SEXUAL SELECTION AND THE HUMAN FACE: BEAUTY IN THE FACE OF THE BEHELD AND IN THE EYE OF THE BEHOLDER

Anthony Charles Little

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Sexual Selection and the Human Face: Beauty in the Face of the Beheld and in the Eye of the Beholder

by
Anthony Charles Little

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Supervisor: Professor David I. Perrett

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 – 1346

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Abstract

Evolutionary theory has been proposed to provide an answer to the question of why some faces are perceived to be more attractive than others are. The first part of this thesis provides an introduction to an evolutionary approach to studying attractiveness (Chapter 1) and reviews sexual selection theory (Chapter 2) and how this theory has been applied to help understand human facial attractiveness (Chapter 3). The thesis focuses particularly on symmetry and secondary sexual characteristics in faces, two of the main factors that relate to attractiveness from an evolutionary perspective as they are both proposed to be associated with genetic benefits to the choosing individual.

The empirical work in the first part of the thesis is consistent with both masculinity and symmetry in males reflecting adaptive selection for high quality mates. Facial masculinity was found to be associated with personality attributions that appear consistent with masculinity reflecting testosterone level in males. Masculinity was associated with some negative personality attributions and when controlling for such attributions masculinity in male faces was found to be of increased attractiveness (Chapter 4). Facial symmetry was found to be preferred in opposite-sex faces by both males and females when images were presented upright and less so when the images were inverted (Chapter 5). Symmetry was also found to be preferred in familiar faces and both this preference and preferences differing according orientation are consistent with the notion that symmetry preferences are an adaptation to identify high quality mates.

The second part of this thesis presents views on the existence of individual differences in attractiveness judgements that are consistent with evolutionary theory.

Evidence is reviewed regarding how individual differences in preference could be more adaptive than a single species wide strategy (Chapter 6). Chapters 7 and 8 present studies showing that preferences for sexual dimorphism and symmetry differ between women in ways that may have been adaptive over evolutionary time. Women who are attractive prefer higher levels of masculinity and symmetry than less attractive women (Chapter 7) and women judging for short-term relationships or women who already have current partners prefer more masculinity in male faces than those judging for long-term relationships or women who do not have a partner (Chapter 8).

Chapter 9 again shows that individual differences in mate-choice do exist and can be consistent with evolutionary theory showing that individuals choose partners resembling their opposite-sex parent, a phenomenon that may reflect imprinting-like effects in humans.

This thesis presents data that is consistent with the notion that sexual dimorphism and symmetry may advertise quality in human faces (Part 1) and data on several potentially adaptive individual differences in human face preferences (Part 2). Individuals can both agree, on average, on what is attractive and unattractive and yet still demonstrate variation in judgements. In this way beauty can be said to be both in the face of the beheld and in the eye of beholder.

Publication list

Parts of this thesis are adapted from the published manuscripts listed below:

Journal articles

Little AC, Burt DM, Penton-Voak, IS, & Perrett DI (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London, B, 268,* 39-44.

Little AC & Perrett DI (2002). Putting beauty back in the eye of the beholder: evolution and individual differences in face preference. *The Psychologist, 15,* 28-32.

Little AC, Jones, BC, Penton-Voak IS, Burt DM, & Perrett DI (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society of London, B, 269,* 1095-1100.

Little AC, Penton-Voak IS, Burt DM, & Perrett DI (2003). Investigating an imprinting-like phenomenon in humans: partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behaviour, 24*, 43-51.

Little AC & Jones, BC (2003). Evidence against perceptual bias views for symmetry preferences in human faces. *Proceedings of the Royal Society of London, B., 270,* 1759-1763.

Book Chapters

Little AC, Penton-Voak IS, Burt DM, & Perrett DI (2002). *Evolution and individual differences in the perception of attractiveness: how cyclic hormonal changes and self-perceived attractiveness influence female preferences for male faces.* In G. Rhodes and L. Zebrowitz (Eds.), *Advances in Social Cognition Volume 1: Facial Attractiveness,* pp 59-90. Westport, CT: Ablex.

Little AC, Perrett DI, Penton-Voak IS, & Burt DM (2002). *Evolution and individual differences in the perception of attractiveness.* In A. Kenichi and T. Akazawa. (Eds.), *Human Mate Choice and Prehistoric Marital Networks,* pp 101-115. International research center for Japanese studies: Kyoto, Japan: Tanaka Printing Co. Ltd.

Part 1: Beauty in the Face of the Beheld

"What is beauty anyway? There's no such thing."

Pablo Picasso

1 Introduction: An Evolutionary Approach to Studying Facial Attractiveness

Synopsis

This first Chapter introduces the importance of faces in everyday life and the impact beauty has on human lives. Notions of universal criteria for attractiveness are discussed and an evolutionary account of why we find some faces more attractive than others is put forward. It is concluded that an evolutionary account of the importance of faces in mate-choice may help explain the large amount of attention faces receive.

1.1 The importance of faces

The human face has been a source of great interest to psychologists and other scientists in recent years because of the extraordinarily well-developed ability of humans to process, recognise and draw information from other's faces. Scientists are not alone in their interest in human faces and it is of course obvious that every human being appears to be fascinated by the faces of others.

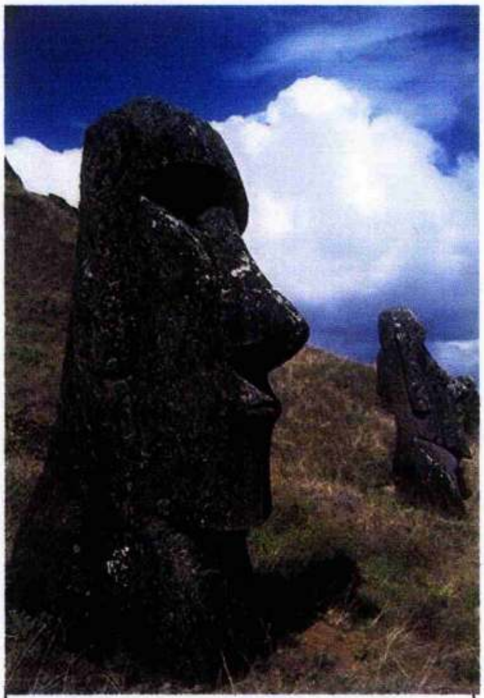

Figure 1: Stone heads on Easter Island

Faces cover our magazines and posters, television and movie cameras focus our attention on the face, and a portrait without a face is a very odd thing indeed. Faces dominate our works of art, ancient and modern, (e.g., Figure 1) and our sensitivity to faces is highlighted when we see faces in many everyday shapes under ambiguous conditions, such as in clouds or the face of the man in the moon.

Faces come in a remarkable number of shapes and sizes and are covered in an incredible number of muscles, which add to facial complexity (Bruce & Young, 1998). While some people may have other distinctive features, such as large hands or feet, the differences between people in these features are not as readily used to distinguish between individuals we meet[1]. The face is also the main seat of four of the five senses – we see, hear, smell, and taste with various parts of our face. We speak using our mouths, and so the human ability of language is also firmly seated in the face. We focus on others faces because we want to see, hear and speak to them requiring us to point our face at them, and to do the same they must point their face at us.

The importance of faces in human life is highlighted by much empirical research. Human infants only minutes old attend particularly to face like stimuli compared to equally complicated non-face stimuli (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991). We rely on faces to recognise the myriad of individuals we encounter in our lives (Bruce & Young, 1986) and hence thieves, bank robbers, and super heroes wear masks to conceal their identity. Our

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[1] Part of the apparent diversity of faces may lie not in the size of the difference between features of the face but in our sensitivity to those differences: "*The difference in human features must be reckoned great, inasmuch as they enable us to distinguish a single known face among those thousands of strangers, though they are mostly too minute to measure. At the same time they are exceedingly numerous.*" (Galton, 1883, p. 3, cited in Bruce & Young, 1998). In other words, independently of how great the diversity between them, humans appear to be particularly tuned to the differences between faces.

faces also constantly display our current feelings about events through facial emotion (Darwin, 1872; Ekman & Friesen, 1976).

The face is obviously an important source of information, for recognition and for decoding a person's emotional state, and it is the focus of our attention for a variety of reasons outlined above. The face is usually the first type of visual information available to a perceiver and is available continually through almost all types of interaction. A fundamental question in social perception, and thus in understanding the social world of humans, is exactly what information a human face conveys. Although other information may be more meaningful than that acquired from faces (such as whether a person is aggressive, which can be indicated by how violently they behave towards others in a number of different situations) it takes more time to acquire (e.g., repeated observation over time), and this means that humans readily draw a number of conclusions about complete strangers solely on the basis of facial information.

1.2 The power of beauty

Our magazines and television screens are not just filled with any faces – they are filled with attractive faces, and it is obvious that both women and men are highly concerned with good looks in a potential partner. Beauty impacts on our lives in many ways not only because we are attempting to attract the attentions of beautiful people to be our partners, but also because attractiveness affects the way that people behave towards us.

Physical attractiveness is a major asset in sexual exchange. Beauty is associated with upward economic mobility, especially for females (Elder, 1969;

Holmes & Hatch, 1938). Attractiveness is also a major determinant of whether people want to date you. Attractive people have more dates than less attractive people (Berscheid, Dion, Walster, & Walster, 1971) and Walster, Aronson, Abrahams, and Rottman (1966) found that after random pairing for a computer date dance that the main determinant of whether participants would like to date their partner again was that partner's independently rated physical attractiveness. In a more ecologically valid setting the same result has been found using real dating frequencies from a computer dating agency, with independently rated attractiveness being the best predictor of those selected most often by others for dates (Riggio & Woll, 1984).

Experimental studies have also demonstrated the many advantages of attractiveness. It has long been noted that there exists a "What is beautiful is good" stereotype (Dion, Berscheid, & Walster, 1972), whereby attractive individuals are perceived to possess a variety of positive personality attributions. For example, in Dion et al.'s study attractive individuals were thought to be able to achieve more prestigious occupations, be more competent spouses with happier marriages and have better prospects for personal fulfilment (Dion, Berscheid, & Walster, 1972). There have been a wealth of studies examining this attractiveness stereotype, mainly demonstrating that attractive people are seen in positive light for a wide range of attributes compared to unattractive people (although some negative attributes, such as vanity, do get attributed to attractive individuals, e.g., Dermer & Thiel, 1975). In mock interviews attractive people are more likely to be hired than less attractive individuals (Cash & Kilcullen, 1985) and attractiveness can also influence judgements about the seriousness of committed crimes (Sigall & Ostrove, 1975). Feingold (1992) reports that, for both males and females, attractive individuals report more satisfying and more pleasurable interactions with others than less attractive individuals. Outside the laboratory attractive people also appear to lead favourable lives; attractive individuals pay lower bail (Downs & Lyons, 1991) and are more likely to be hired for jobs (Chiu & Babcock, 2002; Marlowe, Schneider, & Nelson, 1996) than less attractive individuals. On the basis of such studies it has been suggested that there exists a positive stereotype associated with physical attractiveness (see Eagly, Ashmore, Makhijani, & Longo, 1991; Feingold, 1992; Langlois et al., 2000 for meta-analytic reviews of research on physical attractiveness stereotypes).

The social impact of facial appearance is not restricted to adulthood – attractiveness appears to elicit more positive reaction from infancy. Langlois, Ritter, Casey, and Solwin (1995) found that mothers are more nurturing to attractive babies than unattractive babies, using both self-report and observational methods, and Barden, Ford, Jensen, and Salyer (1989) found a similar pattern in facially deformed babies, with deformed babies receiving less 'loving' behaviour than a control group. In both of these cases the mothers were unaware that their behaviour was less nurturing. In pre-schoolers it has been found that both boys and girls preferred pictures of attractive peers as potential friends and rejected unattractive children and that attractive peers were expected to behave pro-socially and unattractive peers to exhibit antisocial behaviour (Dion & Berscheid, 1974). In natural situations, experiments on group membership in children have also shown a positive correlation between facial attractiveness and acceptance by groups (Krebs & Adinolfi, 1975).

In a classic study, Snyder, Tanke, and Berscheid (1977) found evidence that beauty may impact on the behaviour of the perceived. In a telephone conversation, males who believed the female they were conversing with was attractive were judged to be more positive and socially interested in the person on the phone by independent judges than those who thought they were interacting with an unattractive person. The behaviour of the women interacting with the men also changed according to whether the person talking to them thought they were attractive or unattractive. Those women that had a partner who thought that they were attractive behaved in a more confident way and also believed that the partnered male liked them more than those in the group where the partnered male was told the woman was less attractive. Thus, not only does attractiveness change the way others interact with us, it also changes the way we interact with them.

The data reviewed in this section indicates that attractive people appear to be treated differently to unattractive people despite a prevalent belief, at least in Western society, that one "should not judge a book by its cover". This highlights the influence that facial attractiveness can have on our social interactions as well as our mating behaviour. However, despite the findings of what facial attractiveness can influence, there is still much debate about what is attractive about attractive faces and what is unattractive about unattractive faces.

1.3 The universally attractive face

Beauty has major social consequences but exactly what it is that makes a face beautiful is poorly defined. One of the major deterrents in determining the features of an attractive face lies in the widespread belief that standards of attractiveness are learned gradually through exposure to culturally presented ideals (e.g., through the media in western society) and this has also led to a general belief that cultures vary dramatically in what they perceive to be attractive. If this were true it would mean that attractiveness was arbitrary and what is beautiful now could, in a different time or place, be considered unattractive. The well-known phrase "beauty is in the eye of the beholder" is a testament to our belief that attractiveness is ephemeral. For example, the philosopher David Hume is often quoted for making the argument that beauty, "is no quality in things themselves: it exists merely in the mind which contemplates them; and each mind contemplates a different beauty" (Hume, 1757, pp.208-209).

Figure 2: A Padaung woman She wears neck rings, which may be a signal of status and this may be attractive to Padaung men.

Darwin (1871) was also struck by cultural differences, such as preferences for skin colour, body hair, body fat, and practices such as lip ornamentation and teeth filing, "*It is certainly not true that there is in the mind of man any universal standards of beauty with respect to the human body.*" (Darwin cited by Berscheid & Walster, 1974). Such convictions were supported by early cross-cultural work by Ford and Beach (1951) who catalogued differences between cultures in preferences for body weight, breast size and other aspects of female physique suggesting little consensus (e.g., Figure 2).

While individual and cross-cultural differences exist (see Chapters 6, 7, 8, and 9 for further discussion of individual differences) something in this politically correct view of beauty just does not ring true. Admittedly the latest movie star is not everyone's favourite pinup but it is undeniable that on average Hollywood stars are generally more attractive than the people we meet in the street. You may disagree over your best friend's choice of partner but there are countless individuals that you and your friend could agree were more or less attractive than each particular partner (e.g. Figure 3). So this is the problem with beauty being only in the eye of the beholder: some people are beautiful and some people are not and most people agree on who is and is not beautiful. In Figure 3 the two faces are both symmetric and have smooth skin, yet the composite model face is systematically different from and more attractive than the composite student face in both shape and colouration (coding for differences such as make-up use, age, head pose etc.).

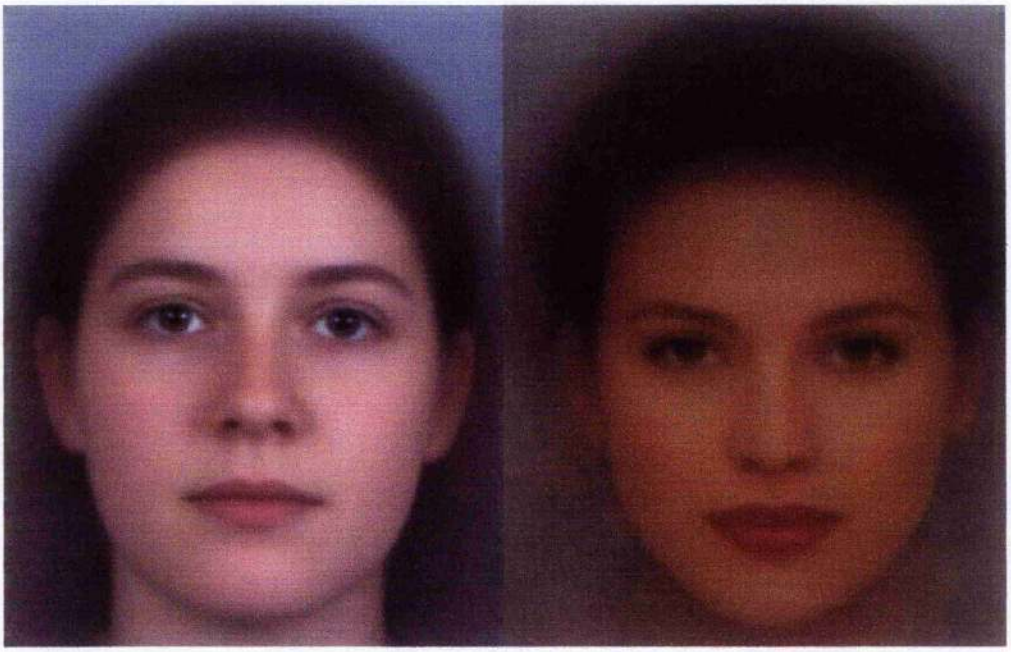

Figure 3: Female student and female model composites

Each picture is a composite of about 50 female faces, students (left) and models (right). People usually agree which of this pair is the most attractive

It appears then that there are certain features of faces that are attractive to all (or at least the majority of) judges. In fact, agreement between individuals is one of the best-documented and most robust findings in facial attractiveness research since the 1970s. Across many studies it has been found that there is a high degree of agreement from individuals within a particular culture (e.g., Chapter 4), and also high agreement between individuals from different cultures (e.g., Cunningham, Roberts, Barbee, & Druen, 1995; see Langlois et al., 2000, for a meta-analytic review). If different people can agree on which faces are attractive and which faces are not attractive when judging faces of varying ethnic background then this suggests that people everywhere are all using the same, or at least similar, criteria in their judgements.

Further evidence for universal attractiveness criteria comes from studies of infants. When infants (3-6 months of age) are shown faces that have been judged by adults for attractiveness they prefer to look at faces which are rated more highly for attractiveness than at those faces rated lower (Langlois et al., 1987; Samuels, Butterworth, Roberts, Graupner, & Hoyle, 1994). Langlois, Ritter, Roggman, and Vaughn (1991) have demonstrated that this preference in infants for attractive faces also holds across cultures (using Caucasian and non-Caucasian faces). It therefore appears that before any substantial exposure to cultural standards of attractiveness infants demonstrate a preference for attractive faces that are in agreement with adult judgements. Again, this suggests a set of criteria for attractiveness that are possessed by attractive faces and not possessed by unattractive faces.

From the studies outlined in this section it has been suggested that there is something innate about attractiveness, that human children (and adults) have a biologically based, universal attractiveness detector (e.g., Langlois & Roggman, 1990). A different explanation also put forward by Langlois and Roggman (1990) is that the basic function of prototype formation in the visual system, which forms the basis of many models of face processing (see Bruce & Young, 1986), is reflected in our preferences for faces that appear more typical of the category of faces. At the very least, the studies suggest that attractiveness is recognised at a much earlier age than most would expect and that contrary to popular belief there is much agreement in what is and what is not attractive about faces across human cultures. Both early developmental and cross-cultural agreement on attractiveness are evidence against the notion that attractiveness ideals are slowly absorbed by those growing up within a particular culture and this suggests that there is something universal about attractive faces (and unattractive faces) that is recognised both across individuals and cultures, and in adults and very early in infancy. While the rest of this Chapter and Chapters 2, 3, 4, and 5 discuss issues associated with agreement on attractiveness this is not to say individual differences do not exist and an evolutionary account for individual variation is discussed further in Chapters 6, 7, 8, and 9.

1.4 Evolution and attractiveness

Evolutionary theory has been proposed to be able to cast light on what features are attractive and what makes people seek out and desire to mate with attractive individuals[2]. Evolutionary theory also offers a good explanation for why humans are

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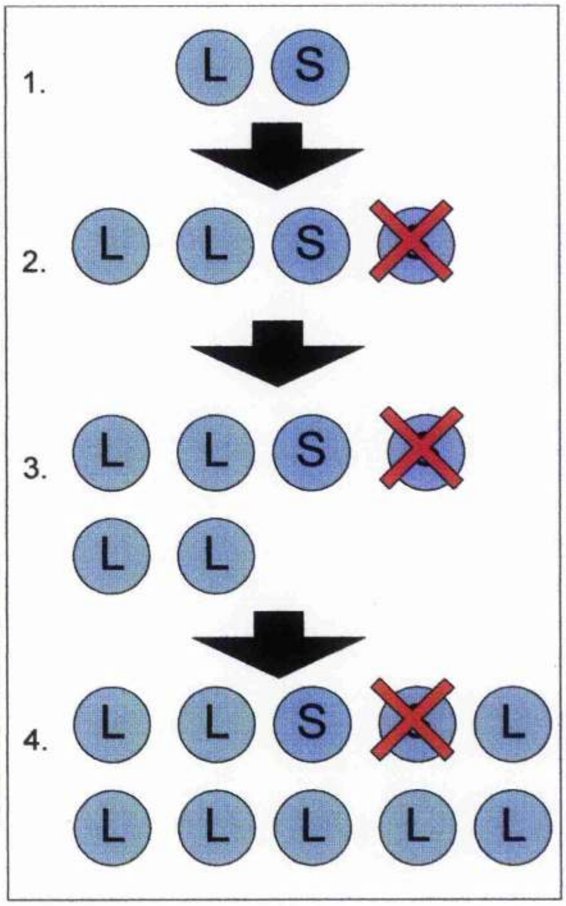
[2] While the following account considers the basic tenets of evolutionary theory in a simplistic manner it is included for completeness and as an example of the type of evolutionary reasoning developed in Chapters 2 and 3.

in agreement over the characteristics that are possessed by an attractive partner. Modern understanding of evolution began when Charles Darwin published his classic work, *On the Origin of Species,* in 1859 and in it he proposed a theory of evolution on the basis of natural selection. The basic idea behind natural selection is a simple one - characteristics, mental as well as physical, that promote survival and the ability to reproduce will be passed down from one generation to the next, while harmful characteristics, interfering with the organism's ability to survive and reproduce, will be less likely to. The mode of transmission between generations is the gene (Mendel, 1866) and mutation and random mixing of genes of parents creates individual variability. It is the non-random survival (selection) of genes in a population that allows evolution to occur. For example, a mutation for genes producing longer legs would increase in a population if long legs allowed individuals to avoid being eaten by predators. Thus long-legged individuals would be more likely to survive and reproduce whereas those with shorter appendages would be more likely to be eaten and so would leave fewer copies of their genes in the next generation (see Figure 4). It should be noted that evolution is a very slow process; billions of years separate the first life forms from the first hominids (the beginning of the lineage of modern humans) and humans have changed very little physiologically for over 100,000 years (the first fossils identifiable as possessing modern human anatomy are found around this time, Aiello, 1993).

Figure 4: The spread of genes that convey an advantage

This simple haploid model has only 2 genes – long and short legs. Each individual produces two offspring each generation, however individuals with short-leg genes are less likely to survive to reproduce and so only half of their offspring can contribute to the next generation (those marked with a red cross have not managed to reproduce). As can be seen, long-leg genes are much more frequent in the population in just a few generations.



The two major problems faced by an organism are survival and reproduction and it is *differential reproductive success* that is the key to evolution. Reproduction is more important than survival because without offspring an organism's genes die with it – in evolutionary terms it is better to lead a very short life producing lots of offspring than a long life and producing none. From this it can be seen that evolutionary success can be measured by how well an organism succeeds in passing on its genes into the next generation and beyond. It is unsurprising then that organisms invest so much in efforts to reproduce.

The second powerful force postulated in evolutionary theory, apart from natural selection, is that of mate-choice, which is a form of sexual selection (Chapter 2 for more detail on sexual selection). There is a diversity of non-human species that rely on external factors (such as feathers, fur, etc.) to attract mates and humans appear no different. In humans, individual males and females differ in their physical attractiveness to members of the opposite gender - there appears to be no human culture yet found in which individuals do not express a preference for some members of the opposite-sex over others (Buss, 1989; Symons, 1979). Such discrimination begs the question of why we are so choosy.

The evolutionary view suggests that choosiness may reflect preferences that drive us to acquire high quality mates - the traits we find attractive in individuals may be directly linked to their value as mates (Symons, 1987). High quality/value mates are those who can best enhance the reproductive success of the judge. Women and men should both be sensitive to cues that indicate higher mate value because individuals who were attentive to cues of high mate value, and based mate-choice decisions on them, left behind more offspring, which would be healthier and more fecund, than those who failed to attend to these cues. For example, males, more than females, value youth in a partner (Buss, 1989) and one explanation for the attractiveness of youth is that fertility, which has a direct impact on reproductive success, decreases with age in females more steeply than it does in males (Buss & Schmitt, 1993). In other words, an evolutionary argument could be constructed in which younger females are proposed to have a higher mate value than older females if youth and fertility are linked. Over evolutionary history males with a genetic predisposition to prefer younger partners could produce more offspring than males who where predisposed to choose older partners. This differential reproduction would potentially continue until a preference for younger partners became universal and species typical in the male population. A preference for younger females does indeed appear to be in place in the human male psyche: males report valuing relative youth in a potential partner more than females do in 37 different cultures (Buss, 1989). Of course, there is more to mate-choice than just age and this leaves those interested in the study of attractiveness the task of finding which characteristics are associated with high and low mate value.

To summarise this section, an evolutionary view assumes that perception and preferences serve an adaptive function: the external world provides information to guide biologically and socially functional behaviours (Zebrowitz-McArthur & Baron, 1983). If in our evolutionary past, information were presented about a person's value (e.g., genetic quality) in any way, then an advantage would accrue to those who utilised these signs and those individuals would leave more genes behind in the next generation. Theoretically then, preferences guide us to choose mates that will provide the best chance of our genes surviving (other views are presented in Chapter 2).

1.5 Discussion: Evolved preferences for human faces

We are aware of the huge amount of attention paid to faces (Section 1.1) and also the many social advantages enjoyed by attractive individuals (Section 1.2). In humans, facial attractiveness is entwined with mate selection - how observers use faces to judge attractiveness and what traits in faces are attractive to judges. There appears to be a universally attractive face, some criteria of attractiveness are agreed upon across both individuals within a culture and between different cultures, and even infants appear to have similar preferences to adults (Section 1.3). Such findings are indicative of biological underpinnings to beauty.

The evolutionary view may provide an answer to both our interest in faces (Section 1.1) and agreement on cues to attractiveness (Section 1.3). Evolution will have favoured the choice of particular facial traits that increase the number of offspring the choosing individual can produce. From this it is easy to imagine that selection pressures will act so as to promote genes for attentiveness to face traits and possibly even genes coding for preferences for face traits, particularly those associated with benefits to choosing individuals, such as genetic quality (e.g., Section 1.4, other explanations for the origin of preferences are discussed in more detail in Chapter 2 and 6). In this way our interest and attraction to certain faces probably reflects evolutionary pressure to select high quality mates. Thus, the human face is likely an ornament, both to be displayed and to be judged, displaying our emotions and identity and also testifying to our value as mates to some degree. Of course there are many facets of what can be referred to here as "mate-value" (e.g., Pawlowski & Dunbar, 1999). Chapter 2 examines theories of evolutionary selection applied to preferences in more detail.

2 Sexual Selection and Theories of Attractiveness

Synopsis

This Chapter introduces ideas of sexual selection for particular traits (Section 2.1). Fundamental differences between males and females inform the strength of competition for access to males and females (Section 2.1.2). Sexual selection is thought to occur through either competition between members of the same-sex (Section 2.2) or through mate-choice (Section 2.3). Mate-choice has received much attention and there are several ideas about the evolution of preference, including good-taste views whereby preference and traits are linked by aesthetic preference (Section 2.4.1) and good-sense views, whereby preference for traits is related to an advantage in choosing mates in possession of that trait (Section 2.4.2).

2.1 Introduction to sexual selection

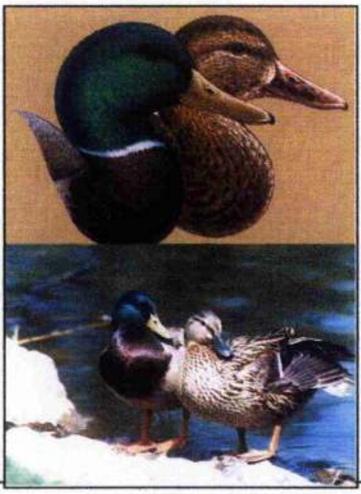


Figure 5: Male (left) and female (right) mallard

While natural selection is proposed to lead members of a species to all possess the same traits (Chapter 1, Section 1.4) the difference between the male and female in some species is often dramatic. For example, Linnaeus (1758) classified into two species the female (mottled brown) and male (metallic green head and neck) of what we now know as both forms of mallard ducks (*Anas platyrhynchos*, Andersson, 1994). Both male and female members of a species are usually under similar pressures from natural selection and so some other force may account for these differences. Darwin

(1871) was the first to point to a force he called sexual selection to account for the seemingly inexplicable differences between the sexes of some species and suggested that sexual selection arises from differences in reproductive success caused by competition over mates. Indeed, the selective forces that operate on males and females as a result of the phenomena of sexual reproduction have been found to have profound effects on both the morphology and behaviour of animals (for comprehensive overview see Andersson, 1994).

2.1.1 Natural versus sexual selection

"Sexual selection…depends, not on the struggle for existence, but on a struggle between the males for possession of the females; the result is not death to the unsuccessful competitor, but few or no offspring" Darwin, 1859, p. 88).

Sexual selection occurs when members of one sex mate disproportionately with members of the opposite-sex on the basis of certain traits, both behavioural and morphological that varies amongst that sex. Whilst some traits favoured by sexual selection may also be favoured by natural selection, others may not (Andersson, 1994). Extravagant and costly characteristics such as the peacock's tail appear to be a hindrance to the survival of the organism. Sexual selection theory explains that these traits, whilst not favoured by natural selection, give those that possess them a reproductive advantage.

Darwin (1871) was the first person to recognise the possibility of sexual selection, having noted features of species that did not serve to aid in the survival of an individual; he posited that these traits could evolve if they were attractive to females. In other words, sexual selection is driven by the differential reproductive success of individuals in competition for access to potential mates. Darwin (1871) defined sexual selection as the effects of "*a struggle between the individuals of one sex, generally the males, for possession of the other sex*".

Darwin suggested that female choice could be the driving force behind such traits as elaborate plumage in some bird species that were problematic to an adaptationist argument. Darwin never looked for an explanation for this differential preference or choosiness, rather he was content with the notion that many species possess a sense of what is beautiful. Darwin did not link sexual selection to reproductive success in general – some traits linked to fertility and reproductive success may not be linked to competition but in discussion it is useful when explaining the traits favoured by sexual selection to postulate that sexual selection does require an increase in the frequency of genes via attracting mates and success in within-sex competition over mates:

Types of selection and traits selected

1. Natural selection – traits favoured by non-sexual aspects of survival (e.g., metabolic efficiency)
2. Sexual selection – traits favoured in competing for mates but disfavoured by (or neutral to) natural selection (e.g., bright colours, courting displays)
3. Natural and sexual selection – traits favoured by both (e.g., pathogen resistance)

Examples of sexual selection can be seen in such traits as the antlers of stags, peacock's tails, bird song, and the extravagant colours of many species of birds and fish. These traits have no obvious input into the survival of an organism, and in fact many of them prove detrimental to the survival of the possessor, and at the very least have a cost to the individual to produce them. For this reason these traits are problematic for a theory of evolution by natural selection. As noted, Darwin suggested both natural and sexual selection but it is best not to overstate the distinction. Given that both types of selection involve the differential survival of genes, whether an individual survives to reproduce because they can run fast to avoid predators or because they are successful in attracting mates, the same principle is in operation in both natural and sexual selection.

2.1.2 Asymmetry in investment to offspring and competition over mates

To understand some of the principles of sexual selection it is useful to know some fundamental differences between males and females. Humans, like many other species, reproduce sexually, with the male depositing sperm inside the body of the female. One of the most important factors in determining the intensity of sexual selection is the relative parental investment each gender provides (Trivers, 1972). The gender investing the least should be the most involved in intrasexual competition, whereas the gender that invests the most should be more discriminating in their partner choice. Trivers (1972) defined parental investment as:

> *"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."* (Trivers, 1972, p. 139)

From this, Trivers concluded that the optimum number of offspring would be different for each parent. In species where male investment is low (e.g., most mammals), males have the potential to sire more offspring than a single female could ever produce and so males can be expected to seek copulations with more than one female.

Sexual reproduction involves the combination of genetic material, half from each parent, so each parent has a roughly 50% share in the offspring's genetic material. In humans this is where the symmetry of parental investment ends. Males and females produce gametes of different sizes (anisogamy), females produce a small and finite number of gametes that are large and energy rich, whereas, in males the gametes (in the form of sperm) are many, smaller, and more mobile. Male investment in this initial phase of reproduction is therefore lower than the investment of the female[3]. It has been suggested that this asymmetry in itself, could generate male competition for access to mates (Trivers, 1972), however, there is a further asymmetry in investment. In humans, infants are cared for inside the mother's body for nine months after insemination and after birth the mother will also produce milk for the child. Another way this asymmetry can be looked at is in terms of the interval between one conception and the opportunity for another. A human female, for example, who has conceived cannot do so for at least nine months as opposed to a man who can theoretically conceive several times a day, with different females.

Females thus make a greater investment in each offspring than males do. Trivers (1972) has argued that, because of this greater investment, females need to look for quality in a mate, so that each child has a good chance of surviving and reproducing. The effort required to produce each offspring means that it pays a female to pick a good mate. Males should be less choosy and desire quantity, as any mate will give a chance of offspring. In this way evolution will have favoured choosy

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[3] The importance of the difference in gamete size between males and females may be overstated as evidence of unequal investment. Sperm are many times smaller than ova but males have to produce millions of sperm, as well as seminal fluid, for a chance to inseminate a single ova produced by a female. Thus, the male's contribution may be as much or even more than the female's.

females and sexually competitive, less discriminating males. This pattern is supported by its exceptions, such as the sea horse, where the females compete for the males, as it is the male who makes a larger parental investment (Clutton-Brock, 1991). This has resulted in a basic asymmetry in mate-choice in many species - males compete for access to females in the vast majority of species (see Daly & Wilson, 1983).

Competition over mates is most apparent in polygynous species. Male choice is also important in species where a partnership with a female reduces a male's chances of achieving other mates. In this instance both males and females are expected to be more selective in their choice of partner. Competition can also occur in monogamous species where mates differ in quality (both in terms of direct and indirect benefits offered, see Section 2.4). As males and females have more similar parental roles in monogamous species we would also expect that female choice of males is also more pronounced in such species.

Bateman (1948) in his classic work with *Drosophila* was the first to quantitatively document that males and females differ in their variation in reproductive success. Males show greater variability in reproductive success than do females and this has come to be known as Bateman's principle. Trivers (1972) revived work in this area by showing that in the Jamaican lizard (*Anolis garmani*) variation in reproductive success was greater in males than in females and that larger males had greater reproductive success. This difference indicates the operation of intrasexual competition. Higher male variance implies that the mating system is in some way polygynous – some males are mating with more than one female and some males are not attaining mates at all.

