offspring? It has been argued that feminine characteristics in females also signal good immunocompetence (Thornhill & Grammer 1999), this may explain, in part, why men show strong preferences for feminine characteristics in women, such as low waist-to-hip ratio (Singh 1993b) and feminine facial characteristics (Ishi et al. 2004; Perrett et al. 1998). Thornhill and Grammer (1999) suggest that oestrogen produces honest signals, perhaps acting as a handicap in the manner posited by Folstad and Karter (1992). Evidence from this is based on oestrogen acting as a suppressant on T-cell activity (Da Silva 1999) and its possible role in cancer (Service 1998). However, unlike testosterone, wherein there is some evidence that it acts to suppress the immune system, oestrogen and progesterone appear to bolster the immune system (Da Silva 1999; Kumru et al. 2004; Seli & Arici 2002) and signals of higher levels of oestrogen and progesterone are direct evidence of superior immunocompetence. The role of gonadal hormones on immunity is complex and inexact, thus hypotheses relating them to honest signals of health or to the immunocompetence handicap principle remain speculative.

Oestrogen is necessary for women's fertility (Lipson & Ellison 1996), thus men should prefer those characteristics that reliably signal female reproductive health and fitness. Daughters of males with good immunocompetence would benefit directly from the ability to resist disease and parasites, and in addition they could gain advantages over other females by signalling their superior genes to courting males. This is especially true in bi-parental care species where both males and females form pair-bonds and devote their time and resources to offspring. However, even in lekking species we find males give preference to signals of genetic quality in females (Dosen & Montgomerie 2004; Werner & Lotem 2003). If oestrogen can suppress aspects of immunocompetence, we might expect to see signals in the form of more feminine facial characteristics evident in daughters of more masculine fathers.

2.1.3 Human sexual dimorphism

Epigamic traits in humans are moderate compared to many other species, including other primates such as gorillas and orang-utans and to some degree chimpanzees (Lee 2001). Human males are slightly larger than females, about 20% heavier, and more muscular on average (Alexander et al. 1979), and other differences include secondary sexual characteristics (e.g. male facial hair, female breasts, female low waist-to-hip ratio). These differences, though perhaps slight, have garnered much attention and their significance within human mating strategies and behaviours has been increasingly studied. In particular, there has been a great deal of research focused on the differences between male and female facial characteristics (Cunningham et al. 1990; Hume & Montgomerie 2001; Ishi et al. 2004; Johnston et al. 2001; Penton-Voak & Chen 2004; Penton-Voak et al. 2001; Penton-Voak et al. 2003; Penton-Voak & Perrett 2001; Perrett et al. 1998; Swaddle & Reierson 2002). Humans, like all other animals, are subject to sexual selection, and evidence for it should be testable. In this study, we make the assumption offspring inherent genetic contributions from their parents, and examine two possible genetically heritable trait characteristics: attractiveness and sexual dimorphism, using photos taken in the laboratory and facial images from family photographs, and base predictions on theories of sexual selection. Our overarching hypothesis is that parental facial characteristics should relate to offspring facial qualities. All sexual selection models rely on traits being heritable, and therefore predict commonality in facial appearance across generations. Theories can be used to predict specific relationships.

2.1.4 Hypotheses

<u>*Same sex parent-to-offspring relationships.*</u>

(1) If Fisherian processes are contributing to male-facial characteristics, then we should expect to find strong paternal influences on male-offspring facial characteristics. Fisherian selection for dimorphic traits leads to Hypothesis 1a: father's masculinity predicts son's masculinity. A good-genes process makes a similar prediction, and a father should pass on his genetic quality to his offspring. Thus, male offspring should signal the inherited benefits of father's good-genes and display comparable masculinity in facial characteristics. Fisherian selection could also exist for traits other than masculinity. Genes for good immunocompetence should manifest themselves phenotypically in the form of increased symmetry, averageness, and skin quality. Since these qualities affect attractiveness independent of masculinity, Fisherian processes and good genes theory leads to Hypothesis 1b: father's attractiveness predicts son's attractiveness.

(2) If Fisherian processes are contributing to female facial characteristics, then maternal influences should be apparent in female-offspring. Likewise, good genes theory also predicts maternal influences in offspring. This leads to predictions similar to those for males. Specifically, mother's facial characteristics will be positively correlated with daughter's facial characteristics, thus Hypothesis 2a mother's femininity predicts daughter's femininity and Hypothesis 2b mother's attractiveness predicts daughter's attractiveness.

Opposite sex parent-to-offspring relationships.

(3) From correlated response theory (Lande 1980) paternal characteristics may also appear in opposite sex offspring; however, natural selection might weaken manifestation of paternal traits, particularly masculinity traits, in daughters since high androgen and low oestrogen would impact negatively on female fertility. Hypothesis 3a: daughter's facial characteristics correlate (positively) with father's facial masculinity. While correlated response theory is not traditionally used to explain male characteristics, for the sake of parity Hypothesis 3b: son's facial characteristics correlate positively with mother's facial femininity.

Good genes consideration predicts correlation in father and daughter's facial attractiveness from signals of a healthy immune system, that being symmetry, averageness, and skin condition. This leads to Hypothesis 3c: father's facial attractiveness predicts daughter's facial attractiveness. One can derive similar predictions from considering the heritability of physiognomy; facial appearance of offspring should reflect in part genes from father and from their mother. Hypothesis 3c could contradict hypothesis 3a, since femininity and attractiveness are closely linked in females, attractive facial characteristics in daughters would necessarily be feminine characteristics (not masculine as Hypothesis 3a suggests). This contradiction is also echoed by considering good genes theory combined with the immunocompetence handicap principle. That is if father's immunocompetence is passed on to daughters and if oestrogen acts in as an immunosuppressant (Da Silva 1999; Seli & Arici 2002; Thornhill & Grammer 1999), then daughters who inherit father's superior immunocompetence should be capable of producing higher levels of oestrogen thus Hypothesis 3d: father's facial masculinity should predict daughter's facial femininity.

Mirroring Hypothesis 3c stemming from good genes theory, we can predict that mother's femininity and son's masculinity should correlate (Hypothesis 4a) but the direction of the relationship is not known. We can predict that mother's facial attractiveness should predict son's facial attractiveness (Hypothesis 4b).

(5) Both males and females are choosy which predicts assortment of attraction in parental characteristics. Hypothesis 5a: attractiveness of mothers and fathers should correlate. Attractive feminine women prefer masculine male faces for long-term partners (Little et al. 2002). Given that men appear to prefer femininity in female faces (e.g. Cornwell et al. 2004) we can predict that feminine women will partner with masculine men. Hypothesis 5b: mother's femininity correlates with father's masculinity.

2.2 Study 1: Females

We conducted two studies, the first examining the relationship between parents and female offspring and the second study examining the relationship between parents and male offspring.

2.2.1 Methods

Stimuli

Over a three year period, students were asked if we could contact their family to obtain family photos. For those students who gave permission, a letter was sent to their parent(s) explaining the nature of our work, a short questionnaire, along with the request for a number of family images. The short questionnaire asked for the ages of the individuals in the photos at the time that the photo was taken, as well as information on biological relatedness (e.g. whether the individual is the biological parent or step-parent). Only images of biological parents were included in our study. We collected images from the families of 130 female undergraduates (Mean age = 19.69, SD ± 1.52, age range = 17-23), with a final count of 96 images of biological father (Mean age = 48.4, SD ± 7.47, age range = 25-73) and 104 images of biological mother (Mean age = 46.44, SD ± 6.54, age range = 23-64).

All images were scanned using an Epson 1200s, cropped to expose only the face, and sized to approximately 4.0MB, uncompressed and then converted to JPGs. These scanned images were presented unmasked.

Photos of the students were taken in a lab setting, under diffuse lighting. Students were asked to pose with a neutral expression. A digital camera captured the images uncompressed, at a resolution of 1200 X 1000 pixels, with 24-bit RGB (red, green, blue) colour encoding.

Participants

Participants judging the photos were undergraduates recruited from the University of St Andrews (14 females, age range = 19-31, mean age = 22.5; 3; and 3 males age range = 22 – 23, mean age = 22.3).

Presentation

Images were presented in randomised blocks, and each block consisted of randomised images of mothers and fathers, female students, as well as filler items. Participants were asked to rate each image on masculinity and attractiveness. For the masculinity scale, participants were asked "Does this student (or 'parent') look more masculine or feminine?" and could choose from 1 of 8 possibilities: (1) androgynous female; (2) slightly masculine for a female; (3) normally feminine for a female; (4)

very feminine; (5) androgynous male; (6) slightly feminine for a male; (7) normally masculine for a male; (8) very masculine. Attractiveness ratings were done on a 7-point Likert type scale with very attractive and not at all attractive as the end points.

Analyses

To determine the relationship between each parent and their offspring, we employed linear regression analyses. Before the analyses, a series of steps were required in order to control for factors such as parent and student age, and to meet the assumptions necessary for our final linear regression analyses. We controlled for age for two reasons: (1) the parent images varied greatly in age from early 20s to early 70s; (2) zero-order calculations revealed that age was positively correlated with father's masculinity ($r_{95} = .253, p = .013$), negatively correlated with mother's femininity ($r_{104} = -.197, p = .045$) and attractiveness ($r_{104} = -.212, p = .031$), and there was a negative trend for female student's age and femininity ($r_{130} = -.136, p = .122$). Therefore, prior to running our zero-order calculations to evaluate the relationship between students' perceived attractiveness and masculinity and that of their parents, we ran an initial linear regression analyses to adjust for effects of age. Each of our dependent variables (mother's masculinity, mother's attractiveness, father's masculinity, father's attractiveness, student's masculinity, and student's attractiveness) were run with the appropriate age (e.g. mother's age or father's age) as the independent variable with the standardized residuals retained. All further analyses will use these residuals (e.g. attractiveness or masculinity controlling for age).

2.2.1 Results

Cronbach's alpha

Ratings were examined using Cronbach's alpha for observed reliability co-efficient. For mothers' images judged for attractiveness, $\alpha = .92$, masculinity $\alpha = .87$; fathers' images judged for attractiveness, $\alpha = .92$, masculinity $\alpha = .71$; female students' images judged for masculinity $\alpha = .89$; and student images judged for females attractiveness $\alpha = .93$; and male attractiveness $\alpha = .87$.

Zero-order correlations

Our Spearman's rank zero-order correlations revealed that among our female students, attractiveness and femininity (for clarity, we will substitute the term 'femininity' rather than 'masculinity' when discussing the sexual dimorphic characteristics of females) were positively correlated ($r_{130} = .801, p < .001$), as was mother's attractiveness and femininity ($r_{104} = .825, p < .001$). For fathers we found no relationship between attractiveness and masculinity ($r_{95} = -.030, p = .772$).

In terms of parent-offspring relationships, we found that mother's femininity and daughter's (female students) femininity ($r_{104} = .306, p = .002$) *(Figure 2.1)* and attractiveness ($r_{104} = .296, p = .002$) were positively correlated. Mother's attractiveness and daughter's attractiveness ($r_{104} = .306, p = .002$) and femininity ($r_{104} = .301, p = .002$) were also positively correlated. Father's attractiveness was found to relate both to daughter's attractiveness ($r_{95} = .349, p = .001$) and daughter's femininity ($r_{95} = .403, p < .001$), while father's masculinity was not found to relate to either daughter's attractiveness ($r_{95} = -.141, p = .172$) or daughter's femininity ($r_{95} = -.053, p = .611$).

We also looked at the relationship between mothers and fathers and found that father's attractiveness was positively correlated with both mother's attractiveness ($r_{91} = .297, p = .004$) and femininity ($r_{91} = .302, p = .004$). We also found that father's masculinity was negatively correlated with both mother's attractiveness ($r_{91} = -.209, p = .047$), and mother's femininity ($r_{91} = -.219, p = .037$).

Linear Regression

The data were checked for normality using SPSS collinearity diagnostics, and a tolerance value of .943 met the criteria for linear regression. Mahalanobis distances were inspected, and there were no outliers outside the critical value. A standard linear regression analysis was performed between the dependent variable – female student attractiveness – and the independent variables father's attractiveness and mother's femininity. Because mother's femininity and attractiveness were highly correlated, only one of these two variables could be used in our analysis, and as mother's femininity revealed a marginally stronger correlation than mother's attractiveness with our dependent variables, we chose the former for our linear regression analyses. The two variables explained 20% of the variance $R^2 = .202$ (Adjusted $R^2 = .183$), $F(2,85) = 10.753, p < .001$. Father's attractiveness was a stronger predictor ($\beta = .302, p = .003$) than mother's femininity ($\beta = .271, p = .008$) of daughter's attractiveness.

Similar analysis revealed that daughter's femininity is predicted by father's attractiveness and mother's femininity. $R^2 = .208$ (Adjusted $R^2 = .189$), $F(2,85) = 11.13, p < .001$. Dad's attractiveness was again a stronger predictor ($\beta = .330, p = .001$) than mother's femininity ($\beta = .248, p = .014$).

2.3 Study 2: Males

2.3.1 Methods

Stimuli

Images were collected in the same manner as Study 1, and again only images of biological parents were included in our study. We collected images from the families of 75 male undergraduates (Mean age = 20.2, SD ± 1.66, age range = 17-24), with a final count of 66 images of biological father (Mean age = 47.32, SD ± 10.52, age range = 18-67) and 68images of biological mother (Mean age = 46.09, SD ± 8.94, age range = 20-61).

All images and photos were processed in the same way as in Study 1.

Participants

Participants judging the photos were undergraduates recruited from the University of St Andrews (20 females, age range = 18-41, mean = 21.4; 14 males, age range = 18-22, mean = 19.07).

Presentation

Images were presented in randomised blocks, and each block consisted of randomised images of mothers, fathers, or male students as well as filler items. Because we collected fewer family images from male students than from female students, we opted to use a more sensitive scale to investigate the heredity of facial masculinity and changed our rating scale from a 4-point to a 7-point scale. Thus, participants were asked to rate each image on masculinity and attractiveness on 7-point Likert-type scales.

Analyses

Analyses for the second study are carried out in the same manner as Study 1.

2.3.2 Results

For our analyses, we will be conducting a substantial number of multiple correlations in order to investigate the relationships between parent and offspring facial characteristics. It is often recommended to perform Bonferroni adjustment of probability estimate when making multiple comparisons to reduce the possibility of a Type I (false positive) error when conducting multiple comparisons, we have opted not to perform this statistic because it is too conservative. Bonferroni does reduce the chance of a Type I error for an individual test, however it increases the chance of making a Type II error (false negative) (Rothman 1990). Additionally, the possibility of a Type II increases as the number of comparisons increase (see Perneger 1998).

Cronbach's alpha

Ratings were examined using Cronbach's alpha for observed reliability co-efficient. For mothers' images judged for attractiveness, $\alpha = .97$, masculinity $\alpha = .97$; fathers' images judged for attractiveness, $\alpha = .93$, masculinity $\alpha = .89$; male students' images judged attractiveness $\alpha = .94$; and student images judged for male masculinity $\alpha = .94$.

Zero-order correlations

Prior to our Spearman's rank zero-order calculations, we ran linear regressions on each of our variables to control for age, and the standardized residuals retained. As with Study 1, the parent images spanned a large age range (20s – 70s); and, as previously found, mother's age was negatively correlated with both attractiveness ($r_{68} = -.294, p = .001$) and femininity ($r_{68} = -.330, p = .006$). We also found a positive trend between father's age and masculinity ($r_{66} = .182, p = .143$). All further analyses were performed using these residuals (e.g. attractiveness or masculinity controlling for age).

Our zero-order correlations revealed that among our male students, attractiveness and masculinity were positively correlated (r_{67} = .298, p = .014), as was mother's attractiveness and femininity (r_{63} = .934, p < .001). For fathers, unlike Study 1, we found a relationship between attractiveness and masculinity (r_{66} = .455, p < .001).

In terms of parent-offspring relationships, we did not find a relationship between mother's femininity and son's (male students) masculinity (r_{59} = - .020, p = .878) or son's attractiveness (r_{59} = .088, p = .509). Nor did we find that mother's attractiveness and son's attractiveness (r_{59} = .090, p = .499) or son's masculinity (r_{59} = - .015, p = .912) were related. We also did not find a relationship between father's attractiveness and son's attractiveness (r_{62} = .886, p = .019) or son's masculinity (r_{62} = .064, p = .619). However, we did find a relationship between father's masculinity and son's masculinity (r_{62} = .314, p = .013) *(Figure 2.2)*, but there was no relationship with son's attractiveness (r_{62} = -.077, p = .553).

As in Study 1, we also looked at the relationship between mothers and fathers, and found that father's attractiveness was positively correlated with both mother's attractiveness (r_{61} = .335, p = .008) and femininity (r_{61} = .282, p = .028). We did not however, as in Study 1, find any relationship between father's masculinity and mother's attractiveness (r_{61} = -.041, p = .755), or with mother's femininity (r_{61} = -.098, p = .454).

As we only found contribution of father's masculinity evident in male offspring trait characteristics, linear regressions are unnecessary and will not be run.

2.4 Discussion

We made one overarching hypothesis: parents' facial characteristics would be apparent in their offspring's facial characteristics. More specifically we made five sets of hypotheses pertaining to particular mate selection theories, and our data appear to support some but not others. We shall go through each hypothesis individually, and afterward we shall discuss implications and introduce any speculations and need for further investigation.

Our first prediction (Hypothesis 1a) is based on Fisherian processes and 'good genes' theory that father's masculinity would predict son's masculinity. Our data supported this hypothesis. Also under the rubric of Fisherian processes and 'good genes' theory, we predicted (Hypothesis 1b) that father's attractiveness would predict son's attractiveness, however this was not supported.

In our next set of predictions, we hypothesized (Hypothesis 2) if Fisherian processes were contributing to female facial characteristics, maternal influences should be apparent in female offspring. This hypothesis was supported, as mother's facial femininity was found to predict both daughter's facial femininity (Hypothesis 2a) and attractiveness. It should be noted that femininity and attractiveness were highly correlated for both mothers ($p < .001$) and daughters ($p < .001$), thus one can also state that mother's attractiveness predicts daughter's attractiveness and femininity (Hypothesis 2b).

We also evaluated the correlated response theory (Lande, 1980) (Hypothesis 3a) that paternal masculine facial characteristics would influence daughter's facial characteristics. We did not find support for this hypothesis. Nor did we find support the mirror hypothesis (3b) that mother's femininity related to son's facial characteristics.

We did find support for Hypothesis 3c that daughter's facial attractiveness and femininity were predicted by father's facial attractiveness, supportive of good genes theory. However, we did not find support for Hypothesis 3d based on good genes theory and immunocompetence handicap principle that father's facial masculinity should predict daughter's femininity. The relationship we found between father and daughter aligns most closely with the good genes theory and not the immunocompetence handicap principle.

We did not find support for either Hypothesis 4a or 4b that mother's facial characteristics would influence son's facial characteristics.

In our final set of hypotheses based on assortative mating, we predicted (Hypothesis 5a) that attractiveness of the parents should correlate and this was supported by the data. That is mother's attractiveness and father's attractiveness are positively correlated. However concerning Hypothesis 4b, we did not find that father's masculinity and mother's femininity were correlated, and in fact found that mother's attractiveness and father's masculinity were negatively correlated in Study 1.

While we did not make predictions concerning male masculinity and attractiveness, our data from the two studies are inconsistent. In the first study we did not find a relationship between father's masculinity and attractiveness ($r_{95} = -.030$, $p = .772$); however, in Study 2 we found that father's masculinity and attractiveness were positively correlated ($r_{66} = .455$, $p < .001$) and son's masculinity and attractiveness were also positively correlated (r_{67} = .298, p = .014). We will discuss the possible reasons for this discrepancy later in the paper.

Female offspring

Our findings are supportive of both Fisherian processes and good genes theory. Both parents contribute to the attractiveness and femininity of daughters. We found that daughter's attractiveness is predicted independently by father's attractiveness and mother's femininity (and therefore by default, mother's attractiveness). Fisherian selection processes would suggest that men have evolved preferences for sexually dimorphic facial characteristic in opposite sex partners, and through human evolution these preferences have increased the frequency of feminine facial characteristics such as a slender chin, full lips, and large eyes in women. Good genes theory predicts the same finding, however it suggests that feminine facial characteristics must by definition signal good quality, including possible cues to immunocompetence, fertility, youthfulness, health, and perhaps even maternal tendencies (Deady et al. 2004). Our study was not designed to determine the honesty of or the information conveyed by the signals of attractive or sexually dimorphic facial characteristics, thus we cannot differentiate between Fisherian processes and good genes theory. However, we should note that one prediction based on good genes theory in which masculinity is a signal of superior genetic quality (e.g. Gangestad & Simpson 2000; e.g. Thornhill & Gangestad 1999a) would be that masculine fathers would produce attractive (e.g. feminine daughters), yet we did not find any support for this prediction.

Immunocompetence handicap principle as proposed by Folstad and Karter (1992) makes a much more specific assertion, in that testosterone acts as an immunosuppressant and thus only those men with the constitution to withstand the ill-effects of testosterone are capable of producing exaggerated sex-specific testosterone mediated traits. The prediction based on immunocompetence handicap principle was that masculine fathers would produce attractive and feminine daughters; however, we found no evidence for this. On the other hand, Thornhill and Grammer (1999) suggested that oestrogen could also act as an immunosuppressant, and thus feminine looking mothers would be expected to produce feminine looking daughters. While we did find that maternal femininity predicts daughter's femininity, we shy away from making any claims as having evidenced immunocompetence handicap principle because, as previously noted, oestrogen and progesterone appear to enhance immunity. Still, we cannot rule out our finding as having supported Thornhill and Grammer's proposition.

We can rule out evidence to support Lande's correlated response theory as father's masculinity did not predict any facial characteristics in daughters.

Male offspring

In males, we found only father's masculinity influenced son's facial characteristics. We did not find any evidence that father's attractiveness or mother's femininity or attractiveness influenced the facial characteristics of male offspring. Thus we can rule out good genes via mother's contribution and correlated response theory.

Our finding that male facial masculinity is passed down from father to son is supportive of both Fisherian processes and good genes theory. It also supports immunocompetence handicap principle, in that son may inherit the genes coding for superior immunocompetence and thus can support higher levels of testosterone which in turn will produce exaggerated sexually dimorphic traits.

We do have some reservations however concerning the lack of evidence for the inheritance of attractiveness. The term 'attractiveness' is somewhat tautological in that it is often used to denote that which 'attracts' another individual. It can also indicate that which is pleasing. While there is generally agreement on the facial features defined as sexually dimorphic, the features of 'attractiveness' are somewhat elusive. We have suggested that features such as symmetry, averageness, skin condition, skin colouration, and brightness of eyes could all contribute to facial attractiveness. Characteristics that signal demeanour could also contribute to facial attractiveness. Some facial features could possibly signal good immunocompetence, others could signal psychological well being (e.g. stability as compared to neuroticism and anxiety), and still others could signal aspects of parenting quality. The facial characteristics could therefore signal genetic influences, environmental influences, or more likely both. In any case, we expected to find an influence of parent's facial attractiveness on son's facial attractiveness. We are perplexed as to why we did not find any evidence for the inheritance of attractiveness in males, either through the female or male parent. Attractiveness, by its own definition, should be sexy – and while we found evidence for sexy parents-sexy daughters, we do not find the parallel in male offspring. While masculine dads produce masculine sons, sexy parents do not produce sexy sons.

<u>*Assortative Mating*</u>

Our final set of hypotheses concerned assortative mating. Parents represented real mating effort. We therefore predicted (Hypothesis 5a) that attractive mothers would be paired with attractive fathers, and (Hypothesis 5b) feminine mothers would be paired with masculine fathers. We found support for the first, but not the second hypothesis.

How do these findings tally with the sexual selection hypotheses we have explored? Let's revisit the broad aspects of Fisherian processes and good genes theory. Both posit that members of one sex are selecting for traits in the opposite sex, and that these traits are then passed on to offspring. Above we outlined the evidence for some traits being passed on from parent to offspring, but that is only half the question. What about the selection process? While our study was not initially set up to fully explore sexual selection in parents, the data are too enticing to ignore.

Let's begin with the tidiest findings: Men select for traits of femininity and attractiveness in opposite sex partners and these traits are then passed on to female offspring. This is clearly supportive of Fisherian processes, good genes theory, and possibly supportive of immunocompetence handicap principle. Next we find that women select for attractiveness in opposite sex partners, and these traits are passed on to daughters. If only we could stop here and not have to subject ourselves to the messiness of the next few findings.

While we find that women select for attractiveness in male partners, we did not find any evidence of selection pressures resulting in attractiveness as a heritable trait being passed on to son. It is possible that attractiveness cues relate to non-heritable direct and indirect benefits, such as cues to good parenting skills or commitment. However this is highly speculative, and in our opinion is not the most parsimonious explanation of our data.

