Darwinian aesthetics: sexual selection and the biology of beauty

KARL GRAMMER[1], BERNHARD FINK[1,*], ANDERS P. MØLLER[2]
and RANDY THORNHILL[3]

[1] *Ludwig-Boltzmann-Institute for Urban Ethology, Althanstrasse 14, A-1090 Vienna, Austria.*

[2] *Université Pierre et Marie Curie, Laboratoire de Parasitologie Evolutive, CNRS UMR 7103, Bâtiment A, 7ème étage,
7 quai St. Bernard, Case 237, FR-75252 Paris Cedex 05, France.*

[3] *University of New Mexico, Castetter Hall, Department of Biology, Albuquerque, NM 87131-1091, USA.*

ABSTRACT

Current theoretical and empirical findings suggest that mate preferences are mainly cued on visual, vocal and chemical cues that reveal health including developmental health. Beautiful and irresistible features have evolved numerous times in plants and animals due to sexual selection, and such preferences and beauty standards provide evidence for the claim that human beauty and obsession with bodily beauty are mirrored in analogous traits and tendencies throughout the plant and animal kingdoms. Human beauty standards reflect our evolutionary distant and recent past and emphasize the role of health assessment in mate choice as reflected by analyses of the attractiveness of visual characters of the face and the body, but also of vocal and olfactory signals. Although beauty standards may vary between cultures and between times, we show in this review that the underlying selection pressures, which shaped the standards, are the same. Moreover we show that it is not the content of the standards that show evidence of convergence – it is the rules or how we construct beauty ideals that have universalities across cultures. These findings have implications for medical, social and biological sciences.

Key words: attractiveness, beauty standards, Darwinian aesthetics, face, humans, mate choice, sexual selection.

CONTENTS

  * Address for correspondence: Ludwig-Boltzmann-Institute for Urban Ethology, University of Vienna, Althanstrasse 14,
A-1090 Vienna, Austria. Tel: +43 1 4277 54769. Fax: +43 1 4277 9547. E-mail: bernhard.fink@ieee.org

I. INTRODUCTION

Human assessments of beauty and human beauty standards have attracted considerable attention in recent years. Given the interest of this subject to biologists, psychologists, social workers, medical doctors and lay people, it seems surprising how little general emphasis has been put on interpreting these phenomena in a sexual selection and general evolutionary context. Here we review the subject. We start out by putting the study of beauty standards and assessment of beauty into a sexual selection context. Next, we address the relationship between beauty and health and describe the consequences of such assessment for individuals. In the following sections we address research on attractiveness of beauty of different parts of the human body and the functional significance of such attractiveness by presenting arguments supporting ('pros') and criticizing ('contras') current theories. We end the review by discussing the ways in which beauty is perceived and the consequences of such general assessment. Finally, we present a list of topics for future research.

II. SEXUAL SELECTION AND MATE CHOICE

It is a widespread notion that humans differ fundamentally from all other animals and so much that comparisons are invalid. It is also a widespread belief that somewhere in the world it is possible to find a culture where people live in harmonious, non-competitive, altruistic bliss with each other, and were it not for the existence of Western culture we would be able to achieve this ideal state. Both claims are erroneous. Humans carry an incredibly large baggage of evolutionary history, and the mere fact that our DNA sequences are similar to those of our nearest relatives among the great apes by as much as 99% makes it a highly unlikely claim that we could just step out of our ape dress. Human nature is to a large extent universal. This includes certain beauty standards and the ways in which males and females interact, as we will show below.