Asymmetry in investment in offspring has consequences for the type of sexual selection found in any particular species. In humans both males and females invest heavily in offspring and so we expect competition to acquire attractive mates in both sexes. However, the costs and benefits to short- and long-term mating for males and females are very different, with the consequences of a poor choice of mate being potentially more deleterious for females than for males. Thus while we might expect equal choosiness for long-term mates in men and women, there are likely sex differences in preferences for short-term mates. In fact it does appear that women are as choosy as men for short-term as long-term relationships whereas men are less choosy than women for short-term relationships (Buss & Schmitt, 1993). Such theorising also suggests that attractive males will be more able to pursue short-term relationships, a notion I return to in later Chapters (3, 6, 7, & 8).

2.2 Forms of competition and selection

There are two main mechanisms that are proposed to be involved in sexual selection:

1. Intrasexual selection (intra = within) - results from same-sex competition for mates.
2. Intersexual selection (inter = between) - results from the choices of the opposite-sex. Choosiness drives intersexual selection; some males and females are preferentially chosen as mates by the opposite-sex.

Intrasexual competition occurs where members of the same-sex directly compete with each for mating opportunities. This first mechanism has resulted in an array of evolved weapons in the competing sex, usually males, and the role of traits such as antlers and horns in male-male competition is uncontroversial. The second mechanism involves intersexual selection, which is the differential selection of mates by the opposite-sex. The main effects are seen in the chosen sex, usually males, which are differentially selected by the choosier sex, usually females (Section 1.1.3). Intersexual competition is sometimes clouded with intrasexual competition – females of some species encourage males to fight and then mate with the winner (e.g., the spider *Linyphia litigosa*, Watson, 1990). At the gene level the distinction between the two mechanisms is even more blurred – both types of selection involve competition between male genotypes, whether attracting females or fighting males. To understand human mating systems we must consider both types of sexual selection.

2.3 Intrasexual selection and sexual dimorphism

Sexual dimorphism refers to differences between males and females of a species. Intrasexual competition is often thought to be a prime reason for differences between the sexes[4] and indeed fighting between males over access to females is a common sight (as females are in demand, Section 1.1.3). Such intrasexual contests will lead to evolutionary arms races for bigger or better-armed males. There is a limit to size and weaponry though – there are costs associated with bigger and better. It has even been suggested that the trend towards larger size among some ancient mammals may have led to their extinction (Maynard Smith & Brown, 1986).

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[4] Sexual dimorphism can come about in ways other than intrasexual competition. Darwin (1871) suggested the large size of females in some species may be due the fact that larger size favours increased egg production. Rabbits are an example of a species where the females are bigger than males and indeed there appears to be reproductive advantages associated with size, with large mothers giving birth to larger infants, which have a better chance of survival (Ralls, 1976).

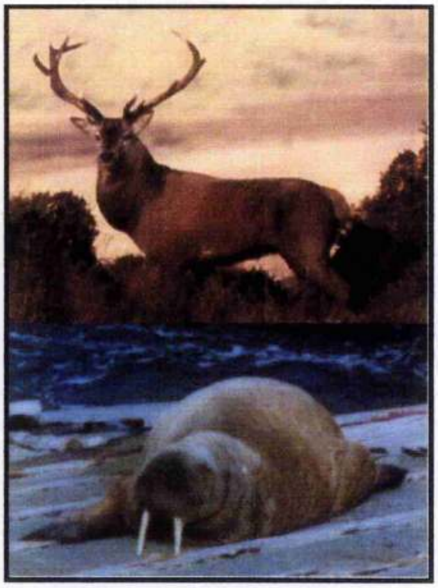

Figure 6: The deer and the walrus: examples of intrasexual selection
Both deer and walrus are sexually-dimorphic in size and have large weapons that they use in male-male contests.

Male-male competition has also been proposed to have led to a general increase in size in males as opposed to females. The importance of size is illustrated by a number of seal species[5]. Male bull elephant seals (*Mirounga angustirostris*) engage in a contest of head-butting during the breeding season and this fighting has led to a strong selection pressure in favour of size. Male seals are consequently several times larger than females (a typical male is about three times heavier than a typical female) and elephant seals are amongst the most sexually dimorphic of all animals. This mating system is called female defence polygyny and to defend a group of females a male needs to be large. Consequently variance in male reproductive success is large as the largest males acquire the majority of mates.

Support for size dimorphism being linked to competition also comes from species where sex roles are reversed – where the male makes a greater investment in offspring and females compete for access to males. Petrie (1983) has shown that in the common British moorhen (*Gallinula chloropus*), where males invest heavily in offspring, competition amongst females for males is more intense than vice versa and that heavier females win fights more often. Under these conditions females are found

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[5] In male-male contests it may also be of benefit to possess weapons. Walruses, elephants, and hippopotami all carry conspicuous tusks and out of the 40 species of deer left today, 36 develop antlers (in 35 of these species antlers are exclusively a male characteristic). Further examples can be seen in beetles such as the stag beetle, where males have large horn-like jaws that are used to fight other males.

to be larger than males on average. The greater the potential pay-off to the male from male-male competition the greater the degree of sexual dimorphism. Alexander, Hoogland, Howard, Noonan, and Sherman (1979) have shown that for both seals and ungulates the average size of a harem in a species is closely related to sexual dimorphism – the more females at stake, the greater the sexual dimorphism.

Sexual size dimorphism is certainly evident even in humans, with males being generally larger than females (Alexander et al., 1979) and facial shape differing between males and females. It is possible that male-male competition may be part of driving selection for these differences (Chapter 3 discusses sexual dimorphism in human faces in more detail) though in the case of human faces intersexual selection, or the consequences of mate-choice, has received the most theoretical attention.

2.4 Intersexual selection: Evolution of choice and the origin of preferences

In non-human species mating involves discrimination, at the very least usually only occurring within a species. It is obvious than both human males and females are particularly choosy in their choice of mate and there appears to be no human culture yet found in which individuals do not express a preference for some members of the opposite-sex over others (Buss, 1989; Symons, 1979).

Mate choice by one gender can exert a selective pressure on both the morphological and behavioural features of the opposite gender. This is the basis for intersexual selection. It is this form of sexual selection that has been most prominently applied to research on human facial attractiveness.

2.4.1 Fisher and runaway sexual selection

"It appears that in a state of nature female birds, by having long selected the more attractive males, have added to their beauty"[6] (Darwin, 1871)

Darwin never wrote about how such preferences may arise (Section 1.1.1), in fact he suggested birds have a sense of aesthetics in the same way that humans have preference for art (Cronin, 1991). Morgan (1903) in a sarcastic response to Darwin's lack of explanation for a starting point for preferences wrote:

> *"Shall we assume that still another process of selection is going on, ...that those females whose taste has soared a little higher than that of the average (a variation of this sort having appeared) select males to correspond, and thus the two continue heaping up the ornaments on one side and the appreciation of these ornaments on the other? No doubt an interesting fiction could be built up along these lines, but would anyone believe it, and if he did, could he prove it?"* (Morgan, 1903, cited in Andersson, 1994).

Fisher (1915, 1930), although not referencing this work, took this idea further, proposing that indeed female preference and male traits may be self-reinforcing - he proposed a process whereby:

1. There initially exists genetic variation in a trait (trait A) that is linked with survival advantage (e.g., positive correlation between tail length and agility

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[6] Evolution of male traits by female choice met much scepticism in Darwin's day (see review in Cronin, 1991). Darwin's emphasis on a notion of aesthetics being similar between humans and other animals also led to criticism.

with agility linked to survival) and there is also initially genetic variation in preference for trait A in the opposite-sex.

2. Individuals with preferences for trait A will produce offspring with the advantage (e.g., those preferring long tails will have more agile offspring and thus more surviving offspring). Thus individuals who possess both genes for trait A and genes for preferences for trait A will become more and more common in the population.
3. There reaches a point in this process when not only is trait A favoured by survival but also by mate-choice due to the increased frequency of the genes for the preference for trait A. Thus the mating advantage adds to the other advantages of trait A and the genes for the preference for trait A are carried to higher proportions in the population. This is then a feedback, "runaway" process which develops at an accelerating pace (e.g., males with the longest tails are chosen as mates whereas those with shorter tails are not increasing the number of long tail genes in the population).
4. Runaway processes reach a limit when trait A becomes so exaggerated that it no longer provides an advantage in terms of natural or sexual selection (e.g., tail size reaches a point where predation negates any benefits of extra size).

Such self-reinforcing selection is often described as "runaway" sexual selection (Fisher's idea are also related to the "sexy-son" hypothesis[7]). In simpler terms, after a preference for any particular trait has arisen, for example, a preference for long tails in

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[7] Reiterating Fisher's theory in terms of sexy sons, if a preference for long tails arose in females in a species then a female not preferring long tails is at a disadvantage – her sons will not have long tails and therefore will not be attractive to other females. Those who do find long tails attractive will have "sexy sons" – attractive to other females because of their long tails. Only when the cost of the ornament outweighs the advantage in terms of attractive mates does the ornament's size or display become stable.

a bird species, females begin to reproduce with males in possession of long-tails to produce offspring with both genes for long tails (in males) and genes for a preference for long tails (in females). A feedback loop between genes for traits and preferences produce stronger preferences and ever larger or more elaborated expression of traits and in a few generations the origin of the preference for the trait is less important than the possession of the trait itself. Linkage between trait and a preference for the trait drive the development of the trait furthur.

How preferences arise: species recognition and sensory bias

In order for runaway selection to work there needs to be reason for a preference for a trait to arise. Fisher (1930) points out that the "grossest blunder in sexual preference which we can conceive of an animal making would be to mate with a species different from its own." Improvement of species recognition is a plausible reason for spread of traits (e.g., Fisher, 1930). Sex recognition has also been postulated to be a viable reason for evolution of preference and trait (e.g., Noble & Vogt, 1935)[8].

Fisher (1930) also suggested that mutations that change female responsiveness to male traits can lead to new preferences but so can mutations in male morphology that fit female preference bias (Andersson, 1994). The initial preference could come from a sensory disposition evolved for another purpose (e.g., Ryan & Rand, 1990). Sexual selection should favour signals that most efficiently stimulate the perceiver, signals that are intense, persistent or otherwise conspicuous (reviewed in Ryan, 1990). For example, the peacock's tail with its many eye spots might exploit a widespread sensitivity to eyes in many animals (Ridley, 1981). In recent years the idea that male

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[8] Sexually dimorphic traits are usually evolved far beyond that needed for recognition, but, as already noted, the initial pressure need only be slight to drive runaway selection.

or female morphology may be attractive because it exploits an already existing preference for something else in the opposite-sex has been called the perceptual bias view (e.g., Enquist & Arak, 1993). There is some evidence that in some species one sex may take advantage of pre-existing preferences in the other sex. For example, in the guppy (*Poecilia reticulata*) there is preference in females for red-throated males but this preference may reflect a colour preference in females that is an adaptation for food selection (Rodd, Hughes, Grether, & Baril, 2002) rather than the colour being preferred due to an advertisement of mate quality (e.g., Houde & Torio, 1992)[9].

Empirical tests of Fisher

One way to test the notion of runaway selection is to examine the geographical association between trait and preference – they should be found close together if Fisher's ideas are correct. In guppies (*Poecilia reticulata*) it has been found that the geographical distribution of bright orange colour in males is strongly positively correlated with the strength of female preference for orange within that population (Endler & Houde, 1995).

Studies of guppies and sticklebacks have shown that a male trait and a female preference for that trait appear to have co-evolved (see Andersson, 1994; Dugatkin & Godin, 1998, for reviews). For example, Bakker (1993) bred from male sticklebacks with either dull or bright red nuptial colouration. Sons of bright red males tended to have bright red patches and daughters were found to prefer males with red patches over males with dull patches. Daughters of dull males showed no preference between

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[9] Of course as yet there is no definitive answer to why female guppies prefer red colouration. As with the facial traits discussed in Chapter 3, whether traits arise as by-products of other aspects of the visual system or as an adaptation to choose high quality mates remains in debate.

dull or red males. This supports the linkage that Fisher posited between male traits and female preference. Wilkinson and Reillo (1994) selectively bred stalk-eyed flies over many generations to produce two groups. In one group males had long eyestalks, and in another the males possessed short eyestalks. In support of co-evolution of traits and preferences they found that the females within each group preferred the stalk length of their own group even without developmental experience of males.

Fisher's runaway hypothesis has been modelled mathematically (see Andersson, 1994, for a review) the results of which, though the models are simplistic, indicate that runaway sexual selection (a preferred trait not favoured by natural selection spreading in a population) is theoretically possible (e.g., Kirkpatrick, 1982; Lande, 1981; O'Donald, 1980; Seger, 1985)[10]. A general problem with evidence for Fisherian processes, though, is that the data does not rule other mechanisms.

2.4.2 Good-genes and indicator mechanisms

In contrast to Fisherian processes, which put forward a "good-taste" view of traits and preferences, indicator mechanisms of sexual selection argue that certain traits are preferred because they are associated with either phenotypic or genotypic quality of individuals possessing them and such preferences can be called "good-sense". In other words, individuals find mates attractive because of the advertisement of the quality of their genetic code or the resources they possess.

Wallace (1889) foreshadowed the notion of what have become known as indicator (or good-gene) mechanisms whereby costly male traits are preferred by

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[10] Of course some models have concluded that Fisher's runaway hypothesis cannot work (e.g., see Andersson for review).

female because they are associated with indirect genetic benefits to offspring (high heritable viability), *"This extremely rigid action of natural selection must render any attempt to select mere ornament utterly nugatory*[11]*, unless the most ornamented always coincide with the 'fittest' in every other respect."* (Wallace, 1889, p26, cited in Andersson, 1994)

Fisher (1915), although more usually associated with self-reinforcing selection, was one of the first to outline an indicator mechanism writing of certain features of animals, *"some will be more conspicuous among the healthy, active and biologically fit... Consider then, what happens when a clearly-marked pattern of bright feathers affords... a fairly good index of natural superiority A tendency to select those suitors in which the feather is best developed is then a profitable instinct for the female bird... "*.

Williams (1966), in agreement, argued, *"One of the functions of courtship would be the advertisement, by a male, of how fit he is. A male whose general health and nutrition enables him to indulge in full development of secondary sexual characters, especially courtship behaviour, is likely to be reasonably fit genetically* (Williams, 1966, p. 184).

More recent empirical research has found evidence in favour of indicator mechanisms. Some studies do indicate that male ornamentation is related to offspring survivability (e.g. Peacocks - Petrie, 1994; great tits - Norris, 1993), although other empirical studies of the heretability of fitness appear inconclusive (Andersson, 1994,

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[11] Worthless; useless or invalid.

for review). Andersson (1994) notes that only a very small amount of fitness heretability would be needed to make indicator mechanisms viable. However, increasing a preference for a trait associated with genetic quality causes a problem.

2.4.3 The paradox of the lek

Some have argued that good-gene models have a fatal flaw – they rely on the heritability of fitness. If all females choose males (or even a single male) with the highest genetic quality and associated fitness (as advertised by his physical traits), then such genes rapidly move to fixation in the population: all offspring possess them. The end result is that differences in phenotypic condition are based on environmental not genetic sources, and 'good-genes' models of sexual selection become meaningless. This has been become known as the paradox of the lek (or lek paradox, Kirkpatrick & Ryan, 1991). Such a dilemma is not irreconcilable. One assumption to be made in order for the paradox of the lek to be true is that selection pressures are constant. Once this assumption is violated, the possibility that heritable fitness can be maintained in a population increases (see Andersson, 1994).

2.4.4 Parasites

One possible source of variation in selection pressures is parasites (e.g., Hamilton & Zuk, 1982). Extremely short parasite generation time sets up an 'arms-race' between host and parasite, leading to conditions where a successful genotype (i.e. parasite resistant) in one generation may not be so in the next (Thornhill & Gangestad, 1993). Parasites exert a tremendous selection pressure on their hosts by reducing their survival and reproductive potential. Individuals differ in their susceptibility to parasites because of genetically inherited host resistance and environmental factors.

Sexual selection for healthy partners would benefit choosing individuals with potentially important fitness benefits (Hamilton & Zuk, 1982).

Following from this reasoning, there are several important conditions that need to be in place in order for parasite driven sexual selection to occur and resolve the lek paradox:

1. Host fitness decreases with increasing parasite burden
2. Ornament condition decreases with increasing parasite burden
3. Resistance to parasites has a heritable component
4. Female choice favours the most ornamented males since these are the least parasitized
5. Host and parasite are locked in a genetic arms race – each trying to stay ahead of the other's resistance

It is the last point that forms part of a solution to the paradox of the lek – a constantly changing set of genes will be most beneficial in defeating parasites. Evidence is generally in favour of this hypothesis – in 3 species (guppy, pheasant, and swallow) all conditions above are satisfied (see Andersson, 1994, for a review).

In several species both male vigour and trait expression are reduced by parasites and so female choice for such ornaments results in selection of males with lower parasite loads (Zuk, 1992). Hamilton and Zuk (1982) have shown that the potential advertisement of parasite resistance is higher in species that suffer from higher levels of parasitism. They found that in North American birds, species with heavy parasite loads possessed more extravagant plumage, allowing males in good condition to advertise their quality. In species where parasites were less prevalent Hamilton and Zuk suggested that there is lower scope for sexual selection for parasite resistance and its advertisement and so exaggerated ornaments are less common. The importance of parasite load is also found in human mate-choice, Gangestad and Buss (1993) have demonstrated that although physical attractiveness (potentially advertising parasite resistance) is the most highly regarded characteristic when it comes to males choosing females, this preference is even further accentuated in areas where parasites are more prevalent.

Evolving an efficient immune system is a way of reliably avoiding the detrimental effects of parasites. However, maintaining the immune system in humans is a very costly activity. Given this huge expenditure, parasite driven sexual selection theory is also related to another prominent theory in good-gene advertisement – handicap theory.

2.4.5 Handicaps

Females may find males who carry a costly handicap more attractive because the fact they have survived with the handicap is an indicator of their genetic quality (Zahavi, 1975)[12]. Zahavi suggested the handicap hypothesis in 1975. He pointed out that large morphological features, such as the peacock's train[13], were more often than not a handicap to survival (e.g., a large tail makes it more difficult to escape predators,

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[12] While the focus of non-human animal research has been on female choice for male traits there are many examples of extravagant female traits. In birds, conspicuous crests or beaks often occur in both sexes (e.g. auks and cormorants) and in many species the female is as brightly coloured as the male (e.g. toucans, parrots, hummingbirds). Likewise, in some ungulate mammals both males and females posses horns or antlers. It therefore seems clear that in many animals the female is as ostentatious in her displays as males are (Johnstone, Reynolds, & Deutsch, 1996).

[13] The peacock's train is a classic example of sexual selection, as with many species where the male is brightly coloured, it is employed to attract mates (Hill, 1991). Petrie et al. (1991) investigated the evolution of this extravagant morphological feature showing that peafowl (*Pavo cristatus*) did not mate at random and that a large part of the variance in mating success was attributable variation in male train morphology: females appeared to choose the males with the most elaborate trains.

bright colours draw more attention from predators). Those individuals who could sustain a long train and still survive were then demonstrating their quality by simply surviving with such an elaborate handicap. The handicap then is an indicator of the good-genes of the individual. As well as presenting a handicap to survival there is another cost to such characteristics. Secondary sexual traits, such as peacock's tails, take energy to produce and so males must be in good condition to afford their production. Poor quality males can neither survive with cumbersome traits nor can they afford to divert resources to the development of such characteristics. In this way the handicaps are said to be 'honest' – low quality males cannot 'fake' such traits.

2.4.6 Parasites and handicaps

In combination the ideas of parasite and handicap driven sexual selection are particularly compelling. Secondary sexual characteristics may reliably advertise the quality of an organism's immune system (Folstad & Karter, 1992). Many secondary sexual characteristics develop under the influence of testosterone and other sex hormones. These hormones potentially have an antagonistic effect on the immune system and so it may be that only high quality individuals are able to develop extravagant secondary sexual characteristics and still maintain an efficient immune system, while those with poor immune defences are unable to bear the cost of the hormones[14].

Testosterone is the primary hormone responsible for the development of male secondary sexual traits, particularly in mammals (Owens & Short, 1995). Folstad and Karter (1992) and Wedekind and Folstad (1994) present a feedback model in which

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[14] Møller (1995) offers an alternative to this view, suggesting that both secondary sexual characteristics and the immune system develop in response to individual condition and so the reliability of the signalling system need not be due to negative interactions between androgens and the immune system.

testosterone production is responsive to parasite load. When parasite load is low individuals are proposed to drop their immunocompetence guard and produce more testosterone in order to develop ornaments to attract mates. With rising parasite load organisms should channel their energies away from display to fight the parasites and so should produce lower amounts of testosterone (Folstad & Karter, 1992; Wedekind & Folstad, 1994). Wedekind (1992) has shown that ornamentation does indeed covary with parasite load in the roach (*Rutilus rutilus*), with different parasites preventing the expression of different traits in males.

Males of many species, including humans, show higher levels of disease caused by parasites than females (Zuk, 1992), implying that testosterone, which suppresses immune system responses, may negatively affect male health (Grossman, 1985)[15]. Some empirical studies also show that parasitic infection causes a lowering in steroid hormone levels in mice and rats (Hillgarth & Wingfield, 1997, for review). Thus, it is plausible that secondary sexual characteristics are indicative of hormone levels in many animals, including humans, and that, because immune systems are handicapped by certain hormone levels, secondary sexual characteristics may represent an honest signal of parasite resistance and possibly even general vigour.

2.4.7 Good resources and good behaviour

In leking species a female receives little from a male and so we would expect her focus will be on acquiring good-genes for her offspring. However, in many species males offer more than just their genes. Monogamous species often engage in lengthy

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[15] Males may also suffer increased parisitization due to lifestyle differences rather than direct hormonal causes. Life history studies indicate men live a 'riskier' lifestyle than women, especially in early adulthood (Daly & Wilson, 1983).

courtships, which may reflect the weighing up of potential partners and potential partners may offer resources such as nesting sites, food, territory, and parental care[16].

In some bird species access to food resources and age/experience influence male traits, such as colouration, song or display rate. Food resources and age/experience factors can provide an advantage to females through improved paternal care (review in Andersson, 1994) and so choice of traits, such as colour, could be preferred through a link not dependent on underlying genes for immunocompetence. The importance of good behaviour has been noted in primates. Goodall (1986) has demonstrated that female chimpanzees show a preference for males who groom them, share food with them, and spend time with them. This tendency can also be seen in humans where females report a preference for men that are kind and understanding (Buss & Barnes, 1986).

It is important to note that the benefits of resources/behaviour can be confounded with classical notions of the benefits of good-genes as resources and genes may be linked. For example, males with good-genes for parasite resistance may be most able to provide food or defend large, high quality territory and so selection for good resources/behaviour may reflect selection for good-genes.

2.4.8 Direct benefits versus indirect benefits

As noted above, there is a distinction amongst the benefits acquired from mating with individuals in possession of good-genes. Two types of advantage are plausible:

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[16] Female choice for male parental ability could even be an adaptive behaviour favoured by natural selection as it impacts on offspring survival further highlighting that natural and sexual selection are not mutually exclusive.

1. Indirect benefits - acquiring good-genes from partners that benefit offspring (e.g., 1.4.6)
2. Direct benefits - acquiring factors other than good-genes from partners that benefit the choosing individual (e.g., 1.4.7)

For example, avoiding a parasitized mate has obvious direct advantages whether parasite resistance is heritable or not (e.g., Gibson, 1990) as there are more direct benefits to choosing a parasite free mate. Parasite driven sexual selection may allow individuals to choose mates who are not carrying contagious parasites (which may be passed on to the individual or to offspring) and that are efficient parents, as well as potentially heritable parasite resistant genes for their offspring (Møller, 1990a). In other words there are several reasons why avoiding a parasitized mate is advantageous:

1. Classical good-genes model - the choice of resistant males benefits a female indirectly through the inheritance of resistance in her offspring (e.g. in ring-necked pheasants parasite resistance appears to be heritable, Hillgarth, 1990).
2. Transmission avoidance model - females avoid choosing mates who may pass the parasite to herself or her children.
3. Resource-provisioning model - a female is choosing a mate not weakened by parasites and so is free to provide resources such as parental care.

Ultimately it may be unnecessary to consider the relative weights of indirect and direct benefits; both indirect and direct benefits are likely to be important in evolution and their contributions to attractiveness are difficult to tease apart[17].

2.5 Discussion: Sexual selection applied to humans

In this chapter I have reviewed some of the most prominent ideas in sexual selection theory. An individual's traits may be involved in inter-sex competition for mates or the result of choosiness by the opposite-sex. There are many facets to choosiness and preference and trait may be explained by good-taste views or good-sense views. One of the most important and widely explored notions of sexual selection is that choosing individuals are able to judge a potential mates genotypic quality from "honest" signals. In humans, both symmetry and secondary sexual characteristics have been proposed as such signals.

Section 1.4.2 reviewed the notion that secondary sexual characteristics are a reliable indicator of health and nutritional status as they indicate parasite burden – which decreases male energy that they can channel into producing these characteristics (Hamilton & Zuk, 1982). Preferences for parasite resistance are possible in humans. There is evidence that in a wide variety of organisms secondary sexual characteristics reliably reflect the parasite load of the individual (Møller, 1990a; 1.1.4.6.; Chapter 3). Many studies of both plants and animals have also shown that parasites influence the symmetry of their hosts, generally making them more

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[17] In a very simplified example, in a made-up population, females prefer men with long legs. Men with long legs can acquire more food in a shorter time than those with smaller legs but are also less likely to be eaten by predators. Thus mating with a male with long legs will probably provide a female with both direct benefits to herself and her offspring in terms of food provision and indirect benefits to her offspring from the survival advantages of genes for long legs.

asymmetric, and further these studies have shown that this asymmetry is related to the attractiveness of the individual (Møller & Pomiankowski, 1993; Chapter 3). Other aspects of sexual selection such as preferences based on intrasexual competition, perceptual bias and good resources/behaviour are also possibly involved in driving preferences for symmetry and secondary sexual characteristics in humans (both important factors of human facial attractiveness) and these are dealt with in more detail in the next Chapter. Ultimately it is almost certain that sexual selection has left its mark on human appearance, as it has in many other animals.

3 Theories of Human Facial Attractiveness: Symmetry and Sexual-Dimorphism[18]

Synopsis

This Chapter discusses preferences for two major traits associated with attractiveness in human faces: symmetry and sexual-dimorphism. Most studies on these traits from an evolutionary view have put forward intersexual selection (Chapter 2) as the driving factor to explain preferences. Theoretically both symmetry and sexual-dimorphism are linked to quality and there is some evidence that this may be the case. It is plausible then that both traits are preferred because of their association with good-genes to the choosing individual (though whether masculinity in male faces is an attractive trait is in debate). Other explanations for the importance and preference for symmetry and sexual-dimorphism are also discussed.

3.1 Sexually selected traits in faces

Physical appearance is important to humans and there appear to be certain features that are found attractive across individuals and cultures (Chapter 1, Section 1.3). The same holds true across the animal kingdom: most non-human species rely on external factors, such as the size, shape and colour of adornments (e.g. feathers, fur, and fins) to attract mates. Research on animals has focused on individual traits that are attractive across individuals, and even species, such as symmetry (e.g., Møller & Thornhill, 1998; see below).

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[18] This review is adapted from Little, A. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002b). Individual differences in the perception of attractiveness: How cyclic hormonal changes and self-perceived attractiveness influence female preferences for male faces. In G. Rhodes & L. Zebrowitz (Eds.), *Advances in Social Cognition: Facial Attractiveness* (Vol. 1, pp. 59-90). Westport, CT: Ablex.

In many studies this evolutionary view of attractiveness has been used to predict the specific characteristics of attractive faces (Thornhill & Gangestad, 1999, for review). The three main factors that have been proposed to advertise the biological quality of an individual in human faces, and hence to influence attractiveness as a mate, are averageness, symmetry, and secondary sexual characteristics. I focus on the last two[19], symmetry and secondary sexual characteristics, as preferences as these traits are further studied in Chapters 4, 5, 7 and 8. These factors are not necessarily mutually exclusive and theories for the influence of each factor on facial attractiveness have received empirical support (reviewed below).

3.2 Symmetry in faces

Symmetry refers to the extent that one half of an image (organism, etc.) is the same as the other half. Much work has been done on morphological symmetry and sexual selection in other animals and this forms the basis of theories of symmetry preferences in humans.

3.2.1 Evolutionary based preferences for facial symmetry

Individuals differ in their ability to maintain the stable development of their morphology under the prevailing environmental conditions under which that development is taking place (Møller & Swaddle, 1997). The ability of an individual to develop successfully in the face of environmental pressures is therefore one proposed indicator of genetic quality.

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[19] I have briefly reviewed the relationship between facial averageness and facial attractiveness in Little & Hancock 2002 and Little, Penton-Voak, Burt , & Perrett (2002).

A character demonstrates fluctuating asymmetry (FA) when symmetry reflects the normal development and deviations from this symmetry are randomly distributed with respect to side (Ludwig, 1932; Valen, 1962). Many morphological features of plants and animals demonstrate fluctuating asymmetry. Fluctuating asymmetry is a particularly useful measure of developmental control ability because we know the optimal development outcome is symmetry. Therefore, any deviation from perfect symmetry can be considered a sub-optimal solution that will result in performance problems in the future. Fluctuating asymmetry is also a useful measure as it subsumes a huge amount of individual variation in development, being the outcome of differences in genetic (e.g., inbreeding, mutation, and homozygosity) and environmental (e.g., nutrient intake, parasite load) factors (Møller, 1997).

Selection against developmental instability begins among sperm and eggs within females of species with internal fertilisation. Only a small fraction of gametes make it and it is mainly those with deviant phenotypes that are disadvantaged (Møller, 1997). Selection during development against deviant gametes and zygotes appears to be a widespread phenomenon. Fruit and seed abortion is very common in plants and Møller (1996) has demonstrated that in the flowering plant fireweed (*Epilobium angustifolium*) around three-quarters of all embryos are aborted during the first few cell divisions because of irregular development patterns. This abortion ratio is directly related to the symmetry of the flowers both of the pollen donor and the pollen recipient. Similar phenomena have been reported for both invertebrates and vertebrates, including humans (Møller, 1997).

There is evidence that symmetry is related to developmental stability. Møller (1990a) found that barn swallow's (*Hirundo rustica*) bodies are more symmetrical if they are in good condition during development and less symmetrical if stressed during development. Møller (1992) also noted that the male barn swallows with the longest tails also had the most symmetrical tails and that these swallows were the most successful in mating. If tails were cut asymmetrically then the mating success of these individuals was reduced providing evidence that symmetry of the tails was found attractive by other swallows.

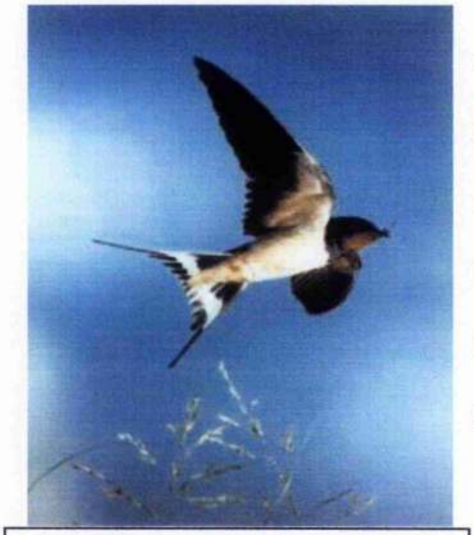

Figure 7: A swallow: much studied in the symmetry literature

Associations between symmetry and trait size are more consistent with a good-genes model of sexual selection than an arbitrary runaway process (Andersson, 1994; Møller & Hoglund, 1991). Within and across bird species, larger ornaments, such as tails, tend to be more symmetrical than smaller ornaments (Møller, 1992; Møller & Hoglund, 1991; see Andersson, 1994). If quality was unrelated to size and symmetry we would expect the cost of ornamentation to create developmental stress for their owners leading to increased asymmetry in large ornaments. However, if only high quality individuals (those with best genes) are capable of bearing the handicap of growing large traits or symmetric traits we would indeed expect size and symmetry of traits to correlate.

Developmental stability and sexual selection have been found to be closely related in many species including plants, insects, fish, birds, and mammals (Møller & Thornhill, 1997a). As symmetry is proposed to relate to performance in general a female with a preference for symmetric males will obtain mates who are able to provide resources and also able to provide genes that will enable more stable growth of her offspring. Meta-analysis's indicate that developmental stability is heritable (Møller & Thornhill, 1997a; Møller & Thornhill, 1997b) though this has been contested (see responses to Møller & Thornhill in J. Evol. Biol., 1997, vol.10, pg. 17-67). If true, this creates a very obvious genetic benefit to offspring and so should lead to preferences in the opposite-sex. The intense developmental selection against asymmetric offspring also means that females choosing symmetric males would benefit in terms of increased fecundity.

3.2.2 Symmetry and actual quality

Whether symmetry is actually related to quality in animals and humans is an issue addressed by a large literature and a complete review is far beyond the scope of this discussion. While the issue is divided, and there is evidence that symmetry is not associated with quality (e.g., Dufour & Weatherhead, 1998), many studies do show links between symmetry and quality (Møller, 1997). For example, in non-human animals, antler symmetry positively related to immune measures in reindeer (*Rangifer tarandus tarandus*, Lagesen & Folstad, 1998) and symmetry is associated with ejaculate quality in three different species of ungulate (Gomendio, Cassinello, & Roldan, 2000). In humans, male body symmetry is positively related to sperm number per ejaculate and sperm speed (Firman, Simmons, Cummins, & Matson, 2003; Manning, Scutt, & Lewis-Jones, 1998) and in human females breast symmetry is positively correlated with fecundity (Manning, Scutt, Whitehouse, & Leinster, 1997;

Møller, Soler, & Thornhill, 1995). The relationship between symmetry and quality is not reviewed in detail here but it should be noted that fitness related characteristics, such as growth rate, fecundity and survivability, are positively associated with symmetry across a number of species and taxa (see Møller, 1997, for review) and ultimately, any link between symmetry and quality, no matter how weak, is sufficient to create a selection pressure on the opposite-sex to choose symmetric mates in order to provide genetic quality benefits to their offspring.

3.2.3 Is symmetry attractive in human faces?

A preference for symmetrical partners is found in many species (see Møller & Thornhill, 1998 for a review). In human males, Thornhill and Gangestad (1994) found that the total number of sexual partners a man reported having was positively related to skeletal symmetry. This finding may not reflect the choice of symmetrical partners per se as it could be a correlate of body symmetry that leads to this choice.

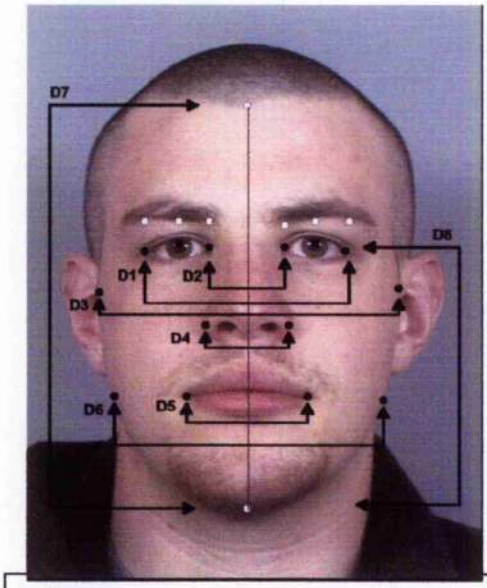

Figure 8: Points used to measure symmetry

From Penton-Voak et al. (2001).