Another possibility is that because the relationship between male attractiveness and male masculinity is equivocal, ratings of attractiveness in males could have been biased by individual differences in masculinity preferences. In females, the positive relationship between attractiveness and femininity is consistent across a wide range of studies. This is not true of male masculinity and attractiveness, where there is far less agreement on the relationship across studies. Between the two studies discussed herein, we find no relationship in Study 1 between father's masculinity and attractiveness while in Study 2 we find a positive relationship between father's masculinity and attractiveness as well as between son's masculinity and attractiveness. We find these disparate findings in the literature as well. In that some studies women show a preference for masculinity in male faces (Grammer & Thornhill 1994; Penton-Voak & Perrett 2001; Scheib et al. 1999), while other studies have found women prefer more feminised male faces (Penton-Voak et al. 2003; Penton-Voak et al. 1999; Perrett et al. 1998; Swaddle & Reierson 2002). Another possible confound is age of parents. While we attempted to control for age effects by running linear regressions to adjust for age and then using the residuals for our analyses it may very well be that the relationship between age and increased masculinity is not a linear relationship. Thus, we submit that the combination of age of parents and the individual differences in preferences for masculinity confound the relationship between parent's facial attractiveness and son's facial attractiveness.

We did find that father's facial masculinity was passed on to son, and suggested that this supported both Fisherian processes and good genes theory. However, we do not find any evidence for the selection process, at least in the parents of university students. In Study 1, feminine and attractive women have selected feminine looking men. In Study 2 we did not find a relationship between father's masculinity and mother's facial characteristics. As mentioned above, the lack of relationship between selection and inheritance is most likely due to individual differences between our raters in combination with the wide age range of the parent photos. It would be best to have recruited photos of the parents at the time of the marriage, which would have reduced the issue of age in our analyses.

Another possible confound that is certainly worth exploring is that our parent cohort were for the most part long-term partners, as we had very few divorced parents among our sample. It has been posited that testosterone in both men and women can increase the likelihood of abandonment and marriage dissolution (Mazur & Booth 1998b). We may have tapped into a sub-group within the general population of men and women selecting for long-term committed relationships, and thus this particular group of women would not have had a strong preference for masculinity traits in a partner. This would require further study of a different population.

There is one more piece of the puzzle which should be addressed in future research: "Are parents' preference also inherited by their offspring?" Research has provided support for offspring mate preferences for characteristics similar to those of their opposite sex parent (Little & Jones 2003; Perrett et al. 2002). The explanation for this relationship has been imprinting during development. However, we cannot rule out that some mate choice preferences of offspring are influenced by heritable traits.

While our evidence for immunocompetence theory was weak in terms of male masculinity, it does not necessarily mean that men and women are not selecting for good immunocompetence. There are possibly other signals to health (Boothroyd et al.

2003; Jones et al. 2001) that individuals are choosing. Symmetry, skin texture and colour, brightness of eyes, and even odour might possibly give cues to superior immunocompetence. As we continue to explore human attraction and mate choice, their secrets will slowly unfold and reveal a complexity for which we are only just now beginning to understand.

Figure 2.1

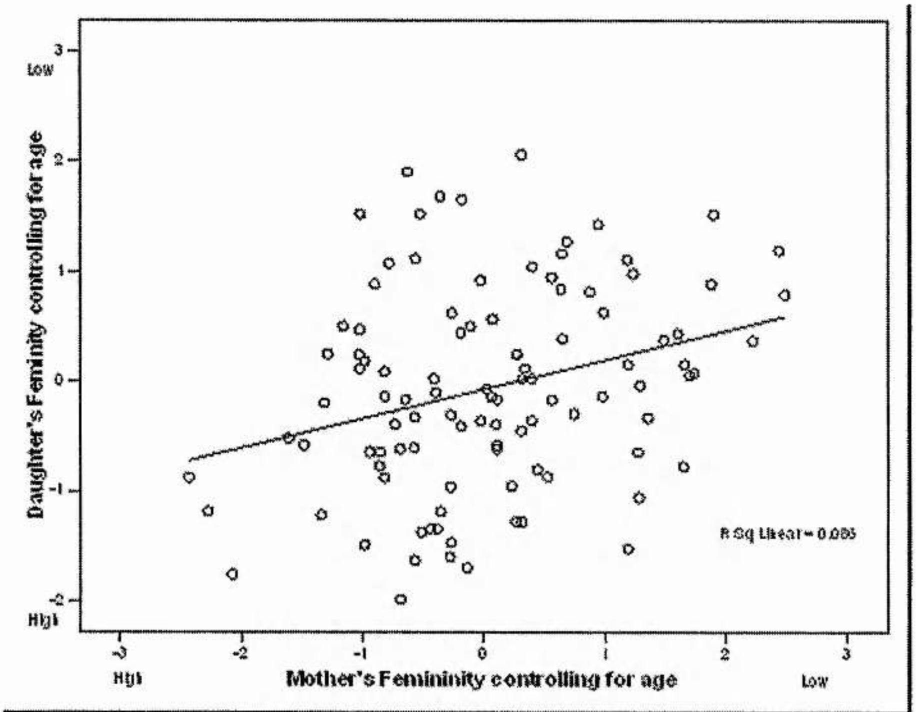
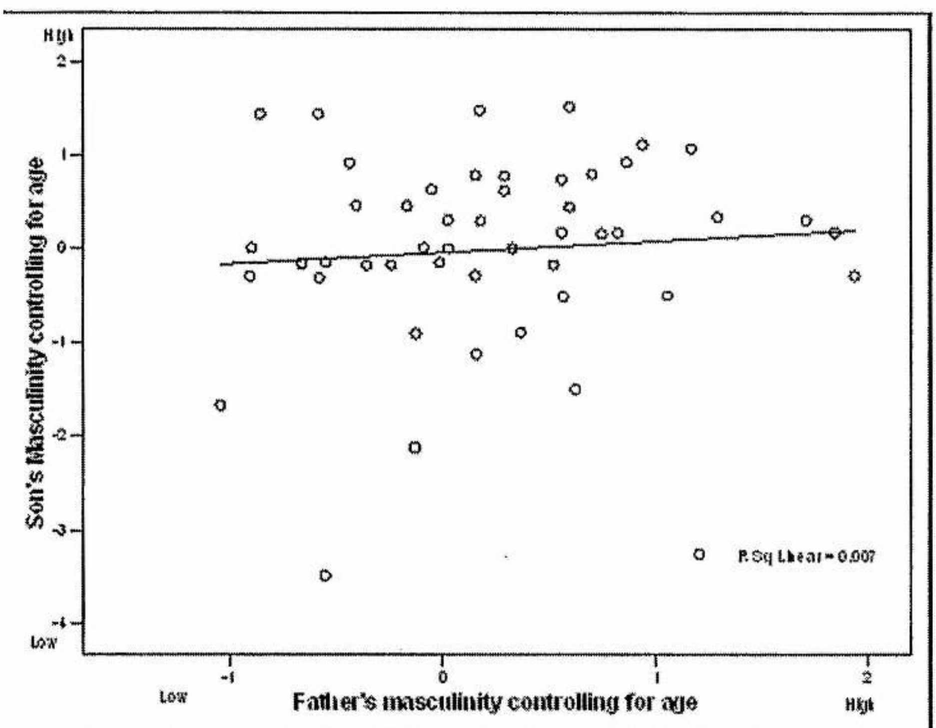


Figure 2.2



3 Developmental stability of facial characteristics: Attractiveness and sexual dimorphism from infancy to early adulthood

3.1 Introduction

Our facial appearance, from the time we are born and throughout our life, influences the way others behave towards us and we toward them. Physical appearance powerfully affects our everyday interactions. The literature is flooded with overwhelming evidence that attractive people, from infancy through adulthood, are generally attributed with more positive attributes compared to less attractive people (Berscheid & Walster 1974; Dion 1972; Dion 1973; Dion & Berscheid 1974; Eagly et al. 1991; Zebrowitz et al. 2002; Zebrowitz et al. 1991). Many aspects of the 'beauty-is-good' stereotype have been studied (see Eagly et al. 1991) including whether or not there is some truth behind it (e.g. Alley & Hildebrandt 1988), or if the stereotype is more of a self-fulfilling prophecy (e.g. Snyder et al. 1977). The last decade has seen a flurry of work exploring Darwinian explanations for perceived beauty and whether or not its characteristics are honest signals of quality. Researchers have begun to explore why humans find particular characteristics beautiful, whether they are universal, and how qualities of beauty influence behaviour (see Fink & Penton-Voak 2002).

Given the evidence that individuals make personality assessments of others based on physical appearance, an important issue arises. Is physical attractiveness stable over development? The more stable it is, the more likelihood that the perceptions of others will have a lasting effect on self-concepts. Alley (1993) found that male and female facial attractiveness showed some stability between five developmental points: 5 to 8 years; shortly before the onset of puberty; mid-puberty;

immediately post-puberty; and at 19 to 22 years of age. He concluded from this that attractiveness could have important effects on development. Zebrowitz et al. (1993) found that facial attractiveness and 'babyfaceness' (neoteny) were stable across a wide-range of ages (10-50 years), and also suggested that as such it would influence personality development due to consistency of social expectations. To our knowledge, no one has studied the stability of facial characteristics from infancy into childhood and on into adulthood.

The influence of our physical characteristics on the behaviour and attitudes of others begins alarmingly early. Caregivers were found to attribute lower competence to unattractive infants compared to those seen as more attractive (Casey & Ritter 1996). Even motherly love and affection appear to be negatively affected if an infant is unattractive (Langlois et al. 1995). Badr & Abdallah (2001) found that among premature infants, those rated as more attractive thrived better, gained more weight, and were released earlier from hospital suggesting they received better care overall than their less attractive peers.

During childhood, physical attractiveness affects perception by peers, with facial attractiveness being associated with more positive peer relationships (Adams & Roopnarine 1994) as well as more positive attitudes in general (Langlois & Styczynski 1979). Adult perceptions of children are also mediated by physical attractiveness, and attractive children are seen as more intelligent, successful, socially competent, and better adjusted than unattractive peers (Adams & Crane 1980; Byrnes 1987).

Before the 1990s, the majority of the work on attractiveness focused on its social implications and how they might shape the individual. Studies of attractiveness overlooked any explanation of *why* humans find particular facial features attractive. Associations between attractiveness and positive attributions were often presented as tautological arguments asserting that culture, expectations of others, and the media were the 'makers' of beauty (e.g. Eagly et al. 1991). As psychologists began to examine the reasons behind beauty from a Darwinian perspective, a different picture of beauty emerged onto the scientific landscape. Beauty was not created by the media, but exploited by it. Nor were the standards of beauty bound by age, culture, or ethnicity (Cunningham et al. 1995; Langlois et al. 1991; Langlois & Roggman 1990). There were good Darwinian reasons why humans, as with other animals, prefer features such as symmetry and sexually dimorphic characteristics (see Thornhill & Gangestad 1999a).

Characteristics of sexual dimorphism, features that most clearly distinguish male from female, were of particular interest to scientists exploring the foundations of attractiveness. Employing theories of sexual selection, researchers began to understand the relationship between male facial masculinity and sex hormones. Following 'good genes' theory and the immunocompetence handicap principle, testosterone, with its influence on facial growth, was advanced as a signal of immunocompetence, thus facial masculinity should be attractive to females (Johnston et al. 2001; Thornhill & Gangestad 1999a). However, the evidence for female preferences linking male masculine features with male attractiveness has not always been consistent (Cornwell et al. 2004; Cunningham et al. 1990; Ishi et al. 2004; Perrett et al. 1998; Swaddle & Reierson 2002). Individual differences due to environment, life history, and hormones are found to mediate preferences for masculine males (Little et al. 2001a; Little et al. 2002; Penton-Voak et al. 2003;

Penton-Voak & Perrett 2000; Penton-Voak & Perrett 2001; Penton-Voak et al. 1999; Perrett et al. 2002). Evidence for female preferences for signals of masculinity is found in voice (Feinberg et al, in press), body (Fan et al. 2005; Maisey et al. 1999b; Singh 1995; Tovée & Cornelissen 2001; Tovée et al. 1998), and weakly in the face (Cunningham et al. 1990). Male attractiveness is correlated with masculinity, but whether women positively or negatively associate the two appears to vary.

Male preferences for female faces have been found to be inextricably linked with preferences for facial femininity (Cornwell et al. 2004; Fauss 1988; Jones 1996; McArthur & Berry 1983; Perrett et al. 1994; Riedl 1990). Female femininity is associated with signals of fecundity, youth, and health (Perrett et al. 1994; Thornhill & Grammer 1999), thus providing a sound Darwinian argument for male preferences for feminine characteristics. Unlike female preferences for opposite sex facial characteristics, while men's strength of preference for femininity might vary (Cornwell et al. 2004) (see Chapter 5), the direction of association between attractiveness and femininity is unwavering.

3.1.2 Attractiveness and Development

Facial attractiveness during development has received a great deal of attention; however, much of the research has ignored Darwinian theory. What goes for adult faces applies to children too. Why are some children attractive and others not? Is attractiveness universal? Are signals of sexual dimorphism meaningful? Are there reasons why what is attractive in an adult should be different from what is attractive in an infant, child, or teenager? While these questions are certainly too ambitious for this current study, we can begin to ask some the rudimentary questions about facial attractiveness and sexual dimorphism during development. Specifically, we examine whether they remain stable across development, and the inheritance of these two facial characteristics.

We examine the stability of two facial characteristics, attractiveness and sexual dimorphism, through development (infancy: 0.3 – 2 years; early childhood: 6-10 years; and early adulthood: 18 – 25 years) in both males and females. We also examine the stability of sexual dimorphism during development and its relationship with attractiveness. In keeping with previous research that attractiveness remains stable between childhood and puberty (Alley 1993), we hypothesise that facial attractiveness will remain relatively stable during three stages of development: infancy, childhood, and early adulthood. Attractiveness at infancy should predict attractiveness in both childhood and adulthood. Likewise, as suggested by Zebrowitz et al (1993) concerning the stability of 'babyfaceness' from peri-puberty (10 years of age) into adulthood, we also hypothesise that facial sexual dimorphism will remain relatively stable. Masculinity of infant faces should predict childhood and adulthood facial masculinity. This brings us to our third hypothesis, that facial attractiveness and sexual dimorphism are related, however the direction and strength of the relationship is dependent upon sex. The correlation between femininity and attractiveness should be both positive and strong throughout female development. In males, as neoteny is attractive in infants, strongly masculine features should be negatively correlated, however as males age this negative trend should weaken and by adulthood become positive.

3.2 Methods

We conducted two studies, the first examining the stability of facial characteristics during development in females and the second study examining the stability of facial characteristics in males. In both Studies we also examine the relationship of parent facial characteristics with infant and child facial characteristics.

3.2.1 Study 1: Females

Stimuli

Over a three year period, childhood snapshots from infancy and early childhood were collected from 130 female undergraduates (Mean age = 19.69, SD = 1.52, range = 17-23 years). Student images were taken in a lab setting, under diffuse lighting; and students were asked to pose with a neutral expression. We collected 120 female infant images (Mean age = 8.93 SD = 3.42, age range = 3-24 mos); and, 115 young female child images (Mean age = 6.89 SD = .95, range = 4-9 years).

Participants

Participants judging the photos were undergraduates recruited from the University of St Andrews (14 females, age range = 19-31, mean = 22.5; 3 males, age range = 22-23, mean = 22.3).

Presentation

Images were presented in randomised blocks, and each block consisted of randomised images of infants, children, and female students, as well as filler items. The sex of the individuals presented was not explicitly stated. Participants were asked to rate each image on masculinity and attractiveness. When judging the images, for the masculinity scale, participants were asked "Does this infant ('child' or 'individual') look more masculine or feminine?" and could choose from 1 of 8 possibilities: (1) androgynous male; (2) slightly feminine for a male; (3) normally masculine for a male; (4) very masculine (5) androgynous female; (6) slightly masculine for a female; (7) normally feminine for a female; (8) very feminine for a female. For all images, attractiveness ratings were done on a 7-point Likert type scale with very attractive and not at all attractive as the end points.

3.3 Analyses

Age impacts on attractiveness and sexual dimorphism (see chapter 2), thus prior to evaluating the relationship between students' current and prior attractiveness and masculinity, initial linear regression analyses were used to adjust for effects of age. Each dependent variable (student, child, and infant's masculinity and attractiveness) was run with the appropriate age as the independent variable with the standardized residuals retained. All further analyses will use these residuals.

3.4 Results

Cronbach's alpha

Ratings were examined using Cronbach's alpha for observed reliability co-efficient. For attractiveness ratings: infants $\alpha = .86$, child $\alpha = .88$, student $\alpha = .93$. For masculinity judgments: infants $\alpha = .95$, child $\alpha = .95$. student $\alpha = .89$.

An initial analysis revealed 5 outliers in our dependent variable, child femininity. Kolmogorow–Smirnov test, and all distributions were normal with the exception of child-femininity. The outliers for child femininity were removed from the appropriate analyses, the data were retested for normal distribution, and the data remained non-normal (df(110) = .154, $p < .001$).

Spearman's rank order correlations

Spearman's rank order correlations revealed a positive relationship between female facial femininity and attractiveness at both infancy (r_{120} =.210, $p = .021$) and early childhood (r_{110} =.679, $p < .001$). Student attractiveness and femininity were also positively related ($r_{130} = .801$, $p < .001$). These findings are in keeping with previous research that has shown a strong positive relationship between adult female facial femininity and attractiveness (see Chapter 8).

We found a relationship between infant and child facial attractiveness (r_{111} =.225, p = .018), and infant facial attractiveness and student facial attractiveness (r_{120} =.237, p = .009). Child attractiveness positively correlated with student attractiveness (r_{115} =.326, p < .001).

Table 3.1

Female Developmental Stability for Attractiveness

	Infant Attractiveness	Child Attractiveness
Child Attractiveness	$r_{111} = .225, p = .018*$	
Student Attractiveness	$r_{120} = .237, p = .009*$	$r_{115} = .326, p < .001*$

We did not find a relationship between infant and child femininity (r_{106} =.109, p = .267); however, we did find a relationship between infant and student femininity (r_{120} =.184, p = .045). There was also a positive correlation between child and student femininity (r_{110} =.243, p = .010).

Table 3.2

Female Developmental Stability for Femininity

	Infant Femininity	Child Femininity
Child Femininity	$r_{106} = .109, p = .267$	
Student Femininity	$r_{120} = .184, p = .045*$	$r_{110} = .243, p = .010*$

<u>Summary</u>

We find that attractiveness remains stable through female development; attractive infants develop into attractive children, who then develop into attractive young adults. Infant femininity remained relatively stable over development, with feminine infants developing into feminine adults.

3.5 Experiment 2: Male Images

Stimuli

Images were collect in the same manner as Study 1. We collected images from the families of 75 male undergraduates (Mean age = 20.2, SD ± 1.66, age range = 17-24), with a final count of 72 male infant images (Mean age = 8.89 SD = 3.44, range = 2-18 mos); and, 68 young male child images (Mean = 6.96 SD = 1.17, range = 3-10 years). Student images were taken in a lab setting, under diffuse lighting; and. students were asked to pose with a neutral facial expression. All images and photos were processed in the same way as in Study 1.

Participants

Participants judging the photos were undergraduates recruited from the University of St Andrews (20 females, age range = 18-41, mean = 21.4; 14 males, age range = 18-22, mean = 19.07).

Presentation

Images were presented in randomised blocks, and each block consisted of randomised images of male students, infants, or children. At the onset of the study, the sex of the individuals presented was made explicit. Because we collected fewer family images from male students than from female students, we opted to use a more sensitive scale to investigate the heredity of facial masculinity and thus changed our rating scale from a 4-point to a 7-point scale. Thus, participants were asked to rate each image on masculinity and attractiveness on 7-point Likert-type scales.

3.6 Analyses

Analyses were conducted in the same manner as Study 1, including linear regressions adjusting for age.

Cronbach's alpha

Ratings were examined using Cronbach's alpha for observed reliability co-efficient. For attractiveness ratings: infants $\alpha = .93$, child $\alpha = .92$, student $\alpha = .94$, mothers $\alpha = .97$, and fathers $\alpha = .93$. For masculinity judgments: infants $\alpha = .94$, child $\alpha = .89$. student $\alpha = .94$, mothers $\alpha = .97$, and fathers $\alpha = .89$.

An initial analysis revealed no extreme outliers. Kolmogorow–Smirnov test, and all distributions were normal with the exception of child-masculinity (df(61) = .132, $p = .010$) and student attractiveness df(67) = .111, $p = .040$).

Spearman rank order correlations

Using Spearman rank order correlations, we found a negative but non-significant relationship between infant attractiveness and infant masculinity ($r_{65} = -.157$, $p = .211$), and no relationship between child attractiveness and masculinity ($r_{61} = -.015$, $p = .906$). We also found, as in the previous chapter, that student attractiveness and masculinity were positively correlated ($r_{67} = .298$, $p = .014$).

For attractiveness, we did not find relationships between infant attractiveness and either child attractiveness ($r_{59} = .186$, $p = .158$) or student attractiveness ($r_{62} = .164$ $p = .201$). However, we did find a relationship between child attractiveness and student attractiveness ($r_{57} = .399$, $p = .002$) .

Table 3.3

Male Developmental Stability for Attractiveness

	Infant Attractiveness	Child Attractiveness
Child Attractiveness	$r_{59} = .186$, $p = .158$	
Student Attractiveness	$r_{62} = .164$, $p = .201$	$r_{57} = .399$, $p = .002$*

Our correlations revealed a positive relationship between infant masculinity and child masculinity (r_{59} =.305, p = .019), but not a significant relationship between infant masculinity and student masculinity (r_{62} =.124, p = .336). We did however find a relationship between child masculinity and student masculinity (r_{57} =.350, p = .008)

Table 3.4

Male Developmental Stability for Masculinity

	Infant Masculinity	Child Masculinity
Child Masculinity	r_{59} = .305, p = .019*	
Student Masculinity	r_{62} = .124, p = .336	r_{57} = .350, p = .008*

Summary

We find that male attractiveness does not track from very early development into adulthood; however, it does relate between childhood and adulthood. Infant attractiveness is unrelated to child attractiveness, however child attractiveness does positively relate to young adult attractiveness. Masculinity steps through male development, with infant masculinity positively relating to child masculinity, and child masculinity relating to young adult masculinity, however there is no apparent relationship between infant masculinity and young adult masculinity.

3.7 Discussion

We had four main hypotheses and found support for some aspect of each of them. The first was that facial attractiveness would be stable from infancy through early adulthood. We found firm support for this in females, with attractiveness tracking from infancy through childhood and into adulthood. We also found that both infant and child attractiveness predicted adult attractiveness. Stability of male attractiveness was apparent between childhood and adulthood, and child attractiveness was predictive of adult attractiveness. These findings are consistent with previous work (Alley 1993) who looked at stability of attractiveness from childhood into adulthood.

Our second prediction was that sexual dimorphism would remain stable over development, and we found some evidence for this in both males and females. In females we found that femininity, while not stable between infancy and childhood, was stable between childhood and early adulthood. These findings are consistent with Zebrowitz et al. (1993) study on babyfaceness stability from childhood into adulthood. We also found that childhood attractiveness was actually more strongly correlated with student femininity than childhood or infant femininity, and was the strongest predictor of student femininity.

We found support for our third prediction that facial attractiveness and sexual dimorphism are related, but the direction and strength of the relationship would depend on the sex of the individual. Female facial femininity and attractiveness were positively related at all three stages of development, however, male facial masculinity and attractiveness moved from non-significant but negative correlations at infancy, to non-significant and neutral at childhood, to a positive correlation between the two characteristics in young adult males.

The developmental trend is confirmed by examining the correlation values between masculinity and attractiveness for male faces at the 3 stages of development. A one-way ANOVA with stage of development (3 levels, infant, child, adult) as a within-subjects factor and masculinity-attractiveness correlation value as the dependent variable, reveals a significant main effect of developmental stage ($F_{2,52}$=16.48, p<0.001). This reflects the fact that consistent across raters masculinity is relatively unattractive in infant male faces but becomes more attractive through childhood into adulthood (see *Figure 3.1*). One can enter rater sex as a between subject variable and find no significant effect of rater sex on this relationship and no interaction between rater sex and developmental stage (both $F<.11, p>.76$).

Our third set of findings helps us to understand the previous two. Facial femininity and attractiveness are always positively correlated in females, thus we should expect that if one characteristic is relatively stable through development then the other should be so as well. It should be noted that the strength of the relationship increased with age (*Figure 3.2*), a point to which we shall return. However in males we have a different story. Masculine looking infants are not seen as being particularly attractive, nor are masculine looking little boys. However, as males mature from infancy though childhood, the relationship between attractiveness and masculinity becomes less antagonistic. This is true even while masculine features in male faces become more pronounced (Enlow 1990). We should expect that if one of our two characteristics of interest was to track throughout development, the other should not. In this case we find that facial masculinity does track from infancy to childhood and from childhood to adulthood and facial attractiveness does not.