Sexual selection theory is concerned with 'the advantages that certain individuals have over others of the same sex and species, in exclusive relation to reproduction' (Darwin, 1871). What is sexual selection and why is it important for judgments of human beauty standards? Sexual selection arises from sexual competition among individuals for access to mates and has given rise to the evolution of such bizarre traits as the antlers of stags, the horns of antelopes, the tail of the peacock (*Pavo cristatus*), bird song, frog croaks, and the extravagant colours of many fish and birds. Darwin in his 1871 treatise was the first person to realize the explanation for the evolution and the maintenance of these bizarre traits that obviously do not enhance the survival prospects of individuals and therefore cannot be explained by natural selection. On the contrary, extravagant secondary sexual characters are costly, often reduce survival prospects and can only be maintained by sexual selection. Two mechanisms are involved in sexual selection: mate competition between individuals of the chosen sex, usually males, for access to females has resulted in the evolution of weaponry such as antlers and horns, but also increases in mere male size that provides some individuals with an advantage over others for access to females. The second mechanism is mate choice by individuals of the choosy sex, usually females, that has resulted in the evolution of many bizarre traits such as the tail of the peacock, beautiful coloration in birds and fish and many kinds of bird vocalizations (Andersson, 1994). Humans are not much different from other organisms by having evolved sexual size dimorphism due to male–male competition [more than 90% of all same-sex homicide involves men in their early twenties when mate competition is intense (Daly & Wilson, 1988)], musculature and other features due to the effects of testosterone at puberty, and female breasts and facial beauty due to the effects of oestrogens and male choice.

Extravagant secondary sexual characters in other species are considered to be beautiful by humans and perhaps also by animals in general. If both non-human animals and humans find similar structures attractive, the likely reason is that animal and human psychologies have evolved to perceive and become agitated by and interested in these impressions. Sugar is only perceived to be sweet by humans because the pleasant and powerful feeling of sweetness during our evolutionary

past has been shaped by the benefits that we obtained in terms of energy and nutrition from eating fruits. In the same way, particular features of faces of women and particular proportions of waists and hips are only considered to be beautiful because our ancestors with such preferences left more healthy offspring than the individuals in the population without the preferences.

III. SEXUAL SELECTION AND WHY BEAUTY MATTERS

Sexual selection can work in a number of different ways because sexual signals may provide different kinds of information to potential receivers. Human evolutionary psychological studies across a wide range of cultures have shown that in consideration of mates men rank female beauty higher than women rank male looks, while women rank male resources higher than men rank female resources (Buss, 1994). Female beauty signals youth, fertility and health while male resources signal male competitive ability and health.

The advantages of sexual selection as seen from the point of view of the choosy partner may derive from the following (review in Andersson, 1994). Females may choose males with exaggerated features simply because such signals indicate the presence of direct fitness benefits that enhance the reproductive success of choosy individuals. Males with a high-quality territory or nuptial gift, males without contagious parasites, and males with sperm of better fertilizing ability all provide females with such benefits (review in Møller & Jennions, 2001). Male displays may also signal benefits that females do not acquire directly, but only indirectly in the next generation through the mating success of the offspring (Fisher, 1930). If the male signal and the female preference both have a genetic basis, choosy females will on average pair up with males with exaggerated secondary sexual characters, and the mate preference and the signal will become genetically coupled as a result of this process. The male trait and the female preference will coevolve to even more extreme versions that enhance male mating success until the mating benefit is balanced by an oppositely directed natural selection pressure, or until the genetic variance in either female preference or male trait become depleted. There is little empirical evidence for this mechanism (Andersson, 1994), but it is likely to work in most contexts although it will work better in mating systems with an extreme skew in male mating success.

An alternative model of female mate preferences that gives rise to indirect fitness benefits is the so-called 'good genes' hypothesis, which is based on the handicap principle. Since secondary sexual characters are costly, only individuals in prime condition may be able to develop and carry such displays. It is only the differential ability of certain individuals due to their genetic constitution that allows them to develop seriously handicapping and costly traits (Zahavi, 1975). The honesty and reliability of such displays is maintained by their costs and their greater cost to low-quality individuals. A choosy female will, by preferring the most extravagantly ornamented male, produce offspring of high viability simply because low-quality individuals with an inferior genetic constitution will not be able to cheat and produce an extravagant character. A particular kind of handicap is the revealing handicap of Hamilton & Zuk (1982), suggesting that males cannot help reveal their infection status by virulent parasites because the presence of such parasites automatically will be discernible from the expression of their secondary sexual characters. Thus, females may obtain reliable information about genetically based parasite resistance by using male secondary sexual characters as a basis for their mate choice. There are a number of studies consistent with this mechanism of sexual selection (Andersson, 1994), and, on average across species, approximately 1–2 % of the variance in offspring viability is explained by the expression of male secondary sexual characters (Møller & Alatalo, 1999).