Studies of naturally occurring human facial asymmetries provide evidence that symmetry is found attractive, though again such studies are similarly confounded by potential correlates. Grammer and Thornhill (1994) estimated the overall asymmetry in male and female faces by marking lateral feature points on a face and connecting them with six horizontal lines. On a perfectly symmetrical face the midpoint of each line should be in line with the midpoint of all the other lines and so the sum of midpoint differences would be zero. Numbers greater than zero therefore provide a measure of the asymmetry present in a face. Using this method it was found that the horizontal symmetry of the faces was positively correlated with attractiveness judgments of both male and female faces (Grammer & Thornhill, 1994). Using a similar technique, Scheib, Gangestad, and Thornhill (1999) also found that symmetry and rated attractiveness correlated in male faces. Interestingly, the relationship between symmetry and facial attractiveness was still observed when only the left or right half of each face was presented. While this technique does not remove all cues to symmetry, the authors note that some covariant of symmetry that can be ascertained from half-faces may influence attractiveness judgements. A third study also shows that attractiveness ratings of women positively correlate with measured symmetry ($rs = .28$, $p = 0.02$, n=66, Penton-Voak et al., 2001). Mealey, Bridgestock, and Townsend (1999) studied symmetry and attractiveness in monozygotic twin pairs. Such twins are genetically but not developmentally identical, and hence manifest differing levels of facial symmetry when adult (in such a study genetic quality is presumably held constant and symmetry is related to developmental stress). Symmetry was assessed by having left-left and right-right chimera image pairs of each of the two twins rated for similarity. Separate raters were then asked to judge the most attractive twin of the pairs using the original images. A significant correlation was found between ratings of symmetry and attractiveness for both male and female twins. These four studies of real faces therefore support the notion that symmetry in faces is attractive though do not discount the notion that it is in fact a correlate of symmetry that is attractive in studies of measured facial symmetry.

It is surprising then that several studies directly manipulating human facial images have found that asymmetry is generally preferred to symmetry (Kowner, 1996; Langlois, Roggman, & Musselman, 1994; Samuels et al., 1994; Swaddle & Cuthill, 1995). Most of these studies have created symmetric face images by aligning one vertically bisected half-face with its mirror reflection (Kowner 1996; Langlois et al., 1994; Samuels et al., 1994). These techniques may induce additional stimulus differences unrelated to symmetry. For example, a mouth of normal width displaced to the right of the midline will assume atypical widths in left-mirrored and right-mirrored chimera face images (see Perrett et al., 1999).

Despite results from experiments using chimeric stimuli failing to detect a preference for symmetry, several studies have demonstrated that symmetry can have a positive influence on attractiveness. Rhodes, Proffitt, Grady, and Sumich (1998) have examined symmetry by blending an original face and a mirror image to create more symmetrical versions of original faces (the symmetrical images were retouched to remove artefacts). Symmetry was found attractive in these faces.

Perrett et al. (1999) have also examined the role of symmetry in facial attractiveness and three experiments manipulating symmetry are briefly described below. In experiment one, symmetry in face shape was improved without changing the symmetry of face textures; natural asymmetries in skin pigmentation were present in both the original and more symmetric remapped versions of the same face (Figure 9). Adults' responses to pair-wise presentation of these two versions of each face indicated a clear preference for the symmetrically remapped stimuli. Experiment two used stimuli with average texture information generated from a set of faces. This average texture was rendered into both the original face shapes and symmetrically remapped shapes of the set of individual faces, giving perfect symmetry in the remapped version. Pair-wise presentation showed a preference for perfectly symmetrical face stimuli. Experiment three used a rating task rather than a forced choice paradigm (stimuli were presented one at a time rather than in pairs), and again participants showed a preference for symmetry in faces, rating symmetric faces as more attractive than more asymmetric faces.

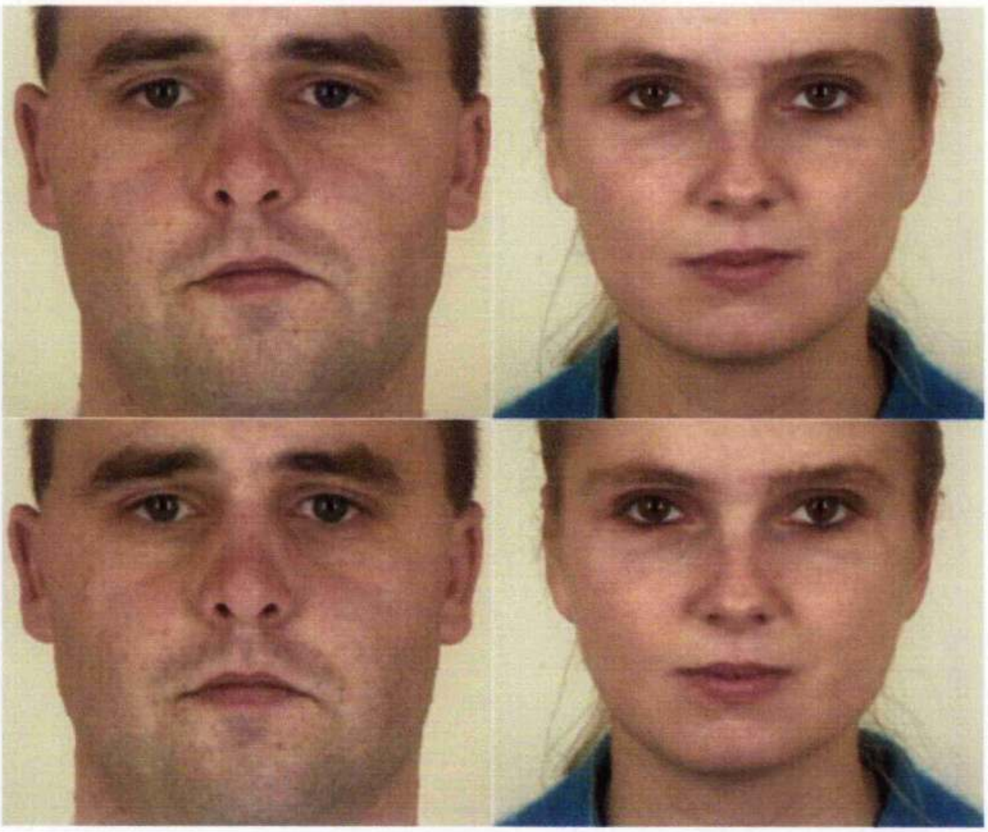

Figure 9: Asymmetric (top) versus symmetric faces (bottom)

Symmetric images are usually found more attractive (e.g., Perrett et al., 1999).

The biggest contender to evolutionary views of symmetry preference is that a preference for symmetry reflects a sensory bias in perception toward symmetric shapes. Such a view implies that symmetry preferences are arbitrary and arise only because of the way in which the visual system operates. For example, computer based neural networks trained to recognise asymmetric stimuli (stimuli with high fluctuating asymmetry) respond most strongly to novel symmetric stimuli which are the average of training stimuli (Johnstone, 1994). Preferences for symmetry can arise in a similar manner in bird species as well. Jansson, Forkman, and Enquist (2002) trained chickens to discriminate between rewarded and non-rewarded stimuli. The stimuli were two asymmetric crosses that were mirror images of each other. On subsequent testing chickens preferred a novel symmetric cross to either asymmetric cross despite the fact it was never associated with reward (Figure 10). So symmetry preference can arise as by-product of the visual system via perceptual experience.

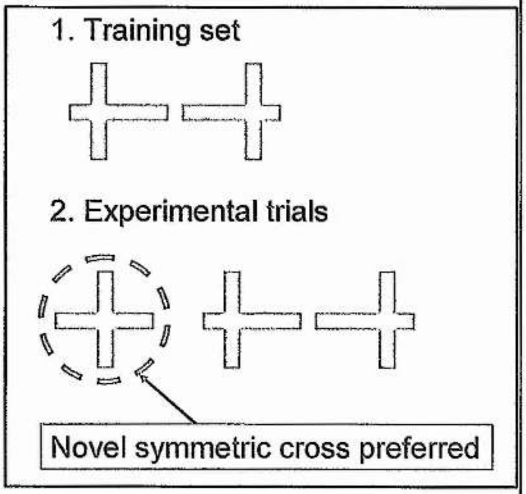

Figure 10: Chickens can learn to prefer symmetry

Chickens were rewarded when responding to two asymmetric crosses, the average of which would be symmetrical. In later trials chickens 'preferred' a novel symmetric cross to either asymmetric cross.

The issue of evolutionary versus perceptual bias accounts of symmetry preferences is discussed further in Chapter 5.

3.3 Secondary sexual characteristics in faces

Male and female faces differ in their shape. Mature features in adult human faces reflect the masculinisation or feminisation of secondary sexual characteristics that occurs at puberty. These face shape differences in part arise because of the action of hormones such as testosterone. Larger jawbones, more prominent cheekbones, and thinner cheeks are all features of male faces that differentiate them from female faces (e.g., Enlow, 1982, see Figure 12 later).

3.3.1 Evolutionary theories of sexual-dimorphism preference

From an evolutionary view extremes of secondary sexual characteristics (more female for women, more male for men) are proposed to be attractive because they advertise the quality of an individual in terms of heritable benefits: they indicate that the owners of such characteristics possess good-genes. The favoured explanation of the importance of these facial traits is that they represent a handicap to an organism (Zahavi, 1975; Chapter 2) and the costs of growing the trait means that only healthy individuals can produce them. In this way, these "honest" handicaps are proposed to indicate the fitness of the owner. For example, secondary sexual characteristics are proposed to be linked to parasite resistance because the sex hormones which influence their growth, particularly testosterone, lower immuno-competence. Testosterone has been linked to the suppression of immune function in many species (see Hillgarth & Wingfield, 1997, for review), including humans (Kanda, Tsuchida, & Tamaki, 1996; Yesilova et al., 2000). Larger secondary sexual characteristics should be related to a healthier immune system because only healthy organisms can afford the high sex hormone handicap on the immune system that is necessary to produce these characteristics (e.g., Folstad & Karter, 1992). For example, in roaches (*Rutilus rutilus*) it has been shown that the size of certain sexual characteristics varies according to parasitic infection, and infection in turn is related to immune system quality (Wedekind, 1992). Female roaches may use sexually dimorphic features to accurately judge infection and immune system quality in males.

3.3.2 Sexual dimorphism and actual quality

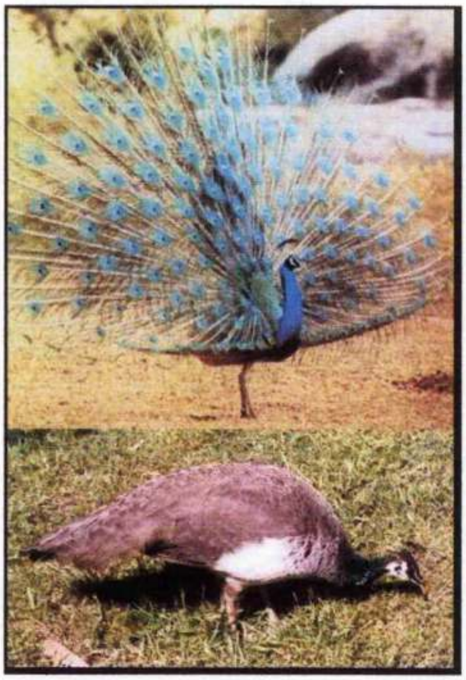

Figure 11: A Peacock and a peahen

There is a large sexual dimorphism in colour and tail ornamentation between peacocks and peahens.

In many non-human animal studies there is a positive association between secondary sexual trait expression and immunocompetence (see Møller, Christe, & Lux, 1999). Peafowl (*Pavo cristatus*) are a good example of an extremely sexual dimorphic species. Peahens are dull and prefer (the much more colourful) peacocks with the most elaborate trains (Petrie et al., 1991). There appears to be an indirect benefit with this choice as the offspring of peacocks with more elaborate trains have greater survival chances (Petrie, 1994) and so preferences for sexual dimorphism in peafowl can be said to lead peahens to acquire males with good-genes.

The relationship between sexual-dimorphism and good-genes in humans is less clear. A recent study by Rhodes, Chan, Zebrowitz, & Simmons (2003), however, has shown that perceived masculinity correlated positively (if weakly, r = .17 n= 154) with actual measures of health[20] in adolescents. If health is heritable then female preferences for masculinity may indeed also reflect the choice of males with good-genes. No relationship was found between femininity and actual health in female faces (Rhodes et al., 2003).

3.3.3 Is sexual dimorphism attractive in human faces?

In females oestrogen dependent characteristics of the female body correlate with health and reproductive fitness and are found attractive (e.g., body shape, Singh, 1993; but see Tovee, 1998). Increasing the sexual dimorphism of female faces should therefore enhance attractiveness as oestrogen also affects facial growth (Enlow, 1982), and indeed there is considerable evidence that feminine female faces are considered attractive. Studies measuring facial features from photographs of women (Cunningham, 1986; Grammer & Thornhill, 1994; Jones & Hill, 1993) and studies of manipulating facial composites (Perrett et al., 1998a; discussed in more detail below) all indicate that feminine features increase the attractiveness of female faces across different cultures. If oestrogenised female faces provide cues to fertility and health then male preferences for such features are potentially adaptive (though the findings of Rhodes et al., 2003, indicate femininity may not indicate health in female faces).

The link between sexual dimorphism and attractiveness in male faces is less clear. Cunningham, Barbee, and Pike (1990) and Grammer and Thornhill (1994) used facial measurements and found that females preferred large jaws in males. 'Masculine' features, such as a large jaw and a prominent brow ridge are reliably

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[20] Annual health scores (1, no illness, to 5, serious illness), based on detailed medical examinations and health histories, averaged across ages 11 to 18.

associated with ratings of dominance in photographic, identi-kit and composite stimuli (Berry & Brownlow, 1989; Keating, 1985; McArthur, 1983-1984; McArthur & Berry, 1987; Perrett et al., 1998a). Despite findings showing a preference for more masculine and dominant faces, several studies have shown that feminine characteristics and faces of low dominance are of increased attractiveness (Berry & McArthur, 1985; Cunningham et al., 1990; Little & Hancock, 2002; Perrett et al., 1998a; Rhodes, Hickford, & Jeffery, 2000).

Cunningham et al. (1990) have suggested that, because both masculine and feminine faces are only rated as moderately attractive, a resolution to this conflict could be that very attractive male faces possess a combination of factors and so reflect 'multiple motives' in female mate-choice (i.e., the desire for a dominant and a co-operative partner, as advertised by a combination of masculine and feminine features). They found that attractive male faces possessed the more infantile/feminine traits of large eyes and a small nose area and the mature features of prominent cheekbones and large chins which indeed may combine both co-operative and dominant signals.

Computer graphic techniques can be used to construct 'average' male and female faces by digitally blending photographs of individuals of one sex. Sexual dimorphism in face shape can then be enhanced or diminished by taking the geometrical differences between male and female face shapes and either exaggerating or decreasing them (e.g., Perrett et al., 1998a). This process simultaneously changes all dimorphic shape characteristics in the face. For example, 'masculinising' a male face shape by increasing the differences between a male and female average increases the size of the jaw and reduces lip thickness because male jaws are larger than female jaws and the lips of men are thinner than those of women.

The shape differences between male and female faces are described by a set of vectors between marked delineation points on the features of the male and female averages (172 landmark points define the outline of the face, the eyes, mouth and nose etc.). Transforms are expressed as a percentage of the distance travelled along these vectors: in a 25% 'feminised' male face shape, each delineation point is moved 25% of the way along the vector to the female average face. The colour information from the original male average is then warped into this new shape. To 'masculinise' male face shapes, the direction of the male-female vector is reversed before the points are moved along it (see Figure 12 for examples of 'masculinised' and 'feminised' male and female face stimuli).

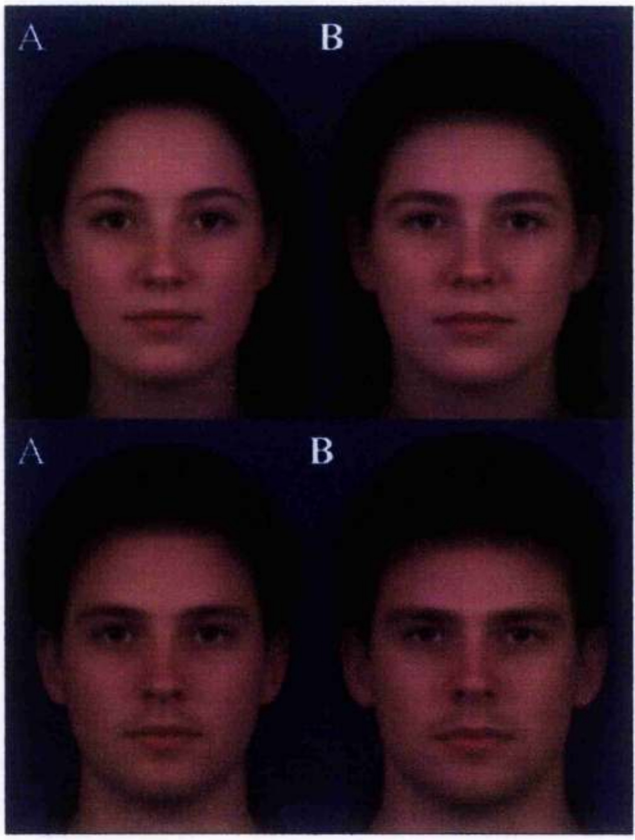

Figure 12: Feminised faces (A) versus masculinised faces (B).

Feminised images are usually found more attractive (e.g., Perrett et al., 1998).

Perrett et al. (1998) presented both Japanese and Caucasian face (average ages for all faces, male and female, was around 21 years) stimuli to 42 Japanese and 50 Caucasian adult males and females (mean age for all participants, male and female was around, 22) in their country of origin. Participants could alter the appearance of a face (increasing the masculinity or femininity of the shape) on a computer monitor by using a computer mouse. For the male face stimuli, the shape selected by Caucasians as most attractive (from the shape range available) was significantly feminised for both the Caucasian male face and the Japanese male face continua. Similarly, Japanese participants also selected significantly feminised versions of the male stimuli for both the Japanese and Caucasian male face continua. Thus, in both cultures it was found that participants showed a preference for feminised male faces.

3.3.4 Masculinity may represent a trade-off in male attractiveness

A preference for 'feminised' male faces seems contrary to predictions from a good-gene view of sexual selection and to some other published studies of male facial attractiveness reviewed briefly above. Rather than preferring typically masculine faces (with prominent brow ridges and large jaws), which are associated with possible immuno-competence benefits, both male and female adults appear to favour a small amount of femininity in men's faces. The explanation may lie in the personality traits masculine and feminine faced males are assumed to possess. Increasing the masculinity of face shape increased perceptions of dominance, masculinity and age but decreased perceptions of warmth, emotionality, honesty, cooperativeness and quality as a parent (Perrett et al., 1998a).

It appears then that 'socially valued' traits such as honesty, warmth, co-operation and skill as a parent are associated with feminised versions of male faces, whilst traits such as dominance are associated with masculinised face shapes. Feminisation of male face shape may increase attractiveness because it 'softens' particular features that are perceived to be associated with negative personality traits. Female face choice may thus represent a trade-off between the desire for good-genes and the desire for a co-operative partner. The relationship between personality attribution, masculinity and attractiveness in male faces is examined further in Chapter 4.

Human males can provide two factors to potential offspring – they can provide paternal investment, directly supporting the child, and they can also pass on potential heritable benefits (e.g., genes for high quality immune systems), providing indirect benefits to the child. The perceived high dominance and lower levels of co-operation point to lower paternal investment from the owners of masculine faces. The perceived lower dominance and greater levels of co-operation point to higher paternal investment from the owners of feminine faces. Although long-term relationships (e.g., relationships lasting months or years that could involve living together, marriage) are generally preferred over short-term relationships (e.g., single dates, one night stands) by females (Buss & Schmitt, 1993), individuals differ in their inclination to take part in short- and long-term relationships (Gangestad & Simpson, 1990; Simpson & Gangestad, 1991). Depending on the type of relationship sought, masculine and feminine faces may differ in their attractiveness to females. In the context of a short-term sexual relationship the perceived cues to high paternal investment in the feminine faced male are of little value to a female. The perceived cues to low parental investment in masculine faced males should have little negative influence on attractiveness in this relationship context. Females should therefore seek to maximise the genetic fitness of potential offspring if they are not extracting any other benefits from their mates and thus may prefer more masculine males. In the context of a long-term relationship the perceived better parenting and increased co-operation of the feminine faced male should be of increased importance, enhancing a feminine faced male's attractiveness. The lower perceived levels of co-operation and decreased value as a parent will detract from a masculine faced male's attractiveness in a long-term relationship. The investment and co-operation benefits may outweigh the benefits of maximising genetic fitness and so feminine males may be preferred as long-term mates (Penton-Voak et al., 1999b). These issues are discussed further in Chapters 4 and 8.

Women with a main sexual partner are more likely to engage in extra-pair copulations at a point in the menstrual cycle when most likely to conceive (Baker & Bellis, 1995). Penton-Voak et al. (1999b) replicated the preference for feminised composite faces, demonstrated by Perrett et al. (1998a), and showed that this preference varies over a woman's menstrual cycle and suggested that there may be certain contexts in which masculinity is found more attractive in a partner. The proposed immunocompetence of masculine males is only of benefit if a female is likely to conceive. Both Japanese and British subjects preferred relatively more masculine male faces during high conception risk than they did for low conception risk, though the preferred face was still feminine. It appears that during the high-risk conception phase females become more influenced by the potential good-gene benefits to their offspring advertised by masculine faced males (Johnston, Hagel, Franklin, Fink, & Grammer, 2001; Penton-Voak, Perrett, & Pierce, 1999a; Penton-Voak & Perrett, 2000).

If females are willing to mate in the short-term with masculine males to maximise possible 'good-gene' benefits, masculine males may respond to such opportunities and pursue a short-term strategy. Feminine faced males may be of less value in terms of good-genes for offspring immunity and so may be forced to offer more parental investment and co-operation to increase their attractiveness. A social cue, such as receiving a lot of attention from females, may predispose men to adopt different strategies. For example, artificially increasing the attractiveness of socially monogamous male Zebra finches (through the use of coloured leg bands) increases the amount of time they spend seeking extra-pair partners and decreases the effort they expend on investing resources in their offspring (Burley, 1986). Similar arguments have been made for humans: males may alter their reproductive tactics based on their apparent mate-value (Gangestad & Simpson, 2000).

3.3.5 Alternative explanations for masculinity preferences

It is plausible that sexual-dimorphism in both males and females is related to intrasexual selection, or competition within a sex to compete for mates. Association between sexual-dimorphism and quality would enable masculine men and feminine women to be better able to compete with others of their own sex, for example, high-quality sexually-dimorphic individuals may be better able to physically fight-off competitors or be able to travel further in the pursuit of mates than lower quality, less sexually-dimorphic members of the same sex. Swaddle and Reierson (2003) have shown that when using slightly different morphing techniques to those outlined above (attempting to use only points that differ between male and female faces under the action of testosterone) that as masculinity increases in male faces they are perceived as more dominant but not more attractive. Thus if we accept the findings of this study it is possible that masculinity in male faces is more related to competition between males than attractiveness to females[21].

Preferences for sexual-dimorphism may also arise in the same way as perceptual bias may account for symmetry preference. Enquist and Arak (1993) used computer neural networks to examine the mechanisms involved in signal recognition. They used these neural networks to model the evolution of female preferences for long tailed conspecifics. Simulated female birds were trained to recognise different patterns that represented males. When shown new patterns it was found that females recognised patterns that were similar to patterns that were first presented but these females also 'preferred' patterns similar to those first presented but exaggerated in size. This result was proposed to suggest that recognition systems could contain "hidden" preferences – that training on discrimination between the category male and female may result in preferences for extremes of sexual-dimorphism. Again there is some evidence that the visual systems of real birds behave as predicted by computer modelling. Chickens trained to discriminate between human male and female faces show just such an effect – after training chickens respond most strongly to faces that differ most greatly in sexual-dimorphism, more than the original rewarded more average male and female stimuli (Jansson et al., 2002).

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[21] The biggest problem with this study is that it is again inconsistent with other studies and does not acknowledge that preferences for sexually-dimorphic traits appear to vary both within (Penton-Voak et al., 1999) and between individuals (Chapters 6, 7, & 8). Thus, without examining the possibility of individual differences known to influence masculinty preference it is presumptious to claim masculinity does not influence opposite-sex mate-choice.

Discussion: Intersexually selected human faces?

In this Chapter I have discussed intersexual selection and other explanations for human preferences for symmetry and sexual-dimorphism in faces.

Intrasexual selection as an explanation for symmetrical and sexually dimorphic traits is an area that requires more work. It is easy to imagine that members of the same-sex perceive some of the same facial information as the opposite-sex but it is unclear so far exactly what they use it for. As both men and women judge masculine face traits in both male and female faces as dominant (Section 1.3.2), selection certainly could act within each sex on these traits. This would be a problem, however, if we found only, for example, that symmetric or masculine men had more sexual partners, as it could be an intra-sex conflict that provided this result (i.e., the most symmetrical, masculine men and the most symmetrical, feminine women are able to discourage lower quality individuals of the same-sex from mating through various means). In fact the majority of this thesis examines the direct relationship between perceptual trait and preference. The computer graphic studies described above (and later Chapters) remove the possibility of confounding mediating variables – individuals directly express their preferences for symmetry and sexual-dimorphism. When rating opposite-sex faces for attractiveness we can assume our focus is on intersexual selection, or mate-choice. It is obvious from the data reviewed here that even if intrasexual selection is linked to symmetrical and sexually dimorphic traits these traits also have a powerful impact on mate-choice.

While a perceptual bias account is also a plausible explanation for opposite-sex preferences with no mediating variables, evidence must be treated with caution.

The first point to note is that while computer models and birds can be trained to exhibit some form of perceptual bias this does not necessarily mean that human brains and perception function the same way. A very general preference for symmetry based on perceptual bias assumes symmetry preference will be constant across stimuli and observers, which does not appear true (an issue taken up in Chapter 5 and later). Likewise, theories suggesting individuals simply prefer sexual-dimorphism as an extrapolation of their recognition systems ability to discriminate male and female, struggle to explain feminine preferences for male faces (Section 1.3.2), changing preferences across the menstrual cycle (Section 1.3.3) and other differences in masculinity preference (Chapters 7 & 8).

Both symmetrical and sexually dimorphic traits do appear to be preferred to varying degrees, even when nothing else in faces is changed, and are theorised to relate to good-genes. As discussed in Chapter 2 there are two main types of possible benefits to acquiring a mate with good-genes, direct and indirect (See Chapter 2). For further discussion and in the studies described later this distinction is best treated as blurred. Whether symmetrical men and women and masculine men or feminine women are chosen either for direct or indirect benefits the result is the same - this attraction results in producing offspring being more attractive to the opposite-sex if the traits in question are heritable. Thus, it is possible that if symmetry and sexual dimorphism are associated with quality then preferences for symmetry and sexual dimorphism also provide good-genes for offspring.

Preferences for symmetry and sexual dimorphism are complicated by the possibility that individuals react to their own traits and experiences. Specifically, as quality increases we expect individuals to make different mating decisions. This is particularly relevant to male facial attractiveness. As discussed in Chapter 2 males have more to gain from short-term relationships and it is possible that highly valued males pursue more short-term relationships. This may mean such males invest less in each partner, forcing women to trade-off good-genes for investment[22]. Again these are ideas that are returned to in the next and subsequent chapters.

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[22] In fact such a system may polarise males into a group of high quality males who can and do adopt a short-term strategy and lower quality males who are forced to invest more to make up for their lower genetic attractiveness.

4 Personality Attribution, Attractiveness and Sexual-dimorphism

Synopsis

This Chapter discusses the importance of personality perception and its link to attractiveness and sexual dimorphism. The two studies presented in this chapter examine how sexual dimorphism is linked to aspects of behavioural attribution. The attributions made to sexually dimorphic faces appear consistent with what would be expected if masculinity in males faces was testosterone dependent and shows that the negative personality attributions elicited by masculine faces impact on their attractiveness.

4.1 The importance of personality attributions

Judging attractiveness of human faces takes only a moment and we also classify faces for broad and tangible qualities like age and sex. Alongside these attributions we also examining more subtle social signals, judging personality, such as deciding whether we think someone is an extravert or an introvert based on their appearance. Facial characteristics influence attributions of various personality characteristics (see below) and, because of their prominent and, in some cases, permanent display, play an important role in social perception. This Chapter examines facial masculinity/femininity, which is linked not only to attributions but also to attractiveness judgements.

There are many studies showing that personality is often inferred from faces. Liggett (1974) found, in a survey of students, that 90% of those questioned believed that faces provided important guides to character. There are also studies showing that observers can make reliable judgements of others' personality traits on the basis of very little information. For example, Albright, Kenny, and Malloy (1988) found that when judges were asked to rate strangers on personality factors, based on no prior acquaintance and in the absence of interaction, a high degree of agreement between different judges on the personality characteristics attributed was found. Further, it was also found that some of the judgements of observers were significantly correlated with the targets' own self-ratings on these factors (most robustly for extraversion and conscientiousness). This paradigm was referred to as "zero acquaintance" and there are many studies confirming these findings. Consensus and accuracy applies between cultures and can be seen using photographs of still faces (Albright et al., 1988), using video footage (Kenny, Horner, Kashy, & Chu, 1992), and using acquaintances' judgements of targets personality in comparison with judges' estimations (Borkenau & Liebler, 1993)[23].

The consistency in attributions must be due to certain visible characteristics in the perceived. For example, males and females differ in facial form and certain behavioural traits such as dominance-submissiveness are thought to be associated with one sex more than the other (whether such a stereotype is accurate or inaccurate). By extrapolation observers may perceive the differences in masculinity of a face within members of the same-sex as relating to the dominance of the owner of that face (Perrett et al., 1998a). As well as potential sex stereotypes, other general

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[23] The listed studies all utilise the five factor model of personality proposed by (Norman, 1963), the factors are, extraversion, agreeableness, conscientiousness, emotional stability, and intellect-openness.

stereotypes also exist. For example, there exists a pervasive "what is beautiful is good" stereotype (Dion et al., 1972; Chapter 1) in which varied positive personality attributions are projected on to those possessing attractive faces (e.g. Feingold, 1992). There also exists a "baby-face" stereotype (Berry & McArthur, 1986) with, individuals whose faces most resemble infants being seen as warmer, less likely to exhibit antisocial behaviour, more submissive, naive, and irresponsible than those with more mature faces (Zebrowitz & Montepare, 1992). This may reflect attribution based on similarity to particular group. Immaturity is associated with childhood and so childlike faces are also perceived as immature (Berry & McArthur, 1985). There are many commonalities between the baby-face/mature-face and masculine/feminine dimensions because male faces change more at puberty than female faces, leaving female faces relatively neotenous (Enlow, 1982).

4.2 Sexual dimorphism, testosterone, and behaviour

Testosterone is proposed to be responsible for masculine male facial traits (Enlow, 1982) and is also linked to male dominance behaviours (Mazur & Booth, 1998), potentially providing a biological link between facial appearance and behaviour.

Testosterone is associated with many dominant and anti-social behaviours (Mazur & Booth, 1998). Increasing testosterone level in adult males is also associated with more troubled sexual relationships. Men with testosterone levels one standard deviation above the mean (estimated from one measurement) are 50% more likely never to marry than men with testosterone one standard deviation below the mean (Booth & Dabbs, 1993). The same study demonstrated that married men with high testosterone were also more likely to suffer troubled relationships, and demonstrated increased incidence of domestic violence and extra-pair sex. Thus whatever good-gene benefits testosterone may be associated with (see Chapter 3) there appears to be a cost to choosing a high testosterone partner in terms of likely paternal investment – high testosterone men may be low investors.

Sexual dimorphism and baby-facedness in faces are also associated with behaviour. There is evidence that baby-faced or mature individuals do to some extent self-report that they have the personality characteristics others attribute to them. Berry and Brownlow (1989) found that ratings of male babyishness were positively correlated with the face owner's self-reported approachability and warmth, but negatively related to self-reported aggression. For female faces, babyishness was associated with low self-reported levels of physical power and assertiveness. Mueller and Mazur (1997) have shown that facial dominance of the graduates from the West Point Military Academy in 1950 predicted their final rank at the end of their careers. Such an environment may reward success in physical male-male competition more than many other walks of life. In the sexual domain, dominant looking teenagers are found to copulate earlier than their less mature faced peers (Mazur, Halpern, & Udry, 1994), suggesting that, at least in teenagers, some masculine facial traits in males are associated with greater sexual access to females.

It appears that data from face shape and behaviour is consistent with what would be expected if sexual dimorphism in faces was related to testosterone. Like high testosterone males, men with masculine faces behave more dominantly (higher rank in military) and have more interest in or opportunity for sex (earlier copulation) than feminine faced men.

4.3 Sexual dimorphism and personality perception

Perceptions of sexually dimorphic faces also appear to reflect the influence of testosterone on behaviour. Increasing the masculinity of face shape increased ranking of perceived dominance, masculinity and age but decreased ranking of perceived warmth, emotionality, honesty, cooperativeness and quality as a parent (Perrett et al., 1998a). High testosterone men are known to behave more dominantly (Mazur & Booth, 1998) and may be less likely to offer high quality or protracted paternal investment than low testosterone men.

A female preference for feminine male faces (Perrett et al., 1998a) can perhaps be partially explained by such personality attributions. Although biological predictions such as handicap theory indicate that females should prefer masculine male faces (Chapter 3), such faces elicit negative personality attributions, which may detract from their attractiveness. Personality traits are reported to be the most important factor in partner choice by both sexes cross-culturally (Buss, 1989; Buss & Barnes, 1986). If desired personality is so important it would appear likely that the personality attributions elicited by a face should impact on its attractiveness.

As facial masculinity may represent a trade-off between the desire for good-genes and the desire for a co-operative partner Cunningham et al. (1990) have also suggested that attractive male faces possess a combination of masculine and feminine features and so reflect ‘multiple motives’ in female mate-choice (see Chapter 3). Age is also potentially a mediating factor in the attractiveness of masculine faces (Perrett et al., 1998a), as masculine faces are seen as older and humans prefer youth in partners (Buss, 1989; Buss & Barnes, 1986). Study 1 examined personality attribution, masculinity, and age and their relationship with attractiveness in faces to explore how masculinity relates to age and personality attribution and its relationship to attractiveness, controlling for such variables.

Given masculinity and testosterone are implicated in short-term attractiveness (see Chapter 3) and proposed to be related to low investment it may be expected that masculine and feminine faced males will differ in personality attributions associated with these issues. Study 2 examined the attribution of desired relationship length (short- versus long-term) to masculine and feminine male faces.

4.4 Study 1: Rating individual faces for perceived attractiveness, personality and sexual dimorphism

4.4.1 Rationale

Masculinity and personality are proposed to be linked and affect attractiveness in male faces. Study 1 examines the inter-relationship between the perception of age, attractiveness, masculinity, and personality in real faces. In line with previous findings (Dion et al., 1972; Perrett et al., 1998a) it was predicted that both attractiveness and masculinity would be associated with personality attribution. Baby-face stereotypes also suggest a role for age in personality attribution though this has not been studied extensively. This Study also investigates the possibility that either age or personality attribution impacts on the attractiveness of masculinity in male faces (Cunningham et al., 1990; Perrett et al., 1998a).

4.4.2 Methods

Participants

Ten female (aged 21-31, mean 23.2 years, 9 Caucasian, 1 Japanese) participants rated faces for their perceived characteristics.