One reason why the previous chapter failed to find a significant relationship between father and son attractiveness was due to the heritability of masculine facial traits, coupled with the fact that opinion is divided amongst observers as to whether or not male masculinity is attractive. If one averages the attractiveness rating between 50% of observers who find masculinity attractive and another 50% of observers who are averse to masculine features, then the combined rating tends to zero: attractiveness in this case can only be defined by characteristics outside masculinity.

Using the meta-analysis technique described here the variability in opinions about masculinity is overcome. If raters are attracted to masculine features in men, then they will rate masculine fathers and masculine sons highly, and feminine fathers and feminine sons with low attractiveness scores. The opposite will be true for those who are averse to masculinity in men; they will score masculine dads and sons low on attractiveness, and feminine dads and sons high on attractiveness. Note however, that both types of raters would show a correlation in ratings between fathers and sons (*Figure 3.2*).

Averaging the correlations between attractiveness ratings of fathers and sons across observers produces a different insight into the heritability of attractiveness and the runaway sexual selection hypothesis. Masculinity is heritable, yes. As a population women do not show an agreement about attraction to masculinity. Some women are positive to masculinity, but some women are negative. If preferences of women are heritable, or if they are passed across generation through culture (or explicit teaching) then the scene is set for Fisherian selection. Note that the population can move either to favour higher degrees of masculinity in the case of the run-away selection and amplification of extreme male traits; or the population can move to select lower levels of masculinity. The selection pressure to amplify masculinity may come if the environment has high levels of pathogens and immunity is a premium, if high degrees of competition between males is advantageous or if becomes the norm for women to bear the burden of child support. Alternatively selection to minimize male masculinity, and decrease the level of sexual dimorphism, may come from environments with low disease prevalence, and cultures favouring high paternal investment or high male-male co-operation. What is essential for rapid adaptation to such environments is that there is variation in levels of male masculinity, variation in women's preferences for masculinity, and that both male traits and female preferences pass between generations. Note that in a stable environment one expects female preference for masculinity to become distributed about a mean equal to the average level of masculinity amongst the males. This is because the advantages for one level of preference (and one level of masculinity) should spread through the population and become fixed. This being so then the average correlation between masculinity and attractiveness of men will tend to zero.

In summary, what our study has made us realise is that attraction to male masculinity does vary between individuals, but that the type of individual attracted to a masculine man will also be attracted to his masculine sons when they become mature adults.

This being said we can turn to the curious case of male infants. Attractive fathers have sons who are like 'ugly ducklings', the sons may turn out to be 'attractive swans' when they grow up, but they start out in life with a handicap. At a speculative level, this is directly attributable to the evaluation of masculinity at different stages of a male's life; masculinity is unattractive as a baby but may become more attractive in later life. The paradox is this, a woman may be attracted to a masculine male as a partner; together they will produce boys who in infancy will look relatively unattractive to the parents. While all parents may bond to and love their own children, the evidence revealed here is that the very same parents would find their baby sons even more attractive if they were more feminine.

There are many possible consequences. If unattractive infants trigger parental and social reactions that are slightly less friendly and engaging, then it is quite possible that traits such as independence and lack of sociability will be encouraged: these are archetypically male traits. What we are suggesting is that masculine-looking babies will trigger adult reactions that may cultivate future masculine behavioural and personality traits. Such behavioural masculinsation is entirely appropriate in an environment where masculinity is itself to be prized and may present a selective advantage.

Neotenous features in both female and male infants have consistently been found to be attractive by adults (Alley 1981; Fullard & Reiling 1976; Geldart et al. 1999; Hall Sternglanz et al. 1977), and neotenous features are also associated with adult facial femininity (Jones 1996). Thus feminine looking infants are viewed as more attractive than masculine looking infants. The characteristics we refer to as being either 'masculine' or 'feminine' are defined as such based on the faces of adults of reproductive age. In other words, they are features of sexual maturity, thus we should expect that as males develop, facial characteristics of masculinity would become more tolerable, especially as individuals enter puberty.

We noted that the strength of the positive relationship between femininity and attractiveness in female faces increased with age. In males, we find that the relationship between masculinity and attractiveness also increases, and more notably moves from a negative (non-significant) relationship to a positive (significant) relationship. One explanation behind these changes is that sexual dimorphic features are associated with sexual maturity, thus exaggeration of these traits too early in development would be viewed negatively. As many studies suggest, very early maturation is often due to psychological and/or physiological problems (Belsky & Draper 1987; Belsky et al. 1991; Dickerman et al. 2004; Jones et al. 1972; Moffitt et al. 1992; Surbey 1990). Outward signals in the form of exaggerated sexually dimorphic characteristics might, for very good reasons, negatively affect perceptions of attractiveness in infants and children. Even though neotenous features are associated with signals of femininity, we still find that among infant faces judgments of sexual dimorphism vary. We do not know what facial characteristics are influencing judgments of either masculine or feminine traits. It does however stand to reason that neoteny is not the only relevant feature in these judgments, as infant faces are by definition neotenous.

In children's faces, we find that tolerance for sexual dimorphic features increases. This is particularly relevant in boys' faces, as masculinity moves from being unattractive in male infants to being neither attractive nor unattractive in childhood. In girls' faces we find that feminine features are not only positively related to attractiveness, but strongly so. Yet, still the relationship is not nearly as strong as we find in young adulthood.

Figure 3.1

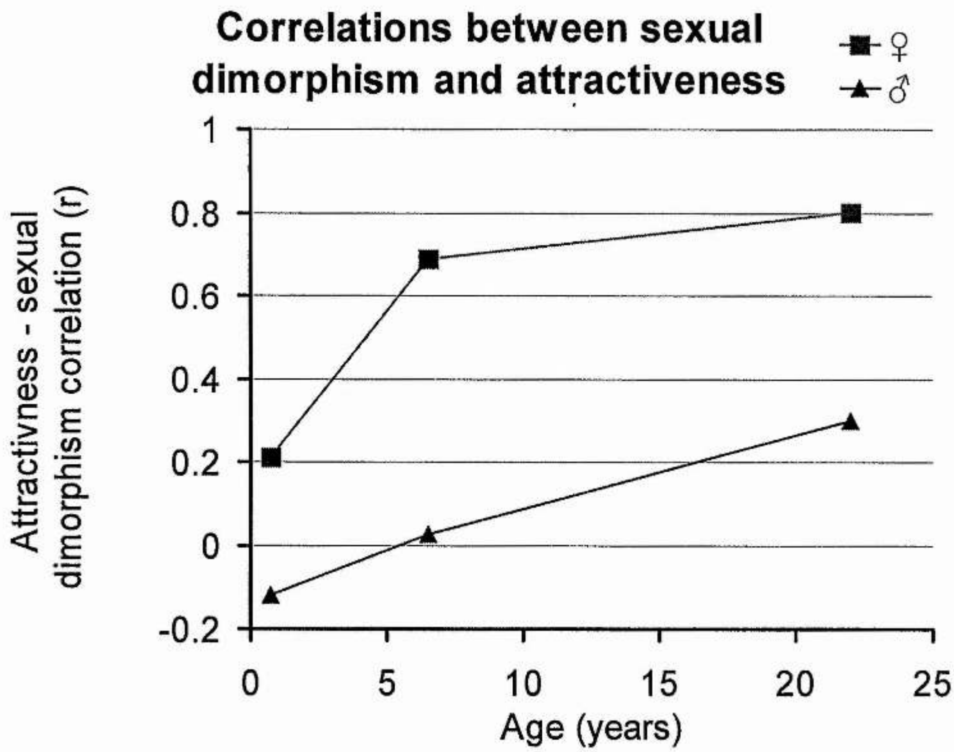
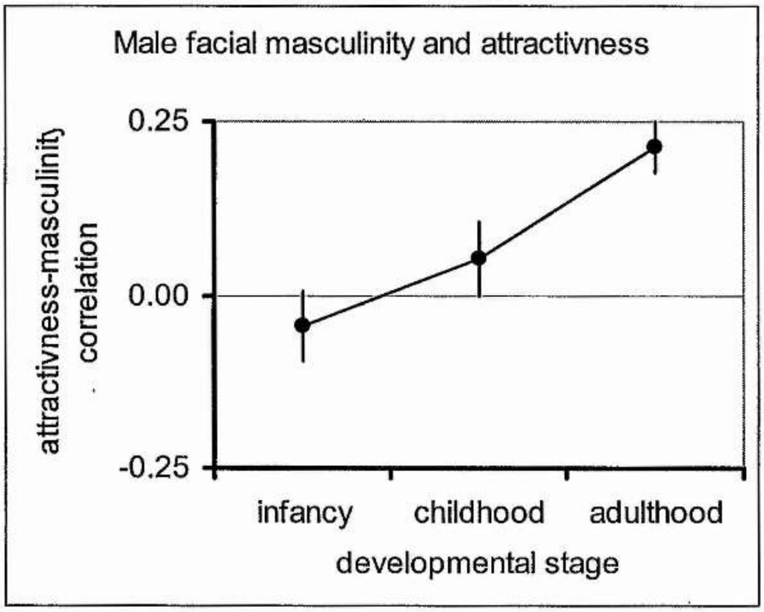

Correlations between sexual dimorphism and attractiveness
♀
♂
Attractivness - sexual dimorphism correlation (r)
1
0.8
0.6
0.4
0.2
0
-0.2
0
5
10
15
20
25
Age (years)

Figure 3.2

Correlations between male facial masculinity and attractiveness



4 An argument for selection of neotenous characteristics in humans: A wee theory

4.1 Introduction

It has long been argued that paedomorphosis, the retention by an organism of juvenile or even larval traits into later life, has profoundly shaped the evolution of humans and other animals (for full review see Gould 1977). Paedomorphosis can come about in either of two ways: acceleration of sexual maturation relative to the rest of development (progenesis) or retardation of bodily development with respect to the onset of reproductive activity (neoteny).

The Dutch anatomist Louis Bolk posited that the human species is an exaggeratedly neotenous form of ape and writes, "Our essential somatic properties, i.e. those which distinguish the human body form from that of other Primates, have all one feature in common, viz they are fetal conditions that have become permanent. What is a transitional stage in the ontogensis of other Primates has become a terminal stage in man" (1926, p. 468). Heterochrony, the phyletic change in the onset or timing of development, was a major theme of Gould's *Ontogeny and Phylogeny*: 'Evolution occurs when ontogeny is altered in one of two ways: when new characters are introduced at any stage of development with varying effects upon subsequent stages, or when characters already present undergo changes in developmental timing.' (1977, p. 4). Recognizing the importance of developmental retardation, however, is only half the battle. For full understanding we also need a selection pressure.

4.1.1 Indirect vs. direct selection

Paedomorphosis has been described across the animal kingdom and explained by a variety of indirect selection pressures. For example, suppose there were direct selection pressures for cooperation and sociability. As hypothesised by Bromhall (2004), this could be achieved through the slowing down of developmental timing. This would be an example of indirect selection in favour of paedomorphosis. I am suggesting something different: a more parsimonious explanation for paedomorphosis as a result of direct selection. I propose that parental preferences for neotenous traits themselves have favoured paedomorphosis in humans: cooperation and sociability are byproducts.

4.1.2 Parenting problems and solutions

Humans, like other mammals, faced particular problems in allocating parental care to offspring. They might apportion it unequally, serving the survival needs of different offspring: perhaps more care might go to the most vulnerable (youngest), or under other conditions to the healthiest offspring. In any case, we should expect parents to develop particular sensitivity to the age and health of their offspring. Offspring, for their part, will strive to elicit as much care as possible from their parents. As Trivers insightfully realised, this whole topic is fraught with conflict.

4.1.3 Parent-offspring conflict

Trivers (1974; 1985) pointed out that young mammals can benefit themselves by postponing weaning, or otherwise prolonging parental care. He developed an ingenious theory of parent/offspring conflict according to which offspring are selected to press for more parental resources than the parent is selected to give, up to a point determined by the child's coefficient of relatedness to its siblings, born or unborn. A parent is expected to resist the pressure to postpone weaning and consequently postpone or otherwise damage future reproductive opportunities. The two parties to the conflict have different weapons at their disposal. The parent has the advantage of physical strength, and direct control of the resources under dispute. The offspring has subtler weapons of manipulation: sophisticated psychological tricks. Trivers suggests that parents would be selected to respond positively to offspring signals, and in turn offspring would be selected to take advantage, in particular by *regressing* to behaviours that appealed to the parents during an earlier stage of development (1985). My suggestion is more general. Paedomorphosis itself evolved in the service of Triversian manipulation by offspring. An offspring that manages to look younger than it is, or younger than its sibling rivals, 'fools' the parent into granting it more resources than its true age would merit. Other paedomorphic manifestations are a byproduct of this primary selection pressure.

4.1.4 Evidence for selection of neotenous traits

Konrad Lorenz (1943) proposed that infantile facial features, such as a high protruding forehead, large eyes positioned in the middle of the face, a small nose and mouth, and chubby cheeks, might serve to elicit caretaking behaviours, a view which has received support (Alley 1981; Alley 1983a; Alley 1983b; Eibl-Eibesfeldt 1975; Hall Sternglanz et al. 1977; Leyhausen 1973; McCabe 1988).

Various psychologists have suggested that the physical appearance of infants and children affects adult behaviour towards them, and these behaviours will in turn have effects upon the child's psychological development (e.g. self-esteem) (Adams & Roopnarine 1994; Byrnes 1987; Dion 1972; Dion & Berscheid 1974; Driver Leinbach & Fagot 1991; Kurdahi Badr & Abdallah 2001; Langlois & Styczynski 1979; Ritter et al. 1991; Zebrowitz et al. 1998). However, while psychologists have entertained ideas vaguely reminiscent of neoteny, they have used a mish-mash of terms used to describe facial characteristics of infants and children. For example, some authors use the term neoteny (Alley 1981; Alley 1983b; Hall Sternglanz et al. 1977; Hildebrandt & Fitzgerald 1979), others speak of 'babyfaceness' or 'baby-faced' (Ritter et al. 1991; Zebrowitz et al. 1993), and still others use the more general, and by far the least meaningful term 'attractiveness' (Badr & Abdallah 2001; Casey & Ritter 1996; Langlois & Styczynski 1979).

I think there is no good reason not to use the term 'neotenous' for a substantial class of those infant features that adults find attractive (Alley 1981; Alley 1983b; Hall Sternglanz et al. 1977). In studies using language like 'babyfaced' or 'babyfaceness', when judged by adults those infants perceived as being older, less baby-faced, are rated as less attractive and as having poorer developmental abilities than those infants assessed as being younger or more baby-faced (Ritter et al. 1991). Among children, the transgressions of more mature looking individuals were less likely to be tolerated, were viewed more negatively, punished more severely, while more chores, and more demanding tasks were assigned to them (Zebrowitz et al. 1991). We also find that attractive infants and children gain greater benefits than less-attractive individuals (Badr & Abdallah 2001; Casey & Ritter 1996; Langlois & Styczynski 1979). I suggest that the facial features discussed in the studies listed above all relate to neotenous facial characteristics.

Given that parents and other adults are giving preferential treatment to children who display more neotenous features, we can easily see how this could have set up a selection pressure in favour of paedomophic evolution. Even with only slight advantages, increased neoteny could easily have been produced. But given that infants and children viewed as attractive (because more neotenous) are given better care, more resources, and more parental devotion, surely being more neotenous than one's sibling or cousin or neighbour has conferred more than just a slight advantage.

4.2 Summary

Past explanations for paedomorphosis in humans have treated it as an indirect consequence of selection for increased intelligence and changes to behavioural traits (e.g. cooperation, reduced aggression). Yet we have a great deal of evidence to support preferences for neoteny itself. Selection for neoteny at the earliest developmental stages (infancy) leading to more complicated behavioural and physiological changes seems so much simpler and economical than selection during late development (adulthood) for various behavioural and physiological changes leading to increased neoteny.

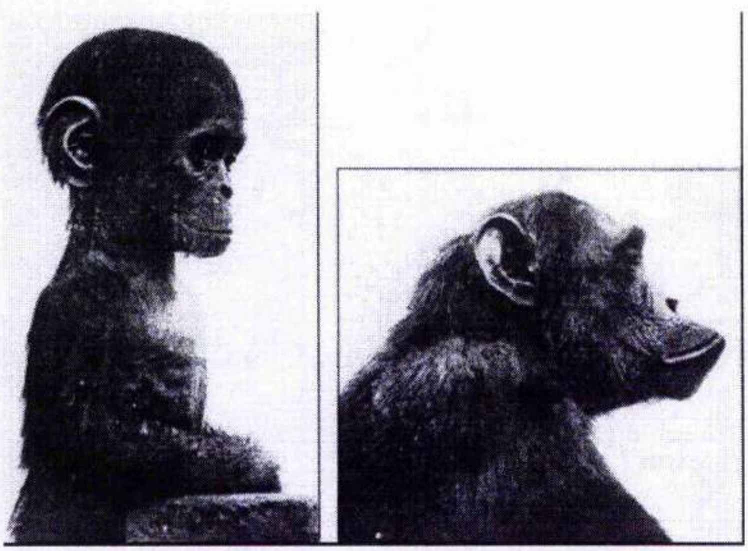


Figure 4.1

Classic example used to highlight the developmental profiles of an infant chimp compared to that of an adult chimp and noting the closer resemblance of the infant to an adult human profile (Naef 1926).

5 The timing of puberty and the development of sexual behaviour in relation to preferences for facial characteristics

5.1 Introduction

Sexual maturation is a key milestone in human development, and much research has focused on multiple factors influencing its timing. These include psychosocial factors (Belsky & Draper 1987; Belsky et al. 1991; Ellis et al. 2003; Ellis & Garber 2000; MacDonald 1999), hormones (Nottlemann et al. 1987; Tremblay et al. 1998), and genetics (Comings et al. 2002).

Timing of puberty, independent of the factors mediating it, influences the social environment of adolescence. Whether one matures early, late, or 'on-time' will shape individual experiences in interactions with peers as well as adults. The outcome of these interactions contributes to the overall psychosocial well-being of the individual during adolescence. Our interest is to go beyond the immediate influences of pubertal timing and sexual maturation on adolescent behaviour and investigate the outcome of sexual maturational timing on adult mate choice and strategies.

We assert that adults who were early sexual maturers, e.g. in terms of both puberty/menarche and initiation of sexual intercourse, will differ from late maturers when making judgments of opposite-sex facial attractiveness. Our over-arching hypothesis is framed by alternative reproductive strategies that are responses to the developmental environment. These differences are reflected in individual preference judgments for particular facial characteristics. We consider three issues: early maturation as a negative outcome due to stress; early maturation as a positive influence due to social status; and preferences due to sexual access and learning.

5.1.1 Alternative reproductive strategies

Alternative tactics to maximise reproductive fitness are found across a wide variety of species, including humans (Gross 1985; Gross 1996; Henson & Warner 1997). The theoretical framework offered by both game theory (Maynard Smith 1982) and evolutionarily stable strategy (Maynard Smith & Price 1973) offers a platform from which investigations into humans' use of alternative reproductive strategies can be launched. Beginning with the most basic assumptions of female/male differences: males are thought to take the approach of capitalising on as many mating opportunities as possible, but are constrained by female choice and demands for investment (Trivers 1972a). Females, on the other hand, should seek out mates who are willing to provide, but they are forced to make trade-offs between good paternal investment and genetic fitness (immunocompetence) (Møller & Thornhill 1998; Perrett et al. 1999; Scheib 2001; Scheib et al. 1999). Research on attraction has successfully used this theoretical framework to explain individual differences in female preferences for symmetric and sexually-dimorphic facial characteristics in opposite sex faces (Little et al. 2002; Penton-Voak et al. 2003).

High-quality individuals have a greater ability to attract high-quality mates and thus procure higher reproductive advantages. A more attractive male can adopt a mating strategy of multiple mating partners, investing less in each partner (Thornhill & Gangestad 1994), with less risk to his offspring (Badyael & Hill 2002; Burley 1986; Gowaty 1996; Sheldon 2000). Females of high-quality cannot only attract high-quality mates, but can enforce demands for parental investment and thereby circumvent the trade-off between good genes and high investment. Individuals of lesser quality cannot successfully employ these strategies, despite their desire to do so, and this gives rise to variation in mate choice strategies. Humans offer us a unique opportunity to investigate the influence of self-assessed quality on mate choice and strategies.

5.1.2 Influence of Puberty on Alternative Reproductive Strategies

The possible environmental factors mediating pubertal timing have been studied since the 1930s, and family, economic, physical, and nutritional stressors have been indicated as having affects on sexual maturation. Despite the amount of research expended, there remains a great deal of controversy as to which particular stressors accelerate and which decelerate puberty timing (Hoier 2003; Romans et al. 2003). Some psychologists have examined the role of environmental stressors and their possible influence on reproductive strategies, including the timing of sexual maturation and mate choice. Humans, it is argued, have been selected to respond to environmental cues by adopting a reproductive tactic most suited to enhance fitness; furthermore, the choice of tactic is sensitive to the environmental cues experienced during development (Belsky & Draper 1987; Belsky et al. 1991; Ellis et al. 2003; Ellis & Garber 2000; Jones et al. 1972; MacDonald 1999; Moffitt et al. 1992; Surbey 1990). It has been asserted that more precocious sexual behaviours indicate a strategy of early reproduction, more offspring, but less investment; whereas later sexual maturity and conservative sexual activity may reflect an investment-biased reproductive strategy with fewer offspring but heavier investment. Adopting either of these strategies may reflect the environment in which the individual was exposed to at specific times during development or throughout development.

5.1.3 Pubertal timing and parental influences

Puberty is the key developmental milestone toward achieving adult sexual status, and its timing has been linked to strong hormonal and genetic influences. There remains debate concerning the contribution of genetic (Pickles et al. 1998) and hormones on development (Dorn et al. 2003). One factor, mother's age of menarche has been found to be the best predictor for daughter's age of menarche (Kirk et al. 2001). Environmental factors also mediate age of menarche, with stressful family situations such as father-absence accelerating menarche (Belsky & Draper 1987; Belsky et al. 1991; Jones et al. 1972; Moffitt et al. 1992; Surbey 1990), while having younger siblings decelerates it (Hoier 2003; Jones et al. 1972). Less work has been done on the effect of father-absence on puberty in males, however, father absence for one year or longer during childhood is significantly associated with earlier spermarche (Kim & Smith 1998; Kim et al. 1997). Early spermarche and puberty have been associated with increased number of romantic partners, sexual partners, earlier onset of sexual interest (dating), and earlier first intercourse (Edgardh 2002; Kim & Smith 1998). In contrast, good relationships with parents, especially between girls and their mothers, can decrease the likelihood of early sex (McNeely et al. 2002)

Since poor relations between parent and offspring is thought to accelerate sexual maturation and negatively affect mate-quality (Boothroyd 2004a), it must be taken into account when investigating the association between sexual development and mate choice preferences. Parental relationships may affect mate choice preferences in a way that is independent of maturation effects, such as through an effect on self-esteem and psychological well-being (Berg 2003; McNeely et al. 2002;

Spencer et al. 2002). We therefore investigate the effect of maturation and relationship with parents on adult partner preference.

5.1.4 Adolescence and peer influences

Adolescence is a time for individuals to explore and come to terms with peer group social hierarchy and their rank within it (Harris 1995; Hawley 1999; Hawley 2003a; Hawley & Vaughn 2003). If adolescence is a particularly sensitive time for determining reproductive strategies, then social status and adolescent sexual behaviour should be of particular importance. While there is evidence that early puberty can have negative psychological, social, and behavioural effects both during and after adolescence, there is also evidence to its positive effects (Dorn et al. 2003; Weichold et al. 2003; Weisfeld & Woodward 2004). Reaching puberty slightly ahead of peers may give distinct advantages in terms of social status, and these advantages may in fact continue on into adulthood. Higher levels of testosterone during early puberty in boys has also been associated with social success (Schaal et al. 1996). Boys who mature earlier are often looked up to by their same sex peers (Peterson & Crockett 1985), and have greater opportunity to affiliate romantically with females (Halpern et al. 1998; Susman et al. 1987). Such affiliations increase the potential for earlier initiation of sexual activity compared to their slower developing peers (Stattin & Magnusson 1990). Girls who mature earlier are more likely to procure the attention of older, more physically-mature boys (Gowen et al. 2004; Magnusson et al. 1985; Stattin & Magnusson 1990; Weichold & Silbereisen 2001), and such girls find older boys to be more attractive than boys of peer age (Kracke 1993). Associating with older boys may give early maturing girls access to social activities and the trappings of higher social status not afforded to slower developing peers, as well as increase the likelihood of engaging in romantic and/or sexual activity (Prokopèáková 1998; Silbereisen & Kracke 1997). These early affiliations with like-developing opposite sex peers may enhance preferences for more sexually mature characteristics. Girls for example, may associate positive experiences with more masculine looking boys and in turn, boys may relate more feminine characteristics in female faces with early sexual rewards. These preferences could continue on into adulthood, and thus associations between early maturation and preferences for exaggerated sexual-dimorphic features would be expected in mate choice for those with early maturation. Another possible influence of sexual development on mate choice is that both early maturing girls and boys may gain social status within their peer groups, and thus enhance self-perceived attractiveness and mate-value. If self-perceptions established during development continue into adulthood, early-maturers are likely to perceive themselves as high-status and high-quality adults. Effects of self-perceived quality have been found to influence adult partner choice. For example, high quality individuals prefer partners of similar quality. This is reflected in their increased preferences for quality markers such as symmetry and exaggerated sexually-dimorphic facial characteristics (Little et al. 2001b; Penton-Voak et al. 2003). For these reasons, we examine the influence of self-rated attractiveness on preferences for sexual-dimorphism in opposite-sex faces.