IV. HUMAN BEAUTY AND SEXUAL SELECTION

Charles Darwin (1871) was the first person to think extensively and write about human beauty standards from a biological point of view. The main problem with Darwin's approach was that he relied extensively on correspondence with missionaries in order to obtain information about the beauty standards in different human cultures. These data often were collected by persons with a British beauty standard and thus do not give evidence for a cross-cultural standard of beauty. Contrary to most other fields of evolutionary biology, which were actually advanced by Darwin's treatments, Darwin actually stagnated studies of human beauty for a century by the claims about lack of general principles. It is only recently that features of human facial and bodily beauty have been cross-culturally validated (Singh, 1993; Perrett, May & Yoshikawa, 1994; Thornhill & Gangestad, 1999; Thornhill & Grammer, 1999). Darwin's claims about the lack of a general beauty standard were at odds with the sheer magnitude of the beauty industry. Although feminist claims may suggest that this obsession with beauty is an outcome of male-initiated capitalist activities (see Wolf, 1992), there is

plenty of evidence for females putting lots of time and effort into their looks as far back as archaeological and historical information can date. The human obsession with beauty in modern Western societies is not much different from similar efforts in other societies, and the mere success of the industry is a reflection of the immense strength of the relevant psychological adaptations and mate preferences. The strong beliefs among women in the wonders of cosmetics and their ability to provide eternal youth obviously are based on the presence of the same psychological adaptations. Any book on the use of cosmetics is a manual of how to accentuate the features that are known to be reliable health and fertility indicators: oestrogenized faces, and symmetric facial features. With the development of plastic surgery these much desired and admired features of human female beauty can be acquired in a more permanent state as compared to the temporary state of cosmetics. Not surprisingly almost all plastic surgery attempts to correct asymmetries and exaggerate traits that are considered to be generally beautiful and reliable indicators of health and fertility.

V. ATTRACTIVENESS AND DAILY LIFE

The human obsession with beauty is not different from similar obsessions in other organisms. Thus it is quite likely that human mate selection criteria, which have evolved through human evolutionary history, are responsible for the shaping of our perception of attractiveness and beauty. In such a view, perception of attractiveness will be sex-specific because both sexes have different aspirations for mates. These different aspirations are a result of a statistical accumulation of problems our ancestors have encountered in our evolutionary past. If those algorithms which were able to process information and solve everyday problems better than others produced more offspring through natural and sexual selection, we are quite likely to have basic adaptations in our thinking (Cosmides, Tooby & Barkow, 1992).

Within cultures the generality of attractiveness is easily accepted. Several rating studies, especially those by Iliffe (1960) have shown that people of an ethnic group share common attractiveness standards. In this standard, beauty and sexual attractiveness seem to be the same, and ratings of pictures show a high congruence over social class, age and sex. This work has been replicated several times by Henss (1987, 1988). Thus it seems to be a valid starting point when we state that beauty standards are at least shared in a population. Moreover, recent studies (Cunningham *et al.*, 1995)

suggest that the constituents of beauty are neither arbitrary nor culture bound. The consensus on which a female is considered to be good looking or not is quite high in four cultures (Asian, Hispanic, Black and White women rated by males from all cultures).

Although we 'are all legally equal', everyone knows that people are often treated differently according to their physical appearance. This differential treatment by others starts early in life. Three-month-old children gaze longer at attractive faces than at unattractive faces. Slater *et al.* (1998) report two experiments where pairings of attractive and unattractive female faces were shown to newborn infants (in the age range 14–151 h from birth). In both experiments the infants looked longer at the attractive faces. Following an earlier suggestion by Langlois, Roggman & Reiser-Danner (1990) these findings can be interpreted either in terms of an innate perceptual mechanism that detects and responds specifically to faces or in terms of rapid learning of facial features soon after birth. Attractive children receive less punishment than unattractive children for the same kinds of misbehaviour. Differential treatment goes on at school, college and into university (Baugh & Parry, 1991). In this part of our lives attractiveness is coupled to academic achievements. It is common knowledge that attractive students receive better grades. Moreover female students even build dominance hierarchies according to attractiveness (Weisfeld, Bloch & Ivers, 1984). Even when we apply for jobs, appearance may dominate qualification (Collins & Zebrowitz, 1995). This differential treatment reaches its culmination perhaps in the judiciary where attractiveness can lead to better treatment and easier convictions. But this is only the case if attractiveness did not play a role in the crime (Hatfield & Sprecher, 1986). We even believe that attractive people are better – 'what is beautiful is good' is a common standard in our thinking (Dion, Berscheid & Walster, 1972).