Stimuli

85 photographs of males (of Caucasian appearance) were provided by the individuals, who were asked to provide a recent passport/passport style photograph of themselves as well as report their current age. Photographs were requested in a national newspaper in Britain. These photos were digitised and cropped to show only the head if more than the head was visible in the original image. The actual age of the individuals in the images ranged from 25 to 83 (mean 50.3, S.D. 13.3).

Procedure

The 85 male faces were presented to the ten raters on a computer screen in a random order with eight questions presented along side. Each question was represented by a 7-point scale with bi-polar opposites at either end. Participants were able to select the level on a particular question by using a computer mouse to click on one of seven numbers. Participants rated each face for 2 physical characteristics (unattractive-attractive, masculine-feminine) and 5 characteristics representing the Big Five personality factors (e.g., McCrae & Costa, 1987). The 5 bipolar descriptors are given below together with the broader personality factors in brackets: broad-interests - narrow interests (openness to experience), insecure - secure (neuroticism), quiet - loud (extraversion), ruthless - soft-hearted (agreeableness), and self-disciplined - weak-willed (conscientiousness). Participants selected a box for the approximate age of the face (broken down into two and a half year increments - boxes were presented to participants from 15 up to 100 years old).

4.4.3 Results

Reliability of ratings

Using Cronbach's α, moderate to high inter-rater agreement was found for all the ratings (quiet $\alpha = .68$, insecure $\alpha = .63$, ruthless $\alpha = .78$, self-discipline $\alpha = .57$, broad-interests $\alpha = .70$, attractiveness $\alpha = .80$, masculinity $\alpha = .71$, and age $\alpha = .97$). High agreement indicates there must exist reliable cues within the faces presented for all of the perceived traits.

Inter-relations between perceived physical traits

Pearson's correlations were performed to examine the inter-relations between the ratings of physical traits. For male faces, rated age was negatively correlated with perceived attractiveness ($r_{85} = -.52$, $p < .001$) and positively correlated with perceived masculinity ($r_{85} = .38$, $p < .001$). Attractiveness was not significantly correlated with masculinity ($r_{85} = -.14$, $p = .19$). These results are summarised in Table 1.

Table 1: Correlations between perceived physical traits in male faces

	Attractiveness	Masculinity
Age	-0.52**	0.38**
Attractiveness	-	-0.14

**Correlation is significant at the 0.01 level /*0.05 level (2-tailed).

Inter-relations between perceived physical and personality traits

Correlations were carried out to examine the relationship between personality perception and the perception of physical characteristics in the male faces. These relationships can be seen in Table 2. Perceived broadness of interests was significantly positively correlated with rated attractiveness ($r_{85} = .53, p < .001$) and negatively with masculinity ($r_{85} = -.35, p < .001$). Perceived broadness of interests was negatively, but not significantly, correlated with perceived age ($r_{85} = -.19, p = .082$). Perceived insecurity was significantly negatively correlated with attractiveness ($r_{85} = -.30, p < .001$) masculinity, ($r_{85} = -.26, p = .002$) and age ($r_{85} = -.26, p = .002$). Perceived level of self-discipline was significantly positively correlated with age ($r_{85} = .40, p < .001$) but not significantly correlated with attractiveness, ($r_{85} = .13, p = .23$) or masculinity ($r_{85} = .02, p = .86$). Perceived ruthlessness was significantly negatively correlated with attractiveness ($r_{85} = -.33, p < .001$) and significantly positively correlated with masculinity ($r_{85} = .49, p < .001$) and age ($r_{85} = .22, p = .040$). Perceived quietness was significantly negatively correlated with masculinity ($r_{85} = -.30, p < .001$) but not significantly correlated with attractiveness, ($r_{85} = -.01, p = .94$) or age ($r_{85} = .07, p = .53$).

Table 2: Correlations between perceived personality traits and physical characteristics in male faces

	Attractiveness	Masculinity	Age
Breadth of interests	0.53**	-0.35**	-0.19
Insecurity	-0.30**	-0.26*	-0.26*
Self-discipline	0.13	0.02	0.40**
Ruthlessness	-0.33**	0.49**	0.22*
Quietness	-0.01	-0.30**	0.07

Regression analysis for attractiveness

In order to derive the best predictor(s) of perceived attractiveness, perceived age, breadth of interest, self-discipline, insecurity, ruthlessness, and quietness were entered into a backwards conditional regression (criterion = .01)[24]. In the first step, for male faces, perceived masculinity, age, broadness of interest, level of self-discipline, insecurity, ruthlessness, and quietness were significant predictors of perceived attractiveness ($F_{7,77} = 16.9, p < .001, r^2 = 0.61$). Within the individual predictors it was found that age ($\beta = -.73, p < .001$), broadness of interest ($\beta = .25, p = .019$), quietness ($\beta = -.37, p < .001$), and insecurity ($\beta = -.37, p < .001$) were independently significant predictors of rated attractiveness. Perceived level of self-discipline ($\beta = .17, p = .082$) and masculinity ($\beta = .18, p = .070$) showed trends towards significant correlations with attractiveness. Ruthlessness was not related to attractiveness in this model ($\beta = .1, p = .95$).

In one step perceived ruthlessness was removed from the model (there were no further removals as the p values of all the remaining variables were below criterion, .01). Overall the model was significant ($F_{7,77} = 20.0, p < .001, r^2 = 0.61$) with an identical r^2 to that with the model including ruthlessness and there were no changes to the above relationships though the p values of all variables decreased slightly, including masculinity ($p = .053$, significant at $p = .05$ if rounded down to 2 decimal places).

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[24] I note that in Chapter 9 I use the non-parametric binomial regression. I feel this difference in analysis is justified as Chapter 9 deals with data that is better described as categorical than the data descibed here. I also note the similarity in results between parametirc and non-parametic versions of this test on the data presented in this Chapter. Using a binary logistic regression, with variables split by mean score, in the first step, reveals the relationship between attractiveness and masculinity is positive ($B = 1.1$ $p = .091$).

Comparing the zero-order correlation of masculinity and attractiveness with a partial correlation controlling for personality

The regression model shows that masculinity is positively related to male facial attractiveness when controlling for perceived age and personality variables. Potentially perceived age may be the mediating factor in increasing the attractiveness of masculinity, however, the correlation between attractiveness and masculinity remained negative when controlling for perceived age ($r_{85} = -.16$, $p = .15$, in fact more negative than the original zero-order correlation), implying that personality attribution accounted for the increased attractiveness of masculine faced males in the regression model.

Further analysis was carried out to test whether the correlation between attractiveness and masculinity significantly changed between the zero-order correlation and the partial correlation. A partial correlation, controlling for perceived age, broadness of interest, level of self-discipline, insecurity, and quietness (as identified by the backwards conditional regression above as the best model) again showed a positive correlation between perceived attractiveness and perceived masculinity ($r_{85} = .22$, $p = .053$)[25]. A Fisher r-to-z transformation was conducted on two correlation co-efficients, the original zero-order correlation between attractiveness and masculinity ($r_{85} = -.14$) and the partial correlation between attractiveness and masculinity, controlling for age and the personality variables (above, $r_{85} = .22$) in order to calculate a value of z to assess the significance of the difference between the two correlation coefficients. This analysis revealed that the zero-order and partial correlations were significantly different ($Z = 2.33$, $p = .020$).

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[25] The p value is identical to that in the regression – this analysis was conducted to provide r for the analysis to compare with the zero-order r between attractiveness and masculinity.

4.4.4 Discussion

Study 1 shows that there is high agreement for a variety of different attributions, including attractiveness, masculinity and personality. The high inter-rater agreement for attractiveness ($\alpha = .91$) is consistent with universal notions of attractiveness (See Chapter 1). There was also high agreement for the personality variables.

Age was positively related to masculinity in male faces. Perrett et al. (1998) have shown that male faces manipulated to look masculine (Chapter 3) look older than feminised male faces. Such findings are consistent with growth of male faces. Masculine male traits develop at puberty and so the difference between youth and adulthood is characterised by an increase in facial masculinity (Enlow, 1982). By extrapolation, increasing masculinity should make males look older. Male faces were also judged as less attractive as they appeared older, which would be expected if youth is valued in partners (e.g., Buss, 1989). Age was also correlated with several of the perceived personality traits. Older individuals were seen as more secure, more self-disciplined and more ruthless than younger individuals. Such findings are consistent with the baby-face stereotype type noted earlier (Berry & McArthur, 1985), though baby-face findings relate to infant resemblance rather than just age. In Study 1 older individuals were attributed with traits more consistent with adulthood than childhood. It is important to note the age range is large between the faces in this study and so the relationship between perceived age and other variables should be treated speculatively.

Masculine faced males were seen as having narrower interests, being more secure, loud and ruthless than feminine faced males in Study 1. This finding replicates some of the pervious attributions found to be made to masculine faced men. For example, (Perrett et al., 1998a) found that masculine faced men were seen as less co-operative and more dominant than feminine faced men. While speculative, it is plausible that the dimensions co-operation/ruthless and dominant/secure are related. It is notable that from what we know about testosterone we would possibly expect masculine faced men (if facial masculinity reflects the action of testosterone) to behave more ruthlessly and to be more secure and confident (Mazur & Booth, 1998).

The traits associated with masculinity could have either positive or negative value. It is possible that broad interests, security and soft-heartedness are all valued traits in a partner and indeed the men who were seen as having broader interests, being more secure and being more soft-hearted were judged as more attractive than men with the opposite cluster of traits. Thus masculinity does appear to be associated with some negative traits (narrow interests, ruthlessness) but also a positive trait (security).

Importantly for the current study, in the zero-order correlations, masculinity was negatively but not significantly correlated with attractiveness, in line with measured preferences for computer graphic manipulated masculinity in male faces (Perrett et al., 1998a; Rhodes et al., 2000).

The regression analysis showed the above variable's relationships with attractiveness were similar controlling for various traits. In the regression, breadth of interest and security were still positively related to attractiveness. Perceived age remained negatively related to attractiveness. Perceived quietness became significantly negatively related to attractiveness when controlling for the other traits. Perceived self-discipline and, importantly, masculinity both showed trends towards significant positive correlations with attractiveness. In the second step of the regression the relationship between masculinity and attractiveness is extremely close to significance (p =.053). Ruthlessness was not related to attractiveness in the regression.

Although the increased perceived age of masculine faces over feminine faces has been posited to detract from the attractiveness of masculine faces (Perrett et al., 1998a), age did not appear to be a mediating variable in the attractiveness of masculinity in male faces. Study 1 also examined whether negative personality attribution detracts from the attractiveness of masculine male faces. Given that masculinity was somewhat negatively correlated with attractiveness and that masculinity was also significantly related to undesirable personality traits it is possible that negative personality attributions to masculine faces could detract from their attractiveness. For male faces the negative correlation between attractiveness and masculinity changed to a positive relationship when controlling for the effects of personality attribution (and was also significantly different from the zero-order correlation) implying that negative personality attribution does detract from the attractiveness of masculine faces.

4.5 Study 2: Sexual dimorphism and perceived sexual strategy in male faces

4.5.1 Study 2.1

4.5.2 Rationale

Study 2.1 aimed to assess whether manipulated masculinised and feminised male facial images are associated with the tendency to seek relationships of different lengths. Given high testosterone males are more likely to have affairs (Booth & Dabbs, 1993) and dominant faced adolescents report having sex earlier (Mazur et al., 1994), then a masculine face shape may be associated with the perception that a man will seek short-term relationships in preference to making long-term commitments (see Chapter 3, Section 3.3.4 for reasons why masculine faced men may be more able to pursue short-term relationships than feminine faced males). By contrast a feminine face shape may be associated with male commitment to relationships.

4.5.3 Methods

Participants

The experiment was broadcast on British television on the BBC's Tomorrow's World programme as part of a nationwide Science week. 18,130 viewers of the BBC's Tomorrow's World MegaLab television program participated in the study. Due to the nature of data collection no other information about the participants was collected.

Stimuli

Two dating adverts were used in the study, one depicting a male seeking a long-term relationship and the other a male seeking a short-term relationship. The same general information is contained in each. They differ in specific cues to the likely temporal context of the relationship.

Short-term advert: Attractive, young (single) professional, back in town for short period, likes pubbing, clubbing, being funny and plenty of sports, would like to meet someone for fun and laughter.

Long-term advert: Attractive, sporty, young, single, male with good sense of humour, professional job, looking to settle, into pubs, clubs etc, seeks someone fun for love and to cherish forever.

Two faces, created using techniques used in previous studies (Perrett et al., 1994; Perrett et al., 1998) were also presented. An original composite face was created by first manually marking a total of 174 key locations around the main features and the outline of 20 male faces (20-25 years of age, mean = 22). The average location of each point in the faces was then calculated. The features of the individual faces were then morphed to the relevant average shape before averaging the images to produce a photographic quality result.

This composite face was transformed in shape to create a masculinised and a feminised version. Composites were made of 50 male and 50 female faces using the techniques outlined above to produce an average male and female shape. The vector difference in shape between the male and female averages was then calculated. This vector can be applied to the points of any of the faces to move them towards either a more feminine or more masculine shape. This study used composite male faces that had been moved to 50% more masculine and 50% more feminine. The only difference between the two faces was the degree of masculinity or femininity. The transformed faces can be seen in Figure 13.

Figure 13: Feminised (left) and masculinised (right) versions of the same male face used in Study 2.1

Procedure

The broadcast was split into two geographical regions and one dating advert was presented in each region. Participants heard one advert read aloud to them by a male actor, while the text of the advert was presented visually on screen. The same actor read both adverts, one to each region. The two faces were then presented, labelled male A and male B, with two phone numbers underneath these faces. Participants were asked to phone in a response, which male, A or B, was most likely to have written the presented advert. Only two responses were possible in each region. These were either the masculine or feminine faced male associated with the short-term advert (region 1) or the masculine or feminine faced male associated with the long-term advert (region 2). Phone lines were open for ten minutes following the display of the numbers. An automated dial-in system recorded the number of phone calls to each line number.

4.5.4 Results

The feminine male face was seen as being more likely to have written both the long and short-term adverts[26]. This difference in association was significant for both the short-term advert (in region 1, 56% > 50% expected by chance, binomial test, corrected Z–score = 13.99, $p < 0.00001$) and for the long-term advert (in region 2, 66% > 50%, binomial test, corrected Z–score = 24.16, $p < 0.00001$). The percentages and actual numbers of responses associating the two faces with the different adverts are presented in Table 3.

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[26] Potentially this may be due to the voice of the actor reading the dating adverts. A young and high-pitched sounding male read both adverts. The youthful and high-pitched voice may be associated with femininity and so the attribution may have been partly to the voice and not the advert alone. There are other possibilities, for example, feminine faced males may be seen as more likely to use dating adverts to acquire mates.

Table 3: Percentage of participants associating the masculine and feminine face with each advert (actual numbers in brackets).

	Short-term advert (Region 1)	Long-term advert (Region 2)
Feminine face	56% (7002)	66% (3755)
Masculine face	44% (5441)	34% (1932)

Of greater interest, the proportion of subjects in region 2 associating the feminine male face with the long-term advert (66%) was greater than the proportion of subjects in region 1 that associated the feminine face with the short-term advert (3755/5687 = 56% corrected *Z*-score = 15.2, $p < 0.000005$). In comparison, the proportion of subjects in region 1 associating the masculine male face with the short-term advert (44%) was more than the proportion of subjects in region 2 that associated the masculine face with the long-term advert (5441/12443 = 34% corrected *Z*-score = 22.9, $p < 0.000005$). In short, the feminine male face was more associated with seeking a long-term relationship while the masculine male face was more associated with seeking a short-term relationship.

4.5.5 Study 2.2: Counterbalancing Study 2.1.

Rationale

The inability to counterbalance the adverts, actors' voices, and lack of other information about participants were all weaknesses of Study 2.1. Thus, the above experiment was repeated using the same adverts, two different pairs of composite male faces (one masculinised and one feminised 30%) and recording more information about the judges.

Participants

One hundred and fifty-four males (aged 16-61, mean = 28.6, S.D. = 9.7) and 287 females (aged 16-60, mean = 25.9, S.D. = 9.3) took part in this experiment. The experiment was administered over the Internet and participants were volunteers following a link from a psychology research web site.

Stimuli

The same two adverts were used as in the above experiment. A second pair of adverts, which reflected the same wording as the first pair but with critical phrases exchanged, was used for counterbalancing.

Counterbalanced short-term advert: Attractive, sporty, young, single, male with good sense of humour, professional job, back in town for short period, into pubs, clubs etc., would like to meet someone for fun and laughter.

Counterbalanced long-term advert: Attractive, young (single) professional, looking to settle, likes pubbing, clubbing, being funny and plenty of sports, seeks someone to love and to cherish forever.

Two composite masculinised and feminised face pairs (made up from different faces from those used in experiment 1) were presented along with the adverts. One composite face was made from 25 male faces (19-23 years of age, mean age = 21) and another made from 21 male faces (19-24 years of age, mean age 21). Both composites had masculinised and feminised versions made using the methods outlined above.

Procedure

Participants were presented with both a masculinised and a feminised face with either the short or long-term advert underneath. Participants were then asked to pair up the adverts with the face of the person most likely to have written it. To pair up faces and adverts two buttons were presented:

1. I think the adverts match the faces
2. I think the adverts should be swapped to match the faces

This meant only two outcomes were possible:

1. Masculine face paired with the long-term advert and feminine face paired with the short-term advert
2. Feminine face paired with the long-term advert and masculine face paired with the short-term advert

The faces were shown in a random order with a random advert pair (original or counterbalanced pair).

Results

In agreement with the findings from Experiment 1, the feminine faces were more often associated with the long-term advert and the masculine faces were more often associated with the short-term advert for both male and female observers (Table 4). Female participants associated the masculine faces with writing the short-term advert and the feminine faces with the long-term advert more than vice versa (face pair 1, corrected *Z*–score = 2.23, $p = 0.013$; face pair 2, corrected *Z*-score = 2.46, $p = 0.007$). Male participants associated the masculine faces with writing the short-term advert and the feminine faces with the long-term advert more than vice versa (face pair 1, corrected *Z*-score = 3.30, $p = 0.0005$; face pair 2, corrected *Z*-score = 3.79, $p = 0.00008$).

Table 4: Percentage of male and female participants associating the masculine and feminine face with the different adverts (actual numbers in brackets).

	Face	Masculine face - long-term Feminine face - short term (%)	Masculine face - short term Feminine face - long term (%)	Total (%)	Significance
Male	1	36.4 (56)	63.6 (98)	100 (154)	<0.001
	2	34.4 (53)	65.6 (101)	100 (154)	<0.001
Female	1	42.9 (123)	57.1 (164)	100 (287)	<0.001
	2	41.5 (119)	58.5 (168)	100 (287)	<0.001

Male participants were also found to be more likely to attribute the masculine faced males as pursuing the short-term relationship and the feminine faced males with the long-term relationship than female participants were (male proportion > female proportion, face pair 1, 63.6 > 57.1, corrected *Z*-score = 2.23, $p = 0.013$; face pair 2, 65.6 > 58.5, corrected *Z*-score = 2.46, $p = 0.007$).

4.5.6 Discussion

Study 2 demonstrates that consistent stereotypical attributions are made to masculine and feminine faced males. Feminine male faces are perceived to be associated with a long-term relationship more than a short-term relationship while masculine male faces are perceived to be associated more with a short-term relationship than a long-term relationship. The perceptual association of facial masculinity and the likely pursuit of short-term relationships appears robust: it has been shown for three pairs of faces, in large samples, across a wide age range of perceivers and for both male and female judges.

There are several possible explanations why judges associate masculine males more strongly with seeking a short-term relationship than feminine faced males. The association with short-term sexual strategies may be part of the general negative expectancies of masculine faces, such as low co-operation (Perrett et al., 1998a). The adverts used in Studies 2.1 and 2.2, however, do not differ in a way that reflects positive or negative personality traits (being "back in town for a short period" versus "looking to settle", looking for someone "for fun and laughter" versus looking for someone "to love and cherish forever"). Instead the adverts just provide cues to the likely length of a relationship and it is therefore unlikely that the relationship attribution is an extension of a negative bias towards masculine faces.

A second possibility is that because males and females differ in their desire to engage in long-term and short-term mating (males show more interest in short-term relationships than females, Buss & Schmitt, 1993; Simpson & Gangestad, 1991), gender based attributes are carried over to those males who more resemble women, and those who are of enhanced masculinity. Feminine faced males would then be thought to possess more typically female personality characteristics and masculine faced males thought to possess more typically male personality traits. This explanation could parallel findings showing that males and females with facial characteristics resembling infants are also thought to possess infant-like personality traits (e.g., immaturity is associated with childhood and childlike faces are thus perceived as immature, Berry & McArthur, 1985). Similar findings have been shown by Friedman and Zebrowitz (1992) who have demonstrated that presenting faces manipulated to posses traits reversing the natural association of gender and facial maturity (i.e. presenting baby-faced males and mature-faced females) resulted in sex stereotypes being weakened or reversed.

A third explanation is that the stereotypic association found in Study 3 may reflect the relative attractiveness of masculine and feminine faced males in different relationship contexts. If females are willing to engage in short-term relationships with masculine faced men to acquire good-genes, then the attribution that masculine men are more likely to pursue short-term relationships than feminine faced males may be accurate. That is, if females do choose more masculine faced men as short-term partners then masculine men can be observed to pursue more short-term relationships than feminine faced men. The reason masculine men are proposed to be more attractive in the short-term is the potential good-gene benefits advertised by their high testosterone so again the link between personality perception and facial masculinity comes down to their relationship with underlying testosterone.

However the associations found in study 2.1/2.2 come about, if, over time, feminine males are perceived to be high investors and masculine males low investors then social cognitive processes, such as stereotyping and self-fulfilling prophecies, may reinforce or exaggerate behavioural predispositions of masculine and feminine featured men.

4.6 General discussion: The importance of personality attributions in the attractiveness of sexually dimorphic faces

From the studies presented in this Chapter, it appears clear that people are happy to attribute a wide range of personality traits on the basis of minimal information. Study 1 demonstrates high agreement for attractiveness, masculinity and personality. Personality was related to both attractiveness and masculinity in male faces and masculinity was also positively linked to the traits of ruthlessness, security, and loudness. Such attributions are in line with what we might expect if facial masculinity is associated with testosterone in males. The attractiveness of masculinity does appear to be mediated by personality in males, suggesting that negative personality attributions do detract from the attractiveness of masculine male faces.

Study 2 demonstrated that feminine male faces are perceived to be associated with a long-term relationship more than a short-term relationship while masculine male faces are perceived to be associated more with a short-term relationship than a long-term relationship. As discussed earlier, the association with short-term sexual strategies may be part of the general negative expectancies of masculine faces;

however, given that masculinity was associated with one positive trait (security) in Study 1 this argument becomes less plausible. An evolutionary explanation that masculinity is desirable for good-genes but reveals likely low investment and so masculine and feminine faced males may differ in their attractiveness as long- and short-term mates does sit well with the data from the two studies. It is interesting to note that the length of relationship may have an important influence on what females consider attractive in a male (a point returned to in Chapter 8).

Studies 1 and 2 both present data on personality attribution and masculinity in male faces that is consistent with what we would expect if masculine traits develop under the action of testosterone. It is possible that individuals attribute traits in line with what they see in the behavioural differences between women and men (e.g., males more physically aggressive than women) to faces more or less resembling women or men. It is also possible that if facial masculinity is related to testosterone within males the stereotypes may reflect the observed behaviour of high testosterone masculine faced men and low testosterone feminine faced men. In this way the attributions seen in Studies 1 and 2 could potentially lead to the adaptive recognition of behavioural propensities based on underlying testosterone levels within a sex.

Personality perception is equally applicable to either male or female judges and so may affect intrasexual competition – in non-human animals male contests not only select for external weapons involved in fighting such as horns but also psychological weapons to signal the potential for victory, *"A sprightly bearing with fine plumage and triumphant song are quite as well adapted for war propaganda as for courtship"* (Fisher, 1930). It is certainly a possibility that sexual dimorphism in personality and appearance may represent a significant factor in intrasexual competition. For example, perceived facial dominance in males is positively related to rank attainment at a military academy and to the final rank of those who graduated from Staff College (Mueller & Mazur, 1996). The same traits that make a male dominant over other males may be the exact traits that females find attractive. For example, high quality males win fights and high quality males can provide resources and genes for high quality. It is thus difficult to disambiguate how personality traits relate to inter- versus intrasexual selection but again the distinction may be overstated – as long as we are examining choice for opposite-sex faces (Chapters 5, 7, 8, and 9) we are dealing with mate-choice, even if this preference is based on intrasexual success.

5 Evolutionary Versus Perceptual Bias Accounts for Symmetry Preferences[27]

Synopsis

This Chapter examines the two major views put forward to explain symmetry preferences: evolutionary advantage and perceptual bias views. Two studies are presented that test some specific predictions of two different aspects of the perceptual bias view and it is concluded that current data are more consistent with symmetry preferences being particularly relevant to mate-choice rather than a simple result of perceptual bias.

5.1 Symmetry is attractive

Symmetry is found attractive by many animals (see review by Møller & Thornhill, 1998; Chapter 3). Studies of naturally occurring human facial asymmetries provide evidence that symmetrical faces are attractive, showing that measured symmetry is positively correlated with attractiveness judgments (facialmetric measures- Grammer & Thornhill, 1994; Jones et al., 2001; Scheib et al., 1999; psychophysical measures - Penton-Voak et al., 2001; Mealey et al., 1999). Consistent with preferences for naturally occurring symmetry in real faces, recent computer graphic studies (Little, Burt, Penton-Voak, & Perrett, 2001; Perrett et al., 1999; Rhodes et al., 1998; Rhodes et al., 2001b; but see Swaddle & Cuthill, 1995) have shown preferences for faces manipulated to increase symmetry. Cross-cultural agreement on the attractiveness of symmetry (Rhodes et al., 2001b) may indicate a biological basis for symmetry

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[27] Adapted from Little, A. C. & Jones, B. C. (2003). Evidence against perceptual bias views for symmetry preferences in human faces. *Proceedings of the Royal Society of London, series B., 270,* 1759-1763.

preference, something universal in humans than transcends culture. The nature of this biological bias for symmetry remains in dispute, however. Two main theories have been put forward to explain universal human preferences for symmetry.

5.2 The evolutionary advantage view reiterated

One explanation for the preference for symmetric faces comes from a postulated link to an evolutionary adaptation to identify high-quality mates (Thornhill & Gangestad, 1999, for review). Symmetry in human faces has been linked to potential heritable fitness ('good-genes') because symmetry is a useful measure of the ability of an organism to cope with developmental stress (both genetic and environmental). As the optimal developmental outcome of most characters is symmetry, deviation from perfect symmetry can be considered a reflection of challenges to development. Only high quality individuals can maintain symmetric development under environmental and genetic stress and therefore symmetry can serve as an indicator of phenotypic quality as well as genotypic quality (e.g., the ability to resist disease, Møller, 1997; Møller & Thornhill, 1998, for reviews). This logic would lead to a preference for high symmetry mates as evolution will have favoured individuals who had preferences for high-quality over low-quality mates. Indeed, morphological symmetry appears to be related to reproductive success in many species, including humans (Gangestad & Thornhill, 1997b; Møller & Thornhill, 1998). For example, more symmetric human males have more sexual partners than less symmetric men (Thornhill & Gangestad, 1994) and symmetric males are also more likely to be chosen as extra-pair partners (Gangestad & Thornhill, 1997a). Thus the link between symmetry and attractiveness could reflect the fact that preferences for symmetrical individuals may be potentially adaptive.

5.3 The perceptual bias view reiterated

A second explanation for a preference for symmetrical faces is that all symmetrical stimuli are more easily processed by the visual system (e.g. Enquist & Arak, 1994; Enquist & Ghirlanda, 1998; Enquist & Johnstone, 1997). This is often referred to as the perceptual bias view. Attneave (1955) demonstrated that humans more easily reproduce symmetrical figures than asymmetric figures and suggested that this was because they possess more redundant information. Another explanation for the preference for bilateral symmetry is that it depends on the human visual system's own bilateral structure. In this framework, human vision is particularly sensitive to bilateral symmetry as ocular musculature is also bilaterally symmetrical (Mach, 1897), or because processing of the left and right visual field in different hemispheres, allowing point-by-point matching, eases symmetry detection (Herbert & Humphrey, 1996). Certainly preferences for symmetry have been observed for stimuli not related to mate-choice, such as everyday objects (Rensch, 1963) and decorative art (Gombrich, 1984; see Figure 14).

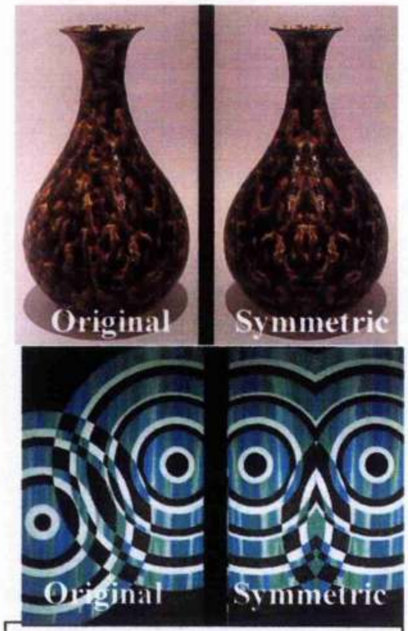

Figure 14: Symmetry in everyday objects. Original (left) and symmetric (right) versions of a vase (top) and piece of modern art (bottom)

A more complicated perceptual bias view for symmetry preference comes from cognitive theories about prototype formation. For each class of stimuli it is possible that the visual system develops an internal prototype. Such a prototype is made up of an average of the characteristics of all the different stimuli of that type that have been seen. When novel stimuli are encountered they are compared against this prototype and similarity to the prototype is positively related to how familiar and attractive we find the new stimuli (e.g., Halberstadt & Rhodes, 2000; Rhodes, Halberstadt, & Brajkovich, 2001a). From this view, symmetry is attractive as when asymmetries in stimuli are randomly distributed the average stimuli are very symmetric (Figure 15). We therefore find symmetry attractive in faces and other stimuli as it represents something closer to our internal prototypes for these stimuli. Certainly faces with average configurations are found to be more attractive than less average faces (e.g., Langlois & Roggman, 1990; Little & Hancock, 2002). Evidence for the possibility of prototype based perceptual bias comes from a recent study by Jansson et al. (2002; see Chapter 3, Figure 10) who trained hens to recognize two asymmetrical mirror stimuli and then measured their responses to a novel symmetrical stimulus that was the average of the two images. The hens responded more strongly to the symmetric stimuli than other hens that were

Figure 15: A composite made up from 15 asymmetric individuals The face looks symmetrical despite the fact that it made up of highly asymmetric individuals (From Penton-Voak et al., 2001)

not exposed to these stimuli. Such results indicate that perceptual experience can produce symmetry preferences without any link between symmetry and genetic or phenotypic quality.

The following studies examine men and women's preferences for symmetry in opposite-sex upright and inverted faces (Study 3) and in familiar faces (Study 4).

5.4 Study 3

5.4.1 Rationale

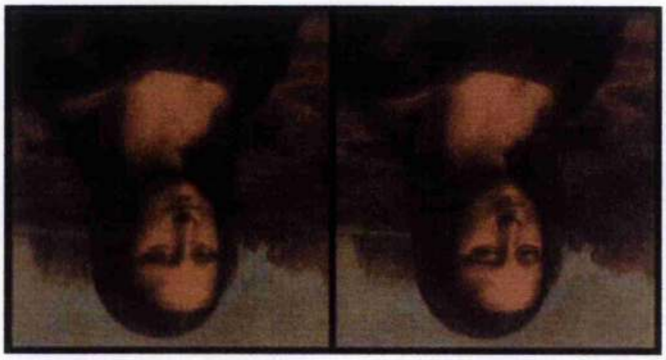

Figure 16: The Thatcher illusion illustrated by the Mona Lisa

The faces should look normal. Turn the page upside to see the differences.

Symmetry is preferred in upright faces but no studies have examined symmetry preferences in inverted faces. Inverting a face maintains its vertical plane of symmetry (where bilateral symmetry is easiest to perceive symmetry, e.g., Rock, 1974) and so according to the simple perceptual bias view should not affect symmetry preference. However, if preference for symmetry is an adaptation to mate-choice we might expect lower preferences for symmetry in inverted faces as inversion does disrupt the perception of faces to the extent that inverted faces are processed in a manner more similar to other objects (e.g., Murray, Yong, & Rhodes, 2000; see Figure 16). In other words, upright faces are an example of mate-choice-*relevant* stimuli in which we expect symmetry preferences from both theoretical positions. By contrast, inverted faces are mate-choice-*irrelevant* stimuli where a perceptual bias view suggests preferences for symmetry equivalent to that for upright faces while an evolutionary advantage view suggests lower preferences than for upright faces.

5.4.2 Methods

Participants

78 women and 41 men (mean age = 23.1, SD= 9.5) participated in Experiment 1. The experiment was administered over the Internet and participants were recruited via email from a participant-pool list asking if the person would like to participate in an experiment. Participants could follow a link from the email to the start of the experiment.

Stimuli

Twenty-eight previously used (Jones et al., 2001; Little et al., 2001; Perrett et al., 1999) stimulus pairs were presented in this study (14 male and 14 female Caucasian individuals between 20 and 30 years). Each pair was made up of one original and one symmetric image. All images were manipulated to match the position of the left and right eyes. To generate the symmetric images, original images were morphed so that the position of the features on either side of the face was symmetrical. Images maintained

Figure 17: Asymmetric (top) versus symmetric faces (bottom). Symmetric images are usually found more attractive (e.g., Perrett et al., 1999).

original textural cues and were symmetric in shape alone. See Perrett et al. (1999) for technical details. An example of an original and symmetrical face can be seen in Figure 17.

Procedure

Subjects were presented with two images of the same individual, an original and a symmetrically remapped version. Each image was seen twice, once upright and once inverted. Participants rated all of the faces with instructions to rate for a long-term relationship. The images were presented side by side on screen with the instructions: “Which face is the most attractive?” and “Please click the face which you feel is most attractive”. Clicking on a box below the faces moved onto the next of the 28 image pairs. Image order and side of presentation were randomised. Participants were also asked their age, which they typed into a box on screen.

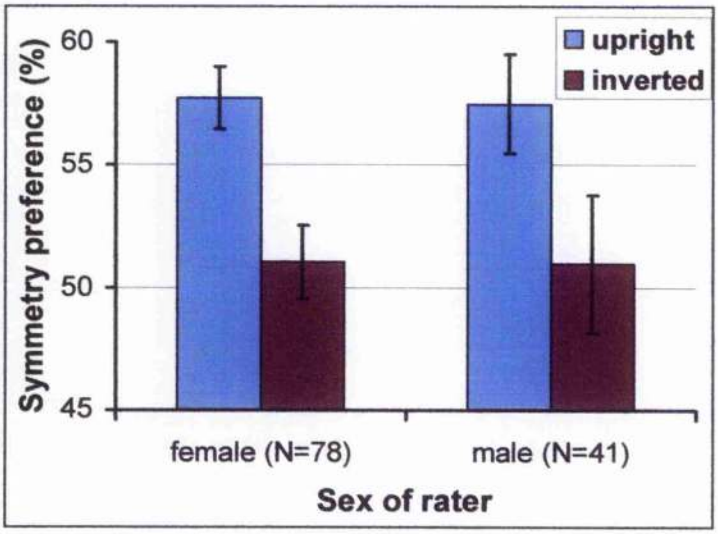

Figure 18: Preference for symmetry in opposite-sex faces according to sex of rater (male and female) and orientation (upright and inverted).