5.1.5 Signals from sexual dimorphic facial traits

Symmetry is considered a positive characteristic for both sexes, as it suggests good immunocompetence during the difficulties of the developmental process (Jones et al. 2001; Perrett et al. 1999). By contrast, the particular growth patterns mediated by sex hormones resulting in epigamic traits are thought to signal both positive and negative mate characteristics (Perrett et al. 1998). Characteristics more typical of the female face include full-lips, large eyes, small nose, and delicate features, which are thought to be associated with higher levels of oestrogen (Jones 1995; Jones 1996). Feminine facial characteristics may signal fecundity (Enlow 1990), and immunocompetence (Seli & Arici 2002). Faces of women with higher levels of oestrogen are rated as more feminine looking than faces of women with lower levels (Law Smith et al., in prep). Feminine features are found attractive by both sexes, and suggest personality merits such as warmth and nurturing (Perrett et al. 1998). The more classic male facial features include square jaw, heavier brow, and thinner lips, which are related to testosterone levels during development. Faces of males with higher levels of testosterone were rated as looking more masculine than faces of males with lower levels (Penton-Voak & Chen 2004). Testosterone is known to depress the immune system (Ahmed & Talal 1990), and Folstad and Karter (1992) argue that only the healthiest males with the best genes for immunocompetence are capable of displaying such epigamic traits (see Chapter 2 for further discussion). Testosterone is also related to male-male competition, and it is reasoned that male characteristics may enhance signals related to male dominance (Mazur & Booth 1998b). Masculine features simultaneously convey both positive and negative signals, including personality attributes such as dominance, high risk taking, aggression, sexual impulsivity, spousal abuse, inability to commit to a relationship, and anti-social behaviour (Mazur & Booth 1998b; Olweus et al. 1988; Perrett et al. 1998). Masculine features therefore are of contrary desirability and women must resolve trade-offs between males with genes signalling high immunocompetence and males signalling affable personality traits and high paternal investment.

5.1.6 Attractiveness: beyond sexual dimorphism

What is 'attractiveness'? In the context of mate preferences it should mean that one individual is 'attracted to' or 'drawn-in' by another individual as a potential sexual partner. It is also used in more general terms, as a sort of rating system. For example, compared to asymmetrical faces, symmetrical faces are generally preferred, thus symmetrical faces are described as being more 'attractive'.

Researchers studying mating strategies need to understand whether attractiveness means the same thing across a variety of individuals. In a meta-analysis, Langlois and her colleagues (2000) found strong agreement between raters on judgments of facial attractiveness, both within and across cultures. Still, while individuals may agree in general who is or is not attractive, there will be some disagreement regarding the degree of attractiveness. We see variation of this sort when examining the influence of hormonal markers on facial preferences. Women's preferences for masculine facial characteristics have been far from consistent across a range of studies. Women have been found to prefer more masculinised male faces in some studies (Grammer & Thornhill 1994; Penton-Voak & Perrett 2001; Scheib et al. 1999), and to prefer more feminised male faces in others (Penton-Voak et al. 2003; Penton-Voak et al. 1999; Perrett et al. 1998). Women are not the only ones who appear fickle, as male preferences for feminine facial characteristics also vary among individuals (Cornwell et al. 2004; Cunningham et al. 1995; Swaddle & Reierson 2002). So, if women and men concur on facial attractiveness but differ on preferences of sexual dimorphism – is there an aesthetic quality in the human face that we do not yet fully understand? And if so, what is its role in mate choice?

Masculine and feminine facial characteristics are signals of mate quality, but strong indicators of sexual dimorphism do not automatically confer attractiveness. For example, Arnold Schwarzenegger's 'Terminator' would certainly be judged as a 'highly masculinised' male, but not all women would judge him as facially attractive. On the other hand, the character Everett, as played by the actor George Clooney in the film 'O Brother, Where Art Thou?', is both masculine and to many women very attractive. Likewise, feminine facial characteristics are not the only feature contributing to a woman's attractiveness. Both Sigourney Weaver and Meg Ryan are highly attractive, and yet Ms. Ryan would likely be judged as being much more feminine looking than Ms. Weaver.

The point we are making is that there are aesthetic qualities that alter our judgements of attractiveness outside of or in addition to feminine or masculine facial characteristics. We assert that these 'attractiveness' characteristics are a signal to mate value, however whether these signals convey the same or different meanings than epigamic facial characteristics is unknown. To investigate whether there is an 'attractiveness' component to the face, we have attempted to isolate it from variations of facial masculinity or femininity by creating a new set of facial images. These images attempt to keep constant sexual dimorphic characteristics and vary on a characteristic we shall at this time refer to as 'attractiveness'. Reciprocally we created images that vary on masculinity and femininity, whilst attempting to keep attractiveness characteristics constant.

If sexually dimorphic traits in faces are the critical signal to determining perceptions of mate quality, then we should find preferences for epigamic facial traits independent of attractiveness. Further, we should not detect any preferences for faces varying on attractiveness when controlling for sexual dimorphism. If, however, both epigamic traits and the attractiveness component convey mate quality information to the receiver, then there should be variation in preference when judging faces that vary on these characteristics independently. While we are attempting to understand the variation found in the literature regarding female preferences for male facial appearance and how these variations relate to mate quality; for the sake of parity we created female face images manipulating attractiveness and femininity.

5.1.7 Apparent Age

Another facial characteristic that has been found to influence choice is apparent age. Masculinity increases apparent facial age (Boothroyd et al. 2003; Perrett et al. 1998), individuals choose partners with reference to their own age (Kenrick & Keefe 1992), and having older opposite-sex parents has been found to increase tolerance for older looking faces when considering long term partners (Perrett et al. 2002). Because participant age and parent age may influence preference for masculinity in faces, we need to include images that manipulate apparent age to differentiate it from sexual dimorphic characteristics. We do not suspect that preferences for epigamic traits are explicitly related to preference for partner age. Still, differential timing of development could have some influence on preferences for maturation cues in the face; these preferences may then relate to epigamic traits. If early maturers prefer other like-maturers, this may increase preference for apparent age in faces. Such effects would be most prominent during adolescence and early adulthood, but may in fact be retained for much longer.

5.2 Predictions

Based on prior research and theories relating to reproductive strategies and assortative mating, we offer three predictions for the effects of sexually-maturation. timing on preferences for facial epigamic traits.

(1) If early timing of sexual maturity is associated with high-stress and therefore producing low-quality individuals, then early-maturing men should prefer low quality female faces, that is less feminine and less attractive faces, while later maturing men should indicate preferences for high quality female faces. Early developing women should indicate preference judgments for low quality males by choosing less masculine and less attractive male faces. However, it should be noted that due to the use of short-term strategies, low-quality women may indicate a preference for high-quality males if they are only considering short-term relationships. (2) If learning occurs, that is to say early developing adolescents have learned to associate increased sexually dimorphic characteristics with potential mates, then we would expect to see early maturers preferring increased sexual-dimorphism but not necessarily indicating a preference for higher facial attractiveness; and (3) If early maturers consider themselves to be higher quality mates due to social learning, then both men and women should choose the high quality mates on both dimensions of facial characteristics, that is more sexually dimorphic and the more attractive opposite sex faces.

5.3 Methods

5.3.1 Rating Original Images

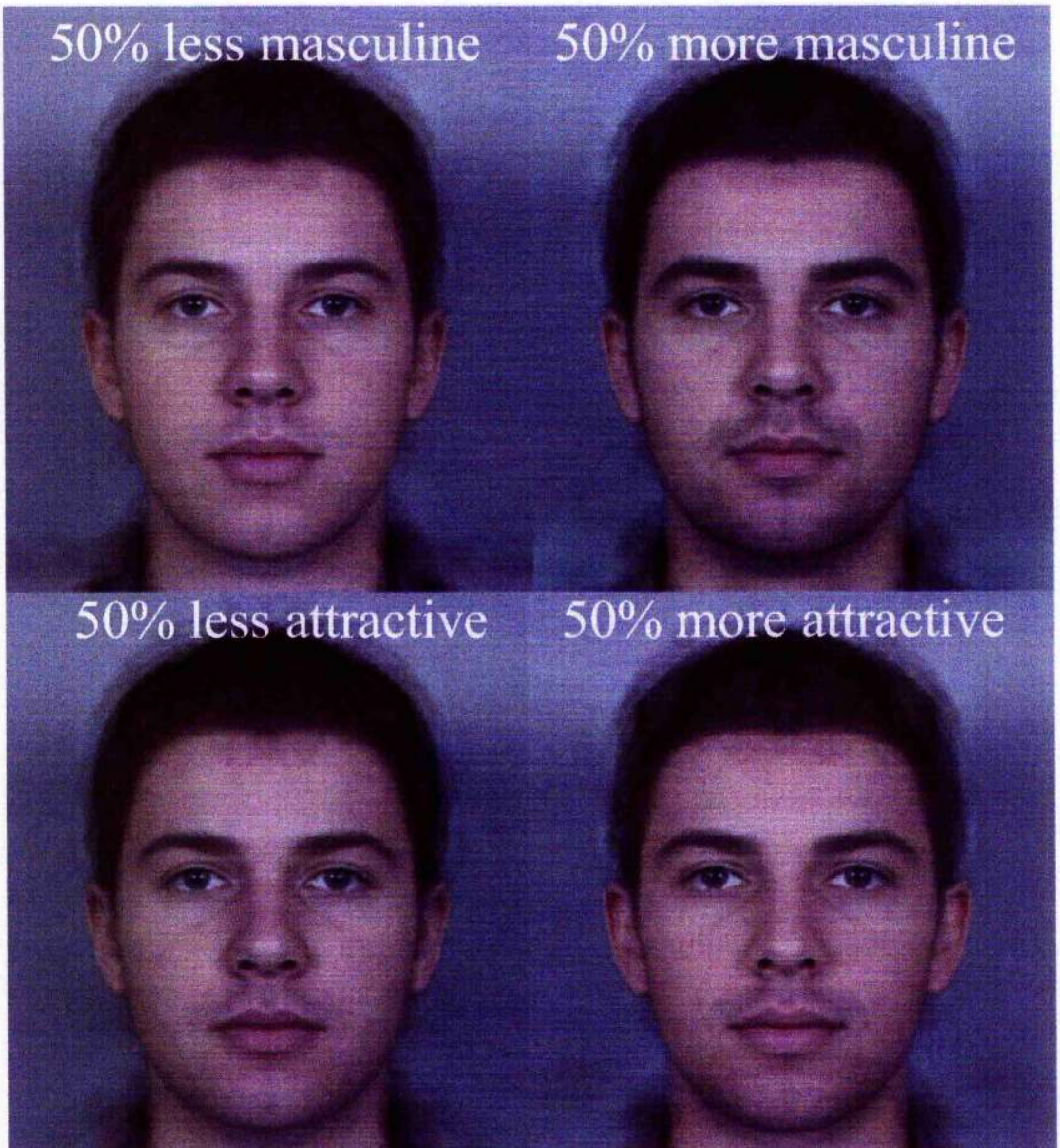
We began with a collection of 701 original face images (>90% Caucasian; 456 female: age mean=20.21 SD=3.18 years; 245 male age mean 21.21 SD=3.58

years). Seventeen participants (11 females) rated attractiveness; and 14 participants (7 females) rated facial femininity of female faces and masculinity of male faces. Images were masked (to exclude hair and clothing) and presented in random. Participants were Caucasian and aged 18-29 years. Each image was assessed on scales of 1 – 7 (1 being low, 7 being high) for attractiveness for both female and male faces, for masculinity on male faces, and for femininity on female faces. Initial correlation analyses revealed that the female rating of male facial attractiveness and facial masculinity were significantly correlated ($r_{196} = .202$, $p = .005$), and correlations between the male ratings of female facial attractiveness and facial femininity were even stronger ($r_{345} = .592$, $p < .001$).

To create our new images we first matched facial images on one dimension, and then from within the matched group we selected the high and low faces on the second dimension. For the attractiveness images, we averaged shape, colour, and texture (n=26-30) of those Caucasian faces that had been rated either high or low on the dimension of attractiveness while rated similarly on the second dimension of male masculinity (see section on Psychomorph methods). This effectively created high and low attractiveness male face prototypes that were matched on the dimension of masculinity (scale: 1-7; mean attractiveness ratings 3.42 vs. 2.43; mean masculinity ratings 4.38 vs. 3.93). The same process was then used to create two male prototypes of high and low masculinity matched on attractiveness (mean masculinity ratings 5.18 vs. 2.88, mean attractiveness ratings 2.85 vs. 2.75), two female prototypes of high and low femininity while controlling for attractiveness (mean femininity ratings 4.98 vs. 2.92; mean femininity 3.10 vs. 2.97), and two female prototypes of high and low attractiveness while controlling for femininity (mean attractiveness ratings 4.22 vs. 2.26; mean attractiveness 4.26 vs. 4.44).

Figure 5.1

Example stimuli used in the studies. (a) Masculinity lowered (left) and raised (right) while keeping attractiveness constant. (b) attractiveness lowered (left) and raised (right) while keeping masculinity constant.



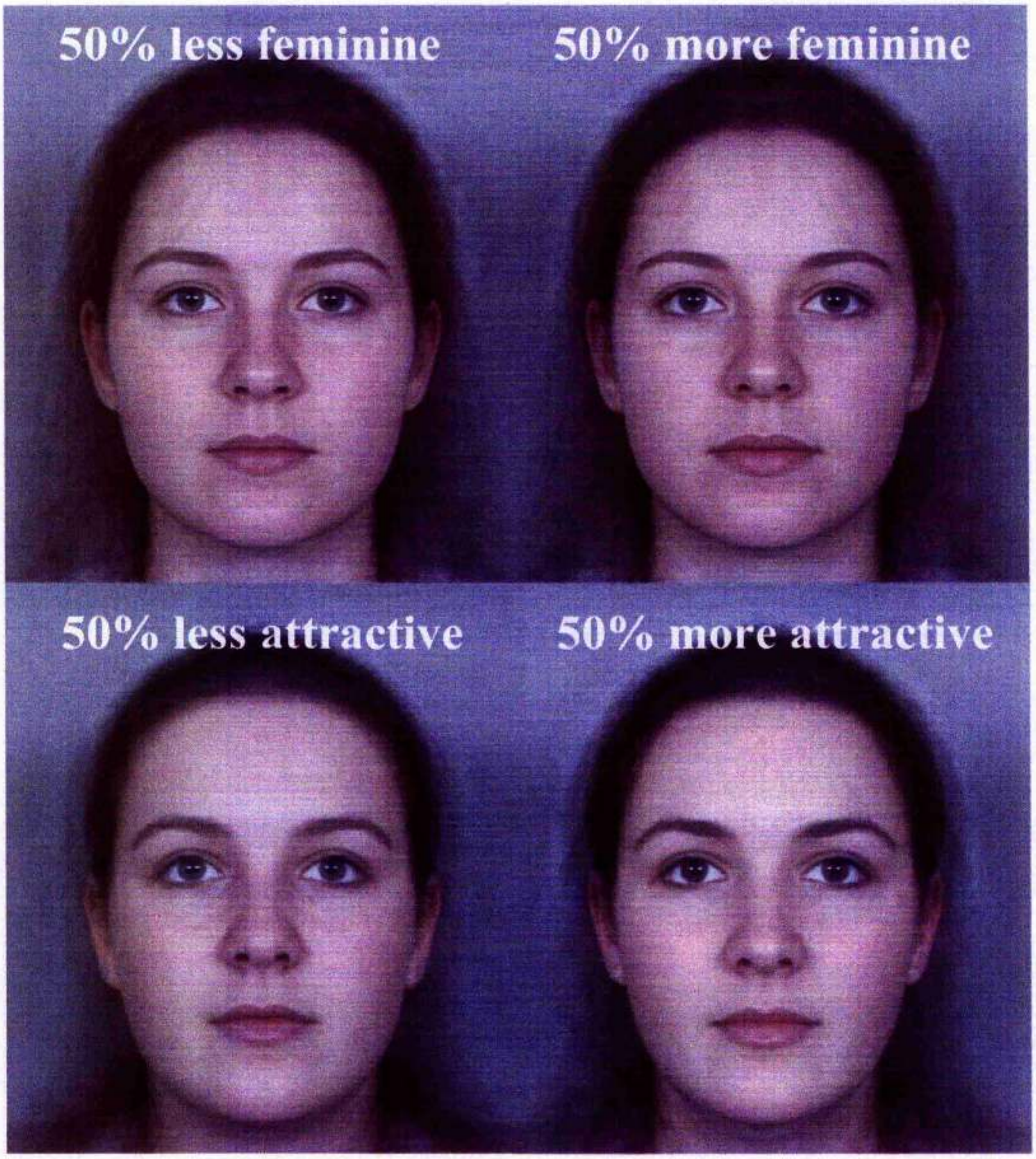


Figure 5.2

Example stimuli used in the studies. (a) Femininity lowered (left) and raised (right) while keeping attractiveness constant. (b) Attractiveness lowered (left) and raised (right) while keeping femininity constant.

5.3.2 Composite Image Calibration

The male face prototypes images were rated on both attractiveness and masculinity and the female faces were rated for attractiveness and femininity. The raters were recruited through an introductory psychology class at the University of Colorado at Colorado Springs for course credit. For our analyses, we included only female raters under 25 years of age ($N = 38$, Mean Age = 18.7 ± 1.2, range 17-23 years) and not taking hormonal contraceptives or pregnant. Male raters were under 25 years of age ($N = 39$, Mean Age = 19.6, ± 1.4, 17-23 years). Analyses are based on opposite sex ratings. Images were presented individually and in random order amongst filler items, and rated on a 7-point scale.

Paired t-test analyses revealed that the high masculine male face prototype ($M = 3.97 \pm 1.03$) was judged more masculine than the low masculine male face prototype ($M = 2.45 \pm 1.01$), $t(37) = 7.3$, $p < .001$, $\eta^2 = .59$. When judged on attractiveness, the high masculinity ($M=3.12 \pm 1.18$) and low masculinity ($M=3.15 \pm 1.31$) face prototypes were found not to be significantly different, $t\ (33) = -.114$, $p = .91$.

For the high and low attractive male images rated on attractiveness we found that the high attractive male face ($M = 3.85 \pm 1.18$) was rated significantly more attractive than the low attractive face ($M = 3.15 \pm 1.11$), $t(33) = 4.112$, $p < .001$, $\eta^2 = .34$. When rated on masculinity the two were not significantly different $t(37) = 1.02$, $p = .31$ (high attractiveness: $M = 3.26 \pm 1.13$; low attractiveness $M = 3.08 \pm .82$). These data show that the intended manipulation of male face prototypes along one dimension while controlling a second dimension was successful.

For the female images, however, the calibration results indicate that segregating attractiveness and femininity in female faces was not successful. The high and low feminine face pairs were rated differently on femininity; high feminine ($M = 2.34 \pm 1.74$), low feminine ($M = 1.62 \pm 1.545$), $t(28) = 3.92$, $p = .001$, $\eta^2 = .354$, but the same images were also judged differently on attractiveness: high feminine ($M = 3.33 \pm 1.43$), low feminine faces ($M = 2.62 \pm 1.12$), $t(20) = 3.25$, $p = .004$, $\eta^2 = .346$. The high ($M = 3.86 \pm 1.389$) and low ($M = 2.90 \pm 1.136$) attractiveness female faces were rated differently on attractiveness $t(20) = 3.301$, $p = .004$, $\eta^2 = .353$; but also differed on rated femininity: high ($M = 2.86 \pm 1.98$), low ($M = 2.07 \pm 1.65$); $t(28) = 3.111$, $p = .004$, $\eta^2 = .257$.

5.3.3 Experimental Images

Three composite 'base' male faces were made by averaging 8 randomly chosen Caucasian male face images, aged between 18 and 24. Three 'base' female faces were similarly created. This created base faces differing in apparent identity which were then transformed by +/-115% of the difference in face shape, colour, and texture between the high and low sexual-dimorphic and high/low attractive prototypes (see Psychomorph methods). Finally a sequence of 25 images was created interpolating between the +115% and –115% end point images. This effectively created 3 face continua (of 25 images) for each sex that differed along one dimension but were matched in other respects (i.e. different apparent masculinity but matched in identity and attractiveness). For illustration see *Figures 5.1 and 5.2*.

These continua were used to create three interactive sequences, with 25 individual images in each sequence. Participants were asked to choose the image that they considered to be the most attractive from the range available (Little et al. 2001a; Perrett et al. 1998).

As sexually-dimorphic characteristics may be associated with age (masculine faces look older, while feminine faces look younger), we included an age transform sequence. These images were made from a different cohort of male and female images, and each image was judged for age by 10 raters. Male composite aging-prototype images were made by creating 3 individual faces from blends of 6 young male faces (perceived age between 15-20 years) and 3 individual blends of 6 older male faces (perceived age between 50-60 years). All images were made symmetrical. The faces were validated via online tests by students at the University of Colorado at Colorado Springs. Twenty-one male and 66 female participants (males: mean age = 20. 65, SD= 5.21; female: mean age = 20.03, SD = 4.67) were asked to enter the estimated age of each face. Interrater reliability for perceived age was high (Cronbach's alpha = .996).

The interactive tests were made by pairing one of the young-aged male composite images with one of the older-aged male composite images. To create the continua between the young and older faces, 35 morphs were made by beginning with the young image and incrementally increasing the facial characteristics of the older image and decreasing those of the young image. The last image of the continua then would be the older composite image. This approximated an increase of 1 year of age to each of the 35 morphs. This process was repeated for the remaining paired male young-old images. Female aging images and continua were made in the same manner.

5.4 Methods

5.4.1 Participants

Heterosexual undergraduate students were recruited from the University of St. Andrews: 46 women not taking hormonal contraceptives or reporting pregnancy (age range 18-23, Mean 19.50 ± 1.36), and 52 men (age range 18-24, Mean 20.62 ± 1.60).

5.4.2 Materials

To assess preferences for facial masculinity and attractiveness, interactive face-sequence trials were used, consisting of three male and three female Caucasian faces.

Participants were also asked to complete a questionnaire, which included life-history questions relating to age of menarche/puberty, and Age of First Sex. For individuals reporting not having had sex or sexual partners: 9 males and 16 females) current age was used as Age of First Sex.

Additionally, family relationship questions included warmth toward father and mother, quality of parent's relationship with one another, and current age of parents, which used a 9-point Likert-type scale. Also relevant to this study was self-rated attractiveness, which used a 7-point Likert-type scale. Father absence was assessed with questions relating to the participant's age at the time of parents' separation.

5.4.3 Procedures

After reading and signing a consent form, participants were asked to complete an on-line questionnaire. After completion of the questionnaire, they were presented with three conditions of interactive face-sequence trials, sexual dimorphism, attractiveness, and age for both opposite-sex and same-sex. Both the conditions and the faces within each condition were randomised. For each face, the participants were asked to select the face they found most attractive by moving the cursor over the image to change through the continua of sequenced faces. By clicking on the mouse, the participant chose the face he or she found most attractive as well as moving them on to the next trial.

5.5 Results

5.5.1 Men

We hypothesised that timing of developmental markers would influence adult mate choice preferences. Correlations indicate that both Age of Puberty (Spearman $r_{49} = -.331$, $p = .020$) and Age of First Sex ($r_{51} = -.286$, $p = .042$) related to preferences for facial femininity. Thus early sexual development was associated with increased preference for feminised facial characteristics.