According to evolutionary considerations on a meta-theoretical level females experience higher cost than males in opposite-sex interactions because they have the higher investment in their offspring (Trivers, 1972). Since females invest more per offspring, their potential fertility is lower than that of males. Females are thus the limiting factor in reproduction and males compete for them. Females in turn choose among males. In humans, sex differences are most prominent in the role that status and physical attractiveness play in mate selection (Buss & Schmitt, 1993). Females value men's socioeconomic status, social position, prestige, wealth and so forth and use these as indicators, more than male attractiveness. By contrast, men attach greater value to women's physical attractiveness, healthiness, and youth; all cues

linked more with reproductive capacity than to female social status. These sex-specific differences in preferences have been found in 37 cultures (Buss, 1989). Men are also more inclined to pursue multiple short-term mates (that is philandering) and are less discriminating in their mate choices (Buss, 1994).

The final piece of evidence consistent with the hypothesis that evolved human mate selection criteria shaped our attractiveness standards and created an obsession with attractiveness would be that 'attractive' people have more or better offspring in the future. But there are several caveats for an approach like this: 'attractiveness' has to be a flexible concept. The reason for this is that a fixed template for attractiveness could unnecessarily narrow down the possibilities in mate selection, as we will show.

VI. HEALTH AND BEAUTY PERCEPTION IN HUMANS AND OTHER ANIMALS

Parasites and diseases have played an important role in human evolution, and perhaps even more so than in many of our close relatives. Parasites exert tremendous selection pressures on their hosts by reducing their longevity and reproductive success. It has been known for a long time that individuals differ in their susceptibility to parasites because of genetically determined host resistance, and sexual selection for healthy partners would obviously provide choosy individuals with potentially important fitness benefits (Hamilton & Zuk, 1982). Parasite-mediated sexual selection may benefit choosy individuals by preventing them from obtaining mates with contagious parasites that could spread both to themselves and their offspring, obtaining mates that are efficient parents, and obtaining mates that are genetically resistant to parasites (Møller *et al.*, 1999*a*). There is considerable evidence for secondary sexual characters in a wide variety of organisms reliably reflecting levels of parasite infections (Møller *et al.*, 1999*a*). Studies of a diverse array of plants and animals show that parasites render their hosts more asymmetric and hence less attractive than unparasitized individuals (Møller, 1996*b*). While secondary sexual characters may reveal parasite infection status, there is an even stronger relationship between host immune response and the expression of secondary sexual characters (Møller & Alatalo, 1999). While virtually any host species may be exploited by more than 100 species of parasites, each with their peculiar ecology, life history and transmission dynamics, hosts should be expected to have evolved generalized immune responses to cope with the most debilitating parasites. This appears to be the case given that immune responses are much better predictors of the expression of secondary sexual characters than are the prevalence or intensity of parasite infections (Møller *et al.*, 1999*a*). This is also the case in humans: people throughout the cultures of the world value physical attractiveness, but the importance of beauty is the highest in cultures with serious impact of parasites such as malaria, schistosomiasis and similarly virulent parasites (Gangestad & Buss, 1993).

Hosts may reliably avoid the debilitating effects of parasites by evolving efficient immune defences, and the immune system in humans is one of the most costly only equalled by that of the brain. Immune defence may play a role in host sexual selection because secondary sexual characters reliably may reflect the immunocompetence of individuals (Folstad & Karter, 1992). Many secondary sexual characters develop under the influence of testosterone and other sex hormones. However, hormones have antagonistic effects on the functioning of the immune system (e.g. Thornhill & Gangestad, 1993; Service, 1998), and only individuals in prime condition may be able to develop the most extravagant secondary sexual characters without compromising their ability to raise efficient immune defences. An alternative version of this model just assumes that both secondary sexual characters and immune defences develop in response to condition, and the reliability of the signalling system is therefore not based on negative interactions between androgens and immunocompetence (Møller, 1995). There is some empirical experimental support for the immune system being involved in reliable sexual signalling in birds, but tests for humans are still unavailable (Møller *et al.*, 1999*a*).