5.4.3 Results

A repeated-measures ANOVA with ‘orientation’ (upright versus inverted) as a within-participant variable and ‘sex’ (male versus female) as a between-participant variable revealed a significant effect of ‘orientation’ ($F_{1,117}$ = 15.6, $p < 0.001$), no interaction between ‘orientation’ and ‘sex’ ($F_{1,117}$ = 0.01, p =

0.93) and no overall effect of 'sex' ($F_{1,117} = 0.01$, $p = 0.96$). Means and standard errors can be seen in Figure 18.

A one-sample t-test against chance (50%) revealed a significant symmetry preference in upright opposite-sex faces across males and females (mean preference = 58%, $t_{118} = 7.1$, $p < 0.001$) but not in inverted opposite-sex faces (mean preference = 51%, $t_{118} = 0.75$, $p = 0.45$).

5.5 Study 4

5.5.1 Rationale

A prediction of the perceptual bias view based on prototype formation is that, for unfamiliar stimuli, stimuli most closely resembling the prototype would be most attractive. This would result in choosing the symmetric version of most stimuli as the most attractive, if asymmetries are random, as on average the prototype image will tend to be symmetric. For familiar stimuli, however, this may not be the case. Familiar stimuli should be preferred over symmetric stimuli as perceptual experience is for the familiar asymmetric version. Thus, from this version of the perceptual bias view we would expect no preference for symmetry in familiar stimuli whereas the evolutionary advantage view predicts no difference in symmetry preferences between novel and familiar faces.

5.5.2 Methods

Participants

15 individuals (9 women and 6 men, mean age = 26.7, SD= 2.7) participated in Study 2. Participants were unpaid volunteers and were selected on the basis of all knowing each other socially.

Stimuli

The 15 participants all had their photograph taken in a neutral expression and under standard lighting conditions. All images were manipulated to match the position of the left and right eyes. Images were then made symmetrical in both texture and shape to produce the symmetric version of the face. Each image was then warped back into its original shape to create the original version of the face. Thus both images possessed symmetrical textural cues and differed in symmetric shape alone.

Procedure

The procedure of presentation was identical to that of Study 1 except that participants rated all of the faces with instructions to rate for attractiveness and not long-term partner attractiveness and that there were 15 image pairs. As well as the 14 familiar face pairs, participants were also shown their own face in symmetric and original versions.

5.5.3 Results

The number of times the symmetric version was chosen over the original version for the 14 face familiar pairs (excluding own face) was calculated for each participant. A one-sample t-test against chance (50%) revealed a significant preference for the symmetric versions of the faces (mean percent of symmetric faces chosen = 69%, $t_{14} = 5.4$, $p < .001$).

For symmetric versus original face preferences for each participants own face a significant preference for the symmetrical version was again seen (11 of 15 participants picked the symmetric version, $\chi^2 = 5.4$, DF = 1, $p = .020$).

5.6 General discussion: Problems with perceptual bias accounts of symmetry preference

Study 3 demonstrates that in both men and women that there is a greater preference for symmetry in upright opposite-sex faces than there is in inverted faces. A lower preference for symmetry in inverted faces is inconsistent with the prediction made by the perceptual bias view that symmetry preferences for faces should remain constant across orientation, as it is the simple symmetry of the image, not any particular relevance to mate-choice, which is preferred. Our findings are more consistent with the evolutionary advantage view of symmetry preference, which predicts viewers should be more sensitive to symmetry when judging the attractiveness of mate-choice relevant stimuli (e.g., upright faces) than when judging the attractiveness of mate-choice irrelevant stimuli (e.g., inverted faces).

Potentially, a lower preference for symmetry in inverted faces is consistent with a prototype formation theory of perceptual bias for symmetry. Upright faces are familiar stimuli and so can be compared to a symmetric-prototype but inverted faces are not often encountered and so no 'inverted face-prototype' has been formed to which other inverted faces can be compared. 'Average faces', images made up of multiple faces, have been found as attractive in several studies (e.g., Langlois & Roggman, 1990; Little & Hancock, 2002) and one explanation for this attractiveness is that highly average faces are close to each individual's internal 'face prototype' and so are familiar (Rhodes et al., 2001a). Familiarity has been found to increase feelings of attractiveness (e.g., mere exposure, Bornstein, 1989; Zajonc, 1968). In Study 2, however, we found symmetry preferences in familiar faces (and also the participants own face) even though a perceptual bias view linking familiarity to attractiveness would predict the familiar original faces would be chosen over the symmetric version. Thus, Study 4 demonstrated that while familiarity may account for some of the preference for symmetry in human faces it might not explain all of this preference.

Other studies have presented evidence that is inconsistent with a perceptual bias view. For example, Jones et al. (2001) have shown that the attractiveness-symmetry relationships may be mediated by perceived health and Little et al. (2001; See Chapter 7) and Penton-Voak et al. (2001) using different methodologies, have shown opposite-sex face sensitivity in symmetry preference. It is worth noting that while these studies provide data more in line with an evolutionary advantage view than a perceptual bias view, the current studies are the first to directly assess competing, specific, hypothesis put forward by these two views.

Study 3 provides no evidence for a general preference for symmetry independent of stimuli. That is, no preference for symmetry was found in the inverted faces. Previous findings showing preferences for symmetry in non-mate-choice relevant stimuli (Gombrich, 1984; Rensch, 1963) would suggest that there should have been some degree of symmetry preference in inverted faces. It is possible, however, that with less subtle symmetry changes or more stimuli we would show preferences for symmetry in inverted faces but that the preference for symmetry in upright faces would still be significantly greater. Thus, we feel that there is reason to believe perceptual bias for symmetry preference may exist, as evidenced by preference for symmetry in non mate-choice relevant stimuli. On top of perceptual biases, however, other mechanisms may be in operation that may make humans particularly attentive to symmetry in mate-choice relevant stimuli. Where others have postulated that preferences for symmetric faces may be based on generalisation of mechanisms that create general symmetry preferences (Enquist & Arak, 1994) it is possible that the reverse is true: general preferences for symmetry could be based on generalisation of an adaptation to prefer symmetric faces and bodies.

Ultimately, any differences in symmetry preference based on familiarity, the judge, context, or orientation are problematic for a simple perceptual bias view. While perceptual bias may account for some level of symmetry preference in many stimuli the evidence for symmetry preferences in human faces thus far suggests that, even if the evolutionary relevant view is incorrect, the perceptual bias account as it stands is insufficient to explain preferences for symmetry in human faces.

Part 2: Beauty in the Eye of the Beholder

"…each mind contemplates a different beauty"

David Hume

6 Evolution and Individual Differences in Face Preferences

Synopsis

This Chapter revisits notions of universality in preferences. Having argued for the universality of attractive traits earlier in this thesis (Part 1), this Chapter reviews some factors that may lead to individual differences in the perception of facial attractiveness and speculates as to how such differences may arise from learning and differences in life history. It is concluded that, although there will be, on average, agreement on attractive versus unattractive traits, individual differences can be consistent with, and even predicted by, an evolutionary view of mate-choice.

6.1 The problem of individual differences

At first glance the evolutionary view appears inconsistent with individual differences as evolution will tend to remove variation if a particular preference is adaptive (see Chapter 1). There are sound reasons to believe there are core motives and psychological mechanisms shared by all members of our species - a universal functional design with the purpose of survival and reproduction. In other words, traits that are adaptive for one individual of a species to posses should also be adaptive for other members of that species. Applying this logic to preferences, if it is adaptive to prefer particular traits then all members of a species should all prefer the same traits as evolution will have favoured those with the adaptation and disfavoured those without it (see Chapter 1).

Each individual within a species, however, is a unique combination of genes and will vary in thousands of ways from others. Human physiology gives a useful example of monomorphic design (a design shared by all members of a species). Although there is a large amount of superficial variation, different sizes and shapes, each organ is present, has the same fundamental design, and has the same function in every member of the species. Tooby and Cosmides (1990) have suggested that human brains may also show monomorphic design suggesting that humans deploy specific cognitive, motivational, emotional, and behavioural strategies to accomplish particular goals. For example, humans learn a diversity of languages, but it has been argued that a language organ has evolved in all humans and shows strong evidence of adaptive design (Pinker & Bloom, 1990).

Such reasoning suggests there should be low variability between individuals though does not preclude differences. Morphs within a species are distinct alternative designs for different adaptive strategies. Male and female within a species are an example of alternative morphs, each possessing different physiological traits. Individuals may also have different personality or preference "morphs", for example Maynard Smith (1979) used the theory of evolutionary stable strategies (EES- derived from game theory) to show that alternative behavioural strategies (such as "hawks" and "doves") can coexist within a species.

6.2 The problem of a universal design

One problem with the notion of a universal design is the obvious differences in mate-choice that are seen in individuals within a species. Across the animal kingdom not all members of a given species engage in the same mating behaviour. Certainly, anecdotally, in humans there is disagreement amongst individuals (e.g., who is the most attractive movie star etc.). Men and women certainly differ in what they find attractive in a mate – at the very least usually choosing members of the opposite-sex as partners. Aside from this broad individual difference it is also important to consider that an individual's life-history may also impact on their preferences. What it is adaptive to find attractive in others may change across the life span.

The relative rarity of studies demonstrating individual differences in mate-choice in humans is no reason to believe such differences do not exist. Given the huge range of possible environments and phenotypes a gene may eventually end up in, an evolutionary view would predict that, in order to maintain an adaptive function, that the gene will be influenced by both environment and phenotype in its expression. Indeed, there may be a range of mating strategies within a species that can be employed based on both the environmental cues and the body that an individual finds itself in. In humans, whilst individuals may share certain basic criteria for finding faces attractive, many factors may influence the specific types of face they find attractive[28]. Thus, individual differences in preference could exist and be adaptive, an issue which is discussed in the next section.

6.3 Adaptive individual differences in preferences

Buss (1991) and Tooby and Cosmides (1990) have considered how individuals may differ in their adaptive strategies. The 'morphs' discussed in Section 1.1 are certainly

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[28] In some other species, females appear to have innate preferences for particular male traits (e.g., Bakker & Pomiankowski, 1995; Price, Schluter, & Heckman, 1993; Wilkinson & Reillo, 1994), however, at the same time mate preferences can also reflect social influences (e.g., Dugatkin & Godin, 1998).

evident in humans. Male and female are heritable alternative strategies which are genetically based and as noted earlier this does impact on preferences.

There may also be an adaptive value to heritable calibration of psychological mechanisms, where the adaptive optimum has changed over time or place, producing heritable variation in a species typical mechanism. In other words, variability may be adaptive in uncertain environments. Traits under selection in fluctuating environments show relatively high heritability (Burger, Wagner, & Stettinger, 1989), and Williams (1975) noted that some organisms facing uncertain environments and scarce resources assume sexual reproduction over asexual reproduction, a mechanism which would maximise variability. These results fit well with the idea that genetic variation in preference and other valued traits serves to facilitate the production of a wide range of variation which allows the occupation of a wide range of possible niches. There is evidence that intra-specific genetic variation is associated with variation in habitat preferences and that genetic variation is linked to environment heterogeneity (Hedrick, 1996; Wilson, 1994). At different times, different parts of a preference distribution may be favoured by natural selection or sexual selection, resulting in, for example, niches for those with high masculinity preferences and those with low masculinity preferences[29].

Aside from variation being linked to discrete morphs and being adaptive in a fluctuating environment there are also other potentially adaptive sources of variation in preferences. It is possible that individual differences in

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[29] Assuming that these fitness differences were not dramatic, the phenotypic distribution will be approximately normal.

morphology could lead to different adaptive preferences between individuals. It is also possible that individual differences in behaviour are the result of individuals reacting to the specific situation they are in or some other environmental constraint. In this way all members of a species would show a particular preference if their situations were identical and variation comes from the fact that individuals rarely are in identical environments and situations. The last source of individual differences under consideration it that development and learning may play a role in shaping mate-choice. Thus, again it is possible to postulate universal psychological mechanisms, but mechanisms which are sensitive to different childhood experiences and that calibrate or set the threshold of a species typical mechanism.

The five potential sources of adaptive individual differences discussed above are summarised below:

1. There may be heritable alternative strategies which are genetically based.
2. There may be heritable calibration of psychological mechanisms of a species typical mechanism.
3. The environment/genetics may create individual differences in ability or morphology that produce differences in the effectiveness with which alternative strategies may be employed (related to 2).
4. There may be situation contingent alternative strategies or individuals may occupy different niches that reliably evoke different behavioural frequencies.
5. There may be developmental calibration of psychological mechanisms, where different childhood experiences calibrate or set the threshold of a species typical mechanism.

(Adapted from Buss, 1991; Tooby & Cosmides, 1990).

The rest of this Chapter discusses the last three potential sources of individual differences in mate-choice (based on individual differences in ability, situational contingent strategies, and developmental calibration) that are followed up in later Chapters.

6.3.1 Individual variation based on inherited phenotypes

The attractiveness of the bodies that men and women find themselves inhabiting will influence the mate they may acquire and so is likely to impact on their mating strategy. In other words, individual differences in ability to attract mates could produce differences in the effectiveness with which alternative strategies may be employed and so result in adaptive individual differences in preferences.

Burley's work with Zebra finches has demonstrated that manipulating the attractiveness of individuals using coloured leg bands changes the mating strategy they employ. The "attractiveness" of the bands was measured by their impact on the other birds; some bands decreased the sexual attention received from opposite-sex birds and some bands increased the amount of sexual attention received from opposite-sex birds. Zebra finches mate monogamously (both in the wild and in captivity) with both males and females equally sharing parental duties. Males given 'attractive' legs bands engaged in polygynous mating whereas those males given unattractive green bands continued to mate monogamously (Burley, 1986). Females made attractive with coloured leg bands were found to spend less time carrying out parental duties than both those typical of their sex and unattractive females but still had higher reproductive success possibly because mates of attractive females spent more time than those typical of their sex carrying out parental duties (Burley, 1986).

Again higher attractiveness allowed females to adjust their strategy and induced partners to behave differently.

More recent work has indicated that condition may also influence an individual's preferences as well as their perceived attractiveness. For example, the red colouration of male sticklebacks' decreases in intensity with parasite load and female sticklebacks demonstrate a preference for intense male colouration. Females in poor condition, however, show an unexpected preference for less intensely coloured (i.e. poorer condition) males (Bakker, Künzler, & Mazzi, 1999).

Increases in attractiveness cause Zebra finches to employ different reproductive tactics and female condition, or attractiveness, influences preferences in sticklebacks. Given these findings, it seems plausible to postulate that attractive humans may be able to adopt sexual strategies different to unattractive individuals, an issue examined in Chapter 7.

6.3.2 Within-individual differences: strategic preferences?

As well as between-individual differences there may also exist within-individual differences. As noted in chapter 3, recent research into male facial attractiveness has revealed that female preferences for male faces may vary over the menstrual cycle, and with personal circumstances. Despite a preference for feminine faces most of the time, during the follicular phase of the menstrual cycle when conception is most likely, women prefer relatively masculine faces (Penton-Voak et al., 1999b). There were trends in the data to suggest that personal circumstances also influence face preferences: women currently in a relationship preferred marginally more masculine faces overall, and tended to undergo a larger shift toward masculinity at peak fertility than women without partners (Penton-Voak et al., 1999b), while women using oral contraception showed no cyclic shifts.

A mixed strategy in female mate-choice has been put forward as one explanation of this finding. Females may choose a long-term partner on the basis of co-operation and high parental care (indicated by a low masculine appearance), whilst occasionally pursuing extra-pair copulations with males with proposed markers of good-genes for immunity (indicated by a relatively masculine appearance) when conception is most likely. These studies show that face preferences can change over even a short period of time (28 days is the standard menstrual cycle model). The suggestion of differences in preference that are linked to current partnerships – women in relationships may look for different qualities advertised in the faces of men than women not in relationships, again suggests definitions of attractiveness change for individuals over time. These ideas are followed up in Chapter 8. If preference changes as a result of partnership it may reflect a situational contingent alternative strategy; women may have two sets of ideal mate characteristics, one for when they do and one for when they do not have a partner.

It is also worth noting that attractiveness is a variable that can change due to accident, disease, or ageing – such changes may, as in Zebra finches, radically alter an individual's sexual strategies and, in turn, impact on their preferences.

6.3.3 Early experience and learning

The information required to produce a competent adult takes years to acquire, and the social setting into which we are born will show us the most important aspects of our society. Draper and Belsky (1990) have suggested that mating behaviour is part of a complex developmental program, which can be made to follow different tracks based on environmental cues. They propose that varied macroecological contexts promote specific rearing experiences, which create psychological mechanisms, which in turn shape reproductive behaviour.

From birth infants are attentive to face-like configurations (Goren, Sarty, & Wu, 1975; Johnson, Dziurawiec, Ellis, & Morton, 1991) and even neonates are able to learn aspects of the mother's facial appearance (Bushnell, Sai, & Mullin, 1999; Pascalis, de Schonen, Morton, Deruelle, & Rabre-Grenet, 1995). Young infants can also abstract prototypical facial proportions rapidly from the different faces they are exposed to (Walton & Bower, 1993) and early visual experience appears critical to the normal processing of facial configuration later in life (Le Grand, Mondloch, Maurer, & Brent, 2001). Thus it would appear unlikely that individuals are born with their ideal mate predetermined in the brain (though some traits may be inherently attractive even to infants, Chapter 1). It is certainly plausible given the proposed role of learning in general face processing mechanisms that these may also effect facial attractiveness judgements later in life, an issue returned to in Chapter 9. Such effects may reflect the developmental calibration of species typical psychological mechanisms.

6.4 Discussion: Evolution can be consistent with individual differences in face preferences

This Chapter discussed how individual differences can initially be seen as contrary to evolutionary predictions (Section 6.1) as evolution tends to remove variation. Indeed, it is highly likely that humans share a universal functional design a suite of adaptive traits shared by all members of our species.

There is, however, a problem with the view of a universal functional design – one template for a human brain, like one template for a human body, is simply not apparent. Humans differ in both shape and behaviour. More importantly, humans also differ in the environment they may find themselves and this environment has the potential for change. In this way a truly adaptive view of a universal functional design would predict that an individual's behaviour and preferences would change according to a variety of factors (Section 6.2).

There are several sources of potentially adaptive individual differences (Section 6.3). These include: the individual's own attractiveness status environmental/situational factors, and early face experience. In the next three Chapters the impact of these factors on face preference or mate-choice is examined.

7 Beauty and the Beast: Attractive Women Prefer More Masculinity and Symmetry in Faces[30]

Synopsis

This Chapter examines how female quality may influence preferences for male traits. A study is presented in which self-perceived attractiveness is used as a measure of mate-quality and shows that those women who consider themselves most attractive have a relatively increased preference for masculinity and an increased preference for symmetry. This finding may reflect a condition dependent mating strategy analogous to behaviours found in other species. The absence of a preference for proposed markers of good-genes may be adaptive in women of low mate-value to avoid the costs of decreased parental investment from the owners of such characteristics.

7.1 Parasites and preferences

In the animal literature there has been much interest in the influence of parasites on male ornaments (e.g., Houde & Torio, 1992; Millinski & Bakker, 1990; Møller, 1990b). These studies are based on Hamilton and Zuk's (1982) theory of parasite driven sexual selection of traits, which suggests that certain traits in males honestly advertise immuno-competence and are consequently selected for by females in mate-choice (see Chapter 3). To reiterate, those with lower quality immune systems are proposed to be more prone to parasites than those with high quality immune systems. This has recently been expanded to predict the attractiveness of secondary sexual

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[30] Adapted from: Little, A. C., Burt, D. M., Penton-Voak, I. S., & Perrett, D. I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London, series B, 268,* 39-44.

characteristics and symmetry in male faces (e.g., Grammer & Thornhill, 1994; Thornhill & Gangestad, 1993).

The question of how parasites influence females' preferences for such male "ornaments" has often been neglected (Lopez, 1999; Poulin & Vickery, 1996, for proposed impact). In humans both males and females vary in their mate value (Symons, 1987). If immune system quality and resistance to parasites is advertised by facial traits such as symmetry and secondary sexual characteristics (Thornhill & Gangestad, 1993) and these traits are in turn related to attractiveness (Chapter 3 for review), we can expect them to relate to mate-value in both males and females.

In a variety of animals it has been shown that parasites can bring about changes in a host's attractiveness and competitiveness, the general finding being that parasite load has a negative influence on the host's mating success (Borgia & Collis, 1989; Millinski & Bakker, 1990; Zuk, 1992). Assortative mating refers to a pattern of mating. Positive assortative mating occurs when individuals possessing similar phenotypes pair up more often than would be expected by chance and negative assortative mating refers to the reverse condition, where individuals of dissimilar phenotypes pair up more often than would be expected by chance (Burley, 1983). When both males and females of a species are choosy (as in humans) and are attempting to avoid infected individuals, we would expect to find positive assortative mating for parasite immunity, with males and females of high immune system quality and males and females of lower immune system quality forming partnerships (Møller, 1994; Møller & Hoglund, 1991).

A tendency for matching for parasite load in mating pairs has been demonstrated in beetles (*Timarcha maritama*, Thomas, Oget, Gente, Desmots, & Renaud, 1999) and the pairing of individuals with similar parasite loads is also seen in other species. For example, Thomas, Renaud, and Cezilly (1996) have shown assortative mating for parasite load in amphipods (*Gammarus insensibilis*) and Møller (1994) presents evidence that a similar matching for parasite load is also found in barn swallows (*Hirundo rustica*). It is difficult to separate out the causes of assortative mating in these studies. One of the suggestions of Thomas et al. (1999) is that the assortative mating in the beetles they studied could be due to the detrimental effect of parasites on breeding condition. If parasitized males and females are delayed in the start of their breeding cycle then they will mate associatively as unparasitized males and females will have paired up earlier. Given that females are usually the "choosy" gender it is possible that female preferences play a role in this assortative mating. Indeed, Møller, (1994) has argued that the matching for parasite load observed in swallows may be due to mutual mate-choice based on tail length (a secondary sexual characteristic negatively associated with parasite infection).

7.2 Condition dependent mate-choice

A second line of evidence suggests that animals are attentive to phenotypic markers of quality in others. In Chapter 6 I discussed the possibility that an individual's attractiveness could influence their mate preferences. Work by Millinski and Bakker (1990) has shown that in three-spined sticklebacks (*Gasterosteus aculeatus,* see Figure 19) parasites reduce the intensity of the red coloration around males' throats. This coloration is important to female mate-choice and females preferentially mate with males with more intense colour. When cues to colour were removed (by using green light to make the differences in red coloration invisible) males that were previously preferred were chosen at levels around chance, although males' courtship displays remained the same. Thus females use the intensity of red coloration to avoid parasitized males and therefore select males with good immune systems. Importantly, the phenotypic quality of an individual affects their preferences for members of the opposite gender. Bakker et al. (1999) allowed female three-spined sticklebacks to choose between computer animations of courting males. The two males differed only in the intensity of red coloration (red versus orange) around the throat and so represented an "attractive" versus "unattractive" phenotype. A significant correlation was found between female condition (condition measured as body weight/body size) and mate-choice. Females who were in better condition showed a greater preference for the red-throated male and those in worse condition showed a preference for the orange male. As these females were raised in laboratory conditions and isolated from males before becoming reproductively active these preferences are not dependent on experience of competition in mating.

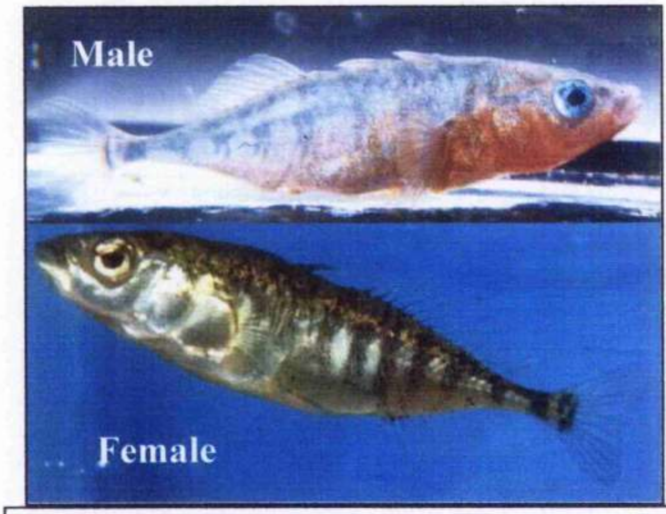

Figure 19: Male and female three-spined sticklebacks (*Gasterosteus aculeatus*)
The red/orange coloured throat of the male is generally more attractive the more intense the colour.

Another example of condition dependent mate-choice comes from Lopez (1999). The parasite *Gyrodactylus turnbulli* reduces the sexual display and colour intensity of male guppies (*Poecilia reticulata*), which makes them less attractive to females (Houde & Torio, 1992). Lopez (1999) examined how this same parasite influences female mate-choice decisions. Infected and uninfected females were presented with a choice of two males, one attractive (high display rate, high colour intensity) one unattractive (low display rate, low colour intensity). When presented with these two males, uninfected females were significantly more likely to choose the attractive male over the less attractive male. By contrast, infected females were less discriminative in their choice of mates and showed no preference for the more attractive male over the less attractive male. Females were raised in laboratory conditions in same gender groups and were virgin when presented with males to choose between thereby minimizing the possibility that learning played any role in the acquisition of these preferences.

7.3 Interpreting condition dependent mate-choice

Why should some females not show a preference for phenotypic signs in males that provide cues to higher quality immune systems? There are some provocative studies in the animal literature showing that in certain species with bi-parental care, high phenotypic quality males invest less in each female than males of lower phenotypic quality. Male pine engraver beetles (*Ips pini*) assist the female in creating tunnels for her brood and defend these nests from potential predators. Studies indicate that large males left the female and her nest (i.e. stopped investing) sooner than smaller males (field study, Robertson, 1998; laboratory study, Reid & Roitberg, 1996). Robertson and Roitberg (1998) note that larger, and therefore higher quality males in terms of flying capabilities, had a greater potential for further reproduction than did smaller males. Larger males therefore benefited by leaving earlier in terms of increased likelihood of achieving a greater number of mates. Conversely, smaller males had less potential for further reproduction and because the duration of paternal care in a given brood was positively related to relative success of that brood, once a small male has a mate he benefits by staying with the female longer.

It may therefore be adaptive for females in poor condition to show a preference for males displaying cues to poorer heritable parasite resistance, as the greater parental investment may be of greater benefit to them and their offspring than the heritable immuno-competence acquired from high quality males. High immune quality females may be able to extract more investment from high quality males than low immune quality females. This hypothesis remains to be addressed. Even if this is not the case, high immune quality females may be better able to cope with decreased parental investment (or gain little from increased male investment).

7.4 Study 5: Self-perceived attractiveness and face preference in women

7.4.1 Rationale

These findings in the animal literature, that a variety of species demonstrate condition dependent mate-choice, suggest that humans might also show different preferences based on condition or self-perceptions of their value as mates. Humans differ in their attractiveness as mates. Pawlowski and Dunbar (1999) use the term "market-value" to specify how much demand there is for a particular individual as a mate, and this will prove useful in our discussion. High market-value (or value) females should be more attentive than lower value females to male traits, such as symmetry and secondary sexual characteristics, which are thought to be phenotypic signals linked to heritable immune system quality. Conversely, females who perceive themselves as less competitive in the mating market may lack these preferences or actively prefer cues to non-immuno-competence related benefits in faces, such as the likelihood of increased parental investment (e.g., feminine faced males are seen as more co-operative and as more likely to make better parents than masculine faced males, Perrett et al., 1998a).

7.4.2 Methods

Preference for Masculinity

Participants

Seventy female participants (age 16-64, mean age = 22.9, SD = 8. 8) judged faces for a long-term relationship and 119 female participants (age 17-47, mean age = 24.1, SD 6.3) judged faces for a short-term relationship. All participants reported being heterosexual.

Stimuli

Attractiveness was measured by giving participants a five-point scale to rate themselves upon (1 = low attractiveness, 3 = average attractiveness, 5 = high attractiveness). Five interactive face sequence trials were constructed from 5 groups of male and female faces (1 Japanese and 1 Caucasian as used in Perrett et al., 1998a, and 3 other groups of Caucasian faces used in Penton-Voak et al., 1999b; each group contributed to a single sequence). For every sequence 174 feature points were delineated on each face image in the group from which the average male and female shapes calculated. Using the linear difference between feature points in the average male and female shape a sequence of 11 face shapes ranging from +50% masculinised to +50% feminised were constructed. The 11 images in the sequence were then calculated by warping, and then superimposing all of the male faces in the group into each of the face shapes. Figure 2 (Chapter 3) earlier shows an example of a masculinised and feminised male face.

Procedure

Participants were presented with 5 interactive face sequence trials followed by an on-screen questionnaire. The face sequence interactive trials were presented in random order with subjects being cued to make judgements based on either short- or long-term relationships by the message "alter the face until you think it is closest to the appearance you would find attractive for a short (or long) term relationship.". During each trial left or right (counterbalanced between trials) mouse-movement instantly altered the shape of the face in the on screen image making it more or less masculine.

Preference for symmetry

Participants

97 female participants (aged 17–46 mean = 20.6, SD = 4.5) took part in the study.

Stimuli

Attractiveness was measured by giving participants a five-point scale to rate themselves upon (1 = low attractiveness, 3 = average attractiveness, 5 = high attractiveness). The 26 stimulus pairs (previously used in Perrett et al., 1999) were 13 male and 13 female face images of Caucasian individuals between 20 and 30 years. Each pair was made up of one original and one symmetric image. All images were manipulated to match the position of the left and right eyes. Symmetric images were warped so that the position of the features on either side of the face was symmetrical. An example of an original and symmetrical male face can be seen earlier (Chapters 3 and 5).

Procedure

Participants were presented with two images of the same individual, an original and a symmetrically remapped version. The images were presented side by side on screen and with the instructions: "Which face is the most attractive?" and "Please click the face which you feel is most attractive". Clicking on the one of the faces moved onto the next of the 26 image pairs. The trial order and side of presentation was randomised.

7.4.3 Results

Self-rated physical attractiveness and preference for masculinity

In line with previous findings, overall, disregarding relationship context and self-rated attractiveness, a significant preference for femininity in male faces was found (mean masculinity preference = -6.86%, s.d. = 15.9, 50% = no preference, one-sample t-test, t_{191} = -2.34, p = .020). Overall, females did not differ in the level of masculinity they chose for short and long-term relationships (mean for short-term = -6.49% masculinised, s.d. = 15.9%, mean for long-term = -7.49% masculinised, s.d. = 16.1%, independent samples t-test, t_{190} = .42, p = .68). Participant age was found to be significantly positively related to a preference for masculinity in male faces (Pearson product moment correlation, r_{191} = .19, p = .008).

Participants were divided by score into low (attractiveness score 1-2, long-term n = 14, short-term n = 17), average (attractiveness score 3, long-term n = 29, short-term n = 71) and high self-rated attractiveness groups (attractiveness score 4, long-term n = 27, short-term n =31). ANOVA's were conducted on the effect of self-rated attractiveness on preference for masculinity for long- and short-term partners separately. Age was entered as a co-variate because it was positively related to masculinity preference. A significant effect of self-rated attractiveness was found for masculinity preference when judging for a long-term relationship ($F_{2,66}$ = 5.43, p = .007). Post-hoc comparisons using Tukey's HSD showed the low group significantly differed from the high group (p = .002) and the difference between the high and average groups was approaching significance (p = .052). The low and average groups did not differ significantly in masculinity preference (p = .12). No significant effect of self-rated attractiveness on masculinity preference was found for short-term relationships ($F_{2,115}$ = 1.1, p = .33). The relationships between self-rated attractiveness and masculinity preference by term of relationship can be seen in Figure 20.

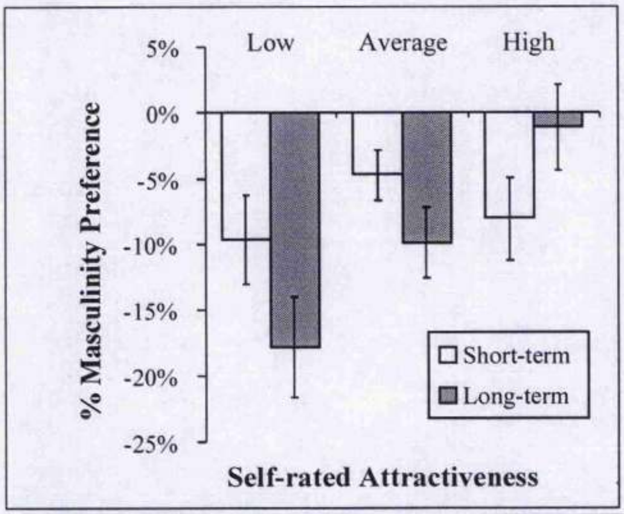

Figure 20: Preference for femininity in male faces as a function of female self-rated attractiveness (+/- 1 S.E.). Preference was measured as the average % masculinity/femininity chosen from interactive continua of five faces.

Self-rated physical attractiveness and preference for symmetry

In line with previous findings showing that symmetry is found attractive in faces, irrespective of self-perceived attractiveness, both male (symmetrical male face chosen 61.5%, one-sample t-test, t_{96} = 7.2, p < .001) and female (symmetrical female face chosen 57.5%, one-sample t-test, t_{96} = 4.1, p < .001) faces were found to be chosen more than expected by chance (6.5 times out of 13). Gender of face had a significant effect on preference for symmetry. Females were found to prefer symmetry in male faces more than they preferred symmetry in female faces (paired samples t-test, t_{96} = 2.2, p = .034).

Participants were divided by score into below average (attractiveness score 1-2, n = 22), average (attractiveness score 3, n = 53) and above average self-rated attractiveness groups (attractiveness score 4, n = 22), as no participant rated themselves 5 for attractiveness and only 3 participants rated themselves as 1. The percentage symmetry preferred refers to the proportion of symmetric faces chosen from a set of 13 faces. Figure 21 illustrates the relationship between self-rated attractiveness and symmetry preference.

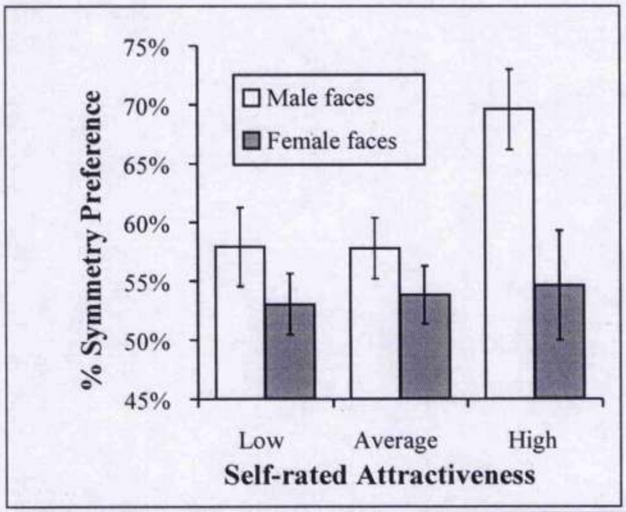

Figure 21: Preference for facial symmetry as a function of female self-rated attractiveness (+/- 1 S.E.). Preference was measured as the number of symmetrical faces chosen from 13 original versus symmetric face pairs and is expressed as a percentage.