Age of First Sex correlated with apparent age of face preference ($r_{51} = .380$, $p = .006$), other correlations between maturation and face preferences for facial age and attractiveness were non-significant (all $p > .25$). While the attractiveness stimuli did not reveal male preferences influenced by sexual development, it is interesting to note that there was a stronger preference overall for the attractive female face (M = 6.50, SEM .043) compared to the feminine female face (M = 2.945, SEM .033; $t_{48} = 5.847$, $p < .001$), and we found a negative trend in the zero-order correlation for preferences for the two stimuli ($r_{49} = -273$, $p = .058$).

Despite findings in previous research linking age of puberty with age of first sex, we only found a positive but non-significant correlation ($r_{50} = .204$, $p = .156$), perhaps due to the small sample size.

5.5.2 Control Variables and Partial Correlations

We used partial correlations to determine whether other known effects (i.e. family background own age and attractiveness) contributed to the current finding of a relationship between male sexual maturation and preference for female facial femininity.

Spearman's Rank correlations revealed that warmth toward mother (r_{52} = .419, p = .002) and warmth toward father (r_{52} = .465, p = .001) were both positively correlated with quality of parents' relationship, and with one another (r_{52} = .587, p < .001). We therefore opted to use quality of parents' relationship as a control variable.

Our partial correlations indicated that the relationship between sexual maturation and femininity preference remained (after controlling quality of parents' relationship, current age, mother's age, and self-rated attractiveness): Age of Puberty (r_{43} = -.302, p = .044); although the relationship with Age of First Sex was marginally non-significant (r_{44} = -.285, p = .055).

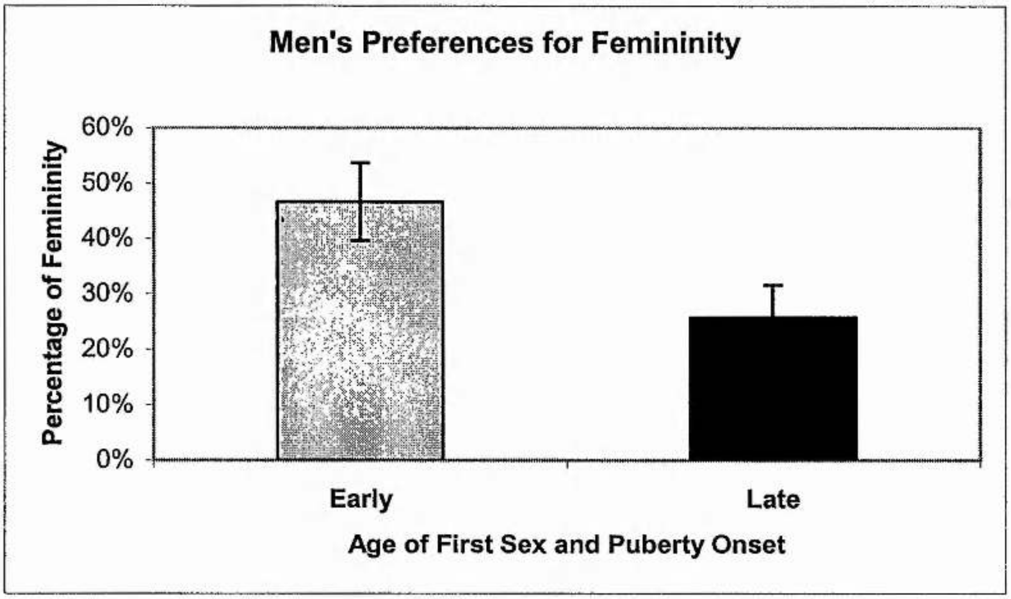
Partial correlations showed that the relation between Age of First Sex and preference for apparent face age also remained significant (r_{44} = .331, p = .024), but other correlations between maturation and face preferences for facial age and attractiveness remained non-significant (all p > .38). Additionally, none of the control variables (quality of parents' relationship, current age, mother's age, and self-rated attractiveness) related to face preferences (all p>.23). We continued to find a negative trend in the correlation between preferences for facial femininity and facial attractiveness (r_{42} = -258, p = .091).

5.5.3 ANCOVAs

To further illustrate the influence of the two developmental milestones, we split males into late and early developers. As age of first sex and age of puberty were unrelated for males, we used a k-cluster analysis (to consider both variables simultaneously) and created early and late Sexual Development groups. Early group: First Sex mean age = 16.14 ± 1.08, range 14-17; Puberty mean age = 13.05 ± 1.79, range 10-17; Late group: First Sex mean age = 19.01 ± .94, range 18 - 24; Puberty mean age = 13.25 ± 1.48, range 10 – 16). Early and Late groups differed on Age of First Sex ($t(48) = 10.25$, $p < .001$), but not on age of puberty ($t(48) = .44$, $p = .660$). The groups did not significantly differ on any other variables of concern (e.g. current age, self-rated attractiveness, and family relationship; all $p > .21$). Nine virgins, aged 18 or older, were placed in the Late development group (note: virgin's current age was used in the mean statistic for Age of First Sex).

Figure 5.3

Early and Late Sexual Development and Femininity Preference



ANCOVA was conducted on the effect of sexual developmental milestones on preferences for facial femininity. We used Sexual Development as a fixed factor, and current age, self-rated attractiveness, mother's age, and parents' relationship as covariates. The early development group ($F_{(1,42)} = 5.14$, $p = .029$, $\eta^2 = .109$) preferred significantly more feminine characteristics (M = .467) compared to the Late group (M = .257, Figure 3). Levene's test for equality of variance $F(46) = .097$, $p = .757$. There were no effects found for covariates (all $F<2.4, p>.128$).

Similar ANCOVA showed the early development group ($F_{(1,42)} = 4.32$, $p = .044$, $\eta^2 = .093$) preferred younger looking female faces compared to the Late group (Levene's test for equality of variance $F(46) = 4.198$, $p = .046$). Individuals reporting higher quality of parental relationship showed a trend to prefer younger looking female faces ($p=0.095$) but there were no effects for other covariates (all $p>.40$).

ANCOVA showed no effect of Sexual Development or covariates on preference for attractiveness (all $p>.13$).

5.5.4 Women

We performed initial Spearman's rank correlations and found that Age of First Sex significantly correlated with preference for masculine facial characteristics ($r_{39} = -.427$, $p = .007$) but not male face age ($r_{39} = -.092$, $p = .578$) and showed a trend to correlate with male facial attractiveness ($r_{39} = .292$, $p = .071$). Women with early sexual experience preferred more masculine looking males, yet showed a reduced tendency to prefer attractive faces. Interestingly, we did not find a significant correlation between Age of Menarche and any facial characteristic preferences (all r_{42} , $p > .314$). In our sample, we did not find a relationship between our two developmental markers, age of first sex and age of menarche ($r_{42} = .047, p = .768$). Additionally, face preferences for attractiveness and masculinity were not significantly correlated ($r_{42} = -.047, p = .769$); nor were attractiveness and apparent facial age preferences ($r_{42} = -.109, p = .492$); but there was a slight trend indicating that as preference for facial masculinity increased so did preferences for increased apparent facial age ($r_{42} = .259, p = .097$).

5.5.5 Control Variables and Partial Correlations

Our Spearman's rank correlations revealed, as with our male sample, both warmth toward father ($r_{44} = .297, p = .050$) and warmth toward mother ($r_{44} = .313, p = .036$) significantly correlated with parents' relationship, as well as with one another ($r_{44} = .585, p < .001$). Thus we chose quality of parents' relationship again as a control variable. Our zero-order correlations indicated a relationship between Quality of Parents' Relationship and a preference for younger looking male faces ($r_{41} = -.387, p = .012$). Our analysis also revealed that self-rated attractiveness was positively correlated with preferences for more attractive males ($r_{42} = .307, p = .048$), indicating that as self perceived attractiveness increased, so did a preference for more attractive male faces. None of our other control variables were found to significantly relate to preferences for facial characteristics (all $p > .180$).

To assess our hypothesis that timing of developmental milestones influenced women's preferences for male facial characteristics, partial correlations were used to control the possibility of other factors known to influence mate choice preferences. We found that the relationship between Age of First Sex and preferences for male facial masculinity remained after controlling for current age, self-rated attractiveness, dad's age, and quality of parents' relationship ($r_{31} = -.423, p = .014$). The other correlations between sexual developmental markers (Age of First Sex and Age of Menarche) and face preferences remained non-significant (all $p > .18$). The relationship between Age of Menarche and male face masculinity was non-significant ($r_{29} = .173, p = .35$). We did not find any other significant correlations with masculinity preferences among our control variables, (all $p > .22$).

To investigate further the relationship of Self-Rated Attractiveness and our dependent variable male facial attractiveness, we ran a partial correlation with Age of First Sex, Age of Menarche, own age, current age, dad's, and quality of parents' relationship as our control variables. The relationship between Self-Rated Attractiveness and preference for male facial attractiveness remained significant ($r_{29} = .431, p = .016$), while the relationship between Self-Rated Attractiveness and masculinity remained non-significant ($r_{29} = .185, p = .320$). Additionally the relationship between quality of parents' relationship and preference for apparent male face age remained marginally non-significant ($r_{30} = -.342, p = .055$) when controlling for Age of First Sex, Age of Menarche, current age, dad's, and Self-Rated Attractiveness.

5.5.5 ANCOVAs

As noted above Age of First Sex or Age of Menarche did not correlate. Moreover the two developmental markers differed on masculinity preference: women who experienced sex earlier preferred more masculine faces, whereas women who experienced sex later (or remained virgins) indicated no preference for facial masculinity ($r_{42} = .159, p = .314$). Additionally, our correlation analyses did not reveal any relationships between Age of Menarche and preferences for facial characteristics. With this in mind, we opted not to create two groups combining the timing of developmental markers as we did with the males, but rather to limit our analyses to Age of First Sex.

We created two groups, Early and Late sexual development based on Age of First Sex. To maintain nearly even groups, women who engaged in first sex prior to the age of 19 (n=20) were placed into the Early group, and those who were 19 or older (n=3), or were still virgins and over the age of 18 (n=16), were placed into the Late group. T-tests indicate that on Age of First Sex the groups significantly differed ($t(37) = 7.16$, $p < .001$) between the Early age of first sex ($M = 17.35$) and the Late age of first sex group ($M= 19.53$). Age of Menarche $M = 12.90$ $M = 12.92$ did not differ between groups ($t(37) = -.22$, $p =.83$). There was a trend for the early sexual maturation group to rate themselves more attractive ($t(37) = 1.69$, $p = .099$) and have younger fathers ($t(37) = 1.89$, $p = .068$) than the Late group. No other factors were found to be significantly different between the two groups.

We ran an ANCOVA with Age of First Sex as a fixed factor (Early vs. Late) and Age of Menarche, current age, self-rated attractiveness, quality of parents' relationship, and father's age as covariates (see Figure 5.4). Analyses reveal that the Early First sex group preferred more masculine faces ($M = .219$) than the Late First sex age group ($M = -.117$) (Figure 2), ($F(1,27) = 6.36$, $p = .019$, $\eta^2 =.188$). Other covariates did not influence masculinity preference (all $F<1.3$, $p >.27$).

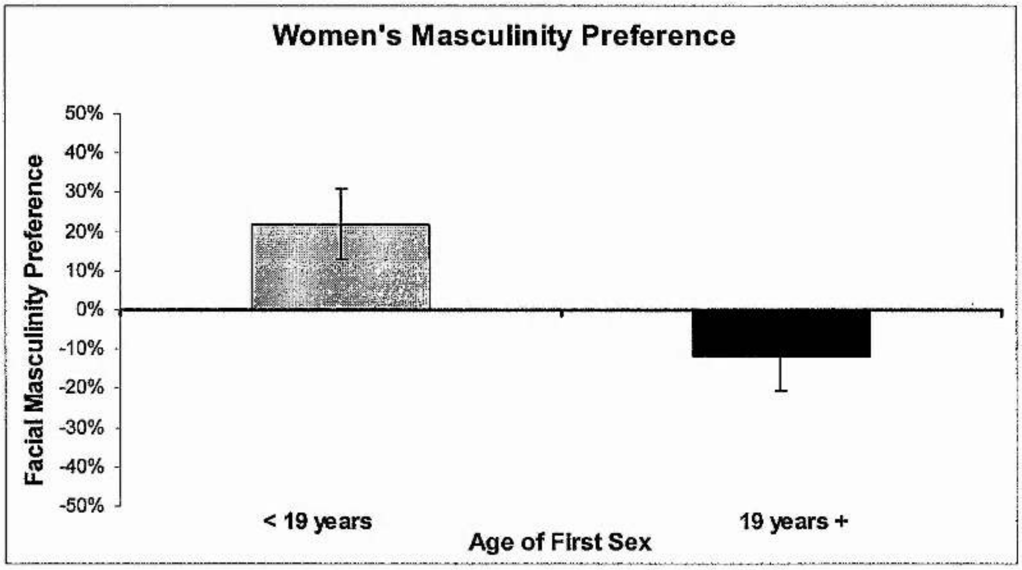


Figure 5.4

Women's preferences for male masculinity

Similar ANCOVA analyses were run for both of the other dependent variables: male facial attractiveness and apparent age of male faces. The results pointed toward the trend seen in our correlations, with women who experienced sex earlier indicating a diminished preference for attractive male faces ($F(1,26) = 2.8$, $p = .10$); however, no group differences were found regarding preferences for apparent age of the male face ($F(1,26) = 1.51$, $p = .23$). Quality of Parents' Relationship, as found previously in our correlations, related to decreased preference in apparent age of male faces ($F(1,26) = 7.35$, $p = .012$, $\eta^2 = .220$). Additionally women with a high quality of parents' relationship also showed an increased preference for male facial attractiveness ($F(1,26) = 7.28$, $p = .012$, $\eta^2 = .220$).

5.6 Discussion

5.6.1 Stimuli

For this experiment we used a new set a stimuli in an attempt to differentiate between sexual dimorphism and another factor we labelled 'attractiveness', and made explicit predictions concerning preferences. Our calibration study indicated that women judged the male attractive faces to vary on attractiveness but not masculinity, and the male masculine faces were judged to vary on masculinity but not on attractiveness. This suggests, as Langlois (2000) implied, that there is a general agreement about attractiveness. Moreover, there is also an agreement as to what constitutes a masculine face, and that these two dimensions for the male face are not necessarily the same. But what about the female face? Our calibration data were less substantive, and male ratings for the high femininity and high attractiveness dimensions were not differentiated. This might indicate that the epigamic traits and the 'attractiveness' traits in the female face are one in the same; however, the data from our facial preference experiment suggest otherwise. The timing of sexual development mediated preferences for more feminine female faces, but it did not affect preferences for our attractiveness face. Perhaps even stronger evidence that these two dimensions differ is the fact that we found a trend for a negative correlation ($p = .058$) between the preferences for the feminine and attractiveness images.

5.6.2 Facial Preferences and Timing of Sexual Maturation

As predicted, the timing of sexual developmental markers was found to influence both men and women's mate preferences, and earlier maturers preferred increased sexual dimorphism in opposite sex faces. Men who had experienced earlier puberty and earlier initial sexual intercourse were found to prefer more feminised female faces compared to those males who matured later. Women who experienced earlier first sex preferred more masculine male faces while those who experienced initial sex later, or remained virgins, preferred less masculinised faces. We did not find as predicted that age of menarche would mediate facial preferences. Other factors known to influence preferences for mate facial characteristics, self-rated attractiveness, parental relationships, age of opposite sex parent, or own age, could not explain the developmental differences in preferences for facial sexual dimorphism.

In addition to our general prediction that timing of puberty and age of first sex would mediate facial preferences, we considered three specific explanations regarding how mating strategies may have been influenced by sexual development. Our data suggests that we can dismiss one, but not two of our alternative explanations.

The explanation that early maturing adolescents would view themselves as having higher social status than their peers was not supported by the data. High status individuals should show increased preference for high quality individuals, and therefore should prefer both sexual dimorphism and attractiveness. We found support for the former but not the later.

Our second explanation had mixed results. We suggested that if early developers are low quality individuals, then as per an assortative mating strategy these individuals should seek low-quality mates. Based on this inference, our data suggests that early maturers are high- and not low-quality individuals. We did not ask participants to choose the most attractive face based on either long- or short-term relationships, so we cannot exclude the possibility that low-condition women were selecting for short- and not long-term mates. It has been suggested that low-condition women will seek out high-quality males for a short-term opportunistic mating in order to obtain better genes for immunocompetence and/or follow a 'sexy-sons' type of strategy. To use this explanation to interpret our data, we do need to make unsubstantiated assumptions: that the early-maturing women were employing a short-term mating strategy; and that a condition dependent preference is exclusive to sexually-dimorphic traits. Our findings suggest that early sexually maturing men select high-quality females because they themselves are high-quality. Thus if anything the results indicate early sexual maturation of both sexes is associated with 'high' quality. We note that it is best to consider early and late maturers as having discrete characteristics of mate quality rather than categorising them as high and low levels of condition. We therefore suggest individuals varying in rates of maturation emphasise different qualities and seek self-similar qualities in others.

The observation that earlier sexual development mediated preferences for facial sexual dimorphism and not for facial attractiveness characteristics supports our second explanation that learning plays a role in adult mate choice. We reasoned early maturing adolescents were more likely to receive positive feedback from early maturing opposite sex adolescents in their early forays into sexual behaviour. Adolescents who matured later would more likely be spurned by early maturing opposite-sex adolescents and could possibly associate negative feedback with these interactions. The signals of early maturation would be associated with exaggerated facial sexual dimorphic characteristics, and these characteristics would be associated with either positive or negative experiences during adolescence. These preferences for epigamic traits would continue on into adulthood. The facial characteristics we have labelled as attractive would not be associated with pubertal timing, and therefore we would not expect to see a strong preference for these characteristics mediated by timing.

5.6.3 Hormones

We have, up to this point, not discussed the possible role of hormones in our findings. It is very possible that the early and late maturation groups differ in gonadal hormone levels and these differences may be mediating our preference findings. The timing of puberty and sexual behaviour and adult hormones is something that needs to be studied. However, the purpose of this study was to examine whether or not timing of sexual maturation influenced adult mating strategies and preferences, and not the biological mechanism by which these strategies are carried out.

5.6.4 Apparent Age

We examined preferences for apparent age and found that males who experienced sex later (or remained a virgin) preferred older looking females compared to those males who had experienced sex at an earlier age. This might reflect a preference for reduced femininity, as older looking faces tend to look more masculine. We suggest our data do not support this conclusion because there was no significant correlation between preferences for apparent age of face and facial femininity.

Women's sexual development did not influence their preferences for apparent age in male faces. Since masculine faces look older than feminised counterparts (Cunningham et al. 1990; Perrett et al. 1998), it is interesting to note that early maturing women like masculine males but not older-looking males. Hence masculinity preference does not reflect age preference.

Preference for younger looking male faces was in evidence for women whose parents had a good quality relationship, but parental relationship was not important for women's preferences for either masculinity or attractiveness. We do not have a theoretical basis to explain these age preferences for either the men or for the women.

5.6.5 Self-Rated Attractiveness and Condition Dependence

Among women, we found that as ratings of self-perceived-attractiveness increased, so too did preferences for our 'attractive' male faces but not preferences for the masculine male faces. Previous work examining condition dependence found that women rated as more attractive preferred more masculine looking males (Penton-Voak et al. 2003). We attribute these contrary findings to the differences between stimuli. Penton-Voak and his colleagues varied their images along a continuum of masculinity in face shape. Our stimuli varied in three ways; in colour and texture as well as shape.

We also went a step further to refine facial dimensions by separating epigamic traits from other facial characteristics signalling mate quality. What we have found is an answer to the question if there is something other than facial masculinity which contributes to mate choice preferences. Questions remain, however, as to what information our male masculine and attractiveness faces convey to women, and why women who rate themselves as attractive prefer one and not the other.

The results may be a manifestation of assortative mating or matching on self-similar qualities (Berscheid et al. 1971; Feingold 1988; Feingold 1990). That is early maturing individuals prefer early maturing (sexually dimorphic) partners while attractive individuals prefer attractive partners. Prior research has not separated maturation and attractiveness in stimuli or observers.

5.6.6 Closing Considerations

Accelerated sexual maturation is associated with preferences for exaggerated sexually dimorphic features in opposite-sex faces in both men and women. We suggest these preferences are due to learning influences during adolescence. It is possible that early maturers are higher-quality, however this conclusion is speculative and requires further investigation. A more parsimonious explanation is that early maturing men and women are seeking out similar individuals in much the same way as more attractive individuals seek out partners with similar attractiveness. Signs of early maturation are most likely to be enhanced sexually-dimorphic characteristics in the face and body shape and seeking out self-similar opposite sex partners would fit-in with the 'matching-hypothesis' (Berscheid et al. 1971; Feingold 1988). We asked individuals to select those faces they found most attractive, without any type of interpersonal or social feedback, this method is perhaps akin to how we might decide who to approach in social situation. Our research suggests that people initially seek out individuals who are more like themselves on the dimension of facial characteristics. Feingold (1988) found that men and women do initially seek out partners who are self-similarly attractive, and there is a mild correlation in terms of attractiveness between partners in long-term relationships – however other components such as socio-economic status, within-group desirability, and interpersonal similarity become much more important. Initial attraction is only a small part of the picture, and it is not surprising that we use facial appearance to sort out initial likes and dislikes.

6 Women's timing of initial sexual behaviour relates to preferences for male facial characteristics: further evidence

6.1 Introduction

In the previous chapter, we examined the relationship between Age of First Sex and preferences for epigamic traits. We found that women who had experienced earlier sex (18 years or younger) indicated a stronger preference for masculine facial characteristics in male faces as compared to those women who had experienced sex later. We suggested that earlier sexual developers preferred to associate with individuals who were early developers themselves, and this was reflected in their adult preferences for more sexually dimorphic male facial characteristics. We framed our findings within the matching-hypothesis (Feingold 1988; Murstein & Christy 1976; Walster et al. 1966), wherein individuals are initially attracted to people who are physically appealing, however, through experience (perhaps through the trial and errors of adolescence) individuals learn to have a more realistic view of what is attainable based on their own allure. Individuals seeking a romantic relationship will more often than not develop a relationship with a partner whose attractiveness more closely matches their own (Feingold 1988).

Initial attraction is likely to be based entirely on physical appearance (Feingold 1988), and yet we find that individuals differ in their perceptions of attractiveness. These individual differences may be influenced by a variety of factors including sexual maturation and age of first sex, self-perceived attractiveness, age, and environmental factors such as father absence, number of siblings, or social-economic status. But individuals also learn through experience to discriminate those who are more likely to reject their romantic interests from those who are more likely to respond positively toward them. Learning then, becomes an intricate part of individual mating strategy and mate choice along with other individual differences.

There is perhaps another explanation to our initial findings that sexual development relates to face preferences, and one that needs to be addressed. We did not examine the possible influence of relationship context on masculinity preferences, and can therefore not exclude the possibility that women who preferred more masculinised faces were in actuality selecting for short- and not long-term relationships. It has been suggested that low-conditioned women (i.e. less attractive and/or more masculine women) when selecting for short-term mating opportunities will seek out men with strong signals for 'good genes', and seek out lower-quality mates for long-term investment (Gangestad & Simpson 2000). This would suggest that they were not matching on self-similar characteristics, but employing a strategy to secure good genes while not expecting any future paternal investment. It has been argued that cuckoldry is a useful strategy for low-quality females to obtain beneficial genes from an 'unretainable' mate whilst securing investment for her and her offspring from a male more likely to invest (Buss & Schmitt 1993; Gangestad & Simpson 2000; Gangestad & Thornhill 1997; Little et al. 2001b; Penton-Voak et al. 2003). Low-quality women, it is then argued, should prefer more masculinised male faces for short-term relationships and less masculinised faces for long-term relationships, while high-quality women should prefer masculinised male faces independent of relationship context.

Early sexual promiscuity in women has often been associated with negative environmental situations (Belsky et al. 1991); thus it might be assumed that girls who begin sexual activity earlier are low-quality females compared to girls who wait longer before engaging in sexual relationships. Further, it could be argued, that girls who begin their sexual activity earlier are pursuing a strategy associated with low-quality females. That is, seeking high-quality (more masculine) males for short-term mating opportunities and lower-quality (less masculine) males for a stable, long-term relationship. While this argument is not without merit, sexual activity during secondary school is not unusual and to assume that only low-quality females are taking part in sexual activities could be viewed as a simplistic view of female behaviour. Indeed, the many factors that influence sexual activity in adolescence are widely varied and complex, and they are not necessarily always negative (Santelli et al. 2000; Spencer et al. 2002; Weisfeld & Woodward 2004).

In the following study we look at whether or not relationship context mediates preferences for facial masculinity. If women who engage in earlier sex are indeed lower quality women then we should find that they prefer more masculine male faces for short-term relationships and less masculine male faces for long-term relationships. If however women who engage in sex earlier are not low quality, then we should find that relationship context does not alter their masculinity preference.