VII. ATTRACTIVENESS AND PHYSICAL FEATURES

Early approaches to assess physical attractiveness were done by measuring different distances in faces, having these faces rated for attractiveness and comparing the facial distances to these ratings. Features like a high forehead, large eyes, small nose and a small chin have been mentioned in many studies as traits of 'babyness' (Rensch, 1963; Cunningham, 1986; Johnston & Franklin, 1993). Other studies could not replicate the appeal of babyness features (Grammer & Atzwanger, 1994; Grammer & Thornhill, 1994). A female trait, which is linked to attractiveness, replicated by all the above authors, is a small size of the lower face. Another feature that could be replicated several times for female faces is 'high and prominent cheekbones'. This maturity feature clearly contradicts the presence of an

attractive babyness feature (Zebrowitz & Apatow, 1984), which would consist of high foreheads, big eyes and blown up cheeks. There is only one male facial feature where a positive correlation with attractiveness has been replicated several times: 'wide jaws and big chins' and generally bigger lower faces (Grammer & Thornhill, 1994; Mueller & Mazur, 1997; Thornhill & Gangestad, 1999).

When we move on to single attractive features of the body, there are some hints from the literature, e.g. that female breast size (Hess, Seltzer & Shlien, 1965) and male shoulder width may correlate with attractiveness for the other sex (Horvath, 1979, 1981). We will come back to these two measures later. In addition to this a 'positive pelvic tilt' in females is one of the bodily features judged as being most attractive by males. In regard to females judging males we mainly find negative aspects in judgments: male bellies and male overall fatness are judged as unattractive (Salusso-Deonier, Markee & Pedersen, 1991).

(1) Theories of feature processing: pro

Many researchers have taken measurement data and tried to put them into an evolutionary framework, but the general approach has changed in recent years. Most new hypotheses are no longer *post-hoc* explanations of existing phenomena, so-called 'evolutionary story telling', instead most of what we know today is derived from empirical testing of *ad-hoc* hypotheses generated from evolutionary theory on a meta-level which uses biological constraints. If attractiveness has any relation to mate selection then we would expect two basic differences in the evaluation of traits in the opposite sex: first, traits which guarantee optimal reproduction, i.e. youth, should be valued, and second, these traits should be basically those which are sexually dimorphic. This should be the case because sexual dimorphism is a result of sex-specific adaptation of a body to the requirements of the evolutionary past, i.e. survival and reproduction.

In the human face the basic proportions are sexually dimorphic, male traits develop under the influence of testosterone (male sex hormones) and female traits develop under the influence of oestrogens (female sex hormones). In the case of the broad male chin as a feature of attractiveness the constraints seem to be known. If females want dominant males, broad chins may signal a tendency to dominate others. This is indeed the case. Keating, Mazur & Segall (1981) have shown that males with broad chins are perceived in eight cultures as those who are likely to dominate others. Comparable results have been put forward by Mazur, Mazur & Keating (1984). These authors describe

careers of West Point cadets – those with broad chins at entrance to West Point rose higher in the military hierarchy than others. In addition, college men with broad chins copulate more often and have more girlfriends (Mueller & Mazur, 1997). Winkler & Kirchengast (1994) have shown among the !Kung San bushmen that those males with broad chins and a more robust body build had a higher reproductive success.