ANOVAs were conducted on the effect of self-rated physical attractiveness on preferences for symmetry in male and female faces. A significant effect was found of self-rated attractiveness on a preference for symmetry in male faces ($F_{2,94} = 4.52$, $p = .013$). Post-hoc comparisons using Tukey's HSD showed that neither the low or medium self-rated attractiveness groups differed in their preference for symmetry in male faces ($p = .82$). The high self-rated attractiveness group differed significantly from both the low ($p = .012$) and medium ($p = .006$) attractiveness groups. No effect of self-rated attractiveness was found for a preference for symmetry in female faces ($F_{2,94} = 0.11$, $p = .89$).

7.5 Discussion: Reacting to your own attractiveness

Study 5 shows that females who consider themselves physically attractive show a greater preference for two proposed markers of phenotypic and genotypic quality: facial masculinity and facial symmetry. Females who consider themselves above average in attractiveness prefer relatively more masculine male face shapes and show a greater tendency to prefer symmetry in male faces than females rating themselves as less attractive. While self-rated attractiveness is not the only measure of mate value it correlates with other-rated attractiveness (Feingold, 1988) and so does reflect one aspect of what males want in a female partner.

The increased preference for masculine faces was only seen when high attractiveness females were judging for a long term-relationship, which indicates the shift in preference is for long-term partners only. The finding that self-rated physical attractiveness had no influence on a preference for symmetry when judging female faces indicates that the change in preference for male faces is important only to mate-choice and not to attractiveness judgements in general.

The study also replicates previous findings demonstrating overall preferences for small amounts of femininity (Penton-Voak et al., 1999b; Perrett et al., 1998a) and symmetry (Perrett et al., 1999; Rhodes et al., 1998) in male faces. Overall, a preference for symmetry was more marked when females were assessing male faces than when assessing female faces again indicating that symmetry is relatively more important for judgements reflecting mate-choice than for attractiveness judgements in general. No difference was found in the level of masculinity desired between individuals judging for a long and a short-term relationship, which indicates similar preferences under both conditions. This is in line with previous studies suggesting that females have similar standards for long- and short-term mates (Buss & Schmitt, 1993) but unexpected given that masculinity was perceived to be associated with short-term relationships in Chapter 4. In fact subsequent research does show that term affects preference for masculinity, but only in women who do not report using oral contraception, and this may explain the discrepancy here (see Chapter 8).

Differences in mate preferences may reflect different strategies for individuals. Females of high attractiveness may attempt to maximise phenotypic quality (indicating immuno-competence) in prospective partners and females of low attractiveness may maximise reproductive success by pursuing males most likely to invest/least likely to desert. Such differences would only arise if there existed advantages to low value females not to be as attentive to cues to heritable immuno-competence in a partner as high value females.

Human males may also balance the prospect of seeking further mating opportunities with the amount they invest (e.g., time, resources) in each mate. Males in possession of good immunity genes may spend more time seeking extra mating opportunities relative to males who do not possess these good-genes because they are more likely to be able to pursue a short-term mating strategy. Indeed, more symmetric human males report more sexual partners than less symmetric men (Thornhill & Gangestad, 1994). Males with enhanced secondary sexual characteristics are also associated with lower parental investment. Perrett et al. (1998a) have shown that masculinised faces are associated with the attribution of bad parenting skills. Also Study 2 (Chapter 4) demonstrates that masculinised male faces are more associated with writing a dating advert representing a male seeking a short-term than a long-term relationship whereas feminised male faces are associated with the long-term advert more than the short-term advert.

If males in possession of good-genes are less likely to invest in mates (Gangestad & Simpson, 2000), a preference for high phenotypic quality in males in low market-value females may thus be maladaptive, as the cost of selecting a low investment male might outweigh the benefit of the good-genes acquired from him. High quality females may be either more able to cope with lower paternal investment from high quality males (by being able to provide more investment themselves) or be able to acquire both good-genes and investment from a high quality male (if high quality males are more likely to invest in high quality females). The finding that attractive females are only more attentive to the good gene markers for long-term relationships and the high cost of loss of parental care lends more support to the latter.

It is interesting to note that preferences away from the maximisation of the heritable benefits of immuno-competence may be adaptive for certain individuals. Paradoxically, those males of high mate value (e.g., good-genes for immuno-competence) may not have the highest mate value when being judged by females of low mate value.

Preferences based on self-perceived attractiveness also have implications for assortative mating. In humans there are studies showing that individuals pair up with others of similar attractiveness (Shepherd & Ellis, 1972) and that couples possess faces which are similar to each other (Hinsz, 1989; but see Penton-Voak et al., 1999a). Recent models of assortative mating argue that organisms do not want to mate assortatively but are forced to because of market pressures: their own attractiveness limits the attractiveness of the mates they can acquire (e.g., Burley, 1983; Feingold, 1988; Kalick & Hamilton, 1986). High attractiveness individuals are able to acquire high attractiveness mates and, as they pair up, less attractive individuals are left to pair up with less attractive mates. In this way a species-wide preference for high quality mates can result in a positive assortative mating pattern. This view posits that we are each trying to find the most "attractive" mate. In this study participants actively demonstrated a preference for different faces when the perceivers believed themselves to be of low attractiveness, which provides an alternative mechanism to explain assortative mating (although it is likely to interact with competitive factors). Pairing due to preferences does not preclude the possibilities that pairing can occur because those of high attractiveness pair up or that these preferences are the result of individuals learning their mate value through competition.

Another point arising from this discussion is that condition dependent mate preferences may mean that a male's attractiveness is not necessarily related to quality in terms of good-genes for immuno-competence (also Perrett et al., 1998a). The perceived value of certain mates appears to be dependent on the judging female's mate value. For example, paradoxically, those males without good-genes for immuno-competence may have the highest mate value when being judged by females of low mate value. Females of low mate value may be unable to acquire mates with good immuno-competence genes or else suffer from desertion/low investment by "attractive" male partners. This is a cautionary note that research into attractiveness should not look to heritable benefits of immuno-competence alone in its description of the adaptive nature of preferences.

8 Women's Potentially Strategic Preferences for Sexual Dimorphism in Male Faces[31]

Synopsis

This Chapter discusses potentially strategic preferences in women that would maximise good-gene benefits from masculine faced males. A study is presented that demonstrates that preferences for masculinity are increased when women either have a partner or are considering for a short-term relationship. Such preferences are potentially adaptive, serving to: (1) maximise parental investment and co-operation in long-term relationships by biasing choices towards feminine faced males and (2) maximise possible good-gene benefits of short-term or extra-pair partners by biasing choices towards masculine faced males.

8.1 Situational effects on women's preferences

Studies of male facial masculinity and attractiveness have produced mixed results (see Chapter 3 for review). It is possible, however, that male facial masculinity might differ in its attractiveness under different circumstances as discussed in Chapters 3 and 4. Human males bring two factors to a parenting relationship: a level of paternal investment and potential heritable benefits (e.g., genes for high quality immune systems). The perceived high dominance and lower levels of co-operation point to lower paternal investment from the owners of masculine faces. Although females generally prefer long-term mating over short-term mating (Buss & Schmitt, 1993), individuals differ in their inclination to take part in short- and long-term relationships

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[31] Adapted from: Little, A. C., Jones, B. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society of London, series B, 269*, 1095-1100.

(Gangestad & Simpson, 1990; Simpson & Gangestad, 1991). Depending on the type of relationship sought, masculine and feminine male faces are proposed to differ in their attractiveness to females. In the context of a short-term sexual relationship the perceived cues to high paternal investment in the feminine faced male are of little value to a female. Females should therefore seek to maximise the genetic fitness of potential offspring if they are not extracting any other benefits from their mates and thus prefer more masculine males for short-term relationships. In long-term relationships, better parenting and increased co-operation may outweigh the benefits of genetic fitness, thereby enhancing the attractiveness of feminine-faced males.

8.2 Partnership and the menstrual cycle

An increased preference for genetic fitness over signs of parental investment would also be expected in extra-pair copulations when a woman has already acquired a long-term partner. Support for the notion that female preferences are variable according to the temporal context of relationships and that females may aim to maximise genetic quality in extra-pair partners at peak fertility has come from work related to the menstrual cycle. Women's menstrual cycles usually last between 21 and 35 days and most standard models of the menstrual cycle are based on a mean duration of 28 days. In such models, ovulation occurs on approximately day 14 at the end of the follicular phase (e.g., Chabbert-Buffert, Djakoure, Christin-Maitre, & Bouchard, 1998). Fertility is highest (where a woman is most likely to become pregnant after sexual intercourse) around the 12th day of the cycle during the follicular phase (Barrett & Marshall, 1969). Although peaks in sexual desire and activity have been reported at different stages across the menstrual cycle (Regan, 1996, for review) two studies have reported that women with partners may be more likely to engage in extra-pair sex at peak fertility (extra-pair copulation is 2.5 times more likely during the follicular phase than in the luteal phase, (Baker & Bellis, 1995; Bellis & Baker, 1990). These studies indicate a possible mechanism where women may maximise their chances of becoming pregnant with the offspring of males chosen for extra-pair affairs. Such males may be selected for possessing superior or alternative genes to the woman's current partner.

Women at mid-cycle do appear to be more sensitive to indirect genetic immunological benefits. Wedekind and Furi (1997) examined the influence of female major histocompatability complex (MHC, a set of genes that play an important role in immune function) on male odour attractiveness, using T-shirts worn by males. They found a preference in females for the odours of males with dissimilar MHC profiles (offspring of partners with dissimilar MHC complexes are proposed to have an immune system better able to fight off infection) around day 12 of the women's menstrual cycle. Such preferences were not just absent but reversed in women using oral contraception, implying that the hormonal changes across the menstrual cycle play an important role in MHC odour preferences.

An example of women's preferences favouring signs of immunological quality at a time when they are most likely to become pregnant comes from the demonstration of shifting female preferences for masculine facial traits across the menstrual cycle (Frost, 1994; Johnston et al., 2001; Penton-Voak & Perrett, 2000; Penton-Voak et al., 1999b). Recent research has revealed that female preference for male faces varies over the menstrual cycle. Despite a preference for feminine faces most of the time (though see Johnston et al., 2001), during the follicular phase of the menstrual cycle when conception is most likely, women prefer relatively masculine faces (Penton-

Voak & Perrett, 2000; Penton-Voak et al., 1999b), particularly in the context of short-term relationships (Penton-Voak et al., 1999b). Penton-Voak et al. (1999b) also report non-significant trends to suggest that personal circumstances also influence face preferences: women currently in a relationship preferred marginally more masculine faces overall ($p = 0.07$), and tended to undergo a larger shift toward masculinity at peak fertility than women without partners ($p = 0.08$). Women using oral contraception showed no significant cyclic shifts in Penton-Voak et al.'s study.

A mixed strategy in female mate-choice has been put forward as one explanation of females favouring masculinity at peak fertility (Penton-Voak et al., 1999a; Penton-Voak & Perrett, 2000). Females may choose a long-term partner on the basis of co-operation and high paternal care (indicated by a low masculine facial shape). When conception is most likely they may occasionally pursue additional relationships with males with proposed markers of good-genes for immunity, indicated by a relatively masculine face shape. Of course such a mechanism may also serve to maximise genetic benefits in offspring for women without partners.

8.3 Study 6: Partnership status and temporal context of relationship effects on face preferences in women

8.3.1 Rationale

Study 6 compared women's preference for masculinity in male faces in long- and short-term contexts to assess whether greater levels of masculinity are preferred for short-term partners compared to long-term partners (masculine male faces are seen as likely to want to pursue short-term relationships more relative to feminine male faces, Chapter 4). The study also examined partnership status to assess whether women with partners prefer more masculine faces than women without partners. Use of oral contraception has been found to influence women's preferences for potentially adaptive genetic benefits (e.g., Penton-Voak et al., 1999b; Wedekind & Furi, 1997) and the impact of this variable was also examined.

8.3.2 Methods

Participants

158 females, aged between 16 and 39 (mean age = 21.7, SD = 4.8), took part in the experiment. The experiment was administered over the Internet. All participants were volunteers and were selected for reporting being heterosexual and less than 40 years old.

Stimuli

Five interactive face sequence trials were constructed using composite faces made from 5 groups of male and female faces. Each group of faces contributed to a single sequence trial and was made up of about 20 male and 20 female facial images of young adults in a neutral pose. To construct each sequence trial, 174 feature points were delineated on each face image in the group from which the average male and female shapes were then calculated. Using the linear difference between feature points in the average male and female shape a sequence of 11 face shapes ranging from +50% masculinised to +50% feminised was constructed. The 11 images in the sequence were then produced by warping and then superimposing all of the male faces in the group into each of the face shapes. The images were made perfectly symmetrical by combining them with their mirror image prior to masculinity manipulation. For more details on the averaging and transforming techniques see (Tiddeman, Burt, & Perrett, 2001). Figure 2 (Chapter 3; and Figure 22) shows an example of a masculinised and feminised male face made using these methods. The final stimuli were 5 interactive tests which allowed for the on-screen transformation of a composite male face between a masculinised and feminised version of itself. These interactive tests were used in previous studies as follows: 1 Japanese group and 1 European group used in Perrett et al. (1998) and 3 other groups of European faces used in Penton-Voak et al. (1999).

Figure 22: Left image - 50% feminised male composite and right image - 50% masculinised male composite.

Procedure

Participants were presented with 5 interactive face sequence trials followed by an on-screen questionnaire assessing age, sexuality, oral contraceptive use, (yes/no), whether they had a current partner (yes/no), number of sexual partners and five questions assed on a 5-point scale, happiness with their current relationship (e.g., 1 = very unhappy, 5 = very happy), commitment to their current relationship, their physical attractiveness, their warmth, and their confidence. The face sequence interactive trials were presented in random order with participants being cued to make all their judgements based on either short- or long-term relationships by the message "alter the face until you think it is closest to the appearance you would find attractive for a short- (or long-) term relationship." (i.e. the variable relationship context was manipulated between participants). Ratings for long- or short-term were run in two blocks, initially everyone rated for long-term relationships and later the experiment was changed to collect short-term ratings. During each trial left or right (counterbalanced between trials) mouse-movement altered the shape of the face in the on-screen image making it more or less masculine.

8.3.3 Results

Only the data from participants who answered all questions could be entered into the analysis. Nine participants were removed for scoring 1 or 2 on either the relationship happiness scale (very unhappy, unhappy) or relationship commitment scale (very uncommitted, uncommitted). Individuals unhappy or uncommitted in their relationships may not rate faces as if they were in a relationship (i.e., they may be looking for a partner in order to leave the relationship or be contemplating leaving the current relationship anyway). Removing unhappy/uncommitted individuals increases the likelihood that remaining participants are rating for extra-pair partners rather than replacement partners. The highly skewed nature of scores on happiness/commitment scales (only 9 subjects scored 1 or 2 on these scales and the majority of participants entered 5 on both scales) meant that it was not possible to assess if happiness/commitment was related to masculine preference in this sample. Two participants were also excluded as they reported being pregnant.

In order to assess any differences in personality/self-opinion between those using oral contraception and those not using oral contraception and those in relationships and those not in relationships a 2x2x2 multivariate ANOVA was carried out with three levels, 'context' (short-/long-term ratings), 'partnership status' (partner/no partner) and 'contraceptive use' (use/do not use) as the between participant variables and number of sexual partners, self-rated physical attractiveness, warmth, and confidence as the dependent variables. Age was entered as a co-variate. Ten participants did not provide complete data for these questions and were excluded. This analysis produced only two significant results; significant effects of both age ($F_{1,140} = 54.6, p < 0.001$) and contraceptive use ($F_{1,140} = 9.2, p = 0.003$) were found for number of sexual partners. Age was positively correlated with number of sexual partners (N = 150, $r = .54, p < 0.001$) and women using oral contraceptive reported having had more partners than those not using oral contraceptive (4.5 and 2.6 mean number of partners respectively). All other effects and interactions were non-significant (all $p > 0.095$).

A univariate 2x2 ANOVA was carried out with the two levels 'context' and 'partnership status' as the between participant variables and femininity preference as the dependent variable. Separate analyses were carried out for women who did and did not report that they were using oral contraception. Age was entered as a co-variate in both analyses due to its possible relationship with femininity preference and partnership status. A smaller number of women reported using oral contraception than reported not using it, meaning the statistical power in the oral contraception group was lower. The numbers of participants in the various conditions for the analysis can be seen in Table 5.

Table 5: Number of participants in Study 6 as split in the analysis

Oral Contraception			N
No	Context	Short-term	67
		Long-term	40
	Partner	No	71
		Yes	36
Yes	Context	Short-term	35
		Long-term	16
	Partner	No	12
		Yes	39

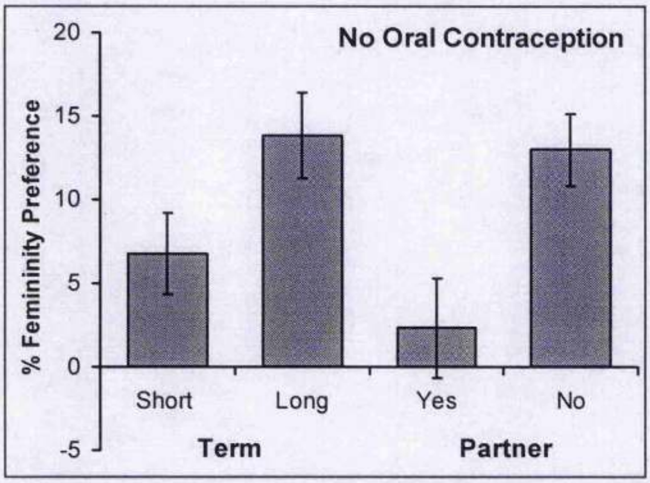

Figure 23: Mean femininity preferences (+/-1 SE) in male faces for participants reporting NOT using oral contraceptive
Scores are presented separately for participants rating for short- and long-term contexts and for participants with and without partners.

For those women who reported not using oral contraception a significant effect of both context ($F_{1,102} = 5.4$, $p = 0.022$) and partnership status ($F_{1,102} = 7.6$, $p = 0.007$) was found. No significant effect of age was found on masculinity preference ($F_{1,102} = 0.5$, $p = 0.50$) and there was no interaction between context and partnership status ($F_{1,102} = 0.2$, $p = 0.65$). These results reflect the lower preference for femininity in women judging for short-term relationships over women judging for long-term relationships and the lower preference for femininity in women with partners than women without partners (Figure 23).

For those women who did report using oral contraception, there were no significant effects of context ($F_{1,46} = .9$, $p = 0.34$), partnership status ($F_{1,46} = 1.3$, $p = 0.26$), and there was no interaction between context and partnership status ($F_{1,46} = 1.3$, $p = 0.25$). Comparing Figures 23 and 24 shows the different preferences for masculinity in women using and not using oral contraception. A significant effect of age on masculinity preference was found in this group of women ($F_{1,46} = 4.9$, $p = 0.033$). Pearson correlations reveal a significant negative relationship between age and femininity preference overall (N = 158, $r = -0.20$, $p = 0.011$).

A univariate 2x2x2 ANOVA with 3 factors, 'context', 'partnership status', and 'contraceptive use', with age as a covariate was carried out on the dependent variable of femininity preference to assess the effects of contraceptive use. Analysis revealed no significant effects of age ($F_{1,149} = 3.0$, $p = 0.087$), context ($F_{1,149} = 0.1$, $p = 0.76$), partnership status ($F_{1,149} = 0.2$, $p = 0.62$) or contraceptive use ($F_{1,149} = 0.1$, $p =$

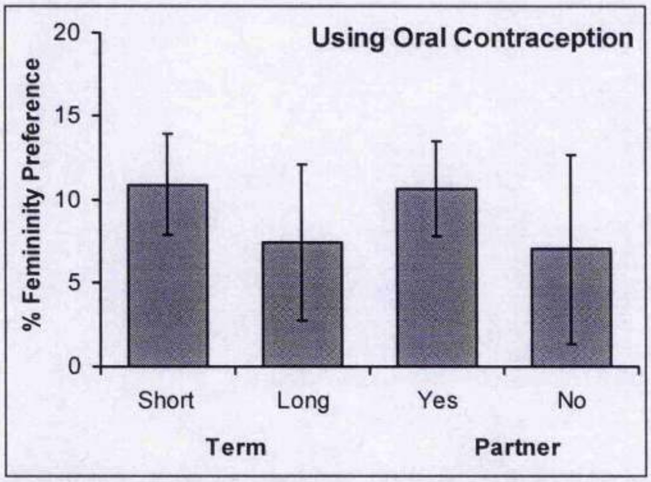

Figure 24: Mean femininity preferences (+/- 1 SE) in male faces for participants reporting using oral contraceptive
Scores are presented separately for participants rating for short- and long-term contexts and for participants with and without partners.

0.76). There was a significant interaction between contraceptive use and context ($F_{1,149} = 3.9$, $p = 0.049$) and between contraceptive use and partnership status ($F_{1,149} = 4.8$, $p = 0.030$). Comparing Figures 21 and 22 it can be seen that these interactions reflect a reversal of the facial femininity preference results of the contraceptive-using group from the results of the group not using oral contraception. There was no significant interaction between context or partnership status ($F_{1,149} = 1.1$, $p = 0.29$) nor was there a significant three-way interaction between contraceptive use, partnership status and context ($F_{1,149} = 0.4$, $p = 0.51$).

8.4 Discussion: Women may act to maximise genetic benefits from masculine faced males

Study 6 shows that human females have different preferences for femininity in male faces in relation to both the temporal context of the relationship they are assessing males for and in relation to their current partnership status. It was found that women showed a higher preference for male face masculinity when judging for short-term relationships than when judging for long-term relationships. A higher preference for male face masculinity was also found in women with partners than women without partners. Women were selected who were happy in their current relationships. The current results may therefore reflect a choice for a potential extra-pair partner rather than choice for a potential replacement for their current partner. Changing preferences as the result of partnership or relationship context was only seen in women who reported not using oral contraception – women using oral contraception did not differ in their masculinity preferences across conditions.

The results show that women have different face preferences for short- and long-term mates. For example, Buss and Schmitt (1993) have found that women do in fact place greater emphasis on a male's physical attractiveness and physical prowess in the context of a possible short-term relationship. Scheib (2001) has also shown that when choosing for an extra-pair partner women are more likely to choose an attractive male lower on co-operation and parenting qualities over a less attractive male with higher co-operation and parenting qualities. In long-term contexts the reverse in true – women choose the less attractive but more co-operative man more often (Scheib, 2001). The effects in Scheib's study appear analogous to our finding that women trade-off good-genes for good parenting between short- and long-term contexts, though in Scheib's study the personality descriptions are explicit (presented in vignettes) rather than the implicit stereotypes associated with masculine faces (Perrett et al., 1998a).

There is some indication that different women may even engage in different selection strategies. Women who are most willing to engage in short-term mating care more about a man's physical attractiveness than do women who are less willing to engage in short-term mating (Simpson & Gangestad, 1992). Such findings may indicate alternate strategies: one that involves maximising male gene quality for immunity by pursuing short-term relationships and one to maximise paternal investment by concentrating on long-term relationships and focusing less on cues to genetic immune quality.

That women with current partners prefer less feminine faces is also consistent with previous studies. For example, women have been found to prefer men with symmetrical bodies (symmetry being another proposed marker of genetic quality) as extra-pair partners (Gangestad & Thornhill, 1997a; Thornhill & Gangestad, 1994). In the current study we might have expected to find an interaction between context and partnership status; those with partners showing the greatest shift towards masculinity preference when judging for short-term relationships. This interaction could be absent because women without a partner may always be influenced by their preferences for a long-term partner (Buss & Schmitt, 1993). By contrast, women with partners may tend to consider a relationship outside their current partnership to be more likely to be short-term (i.e., when choosing a secondary potential partner women are not as constrained by their long-term preferences).

Changing preferences for masculinity in male faces highlights the importance of flexibility in women's mate-choice. In humans, as with other species with bi-parental care, it is important, but not absolutely necessary, for a woman to obtain both paternal care and heritable benefits for her offspring. Masculine male faces and feminine male faces are associated with potential costs and benefits to the reproductive success of females (Perrett et al., 1998a). Heritable immuno-competence benefits may be acquired from the owners of masculine faces but at the potential cost of lower paternal investment. It has been argued that high-quality males are less likely to invest in mates and instead pursue a strategy of maximising their number of lifetime mates (Gangestad & Simpson, 2000). Indeed, men with high body symmetry (a proposed marker of good-genes) appear less inclined to provide paternal care than other men (see Gangestad & Simpson, 2000 for review). It is possible that some females may choose a long-term partner whose low masculine appearance suggests co-operation and extended paternal care and/or choose short-term partners whose higher facial masculinity may indicate better genetic quality. Females may thus trade-off heritable immunity benefits for the benefits of paternal investment. In the case of short-term mating or when a female has already acquired a long-term partner, the importance of paternal investment from a secondary partner is minimised and so females appear to favour male traits advertising heritable immunity benefits.

It should be noted that the results of the study may not reflect that females with a partner or females rating for short-term relationships prefer masculinity: rather the results of the study may suggest that individuals without partners and those looking for men for long-term relationships prefer greater femininity, and hence positive personality attributes, in men. Females without partners and those rating for short-term relationships may not be as demanding of the overall preferred femininity in male faces as they do not expect the relationship to last long or they already have a partner they are happy with and so this variable is simply not as important to them.

There were trends in the data to suggest that older individuals prefer more masculine faces (significant overall negative correlation between age and femininity preference). One obvious explanation may be that masculine faces appear older (Perrett et al., 1998a). Older females may thus prefer older looking male faces for a variety of reasons associated with assortative mating (individuals' pair up with those possessing similar traits to themselves). Older individuals have also grown up under different environments and potentially different portrayals of beauty. For example, the males presented in Hollywood films are potentially different now than twenty years ago. Older individuals may also have needs in a partner that are different from those of younger individuals. Assortative mating for age, different media portrayals of beauty across time, and changing desires are all potential, and possibly additive, mechanisms to account for variations in preferences between younger and older participants.

Little et al. (2001; Chapter 7) found that women who thought they were physically attractive preferred more masculine faces than those women who thought they were less physically attractive. The absence of a preference for proposed markers of good-genes was interpreted as potentially adaptive for women of low mate-value in order to avoid the costs of decreased parental investment/potential desertion from the owners of masculine features. The findings reported in this study appear independent of such effects given that self-rated attractiveness was not found to differ across those rating short- or long-term relationships, those with or without partners or those using and not using oral contraception.

The current study also demonstrates that use of oral contraception appears to disrupt potentially adaptive preferences. Women using an oral contraceptive displayed no effect of either context or partnership status, in fact their preferences appear to be in the reverse direction to women not using oral contraception. Women using oral contraception also do not show potentially adaptive preferences for cycle-based attractiveness judgements of masculinity (Penton-Voak et al., 1999b), odours associated with male facial symmetry (Gangestad & Thornhill, 1998), and odour-based cues to MHC genes (Wedekind & Furi, 1997). It is also worth noting that those using oral contraception reported having more lifetime partners than those not using oral contraception. This may indicate different lifestyle choices for those using and not using oral contraception. By reducing the consequences of casual sex, use of contraception may lead to more promiscuous behaviour or else a desire to engage in sex with a greater number of partners may lead individuals to use oral contraception. It is possible then that it is not just the hormonal effects of contraceptive use that lead to different patterns of masculinity preference between contraceptive users and non-users in the current study – there may also exist behavioural differences between these groups which may also impact on preference. The impact of the use of oral contraception on actual mate-choice remains to be seen but it is certainly an important avenue for future research given its impact on preferences for the potential to maximise offspring fitness.

9 Narcissus and Oedipus: Attraction to Own Traits and Attraction to Parental Traits[32]

Synopsis

This Chapter examines two popular notions in modern society: that we are attracted to our own physical traits and/or our parent's physical traits. Each is consistent with the other given that offspring resemble their parents and there are evolutionarily advantages to mating within someone who shares common genes. A study is described which examined the best-predictor of partner hair and eye colour from own and parent traits, finding that opposite-sex parent traits best predicted partner traits. Such data is consistent with both studies showing self-similar partnerships and studies showing parent-similar partnerships but suggests that such effects are driven by an imprinting-like phenomenon.

9.1 Narcissus and Oedipus

Figure 25: Narcissus falling in love with himself

The notion that we are attracted to images resembling ourselves and also to our parental traits is pervasive in modern society. The dictionary defines narcissism as "excessive or erotic interest

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[32] Adapted from: Little AC, Penton-Voak IS, Burt DM, & Perrett DI (2003). Investigating an imprinting-like phenomenon in humans: partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behaviour, 24,* 43-51.

in oneself and one's physical appearance" (Concise Oxford Dictionary, 10th ed). The word narcissism comes from an extreme example of self love - Narcissus, a character from Greek mythology that falls in love with his own reflection when walking past a pool and dies because he is unable to pull himself away from the beauty of his own image (Figure 25).

The Oedipus complex, put forward by Freud (1927), has also entered common usage, defined in the dictionary as, "(in Freudian theory) the complex of emotions aroused in a young child by an unconscious sexual desire for the parent of the opposite-sex." (Concise Oxford Dictionary, 10th ed). Again the name comes from an extreme example from Greek literature; Oedipus killed his father and married his mother.

Most individuals never come anywhere near the extremes of Narcissus and Oedipus and there is no reason to think that because these ideas are popular in culture that they are real effects. There are also, however, theoretical evolutionary reasons to expect preferences for self- or parent similarity in partners. The theory and evidence for self- and parent-similar attractiveness are briefly reviewed below.

9.2 Look-alikes

Positive assortative mating occurs when individuals form pairs in which the individuals involved are more similar to each other than would be expected by chance (e.g., Burley, 1983; Thiessen & Gregg, 1980). In humans, mating with similar individuals to oneself may have genetic benefits. For example, Thiessen and Gregg (1980) have proposed that if you mate with similar looking individuals this increases the chances that those individuals have genes in common with you and that mating with such individuals can be advantageous (also Rushton & Nicholson, 1988)[33]. Aside from genetic benefits, assortative mating may also simply result in more stable partnerships as it has been shown that couples who are similar on a variety of traits are less likely to break up (Hill, Rubin, & Peplau, 1976), possibly due to increased behavioural compatibility (e.g., assortment for personality results in similar interests).

Early research on assortative mating in humans examined correlations in physical characteristics between partners, such as arm length, and reviews of these studies find that the overall pattern shows low positive correlations (0.01- 0.35) for many physical features between partners (e.g., Spuhler, 1968).

Three studies have examined the perceived facial similarity between married couples. Griffiths and Kunz (1973) took photos of married couples who were then split into six groups by the length of the marriage. Participants were asked to match up photos to their partner. Couples married for less than ten years were matched at levels above chance but subjects failed to match couples married for between ten and twenty years. Couples married for over 20 years were again successfully matched by participants. This is a difficult result to interpret but the small stimuli sets used (five couples in each group) may help explain these findings.

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[33] There are also costs to positive assortment, however, such as inbreeding, which place a theoretical ceiling to the self-similarity that should be tolerated and so it has been hypothesised that there exists an ideal level of preferred similarity that maximises the benefits and minimises the costs ('optimal-outbreeding', see Bateson, 1980).

Zajonc (1987) performed a similar experiment, hypothesising that couples do not pair due to similarity, but become more physically alike over time due to sharing similar diets, lifestyles and emotional experiences. They used two photographs from each individual in twelve married couples. One photo came from the first year and the second was taken in the twenty-fifth year of the marriage. Target faces were presented with six opposite-sex test faces, one of which was the target's real life partner. The subject's task was to rank either the similarity or the likelihood of marriage between the test faces and the target, depending on the condition. Photos from the first year were not perceived as more similar (or more likely to be married) than expected by chance. Photos from the 25th year of marriage were ranked as more similar and more likely to be married than chance would predict. These results differ from Griffiths & Kunz (1972) who did demonstrate similarity between newly wed couples. The 'similarity' and 'likelihood of marriage' rankings were almost identical, indicating participants' associated facial resemblance with the likelihood of marriage between individuals. This means that people assume that people marry people who look like themselves (e.g., Figure 26).

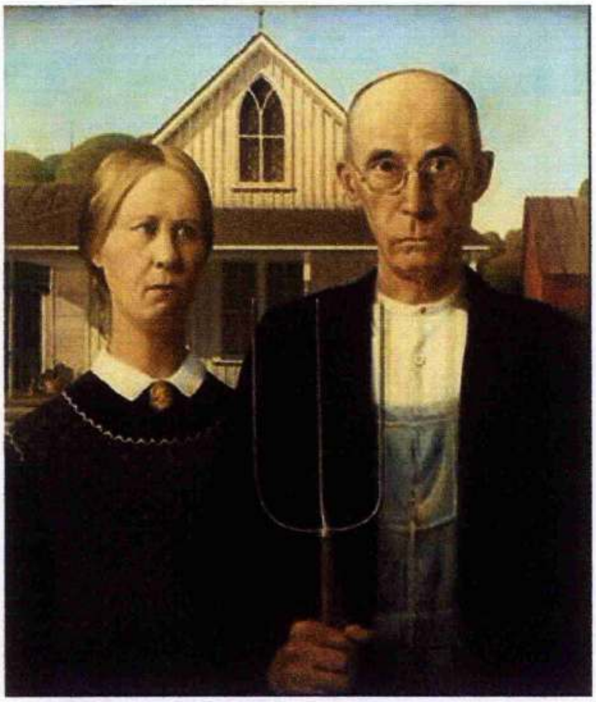

Figure 26: American Gothic.
This is a portrait by Grant Wood from 1930 and provides a famous example of the belief that similar looking individuals pair up together.

Hinsz (1989) also studied facial similarity in real couples. Photos were of two groups, engaged couples and couples married for around 25 years. Participants were presented with opposite-sex pairs of photos, and asked to rate the similarity between the two faces. Half of the pairs presented were actual couples, and half were randomly generated couples. Real couples were rated as significantly more similar than randomly generated couples. Unlike Zajonc (1987), couples that had been together for longer periods of time were not perceived as more similar than new couples.

Penton-Voak et al. (1999a) adopted a novel approach to studying similarity between partners, by studying preferences for faces, rather than looking at real couples. Individual faces were photographed and the resulting images were 'gender transformed' using computer graphics techniques to generate hypothetical opposite-sex 'siblings'. Ratings demonstrated that these computer-generated images were perceptually similar to the original photographs, indicating that the transforms were successful. When the original subjects were asked to rate a set of photographs which included their opposite-sex 'twin', they tended to rate faces similar to their own higher in attractiveness than those to which they were dissimilar. Unfortunately, whether this really represents a preference for self-similar faces is unclear as a preference for averageness could also generate this finding: faces very far from average receive low attractiveness ratings and such atypical faces differ from the faces of most individuals more than average faces, possibly accounting for the result (Penton-Voak et al., 1999a).

In a second study Penton-Voak et al. (1999a) gave subjects the opportunity to adjust average face shapes, making the faces appear more or less similar to the subject's own face. No systematic preference for self-similar characteristics or opposite characteristics was found.

Two other computer graphic studies of facial similarity have been conducted recently. DeBruine (2002) has shown that increasing self-similarity in shape and colour and in shape alone increases trust in a co-operation game with same-sex faces. Platek, Burch, Panyavin, Wasserman, and Gallup (2002) manipulated self-similarity in infant's faces and showed that males but not females found the face merged with themselves as the child they found most attractive, most likely to adopt, and more likely to invest in. The results of these studies show that facial resemblance is important for some decisions (co-operation and investment) but not necessarily mate-choice.