6.2 Methods

6.2.1 Participants

Heterosexual female undergraduate students (94 women, age range 17-24, mean 20.24, ± 1.64, not taking hormonal contraceptives) were recruited from the University of St Andrews.

6.2.2 Materials

To assess masculinity preference, we used trials consisting of 6 opposite sex and 6 pairs of same-sex images (4 Caucasian, 1 African-Caribbean, and 1 East-Asian face(s). The same images had been used in previous studies (Penton-Voak & Perrett 2000; Penton-Voak et al. 1999; Perrett et al. 1998)). Each face image was warped into a 50% feminised 50% masculinised face shape using prototypical female and male faces (see Tiddeman et al. 2001 for full review of technique). This allowed us to create paired images of feminised and masculinised versions of the same face.

Age stimuli were created to manipulate apparent age of both male and female faces. Younger and older appearing male and female prototypes were composite images made from 15 male or female faces 15-18 years-of-age (younger) and 15 male or female faces 25-29 years-of-age (older). All faces used in the transform composites were Caucasian with no facial hair. Individual faces were created by randomly selecting 10 images (10 female/10 male) and making a composite, and all composite images were made symmetrical. These 'individual' base face images were transformed in shape, colour, and texture by adding and subtracting 30% (theoretically 3 years) of the difference between the 2 age-prototypes.

6.2.3 Procedures

Participants were presented with 6 pairs of opposite-sex faces, with one face 50% masculinised and the other 50% feminised (in face shape), apparent age (younger or older) face pairs, and fillers. The faces pairs were presented in blocks and the subject was asked to choose the preferred face for either a long- or short-term relationship and indicate a strength of choice from 4 categories (a) guess (i.e. completely unsure) , (b) slightly prefer, (c) prefer, (d) or strongly prefer. A long-term relationship was defined as a committed relationship possibly leading to co-habitation or marriage. A short-term relationship was described as one that is short in duration, such as a one-night stand or a brief affair. The relationship context was run in two blocks for opposite-sex faces. This created an 8 point preference range for masculine face shape. The blocks were counter-balance and the order of the pairs and side presentation was randomised. Subjects were presented only with opposite-sex faces. Participants also completed a questionnaire concerning personal life-histories: including age of menarche, age of initial sexual intercourse, age of each parent, relationship with mother, relationship with father, relationship between parents (later 3 using a 9-point Likert-type scale), self-rated-attractiveness, and sexual orientation (both using a 7-point Likert-type scale).

6.3 Results

There were 34 women who reported being virgins, and 39 women who did not report virginity status. For our analyses, we needed to include the Age of First Sex; and for virgins who were 19 or older we coded Age of First Sex as current age, while virgins who were 18 or younger were removed from our analyses. Only virgins who were 19 or older (N= 25) were included in any analyses using Age of First Sex as an independent variable.

We preformed initial Spearman's rank correlations and found that Age of First Sex did not significantly correlate with preference for either short-term ($r_{45} = -.195$, $p = .119$) or long-term masculinity facial characteristics ($r_{45} = -.046$, $p = .765$). We did find a trend for women who experienced early sex to prefer older-looking male faces for short-term ($r_{45} = .256$, $p = .090$) and long-term relationships ($r_{45} = .264$, $p = .079$). Consistent with previous research (Little et al. 2001b), we also found that as women's self-perceptions of attractiveness increases, so does their preference for more masculinised faces for long-term ($r_{91} = .353$, $p = .001$) but not short-term relationships ($r_{91} = .118$, $p = .265$). We did not find a significant correlation between

Age of First Sex and Age of Menarche, but there was a weak positive correlation (r_{45} = .240, p = .113). Further correlations did not find any relationship between Age of Menarche and preference for male facial masculinity (all p> .247)

In keeping with previous research, we ran partial correlations and controlled for factors that possibly influence preference for facial masculinity (see previous chapter). These include: age, self-rated-attractiveness, father's age, warmth toward mother, and warmth toward father. In the previous study we found that warmth toward mother and warmth toward father both strongly correlated with quality of parents' relationship. However, in this sample the factor was only correlated with warmth toward father (r_{73} = .564, p < .001) and not with warmth toward mother (r_{74} = .216, p = .065), therefore we opted to use the two 'warmth' factors and not the quality of parent's relationship in our partial correlations.

Our partial correlations revealed that age of first sex was significantly correlated for both short-term (r_{35} = -.388, p = .018) and long-term relationships (r_{35} = - .348, p = .035) and preferences for facial masculinity. The earlier the age of first sex, the stronger the preference for more masculine male faces, independent of relationship term. We also looked at preferences for apparent age and found that earlier sexual activity did not appear to influence preference for apparent age for either short-term (r_{35} = .073, p = .667) or long-term relationships (r_{35} = .05, p = .658). Age of menarche was also not significantly correlated with masculinity preferences for either short-term (r_{47} = -.165, p = .258) or long-term relationships (r_{47} = .043, p = .758). Nor did age of menarche significantly correlate with age preferences for short-term (r_{47} = .0529, p = .718) or long-term relationships (r_{30} = .181, p = .212).

We then performed a partial correlation to control for age of menarche in addition to our other controls. We found that the relationship between age of first sex and masculinity preference remained for both short-term (r_{34} = -.359, p = .032) and long-term relationships (r_{34} = -.384, p = .021).

To further explore the relationship of self-rated attractiveness on preferences for facial masculinity, we ran partial correlations controlling for age of first sex, age of menarche, age, dad's age, warmth toward mother, and warmth toward father. We found the relationship seen in our zero-order correlations continued to hold and as self-rated attractiveness increased, so did preference for more masculine male faces for long-term (r_{34} = .479, p = .003) but not for short-term relationships (r_{34} = .248, p = .144).

6.4 Discussion

We found that women's preferences for male facial masculinity are influenced by age of first sex but this effect does not depend on relationship context. Women who engaged in sex at an earlier age showed a stronger preference for more masculine male faces for both long- and short-term relationships. These preferences were found after controlling for other factors: age, father's age, warmth toward mother, warmth toward father, self-rated attractiveness, and age of menarche. In keeping with previous research (Little et al. 2001b), we found that self-rated attractiveness also influences masculinity preference, but is found only when considering a long-term relationship.

It is curious that age of first sex and self-rated attractiveness affect preferences for masculinity differently. Women who experienced sex earlier prefer more masculinised male faces, independent of relationship context, and women who rate themselves as more attractive prefer more masculinised male faces, but only when considering a long-term relationship. This presents us with two perplexing issues: firstly, contrary to what we found in this experiment, our previous experiment indicated that women's self-rated attractiveness did not affect preferences for male facial masculinity. Secondly, given the results of this current experiment, why would relationship term affect one factor, self-rated attractiveness, and not the other, age of first sex?

The first issue concerns the discrepant findings between our two studies; but given that the stimuli in the two experiments differed, it is not particularly disconcerting. In the previous experiment the masculinity stimuli we used controlled for attractiveness and in the current experiment the stimuli were made using the more traditional face-shape manipulation between an average female and an average male face shape. It is possible that the masculinity images in this experiment are 'contaminated' by elements of attractiveness, which could explain why the women who rate themselves as more attractive preferred the more masculinised faces in this but not in the previous study. As we refined our images to isolate masculinity and attractiveness, differences in preferences emerged that had been previously obscured. When given the opportunity to judge both 'masculinity' and 'attractiveness', those women who engaged in earlier sex prefer the more masculine faces while women who rate themselves as more attractive indicated preferences toward more attractive male faces. The findings may not be contrary at all, but simply they were winnowed to a finer grain in the previous study.

The second issue of why would the effects of self-rated attractiveness on masculinity preferences be exclusive to long-term relationships is a more interesting problem. As noted previously, Little and his colleagues (2001b) found that self-rated attractiveness only affected preferences for long-term relationships. Similarly, we found that ratings for opposite-sex pheromones were concordant with preferences for opposite sex epigamic facial traits but only for long- and not short-term relationship (Cornwell et al. 2004). Presumably when choosing for a long-term relationship, women are looking for a partner who is willing to invest in her and her offspring. She should then take greater care when considering a long-term partner as opposed to a short-term partner, and therefore it is more likely to see preferences surface when making judgments within the context of a long-term relationship. But this does not yet fully explain our data since Age of First Sex affected masculinity preference for both long- and short-term relationships. While more work is needed to understand our anomaly, our working hypothesis is that timing of sexual development does not relate to a quality factor. For example, individuals who developed slightly faster than their peers may not always possess 'attractive' qualities. In other words, fast developers are not necessarily better or worse than slow developers. Seeking out like-developing peers does not necessitate one to evaluate his or her own qualities before selecting a potential partner for either a short- or long-term relationship. This, however, is not the case for self-perceived attractiveness. 'Attractiveness' is a quality sought out by others, and the fortunate individuals who possess highly attractive features can afford to be more choosey. We would expect this choosiness to become more apparent when considering a partner for a long-term compared to a short-term relationship.

Our data in this experiment has strengthened our hypothesis that individuals learn who finds them attractive, and use this knowledge to match on self-similar attributes. We are not suggesting that selecting a self-similar mate via a learning process is non-Darwinian. To the contrary, we are suggesting that learning to find a self-similar mate is the mechanism to finding a suitable mate for successful reproduction. Learning as a mechanism for mate selection is found in a other species (Magurran & Ramnarine 2004; Slagsvold et al. 2002) and evolved for good reasons. The question for humans then is not so much is learning an aspect of mate choice, but how do we learn, when do we learn, and how is it applied.

Humans have a prolonged childhood, and a stable environment throughout this period is important for individual well-being. Poor-parenting, an absentee father, and parental conflicts can all have negative effects on the developmental process. Mating does not guarantee reproductive success, having viable and healthy offspring is certainly more important. In bi-parental species, such as humans, parents who can cooperate and together funnel their energy toward the well-being of their offspring are more likely to enjoy reproductive success then those parents who do not. Finding a partner who is more willing to remain committed in the relationship and to raising offspring is in itself a good mating strategy. Learning who rebuffs us and who doesn't, who we can get along with and who we can't, is critical to successful reproductive fitness.

7 Preferences for attractiveness in same- and opposite sex faces in peri-pubertal adolescents

7.1 Introduction

Male and female prototypical faces differ (Brown & Perrett 1993), thus it is no surprise that men and women's preferences for opposite sex facial characteristics also differ. Men on the whole prefer feminine looking female faces (Jones 1995; Jones 1996; Perrett et al. 1998; Perrett et al. 1994), while women slide between liking slightly masculine (Grammer & Thornhill 1994; Penton-Voak & Perrett 2001; Rhodes et al. 2000; Scheib et al. 1999) and slightly feminised male faces (Penton-Voak et al. 2003; Penton-Voak et al. 1999; Perrett et al. 1998; Swaddle & Reierson 2002). But when do these preferences begin to emerge? One might suspect our preferences for sexual dimorphic facial features parallel our sexual awakening as we commence our journey along the knotty passage of adolescence. While there are an abundance of studies evaluating adolescent sexuality, from condom use to abstinence, we know relatively little about what teens find attractive in the opposite sex.

7.1.1 What do children like?

Our preferences for attractive faces appear to begin at infancy (Langlois et al. 1991; Langlois et al. 1987; Ramsey et al. 2004; Rubenstein et al. 1999; Samuels et al. 1994; Slater et al. 2000; Slater et al. 1998), continue through childhood (Kissler & Bäuml 2000) and into adulthood (Langlois et al. 2000). Adult judgments for facial attractiveness are found to be universal and not culturally manufactured (Bernstein et al. 1982; Cunningham et al. 1995; Perrett et al. 1994), and preferences for attractive faces appear to remain consistent across different age groups, from infancy through adulthood (Kissler & Bäuml 2000; Ramsey et al. 2004; Rubenstein et al. 1999; Slater et al. 2000; Slater et al. 1998). It then stands to reason that children's judgments and preferences for attractive faces are also resistant to cultural or commercial influences – indeed, it is more likely that corporations who market to teens exploit teen preferences rather than influence them.

The term 'attractiveness' is a subjective, even tautological term and does not explicitly describe the type of facial characteristics that go into making one face more attractive than another. Some researchers have attempted to identify possible features contributing to facial attractiveness, and these include symmetry (Jones et al. 2001; Møller & Thornhill 1998; Rhodes et al. 2002; Rhodes et al. 1998), averageness (Rhodes et al. 1999; Rhodes et al. 2001), sexual dimorphism (Little et al. 2001a; Penton-Voak et al. 2001; Penton-Voak & Perrett 2001; Perrett et al. 1994), skin condition (Jones et al. 2004) and colour (Fink et al. 2001; Frost 1994; Law Smith et al. in prep-a).

There is evidence that infants and children prefer and judge facial attractiveness in a like manner with adults. Infants will look longer at those faces adults find more attractive, which is thought to indicate a preference, compared to looking times at faces adults find less attractive (Van Duuren et al. 2003). Infants and adults, however, do not always indicate similar liking. For example Rhodes and her colleagues noted that infants looked longer at more asymmetric and less than average looking faces (Rhodes et al. 2002), which could indicate a preference bias different than those of adults. Or, as the authors suggested, the findings indicate infants' preference for novelty, but this conflicts with evidence that infants prefer familiar faces over novel faces (Walton & Bower 1993). Rubenstein and his colleagues (1999) found that both infants and adults looked longer at averaged faces (computer generated composite average) over individual faces, and in another study, infants were found to prefer attractiveness over youthfulness (Kramer et al. 1995). When considering infant preferences, it must be kept in mind that there remains some controversy over the meaning of looking times as they may or may not indicate preferences (see Bogartz et al. 2000).

In examining children's preferences for attractive faces, they are consistent with those of adults. Judgments for attractiveness were similar between girls, aged 9 and 12 years, and their mothers; however, the strength of the preferences were stronger among the adults compared to daughters (Kissler & Bäuml 2000). Children also evaluate attractive peers more positively, which is consistent with adults' positive evaluations of attractive peers (Langlois et al. 2000; van Leeuwen & Macrae 2004). Children prefer attractive peers as friends, rate them as more socially competent, and, in general, attractive children are more popular (Adams & Roopnarine 1994; Byrnes 1987). The effect of attractiveness as a predictor of peer acceptance is more relevant for girls than boys (Adams & Roopnarine 1994).

Researchers in the area of adult facial attractiveness have examined the influence of sexual dimorphic characteristics on preference judgments. Feminine characteristics in female faces are generally preferred (Jones 1995; Jones 1996; Perrett et al. 1998), while preferences for facial masculinity in males are not universal. Women have shown both a preference for masculinity in male faces (Grammer & Thornhill 1994; Penton-Voak & Perrett 2001; Scheib et al. 1999), as well as preferences for more feminised male faces (Penton-Voak et al. 2003; Penton-Voak et al. 1999; Perrett et al. 1998; Swaddle & Reierson 2002). These apparent inconsistencies have been attributed to individual differences such as menstrual cycle, use of hormonal contraceptives, parent age, parent-offspring relationship, or relationship status (Boothroyd 2004b; Little et al. 2001a; Little et al. 2002; Penton-Voak et al. 2003; Penton-Voak & Perrett 2000; Penton-Voak & Perrett 2001; Penton-Voak et al. 1999; Perrett et al. 2002; Rhodes et al. 2000). Research into whether or not infants or children show preferences for sexually dimorphic features has not, to our knowledge, been conducted. There has been limited research into infant preferences for either male or female faces, and infants were found to prefer female faces when the primary care-giver was female, but male faces when primary care-giver was male (Quinn et al. 2002).

Generally, it is easy for us to discern sex when looking at children, adolescents, and adults' faces (hair and clothing masked) (Cheng et al. 2001; Wild et al. 2000). Even children as young as 8-months old can discriminate between adult males and females (Fagot & Leinbach 1993; Yamaguchi 2000). It has even been suggested that adults can differentiate sex of young infants (Sergienko & Nikkina 2004). Sex discrimination, it has been posited, is possible because the internal structure of the face provides reliable cues to sex (Brown & Perrett 1993; Bruce et al. 1993; Cheng et al. 2001; Wild et al. 2000). In other words, sex-prototypical facial features exist from birth, and either through exposure or innate mechanisms, we assess these cues to categorize individuals into two discrete categories, male and female. But the internal structures of the face we use consist of a number of features such as skin texture, colour, face shape, feature position, and feature size. Each of these can vary along a continuum of more male prototypical (masculine) to female prototypical (feminine). Maleness and femaleness of facial characteristics are less exaggerated in children than they are in adults (Enlow 1990; Wild et al. 2000), but still readily detectable in children as young as 7 years of age (Wild et al. 2000) and possibly even neonates (Sergienko & Nikkina 2004). Masculine-feminine structural facial features of young children and infants are similar, but not precisely so, to those of adults. Adult faces are easier to sex differentiate than children's faces, and Cheng et al. (2001) suggest that we use age-appropriate facial features to discern sex rather than use adult features and apply them to children. The structural differences among children might be due to hormonal influences that direct the distribution of tissue and fat deposits, whereas adult (post-puberty) sex-specific features are a result of hormonal influences on both tissue and skeletal structure. As puberty encroaches, changes in skeletal structure will begin to take on more sex-specific adult-like shape, allowing for new information used to discriminate sex.

Given that we categorize sex of others based on facial characteristics, do we use that knowledge to categorize attributions of personality? Researchers have suggested that we associate sex-stereotypical behaviours and personality with sex-typical facial characteristics. In adults, sexually dimorphic facial characteristics elicit negative attributions such as coldness and dishonesty (Perrett et al. 1998). Baby-faced individuals are more often attributed with childlike traits and are seen as less mature, more warm, more submissive, less physically strong, and more naive (Berry & Zebrowitz McArthur 1986; Zebrowitz & Montepare 1992). And, while baby-faced adults are also seen as more honest, baby-faced children are perceived as being more deceptive (Masip et al. 2003; Masip et al. 2004). The facial characteristics associated with baby-faceness include shorter chin, large forehead, and large eyes, with the placement of the facial features themselves lower on the face (Lorenz 1943). These same baby-face characteristics are also considered to be more female-prototypical

(Jones 1996). It is then reasonable to argue that many of the behavioural attributions associated with baby-faced individuals are likely to be attributed to feminine looking faces (Jones 1995). Logically, this implies that mature looking faces relate to masculine facial features. Indeed, as previously noted, masculine facial shape characteristics are associated with increased age and negative personality traits such as dishonesty or coldness (Perrett et al. 1998) while feminine, 'baby-faced' individuals are seen as honest and warm. However, as we pointed out, baby-faced children are perceived as more dishonest, which is opposite to the attribution made on adult baby-faced individuals (Masip et al. 2004) suggesting that depending on age of the face, our attributions based on facial shape may change.

If adults are making personality attributions based on facial characteristics, are children doing likewise, and do they make these attributions about other children? The attributions made by children based on sex of both peers and adults have been well documented (Adams & Roopnarine 1994; Alexander & Hines 1994; Bukowski et al. 2000; Dion 1973; Dion & Berscheid 1974; Giles & Heyman 2005; Langlois & Styczynski 1979; McDermid et al. 1998; Montepare & Zebrowitz McArthur 1989; Morrongiello & Dawber 1998; Morrongiello & Dawber 2004; Morrongiello et al. 2000; Ollendick et al. 1985; Ramsey & Langlois 2002), and children also attribute sex-stereotypical behaviour based on sex of the individual. This would then suggest that sexual facial characteristics of masculinity and femininity would influence children's attributions toward other children.

7.1.2 Does masculinity in children signal bullying behaviour?

As we noted, adults perceive more masculine looking males as colder and more dominant than less masculine looking males. Many have argued that this stereotype is not without merit. Testosterone levels are positively linked with more aggressive behaviours and dominance in both males (for review see Mazur & Booth 1998b) and females (Grant & France 2001) (this view is not without controversy, see Archer et al. 2005; Book et al. 2001; Van Goozen et al. 1998), and they also regulate the skeletal growth of the face, thus testosterone levels are thought responsible for the masculine face shape (Enlow 1990). Oestrogens, on the other hand, are thought to retard skeletal growth as well as regulate tissue development, giving what we see as a proto-typical female face shape (Jones 1996). While no one would advocate making absolute judgments of personality based on face shape alone, the fact is making snap judgements in certain situations could be beneficial (Macrae & Bodenhausen 2000; Macrae et al. 1997).

In children, researchers have found that facial masculinity is associated with dominance (Keating & Bai 1986) and anti-social behaviours (Udry 1990). The link between personality, aggressive or anti-social behaviours are, like the adult studies, controversial. Some research indicates that testosterone levels are positively associated with social dominance but not physical aggression (Rowe et al. 2004; Schaal et al. 1996), while others have found that androgen levels relate to physical aggression and anti-social behaviours (Maras et al. 2003). These somewhat disparate findings likely indicate strong and complex biological and environmental interactions.

Independent of the complexities of nature and nurture, we humans make attributions based on very limited information – that is, on sexually dimorphic facial characteristics. It appears that infants begin to categorize people into 'male' and 'female' (this is not to suggest that infants actually label sex categories, only that they somehow differentiate between male and female). From this humble beginning, throughout our development we drop lots of different types of items into one of these two categories – and how we categorise them are likely based sex-differentiated preferences (Alexander 2003; Ruble & Martin 1998) and behaviours (Alexander & Hines 1994). Very early on, children hold beliefs attributing boys with more aggressive behaviours (Giles & Heyman 2005) and that boys are less likely to experience injury (Morrongiello et al. 2000); this is despite the evidence that boys take more risks than girls (Ginsberg & Miller 1982; Morrongiello & Dawber 1998; Morrongiello & Dawber 2004; Rosen & Peterson 1990), and are more likely to actually receive injuries (Morrongiello et al. 2000). Perhaps our categories of 'maleness' and 'femaleness' can be summarised in the familiar nursery rhyme:

> *What are little boys made of?*
> *Frogs and snails,*
> *And puppy-dogs' tails;*
> *That's what little boys are made of.*
>
> *What are little girls made of?*
> *Sugar and spice,*
> *and all that's nice;*
> *That's what little girls are made of.*

Our need to categorise combined with our ability to discriminate sex based on facial characteristics can lead us, rightly or wrongly, to make attributions of behaviour and personality based on sexually dimorphic facial characteristics.

Given that adults make specific attributions, such as coldness and dominance, based on sexually dimorphic facial features and the link between facial growth and androgens as well as children's behaviour and androgens, it is reasonable to predict that children also make sex-typical attributions based on the degree of facial masculinity. Behaviours such as dominance, aggressiveness, and bullying are likely to be associated with more masculine looking facial features in other children.

7.1.3 Attractiveness

Adult preferences toward apposite sexually dimorphic facial characteristics fit nicely into evolutionary theory. Preferences for female and male typical characteristics have been selected for because the characteristics themselves represent healthy, genetically-fit, fecund individuals. Strategies for finding the best mate will need to take into consideration the viability of a mate for potential reproduction. Young children should be concerned with care and provisions, and it is not unreasonable to assert that, as women are usually the primary care-provider, they could show a preference for more feminine facial characteristics in both male and female faces (Quinn et al. 2002). However, as children begin to make their way through puberty and sex-hormones start circulating in abundance, preferences for opposite-sex faces might take on more adult-like preferences. The change from childhood to adulthood is painfully slow (for both the individual and the parents), and it would not be expected that adult-like preferences would suddenly arise overnight. While it is not in the scope of this paper to review the literature on the evolutionary implications of adolescence, it can be said that evolution would not waste time on such a process if it were not important to human functioning. An evolutionary perspective of development, and specifically adolescence, is just beginning to emerge. It has been suggested that adolescence is a time to learn expected sex roles, find a place within the social hierarchy, and discover the opposite sex (Hawley 1999; Hawley 2003a; Hawley 2003b; Pellegrini 2002; Pellegrini 2003; Pellegrini & Long 2003; Weisfeld & Janisse 2005).

We conducted three studies to investigate the attributions and preferences of peri-pubertal children based on facial masculinity. In Study 1, we used an interactive task to assess children's (aged 11-12) attractiveness judgements of both same and opposite sex peer relevant faces manipulated along a masculinity continuum. In Study 2 using a forced choice method with a different cohort of children, we examined attributions associated with bullying and facial masculinity for both girls and boys' faces. In our third study, using forced choice and multiple peer-relevant faces, we looked at the effects of facial masculinity on both attractiveness and bullying.

We hypothesise that peri-pubertal children will attribute bullying to increased levels of masculinity in the face of peer relevant boys and girls. Additionally, peri-pubertal children will show similarity to adult facial preferences. Since we are using facial transforms following previous psychological studies using computer graphic methods manipulating facial masculinity in shape (Perrett et al. 1998), we expect boys will prefer femininity in the shape of the girls' faces, and girls will show a preference for a slight degree of femininity in boys' faces. We note that as a null hypothesis attraction to sexually dimorphic facial features may be absent in both boys and girls if preferences reflect mate choice decisions that are still premature for peri-pubertal age groups. From this perspective for children of 11 – 12 years of age, masculinity should not affect facial attractiveness for males or females.

Study 1

7.2 Methods

7.2.1 Participants

The 67 children who participated in this study were pupils at a secondary school located in southern England. The students ranged between 11 and 12 years of age (females: 36, M=11.75, SD = .439; males: 31, M=11.84, SD = .374). Parents were notified of the experiment and given the opportunity to exclude their children from the study, however no parents chose to exclude their child. Permission was granted by the local educational authority, and all ethical guidelines were followed including police checks as mandated.

7.2.2 Materials

Stimuli: The original faces used to generate the face stimuli came from the Haverhill2000 series (see www.haverhill2000.com). The original photographs were taken by Chris Dorley-Brown using a Nikon digital camera commissioned by the Haverhill Town Council as part of a millennium celebration. Permission to use the images to create composite images with the explicit purpose of experimental study was granted by the Haverhill Town Council and the photographer, Dorley-Brown. The original images arrange in age between toddlers to the elderly, from which, for the purposes of this experiment, we used a subset of children's faces. Prior to the creation of the composite images, the individual faces were assessed for age by 10 individuals. We found a strong inter-rater reliability with a Cronbach alpha coefficient of .977 for the female and .981 for male faces. To create peer-relevant faces, we combined those faces judged between 11 and 12 years of age for each sex. For the female image, 27 original photos went into the average face composite, and for the male image 14 individual photos made up the final composite. The male and female composite faces were made symmetrical (see Burt & Perrett 1997 for full review of technique). To assess sexual dimorphic preference we used interactive face-sequence trials. The sequences involved selection of preferred face shape from a range of 50% feminised to 50% masculinised (*Figures 7.1 and 7.2*) (See section on Psychomorph methods).

Figure 7.1

Top left 11-12 year old male face 50% feminised; top right 50% masculinised

Bottom left 11-12 year old female face 50% feminised; bottom right 50% masculinised

7.2.3 Procedures

All testing was conducted during the children's Information Technology (IT) class with the class teacher present throughout the testing. The children were read brief instructions, told that their participation was voluntary, and their responses were confidential. The experiment was conducted over the internet and all data was sent to a secure server at the University of St Andrews. Following the experiment, the children were given a full debriefing and encouraged to participate in a discussion about stereotypes based on physical attributes.

For the experiment, the male and female 11-12 year old face stimuli were randomised amongst filler items and presented in two counter-balanced blocks of female and male faces. By using the mouse and moving the curser to pass from the right- to the left-side of the screen, participants could view a sequence of 31 faces, ranging from +50 masculinised to -50% masculinised. Fifteen faces were masculinised, 15 feminised, and at mid-point one average male or female face. The instructions were for the participant to use the mouse to view the full range of sequential images and finding the face they thought as most attractive, to left click to select that image. Once the participant selected from the range of faces, the one they thought most attractive, they clicked on the left mouse button to record their preference.

7.3 Analyses and Results

For our first set of analyses, we used a one-sample T-test, with a test value equal to zero, which represents the average of either the 11-12 year old female or male face. Negative numbers are associated with masculinised faces, and positive with feminised faces, and the range of possible scores is -1.0 for masculised and +1.0 for feminised.

For all students there was a significant preference for feminised boy's face (Mean = .248, SD = .43, $t(62) = 4.598$, $p < .001$) and girl's face (Mean = .184, SD = .39, $t(64) = 3.777$, $p < .001$). We then looked at whether these preferences held when we split by sex and found that for boys' faces both girls (Mean = .300, SD = .39, $t(31) = 4.326$, $p < .001$) and boys (Mean = .193, SD = .43, $t(30) = 2.333$, $p = .027$) significantly preferred more the more feminised male face. For the girl's face, again both girls (Mean = .133, SD = .37, $t(33) = 2.108$, $p = .043$) and boys showed a preference for more the more feminised face (Mean = .240, SD = .42, $t(30) = 3.201$, $p = .003$).

To see if girls and boys differ on their preferences, we used an independent samples T-test and found no significant differences between the two sexes on either the boy's ($t(61) = 1.000$, $p = .321$) or the girl's faces ($t(63) = 1.109$, $p = .272$).

7.4 Discussion

The data supported our prediction that, given we were looking at peri-pubertal girls and boys, we would find adult-like preferences in children when judging attractiveness of peer-relevant faces. We did find that boys show a preference for the more feminised female face, which parallel male adult attractiveness judgements. Girls showed a very strong preference for the more feminised male face, again consistent with female adult preferences. While we did not make a specific prediction about sex differences, we were surprised to see that the girls and boys' attractiveness judgments did not significantly differ.

Study 2

7.5 Methods

7.5.1 Participants

Study 2 took place at the same time as Study 1, thus participants are the same. It should be noted that more children participated in Study 2 than Study 2. Forty-two girls (Mean age = 11.69, SD = .468) and 56 boys (Mean age = 11.72, SD = .426) participated in the second experiment.

7.5.2 Materials

The stimuli were constructed in the same manner as in Study 1, however in the current study we used a forced choice task to investigate whether children also used masculine facial features to make attribution. During the face-choice task, the children were asked to choose one of two same-sex faces that most represented a bully. Each face pair consisted of a face that had been +50% masculinised and -50% masculinised. The face pairs were randomised and presented in two counter-balanced blocks of female and male faces along with filler items.

7.5.1 Procedures

As in Study 1, the experiment took place during the participants' IT class. For the experiment, the male and female 11-12 year old face pairs were randomised amongst filler items and presented in two counter-balanced blocks of female and male faces. Participants were instructed to select that image of the paired faces they thought looked more like a bully. The term 'bully' was described as someone who physically or verbally picked on other children, especially those children who were unable to defend themselves against the attacks.

7.6 Analyses and Results

Using the same analyses as in Study 1, we examined whether or not masculine facial characteristics had any effect on judgments of bullying behaviour. Selection of the feminised face resulted in a score of 0, and selecting the masculine face registered with a score of 1. One sample T-test (test value = .5) revealed a significant effect of masculinity on bullying attributions (Mean = .65, SD = .48, t(96) = 3.070, p = .003), however this was not found for the girl's face (Mean = .48, SD = .50, t(96) = 1.534, p = .077).

We also looked at whether sex of the participant affected attribution judgments and found that while girls attribute bullying behaviour to more masculine looking faces (Mean = .71, SD = .46, t(41) = 3.037, p = .004), boys' attributions are more ambiguous (Mean = .60, SD = .49, t(34) = 1.500, p = .139). Neither girls (Mean = .62, SD = .49, t(41) = 1.570, p = .124) nor boys' (Mean = .55, SD = .50, t(54) = .671, p = .505) attributions of bullying behaviour based on girls' facial masculinity reached significance. We did not find a difference between girls and boys on bullying attributions for either the boy's face (t(95) = 1.165, p = .247) or the girl's face (t(95) = .721, p = .472).

7.7 Discussion

Like adults, peri-pubertal children do attribute negative behaviours to a more masculine looking male. We did find that this is true of girls' attributions, but not boys (although the direction was the same). Masculine facial cues in the girl's face did not garner a significant attribution of bullying behaviour. It is possible that boys and girls differ in styles of bullying, thus the term bullying might be interpreted by the students as a more male-type behaviour. Another potential problem with both this study and Study 1 is that only one face-stimuli (per sex) for an age-relevant peer was used. We cannot exclude the possibility that our results are due to stimuli effects and are not applicable to the population at large.

Study 3

Study 3 was conducted in much the same manner as Studies 1 and 2; however, this study was conducted one year later, thus giving us a fresh participant pool of children. We also created new faces of peer relevant stimuli in order to exclude the possibility that our findings due to the stimuli rather than a general preference or attribution judgment.

At the time of the first two studies, we found some resistance among the boys to make attractiveness attributions of boys' faces. To avoid this issue, in Study 3 we asked the subjects only to make judgments of attractiveness for opposite sex faces. We also opted to use a forced choice paradigm for both the attractiveness as well as the bullying judgments.

Study 3

7.8 Methods

7.8.1 Participants

The 120 children who participated in this study were pupils at a secondary school located in southern England. The students ranged between 11 and 12 years of age (females: 52, M=11.46, SD = .50; males: 68, M=11.47, SD = .50). Parents were notified of the experiment and given the opportunity to exclude their children from the study, however no parents chose to exclude their child.

7.8.2 Materials

The original images used to create the stimuli are from the same set of children's images noted in Study 1. To create unique identities of 11 – 12 year old children, we randomly selected 6 images from the 11-12 year old age group to make a new composite base image. This was done 4 times to create 4 unique looking individual base images for each sex, thus creating 8 images in total. Each base image was made symmetrical, then warped into either 50% feminised to 50% masculinised using the age relevant (11-12 year old) male or female average.

7.8.3 Procedures

As with Studies 1 and 2, all testing was conducted during the children's Information Technology (IT) class with the class teacher present throughout the testing. Brief instructions were read to the children and they were told that their participation was voluntary and their responses were confidential. Parents had been previously notified about the experiments, however no parents chose to exclude their child. The experiment was conducted over the internet and all data were sent to a secure server at the University of St Andrews. The children were given a full debriefing after the experiment and encouraged to participate in a discussion about stereotypes based on physical attributes.

For the experiment, the 4 male and 4 female 11-12 year old face pair stimuli were randomised amongst filler items and presented in pairs in two counter-balanced blocks of female and male faces. For the attractiveness judgment participants were presented with 4 pairs of opposite-sex faces, with one face 50% masculinised and the other 50% feminised (in face shape). The faces pairs were presented in blocks and the subject was asked to choose which face they found most attractive and indicate a strength of choice from 4 categories (a) guess (i.e. completely unsure), (b) slightly prefer, (c) prefer, (d) or strongly prefer, thus creating an 8 point scale across the face pairs. The blocks were counter-balance and the order of the pairs and side presentation was randomised. To investigate bullying attributions, the same method was used as noted for the attractiveness judgment; however, both same and opposite-sex faces were presented. The participants were asked to choose which face was more likely to be a bully.

7.9 Analyses and Results

7.9.1 Attractiveness

To examine whether any preference for masculinity or femininity were present, we used the average of the 4 face pairs in a one-sample T-test (test value = 3.5, > 3.5 indicates a preference for masculinity). For boys' judging girls' faces for attractiveness, we did not find a femininity preference (Mean = 3.21, SD = 1.32, t (55) = -1.67, p = .100) nor did the girls show a significant preference for feminised boys' faces (Mean = 3.77 = 1.53, t (44) = 1.18, p = .245).

7.9.2 Bullying

For bullying, participants were asked to make attributions for both same and opposite sex faces. Over all, participants were more likely to choose the masculinised faces as bullies for both boys' (Mean = 2.61, SD = 1.34, t(100) = -6.646, p < .001) and for the girls' (Mean = 2.75, SD = 1.37, t(65) = -4.46, p < .001). When we split by sex we find that girls choose both the masculinised female faces (Mean = 2.61, SD = 1.38, t(45) = -4.33, p < .001) and male faces (Mean = 2.53, SD = 1.48, t(45) = -4.40, p < .001) significantly more often as likely to bully. Boys showed the same attributions for boys' faces, choosing masculine faces as more likely to bully (Mean =

2.67, SD = 1.22, t(54) = -5.00, p < .001); however, while the findings were in the same direction, they were non-significant for the girls' faces (Mean = 3.0, SD = 1.35, t(20) = -1.537, p = .141).

In Study 1, we did not include strength of choice, and so to be parsimonious, we converted our attractiveness scale to a binomial rating. That is, any selection for a feminised face was computed to equal 0, and the choice for a masculinised face was computed to equal 1. We then added the 4 scores to see if selection was different than chance using a one-sample T-test (test value = 2). While girls did choose the feminised face more often, it did not reach significance (Mean = 1.67, SD = 1.31, t(44) = -1.701, p = .096). Selections by boys were at chance (Mean = 2.02, SD = 1.1, t(55) = .121, p = .904).

7.10 Discussion

In Study 3, we did not find a preference for either masculinity or femininity for boys or girls' judgments of attractiveness. However, we did find that for attribution of bullying, that facial masculinity does matter. Girls selected masculine faces of both girls and boys as more likely to bully, while boys did similar when considering boys' faces, but were not as likely to choose a more masculine looking girl as a bully.

7.11 General Discussion

We found that peri-pubertal girls and boys judged feminised opposite sex faces as more attractive than masculinised faces in our first study, but this finding did not replicate in the second. There are several possibilities as to why these studies did not replicate. One reason could be due to the difference in stimuli between Study 1 and Study 3. In our first study, we used one opposite sex face pair, and the preference for the more feminised face could be specific to the stimuli rather than a general preference. Another possible confound is that there are group differences of which we are unaware. Due to limits on the questions we were allowed to ask students, we were not able to collect information concerning the children's development. With the onset of puberty, gonadotrophin and steroid hormones levels begin their sharp increase – in boys this occurs, on average, slightly after 12 years of age, and in girls, the onset is slightly earlier, around 10 ½ years of age (Johnson & Everitt 1988). We would expect that if perceptions of attractiveness in opposite sexes change between childhood and puberty, that ages 11-12 years would be transitional. The children we tested were aged between 11 and 12 years, and it is possible that the children in Study 1 differed in terms of their sexual maturation than those in Study 3.

The bullying data are more clear cut, children make negative attributions based on increased levels of facial masculinity. This is consistent with adult perceptions of masculine facial traits (Perrett et al. 1998), and children's association of boys being more physically aggressive than girls (Giles & Heyman 2005). Attributions of bullying in girls was not associated with sexually dimorphic facial characteristics in boys' judgments; however girls did attribute bullying to more masculine looking girls. This may be in part due to the differences between bullying styles between girls and boys. Boys are thought to use physically aggressive styles whilst girls use more relational styles of bullying (e.g. gossip and exclusion) (Bjoerkqvist et al. 1992). Physical aggression in boys has been related to higher levels of testosterone (Susman et al. 1987; Udry 1990), and higher levels of testosterone are related to more masculine looking faces in adults (Penton-Voak & Chen 2004). Testosterone in boys is also related to social dominance (Rowe et al. 2004), and bullying is possibly one way to move up the social ladder (Luthar & McMahon 1996). Patricia Hawley (2003a) argues that adolescence use aggressive behaviours as a method for resource control and social dominance. Girls could use some style of aggressive behaviour to assert dominance and control resources, but perhaps it is more likely to be directed at other girls rather than boys, explaining why the girls in this study linked masculine facial features in other girls with bullying, while the boys did not. There is some evidence that prenatal testosterone exposure can increase aggressive behaviour in girls (Cohen-Bendahan et al. 2005).

It is also possible that the association between increased male facial masculinity and perceived bullying is because feminised faces look *least* like bullies. Baby-faced adolescents (males and females) are rated as physically weaker, more naïve, and less socially autonomous than more mature looking individuals (Zebrowitz & Montepare 1992).

We propose that children are using cues of hormonal influence on the development of facial characteristics to assess likely behaviour. As testosterone is associated with more aggression, both in adults and children, masculine facial characteristics could act as a clue to an increased chance of aggressive behaviours. Further, we suggest that children have learned to associate these facial cues with masculine facial characteristics over time, either through observations of other children or adults. This however would need to be tested empirically across different age groups.

The following chapter is taken from previously published work, Cornwell et al. (2004). Concordant preferences for opposite-sex signals? Human pheromones and facial characteristics. Proceedings of the Royal Society London B, 271, 1046-1051.

8 Concordant preferences for opposite sex signals? Human pheromones and facial characteristics

8.1 Introduction

Studies on human attraction framed by evolutionary theory have concluded that men and women advertise heritable mate qualities, and that their mate choice strategies exploit these signals. While the precise roles of environment and genetic influences are equivocal, suggested visual signals of heritable mate quality include body and face symmetry (Gangestad et al. 1994; Jones et al. 2001; Penton-Voak et al. 2001; Perrett et al. 1999; Rhodes et al. 1998; Thornhill & Gangestad 1994), masculine and feminine face shapes (Penton-Voak & Perrett 2000; Penton-Voak et al. 1999; Perrett et al. 1998), and body shape (Singh 1993b; Tovée et al. 1999). Non-visual signals include body odour (Gangestad & Thornhill 1998; Rikowski & Grammer 1999; Singh & Bronstad 2001; Thornhill & Gangestad 1999b) and vocal characteristics (Collins 2000; Hughes et al. 2002). Rikowski and Grammer (1999) suggest that humans use multiple signals as a way of reducing error when assessing mate quality. Thus, humans seeking a mate should be keenly sensitive to signal concordance; and indeed, concordances have been reported. Women prefer body odours collected from men with a high degree of bilateral symmetry compared to odours from asymmetrical men (Gangestad & Thornhill 1998; Rikowski & Grammer 1999; Thornhill & Gangestad 1999b). Moreover, both men and women indicate preferences for voices recorded from individuals with higher degrees of bilateral body symmetry over those with lower bilateral symmetry (Hughes et al. 2002).

Sexually dimorphic facial features may also signal mate quality, and Enlow (1990) has speculated that distinctly feminine features (e.g. full lips, larger eyes) in women are influenced by hormones and signal fertility. In males, features such as heavier brows and a strong jaw-line may signal increased levels of testosterone, which in turn may signal dominance (Mazur & Booth 1998a) or immunocompetence (Folstad & Karter 1992).

Other possible signals of mate quality include pheromones, which are ubiquitous among animals but only recently have been seriously considered as signals for human mate choice. Indeed, the researchers investigating body odours have speculated that pheromones are key in mediating the effects. We investigate the possible role of three putative human pheromones: the male pheromones 5α-androst-16-en-3-one and 4,16-androstadien-3-one, and the female pheromone 1,3,5, (10) 16-estratetrael-3-ol, as signals of mate quality. For brevity, we shall call them MP1, MP2 and FP respectively. The two male pheromones have been found to be the most concentrated in human semen from among the androgen and 16-androstenes steroids (Kwan et al. 1992). Jennings-White (1995) found that among the androstene steroids, MP2 produced the strongest response in women's vomeronasal organ (VNO), the organ mediating pheromonal signals. Previous research has tended to include only one of the male pheromones, allowing for little comparison to evaluate their similarities as mate quality signals. Comparisons, however, between the female pheromone FP and the male pheromone MP2 have revealed sex differentiated processing in the hypothalamus (Savic et al. 2001b) including sensitivity and surface potential in the VNO to opposite sex pheromones (Jennings-White 1995; Monti-Bloch & Grosser 1991). Pheromones can prime changes in human reproductive function (Morofushi et al. 2000; Rekwot et al. 2001; Schaal & Porter 1991; Wyatt 2003), however its status in signaling human mate quality and affecting mate selection is inconclusive (Black & Biron 1982; Cowley et al. 1991; Cutler 1988; Jacob & McClintock 2000).

8.1.1 Multiple signals, individual differences, and mating strategies

It has been suggested that multiple signals reduce error when evaluating potential mates (Kohl et al. 2001; Rikowski & Grammer 1999). The strength of concordance, however, may depend upon the context under which the judgment is made. For example, an increasing number of studies emphasize individual differences in the assessment of quality signals and have found that preference for facial masculinity is affected by relationship status (Little et al. 2002), age of parents (Perrett et al. 2002) and self rated attractiveness (Little et al. 2001a). We test these assumptions by examining judgments for visual and olfactory signals of potential partners in two contexts: long-term or short-term relationships.

In keeping with research on mating strategies and with the good-genes theory (Andersson 1994; Gangestad & Simpson 2000), we propose that both facial characteristics and pheromones signal mate-quality, and that preferences for cues to mate-quality should co-vary across domains. Women who prefer more masculinised faces should also show an increased liking toward male over female pheromones, while men who prefer more feminised faces should indicate a corresponding inclination toward the female pheromone.

It should not be assumed that the strategies used in seeking a partner are the same across individuals, or across time for any one individual, nor even that they must be rooted in the same biological function. Women might have been selected to seek 'good genes' through cuckoldry (Gangestad & Simpson 2000), to evaluate prospective 'good fathers,' or to replace a current mate (Buss 1994). While the mating system of ancestral hominids is unknown, it is likely that during hominid evolution there had been at least some male investment toward mate and offspring upon which natural selection shaped modern human mating behaviours. Today's world is vastly different from the world in which our ancestors were naturally selected, and immediate psychological motivations, such as the need for self-affirmation or bowing to peer pressure, may have only the most tenuous links to Darwinian selection. Men's risks when engaging in a short-term relationship are fewer, but the strategies in choosing a partner are no less likely to vary. Different selection pressures should be expected to affect signal preference, or attention to specific signals, by both men and women.

The selection pressures underlying the strategies used when seeking a long-term relationship may vary among individuals, but it is possible that for any one individual they are more consistent across time compared to short-term benefits. Those females who were more discriminating when choosing a long-term partner achieved higher fitness than those women who were not so choosey. Women were, in nearly a literal sense, placing all their eggs in one basket. Although women today do not face the same risks which led to the selection of the genes behind this strategy, the evolutionary legacy remains intact. Females, therefore, are selected to desire a healthy and fit partner, and also expect substantial investment by him in both her and all resulting offspring. This Darwinian function would require females accurately to read all available signals and to be sensitive to their consistency (see Møller & Pomiankowski 1993). Selection pressures on males influence the strategies used when investing in a long-term partner, and males sacrifice time, energy, and potential mating opportunities. Males' judgments across multiple modalities should be most strongly correlated when evaluating a potential partner for a long-term relationship. We therefore propose that relationship context, that is long-term versus short-term, will influence concordance of signal judgments for both men and women, though the nature and direction of these effects (particularly for women) are uncertain, and these effects should be sex-specific.

Study 1

The purpose of Study 1 was to investigate whether two proposed signals of mate quality, masculine/feminine facial characteristics and masculine/feminine pheromones, are chosen concordantly and if these judgments are sex-specific. Do women who prefer more masculinised facial shapes also rate putative male pheromones more appealing? Similarly, do men indicate an increased liking of the female pheromone if they prefer more feminised facial shape when judging a partner.

8.2. Methods

8.2.1Participants

Heterosexual undergraduate students (56 women, age range 17-26, mean 20.7, ± 2.12 and 56 men age range 17-26, 21.14 ±2.01), not taking hormonal contraceptives, were recruited from the University of St. Andrews.

8.2.2 Materials

Five odorants were used: two male pheromones, MP1 and MP2; a female pheromone FP[6]; and two filler-items, clove oil, and oil of cade. Solutions were made of each compound (2 mg per 1.0 ml of propylene glycol). 20 µl of the solution was then deposited onto filter paper (Filsinger et al. 1985; Jacob & McClintock 2000). The filter paper was presented to the participant in a glass vial after the experimenter removed the lid. Vials were stored at 5° C when not in use. Experimenters conducting the testing were blind to the identity of the odorants.

To assess masculinity preference we used interactive face-sequence trials consisting of 6 opposite sex and 6 same-sex images (4 Caucasian, 1 African-Caribbean, and 1 East-Asian face(s). The same images had been used in previous studies (Penton-Voak & Perrett 2000; Penton-Voak et al. 1999; Perrett et al. 1998). The sequences involved selection of preferred face shape from a range of 50% feminised to 50% masculinised (see Tiddeman et al. 2001 for full review of technique).

8.2.3 Procedures

Participants were presented with 6 interactive face sequence trials and were asked to select the face they most preferred. Subjects were asked to judge opposite-sex faces for two hypothetical situations: long-term versus short-term relationship. As a control to assess whether preferences are sex-specific, we included judgments of

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[6] The pheromones were obtained from Steraloids, Inc., Rhode Island, USA. 5α-androst-16-en-3-one (MP1) and 4,16-androstadien-3-one (MP2), and the female pheromone 1,3,5, (10) 16-estratetrael-3-ol (FP)

same-sex faces without any such mention of relationship context. If preferences are sex-specific, we would expect our predictions for concordance to be found only between opposite-sex faces and pheromones. They should not apply to the assessment of same-sex friend or foe. As noted, a long-term relationship was defined as a committed relationship possibly leading to co-habitation or marriage. A short-term relationship was described as one that is short in duration, such as a one-night stand or a brief affair. The relationship context was run in two blocks for opposite-sex faces. Blocks and face sequence trials were presented in random order. Participants then completed a questionnaire regarding sexual orientation and oral contraceptive use. They were then asked to smell and rate the 5 'naturally occurring' odorants in terms of pleasantness (7-point Likert-type scale ranging from very unpleasant to very pleasant), or indicate that they could not detect the odour.