Aside from physical traits, assortative mating also takes place for non-physical factors. In fact, stronger correlations are reported between partners for characteristics such as religion, educational level, socioeconomic status and political beliefs than for any measured physical characteristics (Rushton & Nicholson, 1988; Thiessen & Gregg, 1980; Vandenberg, 1972; Epstein & Guttman, 1982). Intelligence is genetically heritable but has a strong environmental influence. Johnson, Ahern, and Cole (1980) reviewed studies from 1928 to 1973 that examine similarity for intelligence and found positive correlations between spouses between 0.12 and 0.76 across many different tests employed. Bouchard and McGue (1981) reviewed 16 standardised IQ studies and found an overall correlation of 0.37 between partners in 3817 couples. There is also evidence that assortative mating occurs for certain abnormalities in personality. Assortative mating has been observed between sufferers of schizophrenia, alcoholism, depression and neuroses (see Thiessen & Gregg, 1980 for review). Looking at matching for personality, Botwin, Buss, and Shackleford (1997) found positive correlations between partners for three of the Big 5 personality traits (see Chapter 4): agreeableness (dating couples, r = .27, married couples, r = .33), conscientiousness (dating, r = .27, married, r = .22) and openness (dating, r = .51, married, r = .38). No assortative mating was found for extraversion (dating, r = .25, married, r = -.10) or neuroticism (dating, r = -.18, married, r = .06).

All these studies point to consistent matching for a wide range of characteristics amongst partners, with similar individuals mating together at levels above chance. Although no preference for self-similarity in physical features has been defined experimentally, and the perceptual basis of actual partners looking alike is unclear there does appear to be some evidence for positive assortment for physical characteristics in humans.

If assortative mating is theoretically beneficial and occurs for a variety of traits in humans then the question remains of how might an individual come to be attracted to (or avoid) self-similar traits[34]. Petrie, Krupa, and Burke (1999) have demonstrated that individuals may examine their own traits to assess genetic similarity. They released a mixed group of related and unrelated male peacocks and found that brothers established display sites very close together. As the birds were raised with

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[34] An assortative pattern of mating is not necessarily caused by assortative preferences (Burley, 1983). Assuming that 'like mates with like' because 'like prefers like' is an oversimplification. In a population where a certain characteristic is universally considered attractive (a type or directional preference) an assortative pattern can still develop. For example, if height is universally considered attractive, tall people will end up with tall partners and short people will end up with short partners. This will happen because tall individuals can compete well for tall partners, leaving short people to pair up together (even if short people were most attracted to tall people).

non-relatives, they could not have been familiar with their brothers' appearance prior to release. This indicates that the birds had a means of kin recognition that did not involve learning the characteristics of relatives. It is possible that peacocks recognise kin through similarity to their own phenotype. For example, individual birds may examine their own tail and recognise others with similar tails allowing 'birds of a feather to flock together'. Thus this is a potential mechanism for assortative mating for traits in other animals.

Research thus suggests that awareness of one's own traits may encourage choice of partners similar to oneself. Seeking out a partner who is similar to you, however, is also consistent with attraction to parental traits, as usually children physically resemble their parents. This leads us to consider the influence of parental characteristics on mate preferences in humans.

9.3 Attraction to parental traits

In animals, the effect of parental traits on later mate-choice has received much attention. Imprinting refers to a phenomenon whereby experience at an early age influences later behaviour including mate preferences. Konrad Lorenz (1943) drew attention to this phenomenon having found that ducklings would imprint on and follow his patterned boots. Young animals see parental traits (such as plumage colour) at an early age and later in life find these traits either unattractive or attractive in mates. Many studies of nonhuman species have examined the effects of early exposure to parental characteristics on later mate preferences, a phenomenon usually described as sexual imprinting. Positive visual imprinting (an attraction to visible parental characteristics) has been demonstrated in both birds (zebra finches - Vos, 1995; quail - Bateson, 1980) and ungulates (sheep and goats - Kendrick, Hinton, &

Atkins, 1998), and there is even suggestive evidence that it occurs in primates (Fujita, 1993).

Although imprinting has been proposed to play a role in human mate-choice, relatively little formal work has tested this hypothesis. Westermarck (1894) argued that children have an innate tendency to develop a sexual aversion to individuals with whom they live closely in infancy and early childhood (usually siblings and parents). Such a mechanism would discourage sibling incest, preventing inbreeding in a population. Westermarck's hypothesis has received empirical support from a series of ethnographic studies where male and female non-siblings are raised together in a way similar to real siblings (Shepher, 1971; Wolf, 1993). Across these studies, children growing up together avoided later sexual interaction, even when in arranged marriages. Westermarck's hypothesis suggests that infants learn to avoid sexual relationships with individuals to whom a strong bond is formed in early childhood. The most documented form of sexual imprinting in animals, however, is positive imprinting – being attracted to the characteristics of those present during infancy as potential mates later in life.

In humans there have been few studies on the effects of parental characteristics on offspring's partner choice, although the idea of attraction to the opposite-sex parent's form is a popular notion, mainly due to the speculation of psychoanalytic theorists (Freud, 1927; Jung, 1926). There are several studies that do indicate that parental characteristics, usually opposite-sex parental characteristics, can influence later choice of partner.

Two studies have examined paternal and partner age in women. Small but consistently positive correlations were found between these variables indicating that the daughters of older men subsequently tend to choose older partners (Wilson & Barrett, 1987; Zei, Astolfi, & Jayakar, 1983). Both studies are thus consistent with sexual imprinting in humans, though the correlations are small (the largest correlation coefficient in both the studies is 0.11). Following from this work showing links between parental age and actual partner age, Perrett et al. (2002) investigated if parental age impacted on preferences for faces of different ages. If offspring are attracted to parental characteristics, individuals born to old parents should be more attracted to older faces than individuals born to young parents. Using computer graphic faces (Perrett et al., 2002) did indeed find that women born to old parents were relatively less impressed by youth and more positive to age cues in male faces than women with young parents. For men judging female faces, preferences appeared to be influenced only by the opposite-sex parent, the mother.

A fourth study by (Jedlicka, 1980; Figure 27) also provides evidence for imprinting-like effects in humans. Jedlicka compared the ethnicity of father and mother to the ethnicity of spouses for individuals on their second marriage and found ethnicity of spouse corresponds to father's ethnicity in 61.4% of brides and 41.4% of grooms. This is reversed for mothers (mother's and spouse ethnicity correspond for 38.6% of brides and 58.6% of grooms). Similar results were also found for 1st marriages. These results indicate that offspring were attracted to, or at least chose to marry, individuals who resembled their opposite-sex parent and that such choices are stable over time as they occur in both 1st and 2nd marriages. There may be additional constraints from social pressures acting on ethnic choice in marriage. For example, mothers may have a stronger influence than fathers on son's choice of daughter-in-law or else there may be pressures from both parents to recreate the parental relationship.

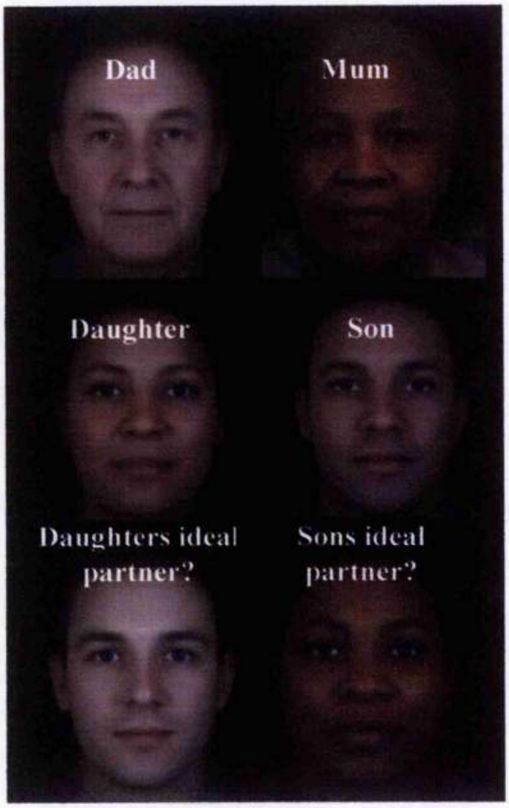

Figure 27: Attraction to parental race traits

Jedlicka (1980) found that children from mixed-race marriages were more likely to marry a partner of the race of the opposite-sex parent.

Apart from age and ethnicity few characteristics are stable in parents throughout upbringing. Hair and eye colour are two further potentially stable parental characteristics that offspring may learn and both appear important in mate-choice. For example, hair and eye colour are often mentioned in lonely heart adverts. For example, Lynn and Shurgot (1984) found 44% of adverts mention the advertiser's hair and eye colour. The impact of parental eye colour on partner choice in women has been investigated. Wilson and Barrett (1987) showed a weak non-significant trend for women to choose partners whose eye colour resembled their father's. Restricting analysis to those reporting partners and parents with blue or brown eye colour showed that women's partners were more likely than chance to have the same eye colour as their father. Women also tended to choose partners that had their maternal eye colour, although this result was non-significant. These results may be confounded by own eye colour. Maternal and paternal eye colours are closely related to own eye colour and therefore women may be choosing partners with eye colour similar to themselves. Wilson and Barrett do not report the overall contingency table results but a 2x2 chi-square with parent eye colour (mother and father) and boyfriend eye colour (same or different to parent) produces an overall non-significant result ($\chi^2 = 4.8$, df = 3, p = 0.19). This analysis suggests that maternal and paternal eye colour did not differentially impact on boyfriend's eye colour in Wilson and Barrett's study.

9.4 Self-similar attraction could be driven by parent-similar attraction and vice versa

Following from Wilson and Barrett's findings it is possible that humans are attracted to parental eye colour characteristics. As outlined above, assortative mating is consistent with imprinting on parental traits, however, parent-partner correlations are also consistent with attraction to self-similar traits. Individuals resemble their parents and so finding that partners look alike or that partners have traits resembling each other's parents is equally explainable by either attraction to self-similar or parent-similar traits. The role of own eye colour in guiding partner choices is given credence by evidence for assortative mating for hair and eye colour in humans. For example, Pearson (1907) reports a correlation of 0.26 between married partners' eye colours. Pearson and Lee (1903) and Schiller (1932) also report positive correlations between married couples for both hair and eye colour. It is worth noting that some studies, however, have not found preferences for self-similar hair and eye colour in partners (e.g., Feinman & Gill, 1978). Assortative mating is thus consistent with imprinting-like effects resulting in acquiring parent, and so self-similar, partners and also with attraction to own traits, which also results in self-similar partners (e.g., Petrie et al., 1999).

9.5 Study 7: Opposite-sex parents versus own traits and partners hair and eye colour

9.6 Rationale

Study 7 aimed to find out whether own or parental colour traits were positively associated with partner colour traits. Own, partner, maternal and paternal hair and eye colour characteristics were examined in an attempt to establish whether there is assortative mating for hair and eye colour and to determine whether such a mating pattern potentially reflects choice of self-similar and/or parent-similar characteristics.

9.6.1 Method

Participants

Three hundred and three females (18-63 years old, mean age 33.2) and 394 males (17-67 years old, mean age 34.6) took part in the study. They were recruited over the Internet and were volunteers. Participants were selected on the basis that they reported being heterosexual, had bi-parental upbringing and had a current partner.

Procedure

Participants were presented with a questionnaire about their own, ideal, partner and family hair and eye colour characteristics as well as a short questionnaire about themselves (gender, age and ideal partner gender).

For each characteristic participants used a pull down menu to select the colour that best described the colour of the hair or eyes of the person being described (own, partner, maternal and paternal). For eye colour the choices were black, dark-brown, light-brown, blue, blue /green, green, and hazel. For hair colour the choices were black, very dark-brown, dark-brown, mid-brown, light-brown, blonde, platinum blonde, light and dark red, and grey. Participants who described any person as having platinum blonde, light and dark red, and grey were excluded from the analysis due to the small sample of platinum blonde, the difficulty of coding light and dark red, and the likelihood that grey did not represent the parental hair colour during childhood.

Participants were also asked if any of the reported persons had dyed hair. Participants reporting dyed hair on any question were also excluded from the analysis.

9.6.2 Notes on the analysis

All correlation coefficients reported were calculated with the nonparametric Spearman's rho. Binary logistic regression was carried out on the data to predict ideal and actual partner hair and eye colour from own, maternal and paternal colour. To determine the best predictor of partner colour traits, backwards-conditional binomial regression was carried out (removal criterion of 0.10). All probabilities are quoted as 2 –tailed.

Eye colour was coded continuously on an 8-point scale from dark to light (1 = black, 2 = dark-brown, 3 = light-brown, 4 = hazel, 5 = green, 6 = blue/green, 7 = blue, 8 = grey). For the binary logistic regression, reported eye colour was recoded into light and dark. Blue, green and hazel eyes were coded as 'light'. Black, dark-brown and light-brown eyes were coded as 'dark'. The label dark is arbitrary, including light-brown but dark colours are relatively darker than the colours in the light category. Hair colour was graded for lightness on a 6-point scale from dark to light (black, very dark-brown, dark-brown, mid-brown, light-brown, and blonde). In order to carry out binary logistic regression on the hair data, hair colour was split into light and dark. Blonde, light-brown and mid-brown were coded as 'light'. Black, very dark-brown and dark-brown were coded as 'dark'.

9.6.3 Results

Female hair colour

Spearman's correlations were carried out on the continuous data. Own hair colour was significantly positively related to maternal ($r_s = 0.35, p < 0.001$) and paternal ($r_s = 0.32, p < 0.001$), but not partner ($r_s = 0.10, p = 0.074$) hair colour. Maternal hair colour was not significantly related to partner ($r_s = 0.08, p = 0.17$) or paternal ($r_s = -0.03, p = 0.65$) hair colour. Paternal hair colour was significantly positively related to partner hair colour ($r_s = 0.13, p = 0.028$). These correlations can be seen in Table 6.

Table 6: Correlations amongst hair colour characteristics for females/males

	Maternal	Paternal	Partner
Own	0.35**/0.55**	0.32**/0.39**	0.10/0.14*
Maternal	-	-0.03/0.16**	0.08/0.15*
Paternal	-	-	0.13*/0.18**

* Correlation is significant at the 0.05 level, ** 0.01 level (2-tailed).

Binary logistic regression was carried out on the data to predict partner hair colour from own, maternal and paternal eye colour. In the first step, own, maternal and paternal hair colour were not significant predictors of partner hair colour (χ^2 = 5.9, DF = 3, $p = 0.12$, Nagelkerke R Square = 0.026). Within the individual predictors it was found that own ($\beta = 0.06$, $p = 0.78$), maternal ($\beta = 0.36$, $p = 0.076$) and paternal ($\beta = 0.38$, $p = 0.075$) hair colour were not significant predictors of partner hair colour though maternal and paternal hair colour were approaching significance.

In one step, removing the worst predictor, own hair colour, created a model that was close to significantly predicting actual hair colour (χ^2 = 5.9, DF = 2, p = 0.053, Nagelkerke R Square = 0.026) and that was not significantly different from the first model (χ^2 = 0.001, DF = 1, $p = 0.99$). Neither maternal ($\beta = 0.40$, $p = 0.089$) nor paternal ($\beta = 0.47$, $p = 0.058$) hair colour was a significant predictor of partner hair colour though both were approaching significance. Removal of variables stopped here as neither remaining variable met the removal criterion of 0.10, though it is worth noting the effects of paternal hair colour are slightly stronger than the effects of maternal hair colour.

Female eye colour

Spearman's correlations were carried out on the continuous data. Own eye colour was significantly positively related to maternal ($r_s = 0.51, p < 0.001$), paternal ($r_s = 0.50$, p < 0.001) and partner eye colour ($r_s = 0.14, p = 0.016$). Maternal eye colour was significantly related to paternal ($r_s = 0.14, p = 0.013$) but not partner ($r_s = 0.06, p = 0.33$) eye colour. Paternal eye colour was significantly positively related to partner eye colour ($r_s = 0.20, p < 0.001$). These correlations can be seen in Table 7.

Table 7: Correlations amongst eye colour characteristics for females/males

	Mother	Father	Partner
Own	0.51**/0.60**	0.50**/0.56**	0.14*/0.14*
Mother	-	0.14*/0.33**	0.06/0.27**
Father		-	0.20**/0.14*

* Correlation is significant at the 0.05 level, ** 0.01 level (2-tailed).

Binary logistic regression was carried out on the binary data (variables recoded into light and dark) to predict ideal and partner eye colour from own, maternal and paternal eye colour. In the first step, own, maternal and paternal eye colour were not significant predictors of partners' eye colour ($\chi^2 = 5.7$, DF = 3, $p = 0.12$, Nagelkerke R Square = 0.025). Within the individual predictors, however, it was found that paternal eye colour ($\beta = 0.59, p = 0.024$) did predict partner eye colour. Own ($\beta = -0.11, p = 0.71$) and maternal ($\beta = 0.08, p = 0.76$) eye colour were not significant predictors of partner eye colour.

In two steps, maternal and own eye colour were removed, leaving paternal eye colour as the single best predictor of partner eye colour ($\chi^2 = 5.3$, DF = 1, $p = 0.021$, Nagelkerke R Square = 0.023, paternal eye colour, $\beta = 0.54$, $p = 0.022$).

Male hair colour

Spearman's correlations were carried out on the continuous data. Own hair colour was significantly positively related to maternal (r = 0.55, $p < 0.001$), paternal (r = 0.39, p < 0.001) and partner (r = 0.14, $p = 0.004$) hair colour. Maternal hair colour was significantly positively related to paternal (r = 0.16, $p < 0.001$) and partner (r = 0.15, $p = 0.002$) hair colour. Paternal hair colour was significantly positively related to partner hair colour (r = 0.18, $p < 0.001$). These correlations can be seen in Table 6.

Binary logistic regression was carried out on the data to predict partner hair colour from own, maternal and paternal hair colour. In the first step, own, maternal and paternal eye colour were significant predictors of partner hair colour ($\chi^2 = 11.2$, DF = 3, $p = 0.011$, Nagelkerke R Square = 0.037). Within the individual predictors it was found that maternal hair colour ($\beta = 0.65$, $p = 0.005$) was a significant predictor of partner hair colour but own ($\beta = -0.33$, $p = 0.17$), and paternal ($\beta = 0.42$, $p = 0.063$) were not.

In two steps, own and paternal hair colour were removed, leaving maternal hair colour as the single best predictor of partner hair colour ($\chi^2 = 6.9$, DF = 1, $p = 0.009$, Nagelkerke R Square = 0.023, maternal hair colour, $\beta = 0.53$, $p = 0.009$).

Male eye colour

Spearman's correlations were carried out on the continuous data. Own eye colour was significantly positively related to maternal ($r = 0.54, p < 0.001$) and paternal ($r = 0.46, p < 0.001$) eye colour, but not partner eye colour ($r = 0.07, p = 0.19$). Maternal eye colour was significantly positively related to paternal ($r = 0.23, p < 0.001$) and partner ($r = 0.16, p = 0.002$) eye colour. Paternal eye colour was not significantly related to partner eye colour ($r = 0.03, p = 0.51$). These correlations can be seen in Table 7.

Binary logistic regression was carried out on the data to predict partner eye colour from own, maternal and paternal eye colour. Own, maternal and paternal eye colour were significant predictors of partner eye colour ($\chi^2 = 10.0$, DF = 3, $p = 0.019$, Nagelkerke R Square = 0.035). Within the individual predictors it was found that it was maternal eye colour ($\beta = 0.75, p = 0.004$) that was mainly responsible for this effect. Own ($\beta = -.13, p = 0.65$) and paternal ($\beta = 0.03, p = 0.90$) eye colour were not significant predictors of partner eye colour.

In two steps, paternal and own eye colour were removed, leaving maternal eye colour as the single best predictor of partner eye colour ($\chi^2 = 9.7$, DF = 1, $p = 0.002$, Nagelkerke R Square = 0.034, maternal eye colour, $\beta = 0.46, p = 0.002$).

Table 8 shows a summary of the results from the backwards-conditional binary logistic regression.

Table 8: Summary of results: best predictors for males and females

	Male	**Female**
Partner hair colour	Mother	Mother and Father
Partner eye colour	Mother	Father

9.7 Discussion: Narcissus, Oedipus and everybody else

Study 7 demonstrates that, from the first step of the binomial logistic regression controlling for own and same-sex parent eye colour, the single best predictor of both male and female partner eye colour is the opposite-sex parents' eye colour. Opposite-sex parents' hair colour is the single best predictor of males' partners' hair colour although maternal hair colour was also found to have a positive effect on female partner hair colour. These results indicate that individuals appear to choose partners that resemble their opposite-sex parent over and above any effects of own or same-sex parent effects. The data also shows evidence of assortative mating for eye colour and hair colour in line with previous findings (Pearson, 1907; Pearson & Lee, 1903; Schiller, 1932). Significant correlations were found between males' eye and hair colour and their reported partners' eye and hair colour. Similar correlations were also found for females although the correlation for hair colour was only tending towards significance ($p = 0.07$).

The finding of an impact of parental traits on mate-choice in this study is consistent with previous findings (Jedlicka, 1980; Wilson & Barrett, 1987; Zei et al., 1983). The current study also replicates and extends the findings of Wilson and Barrett (1987) for eye colour, showing similar results for male participants as well as females. An attraction to visible parental characteristics has been demonstrated in many non-human animals (Bateson, 1980; Kendrick et al., 1998; Vos, 1995; Fujita,

1993) and it is possible that attraction to parental hair and eye colour traits may reflect "imprinting-like" effects (referred to as imprinting from now on) in humans. Imprinting implies that the learning is constrained to infancy but the current experiment does not examine the timing of learning effects. Therefore in this Chapter the term imprinting is used to reflect the learning and attraction to parent characteristics whenever in an individual's life this learning occurs. In this way the use of the word imprinting is more analogous to the term 'social-learning' rather than a more restrictive view of imprinting sometimes used in reference to other animals.

While it is possible the individuals can be attracted to their own traits (Petrie et al., 1999), the findings of Study 7 imply that resemblance to opposite-sex parental traits best explains assortative mating (or self-similarity) for eye and hair colour in partnerships. It is possible that assortative mating/self-similar preferences reflect attraction to parental traits rather than referencing your own phenotype in other domains and this remains an area for future study.

Attraction to parental characteristics may appear to conflict with Westermarck's (1894) hypothesis that children develop a sexual aversion to individuals with whom they live closely in infancy and early childhood. The two phenomena, however, need not be in contradiction. Bateson (1980) has shown in quail that individuals may avoid the particular individuals close to them during childhood but still be attracted to their general characteristics. An individual can both be attracted to the general colour characteristics of their parents while still learning to avoid the actual parent as an inappropriate mate.

Exposure to faces has diverse effects on perception (Valentine, 1991) and it has been shown that brain mechanisms processing faces may become attuned (e.g., Perrett, Oram, & Wachsmuth, 1998b) to the characteristics of the faces that are experienced during life. Such tuning may then influence partner choice in adulthood. Learning effects in faces may occur for parental characteristics. For example, it is well established that people generally respond positively to familiar stimuli (the mere exposure effect - Bornstein, 1989; Zajonc, 1968) and parental facial features may be very salient familiar features. Thus it is possible that individuals choose partners who possess similar hair and eye colour to their opposite-sex parents on the basis that such partners are more familiar than prospective mates with different hair and eye colours. Potentially the finding that individuals are attracted to faces with some characteristics of their parents (age, Perrett et al., 2002) may help explain why the participants in this study report having partners similar to their parents for colour traits. A visual preference for opposite-sex parental colour in partners could explain the results though this is by no means the only potential mechanism.

It must be noted that valuing partners who display parental eye and hair colour does not necessarily indicate that such behaviour is adaptive. Attraction to parental hair and eye characteristics may be an epiphenomenonal consequence of mechanisms for learning the visual characteristics of the parental species (which seems clearly adaptive) or simply a by-product of the way in which the visual system becomes attuned to familiar traits. It is worth noting that if the effects observed in this study were due to a general cognitive effect we would expect equal effects of both parents. Offspring appear to acquire partners possessing colour traits in line with their opposite-sex parent's traits and not the same-sex parent, which is suggestive that the underlying mechanism is not indiscriminate and therefore implies an adaptive function at some level (see Chapters 3 & 5). Such opposite-sex effects are consistent with findings in birds of the effects of parental traits on subsequent partner choice. For example, Vos (1995) has demonstrated the importance of the opposite-sex parent in imprinting in male zebra finches.

The finding of a relationship between parental traits and partner has wide-ranging consequences in human mate-choice. Despite a high degree of agreement both across individuals and cultures about what is and what is not attractive, present results indicate that there are individual differences in what people find attractive (see also Chapters 6, 7, & 8). Learning parental characteristics may explain some individual differences in opinion about which characteristics are attractive in a partner. Attraction to parental characteristics also has implications for assortative mating. Studies showing similarity between partners cannot assume such similarity comes about due to self-similar preferences as similarity is also consistent with attraction to parent traits. For example, the similarity between the faces of married partners (e.g., Griffiths & Kunz, 1973; Hinsz, 1989; Zajonc, 1987) is consistent with imprinting-like effects and it is possible that imprinting on parents may contribute to the causes of assortative mating in humans for a variety of traits.

In summary, the data in this Chapter shows that parental eye and hair colour is positively related to partner colour. The data here are consistent with findings of previous studies showing effects of opposite-sex parents on partner choice and such effects, though small, suggest that an imprinting-like phenomenon does indeed influence human mate-choice.

10 Summary and Conclusions: Beauty in the Face of the Beheld and in the Eye of the Beholder

Synopsis

This final Chapter summarises the findings and the implications of the work conducted as part of this thesis. It is concluded that current evidence suggests that both symmetry and sexual dimorphism in human faces are linked to mate-choice and that individual differences in mate-choice can be consistent with an evolutionary view.

10.1 Beauty in the face of the beheld

Chapter 1 discussed the huge amount of interest by humans in other human's faces. On top of this general interest, as a species, we are generally drawn particularly to attractive faces. In other species, traits influencing mate attractiveness are usually involved in sexual selection (Chapter 2) and so it is highly likely that this interest in faces, particularly the discrimination between attractive and unattractive faces, in some way reflects evolutionary pressures.

Sexual selection helps to explain why we are attracted to particular faces (Chapter 2). There are several ideas about the evolution of preferences and traits. Preference and traits could be linked by general aesthetic preference, arising out of other properties of sensory systems but driving the evolution of a trait in line with a preference. Rather than arbitrary preferences, there are also thought to be preferences for traits related to an advantage in choosing mates in possession of those traits. In other words, the trait is preferred because it advertises a benefit to the chooser. Other sources of preference are discussed in Chapter 2.

There are two major traits associated with attractiveness in human faces discussed in this thesis: symmetry and sexual-dimorphism (Chapter 3). Symmetry and sexual-dimorphism are both theoretically linked to quality and it is possible that both traits are preferred because they advertise good-genes to the choosing individual.

The studies in Chapter 4 demonstrate that the attractiveness of masculinity in male faces is mediated by negative personality attributions (Study 1) and that masculine male faces were associated with seeking short-term relationships while feminine faced men are associated with seeking a long-term term relationship (Study 2). Although speculative, the personality attributions received by masculine and feminine faced men appear in agreement with what we would expect if masculinity in male faces was related to underlying testosterone levels and dominance. Chapter 5 examined symmetry preferences in different face images. As symmetry was not preferred in inverted faces and was preferred in familiar faces these studies suggest that symmetry preferences may not be arbitrary but rather symmetry preferences in human faces may reflect an adaptation to identify high quality mates.

10.2 Beauty in the eye of the beholder

People do generally agree on what is and what is not attractive (Chapter 1; Chapter 4). Although evolutionary theories suggest that attractiveness judgments and partnership choices should reflect a 'best strategy', this does not preclude different individuals following different strategies and being attracted to different faces. In fact, in many instances it is easy to see how individual differences in preference could be more adaptive than a single species wide strategy (Chapter 6).

Preferences for visual cues to levels of masculinity and symmetry differ between individuals. Women who consider themselves most attractive have a relatively increased preference for masculinity and an increased preference for symmetry (Chapter 7) relative to those who thought themselves less attractive. Preferences for masculinity are also increased when women either have a partner or are considering for a short-term relationship relative to when they do not have a partner or are considering a long-term relationship (Chapter 8, also Chapter 4). These findings are consistent with strategic trade-offs we would expect females to make if masculinity in males advertised quality but was linked with decreased paternal investment. The absence of a preference for markers of good-genes may be adaptive in women of low mate-value to avoid the costs of decreased parental investment from the owners of such characteristics. High quality females may be less prone to low investment from high quality men or else more able to afford the costs of low paternal investment. The strategic preferences investigated in Chapter 8 show that women have preferences that would maximise any possible good-gene benefits from masculine faced males in situations when investment becomes of decreased importance.

Chapter 9 does not discuss masculinity or symmetry but does again show that individual differences in mate-choice do exist and can be consistent with evolutionary theory. That individuals' have partners most similar to their opposite-sex parent than their same-sex parent is also potentially evidence that this process is not a simple by-product of another mechanism but is directed in some way. Such data is also consistent with both studies showing self-similar partnerships and studies showing parent-similar partnerships but suggests that such effects are driven by attraction to parental traits.

10.3 Conclusions

Some aspects of human facial appearance are linked to preferences. If a trait reliably advertises mate quality then we would expect individuals in a population to find that trait attractive. Sexual dimorphism and symmetry are both traits in human faces that are linked to preferences and also potentially good-genes. We might expect then that all humans will prefer masculine male faces, feminine female faces and symmetrical faces of both sexes. This thesis presents data that is in line with the notion that sexual dimorphism and symmetry may advertise quality in human faces (Part 1).

Having argued for an overall preference for certain traits advertising quality, it is clear that individual differences in preferences for some traits will prove adaptive and so can be consistent with evolutionary theory. This thesis documents several potentially adaptive individual differences in human face preferences (Part 2). For humans, as with other species, there is no optimal strategy for mate-choice and parenting that applies to all individuals. Indeed the range of personal circumstances (physical, environmental, social) will guarantee that what is a good or adequate strategy, and therefore what is attractive, will depend on the individual. In this way beauty can be said to be both in the face of the beheld and in the eye of beholder.

References

Aiello, L. C. (1993). The fossil evidence for modern human origins in Africa: a revised view. *American Anthropologist, 95*, 73-96.

Albright, L., Kenny, D. A., & Malloy, T. E. (1988). Consensus in personality judgments at zero acquaintance. *Journal of Personality and Social Psychology, 55*(3), 387-395.

Alexander, R. D., Hoogland, J. L., Howard, R. D., Noonan, K. M., & Sherman, P. W. (1979). Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In N. A. Chagnon & W. Irons (Eds.), *Evolutionary Biology and Human Social Behaviour: An Anthropological Perspective* (pp. 402-435). North Scituate, MA: Duxbury Press.

Andersson, M. (1994). *Sexual Selection*. Princeton, NJ: Princeton University Press.

Attneave, F. (1955). Symmetry, information, and memory for patterns. *American Journal of Psychology, 68*, 209-222.

Baker, R. R., & Bellis, M. A. (1995). *Human Sperm Competition: Copulation, Masturbation and Infidelity*. London: Chapman & Hall.

Bakker, T. C. M. (1993). Positive genetic correlation between female preference and preferred male ornament in sticklebacks. *Nature, 363*, 255-257.

Bakker, T. C. M., Künzler, R., & Mazzi, D. (1999). Condition-related mate-choice in sticklebacks. *Nature, 401*, 234.

Bakker, T. C. M., & Pomiankowski, A. (1995). The genetic-basis of female mate preferences. *Journal of Evolutionary Biology, 8*, 129-171.

Balmford, A., & Thomas, A. (1993). Swallowing ornamental symmetry. *Nature, 361*, 628.

Barden, C. R., Ford, M. E., Jensen, A., & Salyer, K. (1989). Effects of craniofacial deformity in infancy on the quality of mother-infant interactions. *Child Development, 60*, 819-824.

Barrett, J. C., & Marshall, J. (1969). The risk of conception on different days of the menstrual cycle. *Population Studies, 23*, 455-461.

Bateman, A. J. (1948). Intra-sexual selection in *Drosophila. Heredity, 2*, 349-368.

Bateson, P. (1980). Optimal outbreeding and the development of sexual preferences in Japanese Quail. *Zietschrift fur Tierpsychologie, 53*, 231-244.

Bellis, M. A., & Baker, R. R. (1990). Do females promote sperm competition? Data for humans. *Animal Behaviour, 40*, 997-999.

Berry, D. S., & Brownlow, S. (1989). Were the physiognomists right? Personality correlates of facial babyishness. *Personality and Social Psychology Bulletin, 15*, 266-279.

Berry, D. S., & McArthur, L. Z. (1985). Some components and consequences of a babyface. *Journal of Personality and Social Psychology, 48*(2), 312-323.

Berry, S. B., & McArthur, L. Z. (1986). Perceiving character in faces: The impact of age-related craniofacial changes on social perception. *Psychological Bulletin, 100*, 3-18.

Berscheid, E., Dion, K., Walster, E., & Walster, G. W. (1971). Physical attractiveness and dating choice: A test of the matching hypothesis. *Journal of Experimental and Social Psychology, 7*, 173-189.

Berscheid, E., & Walster, E. (1974). Physical attractiveness. In L. Berkowitz (Ed.), *Advances in Experimental Social Psychology* (Vol. 7, pp. 157-215.). New York: Academic Press.

Booth, A., & Dabbs, J. (1993). Testosterone and men's marriages. *Social Forces, 72*, 463-477.

Borgia, G., & Collis, K. (1989). Female choice for parasite free male satin bowerbird (*Pitiloryhnchus violaceus*). *American Zoologist, 30*, 279-276.

Borkenau, P., & Liebler, A. (1993). Convergence of stranger ratings of personality and intelligence with self-ratings, partner ratings, and measured intelligence. *Journal of Personality and Social Psychology, 65*(3), 546-553.

Bornstein. (1989). Exposure and effect: overview and meta-analysis of research 1968-1987. *Psychological Bulletin, 106*, 265-289.

Botwin, M. D., Buss, D. M., & Shackleford, T. K. (1997). Personality and mate preferences: Five factors in mate selection and marital satisfaction. *Journal of Personality, 65*(1), 107-136.

Bouchard, T. J., & McGue, M. (1981). Familial studies of intelligence: a review. *Science, 212*, 1055-1059.

Bruce, V., & Young, A. (1998). *In the eye of the beholder: the science of face perception.* Oxford: Oxford University Press.

Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology, 77*, 307-327.

Burger, R., Wagner, G., & Stettinger, F. (1989). How much heritable variation can be maintained in finite populations by mutation selection? *Evolution, 43*, 1748-1766.

Burley, N. (1983). The meaning of assortative mating. *Ethology and Sociobiology, 4*, 191-203.

Burley, N. (1986). Sexual selection for aesthetic traits in species with biparental care. *American Naturalist, 127*(4), 415-445.

Bushnell, I. W. R., Sai, F., & Mullin, J. T. (1999). Neonatal recognition of the mother's face. *British Journal of Developmental Psychology, 7*, 3-15.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioural and Brain Sciences, 12*, 1-49.

Buss, D. M. (1991). Evolutionary personality psychology. *Annual Review of Psychology, 42*, 459-491.

Buss, D. M., & Barnes, M. (1986). Preferences in human mate selection. *Journal of Personality and Social Psychology, 50*, 559-570.

Buss, D. M., & Schmitt, D. P. (1993). Sexual Strategies Theory: An evolutionary perspective on human mating. *Psychological Review, 100*(2), 204-232.