8.3 Analysis

Data from subjects anosmic for a given pheromone (unable to detect the odour) were removed from the analyses for that pheromone. Ratings of the pheromones and the preferred level of masculinity/femininity face shapes were compared using Spearman Rank correlation (two-tailed probability).

8.4 Results

For women, the only significant positive correlation found was between the judgments for male faces for long-term relationships and the ratings of the male pheromone MP2 (r_{42} = .379, p = .017) (see Table 8.1). This correlation suggests that preference for facial masculinity corresponds with a greater liking for masculine smells. Corresponding judgment of faces for short-term relationship was not significantly correlated with ratings of either male pheromone.

Men's preferences mirrored these. Their ratings of the female pheromone significantly and positively correlated with preference for a more feminine face shape in long-term relationship contexts ($r_{34} = .352, p = .045$) but not short term relationship contexts (see Table 8.1).

8.5 Discussion

The prediction that judgments of facial shapes and pheromones would positively correlate was partially supported, and the results were also sex specific. Women showed a greater liking for the male pheromone, MP2, the more they preferred masculinised faces when judging for long-term relationships. Men's preferences for femininity in face shape when judging for long-term relationships corresponded with their ratings of the female pheromone.

One limitation of Study 1 was that the relationship context was tied only to the judgments of face, while the pheromone ratings were not bound to a relationship context. In order to explore these effects and pursue a possible explanation, we did a second study.

Table 8.1 (Study 1).

Spearman rank correlations between odour pleasantness and preference for masculinity in male faces and femininity in female faces. Opposite sex face judgments were performed in the context of short and long-term relationships. Positive correlations indicate like-preferences for the same sexual characteristics (e.g. male pheromone and masculine facial characteristics would be positively correlated if preference for both increased).

	Rater sex	Opposite sex faces short-term relations	Opposite sex faces long-term relations	Same sex faces
5α-androst-16-en-3-one	F	$r_{43} = -.060$	$r_{43} = .222$	$r_{43} = .012$
(male pheromone, MP1)	M	$r_{48} = -.111$	$r_{48} = -.040$	$r_{48} = .040$
4, 16-androstadien-3-one	F	$r_{42} = .097$	$r_{42} = .379$*	$r_{42} = -.184$
(male pheromone, MP2)	M	$r_{37} = -.225$	$r_{37} = .126$	$r_{37} = .068$
1,3,5, (10) 16-estratetrael-3-ol	F	$r_{36} = .170$	$r_{36} = .011$	$r_{36} = .143$
(female pheromone, FP)	M	$r_{34} = .098$	$r_{34} = .352$*	$r_{34} = -.071$

Study 2

The purpose of Study 2 was to investigate further the influence of relationship context on olfactory and visual signals of mate quality. In Study 1, the pheromones were presented as naturally occurring odours with no mention of an association with humans. In Study 2, subjects were explicitly told that the odours were related to humans and asked to what degree they would like a partner to smell of the odour within the context of a long-term or short-term relationship. As with the previous study, subjects of both sexes were asked to select the face they would most prefer for a long- versus a short-term relationship. From Study 1 it was expected that naturally cycling women who indicate preferences for more masculinised faces would rate the male pheromones more favourably than women who prefer more feminised faces. Men should also rate the female pheromone more pleasant if they prefer more feminised faces when selecting for a long-term, but not a short-term partner.

8.6 Methods

8.6.1 Participants

Subjects were 205 heterosexual undergraduates (96 female, age 17-26 years, mean 20.40 ±1.76 and 50 males, 18-25 years, mean age 21.18 ± 1.61). All women included in the study had natural menstrual cycles (neither taking hormonal contraceptives nor reported to be pregnant).

8.6.2 Materials

The three pheromones (2 male and 1 female) were the same as those used in Study 1 and prepared in the same manner. As before, the experimenters conducting the experiment were blind to the identity of the odours.

To examine the generality of results the stimuli used for the facial attractiveness ratings were created from a new set of original images, but in the same manner as for Study 1. Twelve Caucasian images were created (6 of each sex). Each image was then morphed into 50% feminised and the 50% masculinised face shape, creating a total of 24 male and female images (see Tiddeman et.al. 2001 for full review of technique).

8.6.3 Procedures

Participants were presented with 6 pairs of opposite-sex faces, with one face 50% masculinised and the other 50% feminised (in face shape). The faces pairs were presented in blocks and the subject was asked to choose the preferred face for either a long- or short-term relationship and indicate a strength of choice from 4 categories (a) guess (i.e. completely unsure) , (b) slightly prefer, (c) prefer, (d) or strongly prefer. This created an 8 point preference range for masculine face shape. The blocks were counter-balance and the order of the pairs and side presentation was randomised. Subjects were presented only with opposite-sex faces. Following the face choice task, the pheromones were presented in two blocks, with vials containing each of the three pheromones (2 male, 1 female) in each block. Each of the 6 vials was uniquely labelled. The blocks were counter-balanced for long- or short-term partnership. The subjects were told that the odours they smelt were related to humans (the term pheromone was not mentioned), and asked whether they could detect the odour, and then to rate each odour in terms of how much they would like a partner to smell of the odour within the context of term. The scale was a 7-point Likert-type scale ranging from 'not at all' to 'very much so.'

8.7 Analysis

Data from anosmic subjects (as with Study 1) were removed from the analyses for each pheromone. Ratings of the pheromones and the judgments of face shapes were compared with Spearman Rank correlations, two-tailed, within the same relationship context, i.e. short-term versus long-term.

8.8 Results

For women, a significant positive correlation was found between preferences for masculine face shape and the ratings for the male pheromone MP2 when judging in the long-term context ($r_{80} = .240, p = .032$) (see Table 8.2). A positive correlation was found between men's ratings of the female pheromone and their preference for feminine face shape when judging for a long-term partner ($r_{34} = .466, p = .006$), with men who rated the female pheromone more positively also indicated a preference for a more feminised face. No other significant correlations were found (see Table 8.2). Individual correlations may not withstand corrections for multiple tests. The findings, however, replicate across Studies 1 and 2.

Further analysis revealed that the correlation between preferences for MP2 and facial masculinity was present for women in the follicular ($r_{34} = .358, p = .038$) but not in the luteal phase of the cycle ($r_{35} = .068, p = .697$). Thus menstrual cycle phase influences the relationship between face and pheromone preferences, but does not account for it.

Table 2 (Study 2)

*Spearman rank correlations between ratings of naturally cycling women (F) and men (M) for odour pleasantness and preferences for facial masculinity/femininity when judging attractiveness of opposite sex faces in the same context (short and long term relations). Positive correlations indicate like-preferences for the same sexual characteristics. Conventions as Table 1 * p<.05*

	Rater sex	Opposite sex face Long-Term	Opposite sex face Short-term
5α-androst-16-en-3-one (male pheromone, MP1)	F M	$r_{88} = .093$ $r_{37} = .068$	$r_{83} = .067$ $r_{35} = -.269$
4, 16-androstadien-3-one (male pheromone, MP2)	F M	$r_{80} = .240$* $r_{35} = .312$	$r_{86} = .170$ $r_{35} = .096$
1,3,5, (10) 16-estratetrael-3-ol (female pheromone, FP)	F M	$r_{71} = -.039$ $r_{34} = .466$*	$r_{76} = .044$ $r_{34} = .214$

8.9 General Discussion

The aim of the two studies was to illuminate the relationship of signals relevant to human mate choice across two discrete sensory modalities, olfaction and vision. In both studies, concordance was found in the preference for facial characteristics and pheromone odour, and was specific to opposite-sex signals. A strong correlation was found between men's ratings of the female pheromone, 1,3,5,(10) 16-estratetrael-3-ol (FP), and their preference judgments for feminine face shapes. Women mirrored this finding: a significant correlation was found between the rating of the male pheromone 4,16-androstadien-3-one (MP2) and preferences for masculinity in male face shape.

We did not expect to find, as we did, the differences between the two male pheromones. Women who preferred one tended to prefer the other (long term: r75 = .399, p < .001 and short term: r79 = .527, p < .001), yet there were no significant correlations between preferences for 5α-androst-16-en-3-one (MP1) and faces in Study 1 or 2. The lack of significant correlations for 5-alpha means that the statistics for the two pheromones cannot be compared meaningfully. Thus we are presently unable to conclude that the actions of the two substances are similar or dissimilar. Concordant preferences could imply corresponding mate characteristics. Concentration of 4,16-androstadien-3-one (MP2) and degree of masculinity in face shape could independently and simultaneously signal traits such as: testosterone level, dominance, 'good genes', or likelihood of desertion. 5α-androst-16-en-3-one (MP1) appears to signal additional or alternative characteristics.

While these pheromones are structurally similar, they have different concentration in bodily secretions: compared to 5α-androst-16-en-3-one (MP1), 4,16-androstadien-3-one (MP2) is more abundant in men's under-arm hair (Nixon et al. 1988) and semen (Kwan et al. 1992). MP2 is also found to produce a stronger response in the female VNO compared to MP1 (Jennings-White 1995). These and the current findings suggest that the two pheromones may have different consequences for behaviour.

Both our studies showed concordance between olfactory and visual signals when participants judged partner characteristics in the context of a long-term relationship. In the first study, subjects were asked to judge faces within a relationship context while odours were judged as naturally occurring substances and were not specifically linked to humans. Despite the lack of relationship-context, studies 1 and 2 produced similar results. One possible explanation is that individuals' judgments default to a long-term as opposed to a short-term context (Buss, 1994). Concordance, it must be noted, does not imply a preference toward either masculine or feminine characteristics, only that the individual preferences are apparently consistent across multiple modalities. The perplexing question remains as to why individual differences exist at all. In other words, why would some men and women choose lower-quality markers over higher-quality markers? Speculation as to how individual differences develop include learning and differences in life history (Penton-Voak & Perrett 2001; Perrett et al. 2002), self-perceived attractiveness (Little et al. 2001a), and hormonal shifts (Penton-Voak & Perrett 2000). Our findings do not elucidate the mechanisms influencing individual differences, rather it is more enticing evidence to their existence and appeals for further investigation.

When a male or a female is choosing a partner for a short-term relationship, a variety of evolutionary functions may be relevant, such as partner replacement or assessment of mate potential (Buss & Schmitt 1993), cuckoldry (Gangestad & Simpson 2000), or perhaps intra-sexual competition. Psychological motivations influenced by the vagaries of modern life, such as gaining sexual experience or peer pressure, may complicate the picture as we see it today. Diverse strategies could lead individuals to attend to opposite sex signals differently. Long-term investment carries quite different risks and costs, compared to short-term. So, as mating strategies shift between the two, we might expect people to attend to different signals of mate quality. For males cost of investment in a long-term as opposed to short-term relationship is much higher. A female risks pregnancy whether she engages in a long- or a short-term relationship, and thus she must always be particular about whom she chooses as a sexual partner. The data suggest, however, that across two discrete signals, olfaction and vision, women's preferences are more consistent when judging for a long-term partner as opposed to a short-term partner. Therefore, for both men and women the implications of a long-term relationship, which must include limiting if not excluding other mating opportunities, may increase the need to find concordance between signals of mate quality.

9.0 Summary

The global theme and conclusion of this thesis is that development plays a significant role in adult mating strategies, and an important aspect of development is the individual variations of sexual dimorphic characteristics. While the environment plays an important role in shaping individual differences, there are biological components that shape the individual's milieu. The relationship between environment and biology is intertwined, with each affecting the other.

In the first chapter, I suggested that understanding the inheritance patterns of sexually dimorphic and attractive facial characteristics would give us insight into the type of mating strategies men and women would pursue. Facial masculinity in male offspring was found to relate to father's facial masculinity. The data indicate that female offspring inherited facial attractiveness from their fathers, and facial femininity from their mothers. These findings provide evidence for the ground conditions necessary for both Fisherian 'run away' selection and good genes theories in humans.

In Chapter 8, we found evidence that men and women are choosier when selecting for potential pair-bond than when looking for a fling, as they seek signal concordance of sexually dimorphic signals when evaluating face and odour for long- but not short-term relationships. This suggests that when men and women are considering possible pair-bond relationships, where both parents would be expected to invest in offspring, it is important to be more selective. The inheritance data (Chapter 2) are also consistent with this, as the traits selected for in women by men are passed on to daughters. Thus, men's choice of sexual partner will impact on the future of his daughter's ability to attract good quality mates. Further research should be carried out to determine if the preferences are also inherited by offspring (e.g. father's preferences inherited by son, mother's preferences by daughter).

Sexually dimorphic and attractive facial characteristics were also found to be stable across development, from infancy into young adulthood. This stability creates an 'environment' during development that would reflect, in part, the attributions and perceptions of others. In Chapter 3, evidence was reviewed suggesting that attractive children receive better treatment from both adults and children, and this preferential treatment begins from birth. In males, the relationship between masculinity and ratings of attractiveness change from a negative association during infancy to a neutral association in childhood to a more positive association in young adults. Because of this shift in the direction of the relationship, masculinity in males appears stable across development while attractiveness judgments are not. In females, masculinity is always negatively associated with attractiveness, thus because feminine facial characteristics are stable across development, so is attractiveness.

Given that mothers show more care toward attractive infants, it raises the question as to how much environmental factors affect personality of offspring. Male facial masculinity is perceived as being less nurturing and colder than feminine facial features – if more masculine males are less affiliative, how much of these effects are related to testosterone levels and how much is related to having received less affection from others? The same type of question also relates to the data concerning children's perceptions of increased facial masculinity in boys as exhibiting an increased likelihood of participating in anti-social behaviours such as bullying. It is possible that more masculine looking boys, being thought of as bullies and treated like bullies, fall into a trap of fulfilling the expectations of others (e.g. Rosenthal &

Jacobson 1968). While testosterone could increase the possibility of more aggressive behaviour in boys, the expectations of such behaviour could increase the likelihood of phenotypic expression.

The speed of development (Chapters 5-6) also affects the environment of an individual. Children who begin puberty slightly earlier than their peers are likely to experience different peer interactions than those children who mature slightly later than their peers. With the onset of puberty, facial sexual dimorphism increases – with girls' faces becoming more womanly and boys' more manly. Earlier maturation is especially advantageous to boys in terms of social status, as they will appear older and probably more masculine – both characteristics are associated with dominance. Faster maturing boys will also gain access girls who are more sexually mature, and vice-versa. This in turn could shape preferences for more sexually-dimorphic facial characteristics in adult mate-choice strategies, with earlier maturers preferring increased sexually dimorphic features in opposite-sex faces. Thus individual differences in mate-choice preferences could reflect learning during the prolonged period of human adolescence.

While humans are sexually dimorphic, compared to other primates such as gorillas and orang utans, ours is slightly muted, but greater when compared to gibbons. One potential explanation is advanced in the theoretical chapter suggesting that our preference for neoteny in infants led to a Fisherian-type runaway selection for more neotenous, feminine, looking infants. More neotenous looking infants, because they would receive more care, would be more likely to survive than less neotenous (more masculine) looking infants. The evolution of neoteny as a form of run-away selection has implications in regards to the decrease of sexual-dimorphism in humans during the evolution of the genus *Homo*, as well an as increase in brain size.

Sexual dimorphism in humans is, as the data in this thesis suggest, important in terms of mating strategies. The hominid fossil records indicates that there was a much greater degree of sexual dimorphism between males and females during our evolutionary past than exist today (Plavcan 2002; Richmond & Jungers 1995). Fisherian runaway selection is most often associated with *increasing* the degree of sexual dimorphism, yet it can be employed to explain any characteristic for which there is a preference expressed by the opposite sex. As environments change, traits that once provided benefits could in fact become a hindrance. As our ancestral females began to invest more in their offspring, allowing for longer development from infancy to sexual maturity, they might well have found it useful to have more investment from males over a longer period of time. Females could have been selecting for features that signalled more investment potential – leading to a "run-down" of the sexual dimorphism more typical of polygynous species. Additionally, with females demanding more male investment, which would reduce the ability for males to maintain large harems, the necessity of maintaining characteristics for male-male competition would have also been reduced – thus the selection pressures to maintain such expensive physical attributes would have diminished and energies could go toward investment in pair-bonds and offspring. While such arguments are speculative, the thesis has established that one of the requirements necessary for sexual selection, inheritance, exists. This permits directional selection to amplify or stabilising selection to minimize sexually dimorphic traits.

While preferences for some apposite sexual characteristics have been maintained in humans, individual developmental profiles and environment will shape the degree of preferences for them. The choices we make when considering sexual relationships are a result of our individual experiences and biology, and how they interact within the context of family, peers, and society.

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Appendix

Method for sexual-dimorphic transforms

Creating face stimuli

In all of the studies herein, face stimuli were created using Psychomorph software to manipulate face shape, and in some instances face colour and texture. Two basic steps are necessary for the creation of masculinised and feminised faces: firstly, creating male and female averages, and secondly, to exaggerate the differences between these two averages and apply those differences to base faces.

Delineation

Face prototypes (averages) were constructed using full-frontal face photographs, which were then individually delineating by hand. The delineation process is done by assigning feature points at specific targets on the face, for example the outline of the face (along the hairline), the mouth, nose, eyes, brows, cheeks, and ears. There are 172 landmark points used to define facial features, thus creating a template. Key to the process is assigning the delineation points in a similar manner to each individual face-photograph, as these points are used as anchors for tessellating images during the 'warping process'.

Creating prototypes (average face)

Prototypical faces are a result of combining the properties (shape, colour, and/or texture) of several face images into one image. To create the prototypical face-shape, the delineation data are normalised using translation, rotation, and scaling, so that the eyes are aligned with the average eye positions. By normalising each template to the average left and right eye positions, they will conform to the same size and orientation. The result is that while the special relationships between the facial features are maintained, the size and the alignment of the faces are standardised. The average position of the delineation points is then found, and this defines the average shape for the set. Each individual face is 'warped' into the average image using one of a number of possible warping options, including thin-plate splines and linear interpolation over triangles. This prevents any one face from influencing the final prototype face more than any other face (Benson & Perrett 1991; Rowland & Perrett 1995).

After the individual face images have been warped into the average shape, the colour average can be calculated. The average red, blue and green values of each pixel in the average shape image are calculated to produce the prototypical face (see Rowland & Perrett 1995 for details). Such "shape and colour" prototypes lack realistic fine texture detail (e.g. lines and wrinkles), because these are not aligned in the warping stage, and so become blurred in the colour blending state. The appearance of textures in the prototype face can be improved by amplifying the intensity of variations in the image to match the average size of the variations in the original set of faces. The intensity variations are found by filtering the image with a number of spatially localised, oscillating filters of different scales and orientations, known as wavelets. For a complete review of this process see Tiddeman, Burt and Perrett (2001).

Symmetrising

As symmetry in faces increase perceived attractiveness, and asymmetry decreases it, our prototypical faces are made symmetrical to eliminate this potential confound. Using Psychomorph, the prototype face is symmetrised by creating a mirror image of the face and then averaging it with the original prototype face. Thus, face shape, colour, and texture are the exactly the same on the right and left side of the face.

Transforms

To create an image transform, two prototype faces are used to define the differences between two groups. For example, having made a prototypical 20-year old female face and a prototypical 20-year old male face, Psychomorph calculates the differences between male and female 20 year old faces in terms of their shape, colour, and or texture (each can be done independently). The mathematical differences can then be applied to a target face in four stages. First the two prototypes are aligned with the subject's template using rotation, scaling, and translation. The new shape is then calculated by adding the differences between matching points in the prototypes to the same points in the subject's template. The three images (subject and two prototypes) are then warped into this new shape. Finally the colour difference between the two prototypes is found at each pixel and added to the colour of the corresponding pixel in the subject's image. The textures can be transformed using an additional wavelet processing step if required. Psychomorph allows the operator to adjust the degree of difference and direction to be applied. For example, one could increase the difference between male and female face shape toward the male shape and away from the female shape by a given percentage and apply that difference to the target face. This would give you a target face that looks more masculine and less feminine.

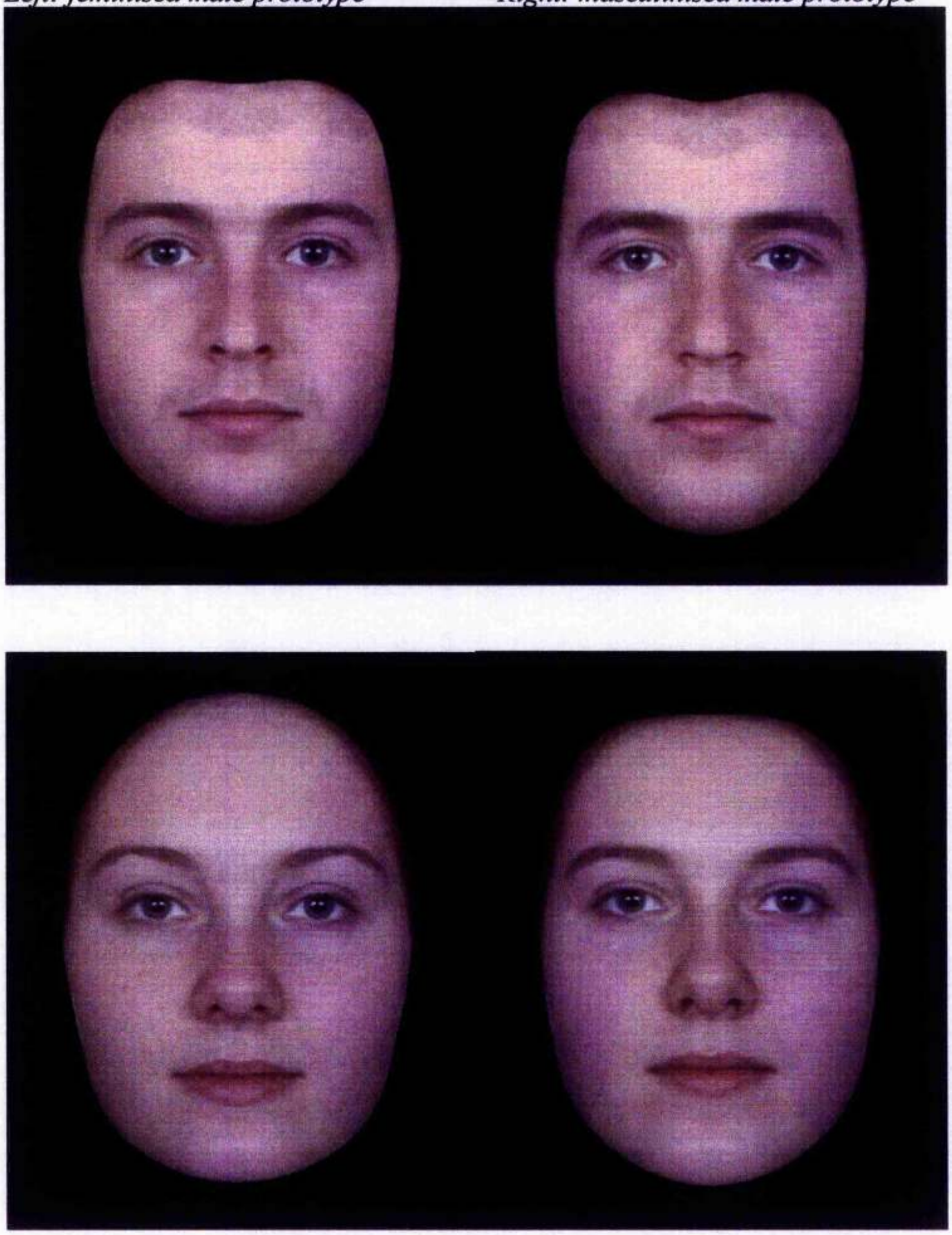
Base faces

Prototype faces are created by mathematically combining individual images of a target group (e.g. males all 20 years of age). Experiments have shown that once about 12 or more randomly selected images are combined, that average will look very much like any other average that has been made using another 12 randomly selected images. However, by using a smaller number of images, around 6 or 8, the average will maintain an 'identity' that will differ from another average made from a different set of 6 or 8 faces. This allows us to make 'individuals' with which we can create the transforms toward or away from masculinity (for example). While we could apply the transforms to images of individual people, the problem with this is firstly since the person is identifiable, the experiment participant could possibly know the individual thus confounding our results (especially true in a small university as is St Andrews). Secondly, as we are manipulating features of the face that are intended to increase or decrease attractiveness, there are some ethical issues concerning the use of an individual's image. Therefore, by creating unique individuals (base faces), we can apply the transform manipulations to many faces, giving us more statistical power, while maintaining the identity of the individuals whose faces went into the base faces. Additionally, by applying the transforms to more than one face, we can increase our confidence that the manipulation rather than the stimulus face is the basis of our findings.

See Figure 1 for examples of masculinity transforms and Figure 2 for examples of base faces.

Figure 1

Left: feminised male prototype *Right: masculinised male prototype*



Left: feminised female prototype *Right: masculinised female prototype*

Figure 2: Base faces for unique identities