Cash, T. F., & Kilcullen, R. N. (1985). The Aye of the Beholder - Susceptibility to Sexism and Beautyism in the Evaluation of Managerial Applicants. *Journal of Applied Social Psychology, 15*(7), 591-605.

Chabbert-Buffert, N., Djakoure, C., Christin-Maitre, S., & Bouchard, P. (1998). Regulation of the human menstrual cycle. *Frontiers in Neuroendocrinology, 19*, 151-186.

Chiu, R. K., & Babcock, R. D. (2002). The relative importance of facial attractiveness and gender in Hong Kong selection decisions. *International Journal of Human Resource Management, 13*(1), 141-155.

Clutton-Brock, T. H. (1991). *The Evolution of Parental Care*. Princeton, NJ: Princeton University Press.

Cronin, H. (1991). *The Ant and the Peacock: Altruism and Sexual Selection from Darwin to Today.* Cambridge: Cambridge University Press.

Cunningham, M. R. (1986). Measuring the physical in physical attractiveness: quasi-experiments on the sociobiology of female facial beauty. *Journal of Personality and Social Psychology, 50*(5), 925-935.

Cunningham, M. R., Barbee, A. P., & Pike, C. L. (1990). What do women want? Facialmetric assessment of multiple motives in the perception of male facial physical attractiveness. *Journal of Personality and Social Psychology, 59*(1), 61-72.

Cunningham, M. R., Roberts, A. R., Barbee, A. P., & Druen, P. B. (1995). "Their ideas of beauty are, on the whole, the same as ours": Consistency and variability in the cross-cultural perception of female attractiveness. *Journal of Personality and Social Psychology, 68*(2), 261-279.

Daly, M., & Wilson, M. (1983). *Sex, Evolution and Behavior* (2nd ed.). Boston: PWS.

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection*. London: Murray.

Darwin, C. (1871). *The Descent of Man, and Selection in Relation to Sex*. London: John Murray.

Darwin, C. (1872). *The Expression of Emotion in Man and Animals.* London: John Murray.

DeBruine, L. M. (2002). Facial resemblance enhances trust. *Proceedings of the Royal Society of London, B, 269*, 1307-1312.

Dermer, M., & Thiel, D. L. (1975). When beauty may fail. *Journal of Personality and Social Psychology, 31*, 1168—1176.

Dion, K., Berscheid, E., & Walster, E. (1972). What is beautiful is good. *Journal of Personality and Social Psychology, 24*, 285-290.

Dion, K. K., & Berscheid, E. (1974). Physical attractiveness and peer perception among children. *Sociometry, 37*, 1-12.

Downs, A. C., & Lyons, P. M. (1991). Natural observations of the links between attractiveness and initial legal judgments. *Personality and Social Psychology Bulletin, 17*(5), 541-547.

Draper, P., & Belsky, J. (1990). Personality development in evolutionary perspective. *Journal of Personality, 58*, 141-161.

Dufour, K. W., & Weatherhead, P. J. (1998). Bilateral symmetry and social dominance in captive male red-winged blackbirds. *Behavioural Ecology and Sociobiology, 42*, 71-76.

Dugatkin, L. A., & Godin, J. J. (1998). How females choose their mates. *Scientific American*(4), 46-51.

Eagly, A. H., Ashmore, R. D., Makhijani, M. G., & Longo, L. C. (1991). What is beautiful is good, but ...: A meta-analytic review of research on the physical attractiveness stereotype. *Psychological Bulletin, 110*, 109-128.

Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect*. Palo Alto, California: Consulting Psychological Press.

Elder, G. H. J. (1969). Appearance and education in marriage mobility. *American Sociological Review, 34*, 519-533.

Endler, J. A., & Houde, A. E. (1995). Geographic-Variation in Female Preferences For Male Traits in Poecilia-Reticulata. *Evolution, 49*(3), 456-468.

Enlow, D. M. (1982). *Handbook of Facial Growth* (2nd ed.). Philadelphia: Saunders.

Enquist, M., & Arak, A. (1993). Selection of exaggerated mail traits by female aesthetic senses. *Nature, 361*, 446-448.

Enquist, M., & Arak, A. (1994). Symmetry, Beauty and evolution. *Nature, 372*, 169-172.

Enquist, M., & Ghirlanda, S. (1998). The secrets of faces. *Nature, 394*, 826-827.

Enquist, M., & Johnstone, R. A. (1997). Generalization and the evolution of symmetry preferences. *Proceedings of the Royal Society of London, B, 264*, 1345-1348.

Epstein, E., & Guttman, R. (1982). Mate selection in man: evidence, theory, and outcome. *Social Biology, 31*(3-4), 243-276.

Feingold, A. (1988). Matching for attractiveness in romantic partners and same-sex friends: a meta-analysis and theoretical critique. *Psychological Bulletin, 104*(2), 226-235.

Feingold, A. (1992). Good-looking people are not what we think. *Psychological Bulletin, 111*, 304-341.

Feinman, S., & Gill, G. W. (1978). Sex differences in physical attractiveness preferences. Journal of Social Psychology, 105, 43-52.

Firman, R. C., Simmons, L. W., Cummins, J. M., & Matson, P. L. (2003). Are body fluctuating asymmetry and the ratio of 2nd to 4th digit length reliable predictors of semen quality? *Human Reproduction, 18,* 808-812.

Fisher, R. A. (1915). The evolution of sexual preference. *Eugenics Review, 7*, 184-192.

Fisher, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford: Clarendon Press.

Folstad, I., & Karter, A. J. (1992). Parasites, bright males and the immunocompetence handicap. *American Naturalist, 139*, 603-622.

Ford, C. S., & Beach, F. A. (1951). *Patterns of Sexual Behaviour*. New York: Harper & Row.

Freud, S. (1927). Some psychological consequences of the anatomical distinction between the sexes. *International Journal of Psychoanalysis, 8*, 133-142.

Friedman, H., & Zebrowitz, L. A. (1992). The contribution of typical sex-differences in facial maturity to sex-role stereotypes. *Personality and Social Psychology Bulletin, 18*, 430-438.

Frost, P. (1994). Preference for darker faces in photographs at different phases of the menstrual cycle: preliminary assessment of evidence for a hormonal relationship. *Perceptual and Motor Skills, 79*, 507-514.

Fujita, K. (1993). Development of visual preference for closely related species by infant and juvenile macaques with restricted social experience. *Primates, 34*, 141-150.

Galton, F. (1883). *Inquiries into the Human Faculty and its Development*. London: Macmillan.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology, 14*, 89-96.

Gangestad, S. W., & Simpson, J. A. (1990). Toward an evolutionary history of female sociosexual variation. *Journal of Personality, 58*(1), 69-96.

Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: trade-offs and strategic pluralism. *Behavioural and Brain Sciences, 23*, 573-644.

Gangestad, S. W., & Thornhill, R. (1997a). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behaviour, 18*(2), 69-88.

Gangestad, S. W., & Thornhill, R. (1997b). Human sexual selection and developmental stability. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary Social Psychology* (pp. 169-195). Mahwah, NJ: Lawrence Erlbaum Associates.

Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings of the Royal Society of London, B, 265*, 927-933.

Gibson, R. M. (1990). Relationships between blood parasites, mating success and phenotypic cues in male sage grouse. *American Zoologist, 30*, 271-278.

Gombrich, E. H. (1984). *The Sense of Order: A Study in the Psychology of Decorative Art.* London: Phaidon.

Gomendio, M., Cassinello, J., & Roldan, E. R. S. (2000). A comparative study of ejaculate traits in three endangered ungulates with different levels of inbreeding: fluctuating asymmetry as an indicator of reproductive and genetic stress. *Proceedings of the Royal Society of London, B, 267*, 875-882.

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behaviour.* Cambridge, MA: Harvard University Press.

Goren, C. C., Sarty, M., & Wu, P. Y. K. (1975). Visual following and pattern discrimination of face like stimuli by newborn infants. *Paediatrics, 56*, 544-549.

Grammer, K., & Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *Journal of Comparative Psychology, 108*, 233-242.

Griffiths, R. W., & Kunz, P. R. (1973). Assortative mating: A study of physiognomic homogamy. *Social Biology, 20*(4), 448-453.

Grossman, C. J. (1985). Interactions between the gonadal steroids and the immune system. *Science, 227*, 257-261.

Halberstadt, J., & Rhodes, G. (2000). The attractiveness of non-face averages: Implications for an evolutionary explanation of the attractiveness of average faces. *Psychological Science, 11*, 285-289.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science, 218*, 384-387.

Hedrick, P. W. (1996). Genetic polymorphism in heterogeneous environments. *Annual review of Ecology and Systematics, 17*, 535-566.

Herbert, A. M., & Humphrey, G. K. (1996). Bilateral symmetry detection: testing a 'callosal' hypothesis. *Perception, 25*, 463-480.

Hill, C. T., Rubin, Z., & Peplau, L. A. (1976). Breakups before marriage: The end of 103 affairs. *Journal of Social Issues, 32*, 147-168.

Hill, G. E. (1991). Plumage colouration is a sexually selected indicator of male quality. *Nature, 350*, 337- 339.

Hillgarth, N. (1990). Parasites and female choice in the ring-necked pheasant. *American Zoologist, 30*, 227-233.

Hillgarth, N., & Wingfield, J. C. (1997). Testosterone and Immunosuppression in vertebrates: implications for parasite mediated sexual selection. In N. E. Beckage (Ed.), *Parasites and Pathogens* . New York: Chapman &Hall.

Hinsz, V. B. (1989). Facial resemblance in engaged and married couples. *Journal of Social and Personal Relationships, 6*, 223-229.

Holmes, S. J., & Hatch, C. E. (1938). Personal appearance as related to scholastic records and marriage selection in college women. *Human Biology, 10*, 65-76.

Houde, A. E., & Torio, A. J. (1992). Effect of parasitic infection on male colour pattern and female choice in guppies. *Behavioural Ecology, 3*, 346-351.

Hume, D. (1757). *Four Dissertations. IV: Of the Standard of Taste.* London: Millar.

Jansson, L., Forkman, B., & Enquist, M. (2002). Experimental evidence of receiver bias for symmetry. *Animal Behaviour, 63*, 617-621.

Jedlicka, D. (1980). A test of the psychoanalytic theory of mate selection. *Journal of Social Psychology, 112*, 295-299.

Johnson, M. H., Dziurawiec, S., Ellis, H., & Morton, J. (1991). Newborns' preferential tracking of face-like stimuli and its subsequent decline. *Cognition, 40*, 1-19.

Johnson, R. C., Ahern, F. M., & Cole, R. F. (1980). Secular change in degree of assortative mating for ability? *Behavioral Genetics., 10*, 1-8.

Johnston, V. S., Hagel, R., Franklin, M., Fink., B., & Grammer, K. (2001). Male facial attractiveness: evidence for a hormone-mediated adaptive design. *Evolution and Human Behaviour, 22*, 251 - 267.

Johnstone, R. A. (1994). Female preference for symmetrical males as a by-product of selection for mate recognition. *Nature, 372*, 172-175.

Johnstone, R. A., Reynolds, J. D., & Deutsch, J. C. (1996). Mutual mate choice and sex differences in choosiness. *Evolution, 50*(4), 1382-1391.

Jones, B. C., Little, A. C., Penton-Voak, I. S., Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Measured facial asymmetry and perceptual judgements of attractiveness and health. *Evolution and Human Behaviour, 22*, 417-429.

Jones, D., & Hill, K. (1993). Criteria of facial attractiveness in five populations. *Human Nature, 4*(3), 271-296.

Jung, C. G. (1926). Marriage as a psychological relationship. In H. Keyserling (Ed.), *The Book of Marriage* . New York: Harcourt Brace.

Kalick, S. M., & Hamilton, T. E. (1986). The matching hypothesis re-examined. *Journal of Personality and Social Psychology, 52*, 673-682.

Kanda, N., Tsuchida, T., & Tamaki, K. (1996). Testosterone inhibits immunoglobulin production by human peripheral blood mononuclear cells. *Clinical and Experimental Immunology, 106*; 410-415.

Keating, C. F. (1985). Gender and the physiognomy of dominance and attractiveness. *Social Psychology Quarterly, 48*, 61-70.

Kendrick, K. M., Hinton, M. R., & Atkins, K. (1998). Mothers determine male sexual preferences. *Nature, 395*, 229-230.

Kenny, D. A., Horner, C., Kashy, D. A., & Chu, L. (1992). Consensus at zero acquaintance: replication, behavioral cues and stability. *Journal of Personality and Social Psychology, 62*, 88-97.

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. *Evolution, 36*, 1-12.

Kirkpatrick, M., & Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature, 350*, 33-38.

Krebs, D., & Adinolfi, A. A. (1975). Physical attractiveness, social relations, and personality style. *Journal of Personality and Social Psychology, 31*, 245-253.

Lagesen, K., & Folstad, I. (1998). Antler asymmetry and immunity in reindeer. *Behavioural Ecology and Sociobiology, 44*, 135-142.

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Science, USA, 78*, 3721-3725.

Langlois, J., Ritter, J., Casey, J., & Solwin, D. (1995). Infant attractiveness predicts maternal behaviours and attitudes. *Developmental Psychology, 31*, 464-472.

Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallamm, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin, 126*, 390-423.

Langlois, J. H., Ritter, J. M., Roggman, L. A., & Vaughn, L. S. (1991). Facial diversity and infant preferences for attractive faces. *Developmental Psychology, 27*(1), 79-84.

Langlois, J. H., & Roggman, L. A. (1990). Attractive faces are only average. *Psychological Science, 1*(2), 115-121.

Langlois, J. H., Roggman, L. A., Casey, R. J., Ritter, J. M., Riser-Danner, L. A., & Jenkins, V. Y. (1987). Infant preferences for attractive faces: Rudiments of a stereotype? *Developmental Psychology, 23*(3), 363-369.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2001). Early visual experience and face processing. *Nature, 410*, 890.

Liggett, J. (1974). *The Human Face*. London: Constable.

Linnaeus, C. (1758). *Systema Naturae* (10th ed.). Stockholm.

Little, A. C., Burt, D. M., Penton-Voak, I. S., & Perrett, D. I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London, B, 268*, 39-44.

Little, A. C., & Hancock, P. J. (2002). The role of masculinity and distinctiveness on the perception of attractiveness in human male faces. *British Journal of Psychology, 93*, 451-464.

Little, A. C., Penton-Voak, I. S., Burt, D. M., & Perrett, D. I. (2002). Individual differences in the perception of attractiveness: How cyclic hormonal changes and self-perceived attractiveness influence female preferences for male faces.

In G. Rhodes & L. Zebrowitz (Eds.), *Advances in Social Cognition: Facial Attractiveness* (Vol. 1, pp. 59-90). Westport, CT: Ablex.

Lopez, S. (1999). Parasitized female guppies do not prefer showy males. *Animal Behaviour, 57*, 1129–1134.

Lorenz, K. (1943). The innate forms of potential experience. *Zietschrift fur Tierpsychologie, 5*, 234-409.

Ludwig, W. (1932). *Das Rechts-links problem im tierreich und beim menschen.* Berlin: Springer-Verlag.

Lynn, M., & Shurgot, B. A. (1984). Responses to lonely heart advertisements: effects of reported physical attractiveness, physique, and colouration. *Personality and Social Psychology Bulletin, 10*, 349-357.

Mach, E. (1897). *Contributions to the Analysis of the Sensations* (C. M. Williams, Trans.). LaSalle, IL: Open Court.

Manning, J. T., Scutt, D., & Lewis-Jones, D. I. (1998). Developmental stability, ejaculate size, and sperm quality in men. *Evolution and Human Behavior, 19*, 273-282.

Manning, J. T., Scutt, D., Whitehouse, G. H., & Leinster, S. J. (1997). Breast asymmetry and phenotypic quality in women. *Evolution and Human Behavior, 18*, 223-236.

Marlowe, C. M., Schneider, S. L., & Nelson, C. E. (1996). Gender and attractiveness biases in hiring decisions: Are more experienced managers less biased? *Journal of Applied Psychology, 81*(1), 11-21.

Maynard Smith, J. (1979). Game theory and the evolution of behaviour. *Proceedings of the Royal Society of London, B, 205*, 475-488.

Maynard Smith, J., & Brown, R. L. W. (1986). Competition and body size. *Theoretical Population Biology, 30*, 166-179.

Mazur, A., & Booth, A. (1998). Testosterone and dominance in men. *Behavioural and Brain Sciences, 21*, 353-371.

Mazur, A., Halpern, C., & Udry, J. R. (1994). Dominant looking males copulate earlier. *Ethology and Sociobiology, 15*, 87-94.

McArthur, L. A., K. (1983-1984). Impressions of baby-faced adults. *Social Cognition, 2*(4), 315-342.

McArthur, L. Z., & Berry, D. S. (1987). Cross-cultural agreement in perceptions of babyfaced adults. *Journal of Cross-cultural Psychology, 18*(2), 165-192.

Mealey, L., Bridgestock, R., & Townsend, G. (1999). Symmetry and perceived facial attractiveness. *Journal of Personality and Social Psychology, 76*, 151-158.

Mendel, G. J. (1866). Versuchce ueber pflanzenhybriden. *Verhandlungen des Naturforshunden Verenines in Bruenn, 4*, 3-47.

Millinski, M., & Bakker, T. C. (1990). Female sticklebacks use male coloration in sticklebacks and therefore avoid parasitised males. *Nature, 344*, 330-333.

Møller, A. P. (1990a). Fluctuating asymmetry in male sexual ornaments may reliably reveal male quality. *Animal Behaviour, 40*, 1185-1187.

Møller, A. P. (1990b). Parasites, sexual ornaments, and mate choice in the barn swallow. In J. E. Loye & M. Zuk (Eds.), *Bird-Parasite Interactions. Ecology, Evolution, and Behaviour*, (pp. 328-343). Oxford: Oxford University Press.

Møller, A. P. (1992). Female swallow preference for symmetrical male sexual ornaments. *Nature, 357*, 238- 240.

Møller, A. P. (1994). *Sexual Selection and the Barn Swallow*. Oxford: Oxford University Press.

Møller, A. P. (1995). Hormones, handicaps, and bright birds. *Trends in Ecology and Evolution, 10*, 121.

Møller, A. P. (1996). Developmental stability of flowers, embryo abortion, and developmental stability of plants. *Proceedings of the Royal Society of London, B, 263*, 53-56.

Møller, A. P. (1997). Developmental stability and fitness: A review. *American Naturalist, 149*, 916-942.

Møller, A. P., Christe, P., & Lux, E. (1999). Parasitism, host immune function, and sexual selection. *Quarterly Review of Biology, 74*, 3-74.

Møller, A. P., & Hoglund, J. (1991). Patterns of fluctuating asymmetry in avian feather ornaments: Implications for models of sexual selection. *Proceedings of the Royal Society of London, B, 245*, 1-5.

Møller, A. P., & Pomiankowski, A. (1993). Fluctuating asymmetry and sexual selection. *Genetica, 89*, 267-279.

Møller, A. P., Soler, M., & Thornhill, R. (1995). Breast asymmetry, sexual selection, and human reproductive success. *Ethology and Sociobiology, 16*, 207-219.

Møller, A. P., & Swaddle, J. P. (1997). *Asymmetry, Developmental Stability, and Evolution.* Oxford: Oxford University Press.

Møller, A. P., & Thornhill, R. (1997a). Developmental Stability is Heritable. *Journal of Evolutionary Biology, 10*, 69-76.

Møller, A. P., & Thornhill, R. (1997b). A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology, 10*, 1-16.

Møller, A. P., & Thornhill, R. (1998). Bilateral symmetry and sexual selection: A meta-analysis. *American Naturalist, 151*, 174-192.

Morgan, T. H. (1903). *Evolution and Adaptation.* New York: Macmillan.

Mueller, U., & Mazur, A. (1996). Facial dominance of West Point cadets as a predictor of later military rank. *Social Forces, 74*(3), 823-850.

Mueller, U., & Mazur, A. (1997). Facial dominance in Homo sapiens as honest signalling of male quality. *Behavioral Ecology, 8*(5), 569-579.

Murray, J. E., Yong, E., & Rhodes, G. (2000). Revisiting the perception of upside-down faces. *Psychological Science, 11*, 492-496.

Noble, G. K., & Vogt, W. (1935). An experimental study of sex recognition in birds. *Auk, 34*, 278-286.

Norman, W. T. (1963). Toward an adequate taxonomy of personality attributes: Replicated factor structure in peer nominated personality ratings. *Journal of Abnormal and Social Psychology, 66*, 574-583.

Norris, K. (1993). Heritable variation in a plumage indicator of viability in male great tits *parsus major*. *Nature, 362*, 537-539.

O'Donald, P. (1980). *Genetic Models of Sexual Selection*. Cambridge: Cambridge University Press.

Owens, I. P. F., & Short, R. V. (1995). Hormonal basis of sexual dimorphism in birds: implications for new theories of sexual selection. *Trends in Ecology and Evolution, 10*(1), 44-47.

Pascalis, O., de Schonen, S., Morton, J., Deruelle, C., & Rabre-Grenet, M. (1995). Mother's face recognition by neonates: A replication and extension. *Infant Behaviour and Development, 7*, 79-85.

Pawlowski, B., & Dunbar, R. I. M. (1999). Impact of market value on human mate choice. *Proceedings of the royal Society of London, B, 266*, 281-285.

Pearson, K. (1907). Reply to certain criticisms of Mr G. U. Yule. *Biometrika, 5*, 470-476.

Pearson, K., & Lee, A. (1903). On the law of inheritance in man. *Biometrika, 2*, 357-462.

Penton-Voak, I., Perrett, D., & Pierce, J. (1999a). Computer graphic studies of the role of facial similarity in attractiveness judgements. *Current Psychology, 18*, 104-117.

Penton-Voak, I. S., Jones, B. C., Little, A. C., Baker, S., Tiddeman, B., Burt, D. M., & Perrett, D. I. (2001). Symmetry, sexual dimorphism in facial proportions, and male facial attractiveness. *Proceedings of the Royal Society of London, B, 268*, 1617-1623.

Penton-Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically - further evidence. *Evolution and Human behaviour, 21*, 39-48.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., & Minamisawa, R. (1999b). Menstrual cycle alters face preference. *Nature, 399*, 741-742.

Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A., & Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior, 20*(5), 295-307.

Perrett, D. I., Lee, K. J., Penton-Voak, I. S., Rowland, D. R., Yoshikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L., & Akamatsu, S. (1998a). Effects of sexual dimorphism on facial attractiveness. *Nature, 394*, 884-887.

Perrett, D. I., Oram, M. W., & Wachsmuth, E. (1998b). Evidence accumulation in cell populations responsive to faces: an account of generalisation of recognition without mental transformations. *Cognition, 67*, 111-145.

Perrett, D. I., Penton-Voak, I. S., Little, A. C., Tiddeman, B. P., Burt, D. M., N., S., Oxley, R., & Barrett, L. (2002). Facial attractiveness judgements reflect learning of parental age characteristics. *Proceedings of the Royal Society of London, B, 269,* 873-880.

Petrie, M. (1983). Female moorhens compete for small fat males. *Science, 220*, 313-415.

Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature, 371*, 598-599.

Petrie, M., Halliday, T., & Sanders, C. (1991). Peahens prefer peacocks with more elaborate trains. *Animal Behaviour, 41*, 323-331.

Petrie, M., Krupa, A., & Burke, T. (1999). Peacocks lek with relatives even in the absence of social and environmental cues. *Nature, 401*, 155-157.

Pinker, S., & Bloom, P. (1990). Natural language and natural selection. *Behavioural and Brain Sciences.*

Platek, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H., & Gallup, G. G. J. (2002). Reactions to children's faces: resemblance affects males more than females. *Evolution and Human Behaviour, 23*, 159-166.

Poulin, R., & Vickery, W. L. (1996). Parasite mediated sexual selection: just how choosy are parasitised females? *Behavioural Ecology and Sociobiology, 38*, 43-49.

Price, T., Schluter, D., & Heckman, N. E. (1993). Sexual selection when the female directly benefits. *Biological Journal of the Linnean Society, 48*, 187-211.

Ralls, K. (1976). Mammals in which females are larger than males. *Quarterly Review of Biology, 51*, 245-276.

Regan, P. C. (1996). Rhythms of desire: the association between menstrual cycle phases and female sexual desire. *The Canadian Journal of Human Sexuality, 5*(3), 145-156.

Reid, M. L., & Roitberg, B. D. (1996). Effects of body size on investment in individual broods by male pine engravers (Coleoptera: Scolytidae). *Canadian Journal of Zoology, 73*, 1396-1401.

Rensch, B. (1963). Vesuche uber menschliche Auslosermerkmale beider Geschlecter. *Zeitschrift fur Morphologische Anthropologie., 53*, 139-164.

Rhodes, G., Chan, J., Zebrowitz, L. A., & Simmons, L. W. (2003). Does sexual dimorphism in human faces signal health? *Biology Letters.*

Rhodes, G., Halberstadt, J., & Brajkovich, G. (2001a). Generalization of mere exposure effects in social stimuli. *Social Cognition, 19*, 57-70.

Rhodes, G., Hickford, C., & Jeffery, L. (2000). Sex-typicality and attractiveness: Are supermale and superfemale faces super-attractive. *British Journal of Psychology, 91*, 125-140.

Rhodes, G., Proffitt, F., Grady, J., & Sumich, A. (1998). Facial symmetry and the perception of beauty. *Psychonomic Bulletin Review, 5*, 659-669.

Rhodes, G., Sumich, A., & Byatt, G. (1999). Are average facial configurations attractive only because of their symmetry? *Psychological Science, 10*(1), 52-58.

Rhodes, G., Yoshikawa, S., Clark, A., Lee, K., McKay, R., & Akamatsu, S. (2001b). Attractiveness of facial averageness and symmetry in non-Western populations: In search of biologically based standards of beauty. *Perception, 30*, 611-625.

Ridley, M. (1981). How the peacock got its tail. *New Scientist, 91*, 398-401.

Riggio, R., & Woll, S. (1984). The role of non-verbal and physical attractiveness in the selection of dating partners. *Journal of Social and Personal Relations, 1*, 347-357.

Robertson, I. C. (1998). Paternal care enhances male reproductive success in pine engraver beetles. *Animal Behaviour, 56*, 595-602.

Robertson, I. C., & Roitberg, B. D. (1998). Duration of paternal care in pine engraver beetles: why do larger males care less? *Behavioural Ecology and Sociobiology, 43*, 379-386.

Rock, I. (1974). The perception of disoriented figures. *Scientific American, 230*, 78-85.

Rodd, F. H., Hughes, K. A., Grether, G. F., & Baril, C. T. (2002). A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proceedings of the Royal Society of London, B, 269*, 475-481.

Rushton, J. P., & Nicholson, I. R. (1988). Genetic similarity theory, intelligence, and human mate choice. *Ethology and Sociobiology, 9*, 45-57.

Ryan, M. J. (1990). Sexual selection, sensory systems and sensory adaptation. *Oxford Survey of Evolutionary Biology, 7*, 157-195.

Ryan, M. J., & Rand, S. (1990). The sensory basis of sexual selection for complex calls in the Tungara frog, *physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution, 44*, 305-314.

Samuels, C. A., Butterworth, G., Roberts, T., Graupner, L., & Hoyle, G. (1994). Facial aesthetics: babies prefer attractiveness to symmetry. *Perception, 23*, 823-831.

Scheib, J. E. (2001). Context-specific mate choice criteria: women's trade-offs in the contexts of long-term and extra-pair mateships. *Personal Relationships, 8*, 371-389.

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry, and cues to good genes. *Proceedings of the Royal Society of London, B, 266,* 1913-1917.

Schiller, B. (1932). A quantitative analysis of marriage selection in a small group. *Journal of Social Psychology, 3,* 297-319.

Seger, J. (1985). Unifying genetic models for the evolution of female choice. *Evolution, 39,* 1185-1193.

Shepher, J. (1971). Mate selection among second generation Kibbutz adolescents and adults: Incest avoidance and negative imprinting. *Archives of Sexual Behavior, 1*(4), 293-307.

Shepherd, J. W., & Ellis, H. D. (1972). The role of physical attractiveness in selection of marriage partners. *Psychological Reports, 30,* 1004.

Sigall, H., & Ostrove, N. (1975). Beautiful but dangerous: Effects of offender attractiveness and nature of the crime on juridical judgement. *Journal of Personality and Social Psychology, 31,* 410-414.

Simpson, J. A., & Gangestad, S. W. (1991). Individual differences in sociosexuality: Evidence for convergent and discriminant validity. *Journal of Personality and Individual Differences, 60*(6), 870-883.

Simpson, J. A., & Gangestad, S. W. (1992). Sociosexuality and romantic partner choice. *Journal of Personality, 60*(1), 31-51.

Singh, D. (1993). Adaptive significance of female physical attractiveness: Role of waist-to-hip ratio. *Journal of Personality and Social Psychology, 65*(2), 293-307.

Snyder, M., Tanke, E. D., & Berscheid, E. (1977). Social perception and interpersonal behaviour: On the self-fulfilling nature of social stereotypes. *Journal of Personality and Social Psychology, 35*, 656-666.

Spuhler, J. N. (1968). Assortative mating with respect to physical characteristics. *Eugenics Quarterly, 15*(2), 128-140.

Swaddle, J. P., & Cuthill, I. C. (1995). Asymmetry and human facial attractiveness: symmetry may not always be beautiful. *Proceedings of the Royal Society of London, B, 261*, 111-116.

Swaddle, J. P., & Reierson, G. W. (2003). Testosterone increases perceived dominance but not attractiveness in human males. *Proceedings of the Royal Society of London, B, 269*, 2285-2289.

Symons, D. (1979). *The Evolution of Human Sexuality*. Oxford: Oxford University Press.

Symons, D. (1987). An Evolutionary approach: Can Darwin's view of life shed light on human sexuality? In J. H. G. W. T. O'Donohoe (Ed.), *Theories of Human Sexuality* (pp. 91-126). New York: Plomin Press.

Thiessen, D., & Gregg, B. (1980). Human assortative mating and genetic equilibrium: An evolutionary perspective. *Ethology and Sociobiology, 1*, 111-140.

Thomas, F., Oget, E., Gente, P., Desmots, D., & Renaud, F. (1999). Assortative pairing with respect to parasite load in the beetle *Timarcha maritima* (Chrysomelidae). *Journal of Evolutionary Biology, 12*, 385-390.

Thomas, F., Renaud, F., & Cezilly, F. (1996). Assortative pairing by parasitic prevalence in *Gammarus insensibilis* (Amphipoda): Patterns and processes. *Animal Behaviour, 52*, 683-690.

Thornhill, R., & Gangestad, S. W. (1993). Human facial beauty: averageness, symmetry, and parasite resistance. *Human Nature, 4*(3), 237-269.

Thornhill, R., & Gangestad, S. W. (1994). Human fluctuating asymmetry and sexual behaviour. *Psychological Science, 5*, 297-302.

Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences, 3*(12), 452-460.

Tiddeman, B. P., Burt, D. M., & Perrett, D. I. (2001). Prototyping and transforming facial texture for perception research. *IEEE Computer Graphics and Applications, 21*, 42-50.

Tooby, J., & Cosmides, L. (1990). On the universality of human nature and the uniqueness of the individual: The role of genetics and adaptation. *Journal of Personality, 58*(1), 17-67.

Tovee, M. J., Reinhardt, S., Emery, J. L., & Cornelissen, P. L. (1998). Optimum body-mass index and maximum sexual attractiveness. *Lancet, 352*, 548.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual Selection and the Descent of Man, 1871-1971.* (pp. 136-179). Chicago: Aldine.

Valen, L. V. (1962). A study of fluctuating asymmetry. *Evolution, 16*, 125-142.

Valentine, T. (1991). A unified account of the effects of distinctiveness, inversion, and race in face recognition. *The Quarterly Journal of Experimental Psychology, 43*, 161-204.

Vandenberg, S. G. (1972). Assortative mating or who marries whom? *Behavior Genetics, 2*(2/3), 127-157.

Vos, D. R. (1995). Sexual imprinting in Zebra-finch females: Do females develop a preference for males that look like their Father? *Ethology, 99*, 252-262.

Wallace, A. R. (1889). *Darwinism* (2nd ed.). London: Macmillan.

Walster, E., Aronson, V., Abrahams, D., & Rottman, L. (1966). Importance of physical attractiveness in dating behaviour. *Journal of Personality and Social Psychology, 4*, 508-516.

Walton, G. E., & Bower, T. G. R. (1993). Newborns form "prototypes" in less than 1 minute. *Psychological Science, 4*, 203-205.

Watson, P. J. (1990). Female-enhanced male competition determines the first mate and principal sire in the spider *Linyphia litigiosa*. *Behavioural Ecology and Sociobiology, 26*, 77-90.

Wedekind, C. (1992). Detailed information about parasites as revealed by sexual ornamentation. *Proceedings of the Royal Society of London, B, 147*, 169-174.

Wedekind, C., & Folstad, I. (1994). Adaptive or nonadaptive immunosuppression by sex hormones? *American Naturalist, 143*(5), 936-938.

Wedekind, C., & Furi, S. (1997). Body odour preferences in men and women: do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London, B, 264*, 1471-1479.

Westermarck, E. (1894). *The History of Human Marriage*. London: Macmillan.

Wilkinson, G. S., & Reillo, P. R. (1994). Female choice response to artificial selection on an exaggerated male trait in a stalk eyed fly. *Proceedings of the Royal Society of London, B, 255*, 1-6.

Williams, G. C. (1966). *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought.* Princeton, NJ: Princeton University Press.

Williams, G. C. (1975). *Sex and Evolution*. Princeton, NJ: Princeton University Press.

Wilson, D. S. (1994). Adaptive genetic variation and human evolutionary psychology. *Ethology and Sociobiology, 15*, 219-235.

Wilson, G. D., & Barrett, P. T. (1987). Parental characteristics and partner choice: Some evidence for Oedipal imprinting. *Journal of biosocial Science, 19*, 157-161.

Wolf, A. P. (1993). Westermarck Redivivus. *Annual Review of Anthropology, 22*, 157-175.

Yesilova, Z., Ozata, M., Kocar, I. H., Turan, M., Pekel, A., Sengul, A., & Ozdemir, I. C. (2000). The effects of gonadotropin treatment on the immunological features of male patients with idiopathic hypogonadotropic hypogonadism. *Journal of Clinical Endocrinology and Metabolism,, 85*, 66-70.

Zahavi, A. (1975). Mate selection: A selection for a handicap. *Journal of Theoretical Biology, 53*, 205-214.

Zajonc, R. B. (1968). Attitudinal effects of mere exposure. *Journal of Personality and Social Psychology, 9*, 1-27.

Zajonc, R. B., Adelmann, P.K., Murphy, S.T. & Niendenthal, P.M. (1987). Convergence in the Physical Appearance of Spouses. *Motivation and Emotion, 11*(4), 335-346.

Zebrowitz, L. A., & Montepare, J. M. (1992). Impressions of babyfaced males and females across the life span. *Developmental Psychology, 28*, 1143-1152.

Zebrowitz-McArthur, L., & Baron, R. M. (1983). Toward and ecological approach to social perception. *Psychological Review, 90*, 215-238.

Zei, G., Astolfi, P., & Jayakar, S. D. (1983). Correlation between father's age and husband's age: A case of imprinting. *Journal of Biosocial Science, 15*, 116-117.

Zuk, M. (1992). The role of parasites in sexual selection: Current evidence and future directions. *Advances in the Study of Behavior, 21*, 39-67.