A broad chin could, however, also signal a handicap (Zahavi & Zahavi, 1997) because testosterone production might be costly due to the suppression of immune function and thereby increased disease susceptibility during puberty (Folstad & Karter, 1992). Immunocompetence is highly relevant because steroid reproductive hormones may negatively impact immune function (Folstad & Karter, 1992). Extreme male features, which are triggered by testosterone, thus advertise honestly that their bearer was sufficiently parasite resistant to produce them. But male facial features cannot become extreme, as we would expect in a run-away selection (Fisher, 1930). Perrett *et al.* (1998) have shown that adding a feminine touch to a male face can make it more attractive to some females. The reason seems to be clear: broad jaws signal high testosterone levels and thus also possible aggressiveness. If females rely on stable relationships male aggressiveness may also turn against them. Thus there is an upper limit for male jaw width – this is when the feature might also become disadvantageous to females. In addition, female chins and lower faces are small when they are attractive – this probably signals the absence of male sex hormones and the presence of female sex hormones, which are a necessary prerequisite for reproduction. Johnston *et al.* (2001) examined the facial preferences of female volunteers at two different phases of their menstrual cycle. In agreement with prior studies (e.g. Penton-Voak *et al.*, 1999), their results suggest that women prefer more masculinized male faces. That is, the attractive male face possesses more extreme testosterone markers, such as a longer, broader lower jaw, and more pronounced brow ridges and cheekbones than the average male face. This finding suggests that women consider such testosterone markers to be an index of good health and that important health considerations may underlie their aesthetic preference (see for recent review Fink & Penton-Voak, 2002). However, pronounced testosterone facial markers were considered to be associated with dominance, unfriendliness, and a host of negative traits (threatening, volatile, controlling, manipulative, coercive, and selfish). The causal relationship between testosterone levels and these behavioural attributes is still controversial (see for review Mazur & Booth, 1998). If such relationships are valid, then the aesthetic

preference of human females may be an adaptive compromise between the positive attributes associated with higher than average testosterone (health cues) and the negative attributes associated with more extreme masculinization.

Jones (1996) favours the sensory bias theory of sexual selection as an explanation for human female facial attractiveness. He shows that the impression of relatively neotenous female faces, i.e. faces that appear to be younger than the actual age of the face, based on certain facial proportions – small lower face, lower jaw and nose, and full large lips – are rated as more attractive by male raters from five populations. He also found that US women models have neotenous faces compared to female undergraduate students. Thus, markers of high oestrogens levels may reliably signal an immune system of such high quality that it can deal with the handicap of levels of high oestrogens (Thornhill & Møller, 1997). Also, there is evidence that oestrogens' by-products are toxic to the body (Eaton *et al.*, 1994; Service, 1998). Thus, markers of oestrogens may honestly signal ability to cope with toxic metabolites (Fink, Grammer & Thornhill, 2001; Fink & Penton-Voak, 2002).

Sexually dimorphic traits in the human body can be found in the distribution of body fat (breast and buttocks), the general structure of the skeleton, i.e. bigger and more massive shoulders in males, and bigger pelvis in females, and finally muscular build. Male muscular build is a main difference. Again muscles are built under the influence of male sex hormones, and muscles will be of use for males in male competition.

The signalling value of body features in the case of females seems to be linked to reproductive stage. Important sex differences in our bodies depend on fat distribution. The amount of fat in the female body is responsible for a stable level of female sex-steroids (fat equals 25 % of body mass; Frisch, 1975). Thus the amount of visible fat can predict if a female is receptive or not. In order to strengthen its signalling value, body fat must be distributed over prominent places like breasts and buttocks. Otherwise its signalling value may be lowered and thus body fat may simply restrict the biomechanical abilities of the body. Indeed, breast size correlates with overall body fat (Grammer, 1995). Furthermore, overall weight is linked to fertility: heavier mothers have more children (Grammer, 1995; Singh & Zambarano, 1997). Appreciation of heavier women in various cultures seems to depend on environmental stability (Anderson *et al.*, 1992). In unstable environments plumpness is linked to status and attractiveness. Besides being sexually dimorphic, the distribution of body fat can also signal youth and neoteny. Firm breasts with small aureole and erect nipples and the breast axis

pointing upward in a V-angle are rated as attractive (Grammer *et al.*, 2001).

Another signal is the absence and presence of body hair, which is also sexually dimorphic, and thus a feature of attractiveness. Females appreciate body hair developed under male sex hormones but males prefer its absence on females. Removal of female body hair thus is more prominent. Length and colour of females' hair of the head are attractiveness traits. Rich & Cash (1993) have shown that blonde hair, although only infrequent in most populations, dominates in pictures of females presented in magazines for males.

Thelen (1983) showed that preference for hair colour depends on the distribution of hair colour in a population. Males prefer the 'rare' colour. The reason for this situation might be a quest for 'rare' genes, which could help in the host–parasite race discussed below. In addition males seem to prefer long hair (Grammer *et al.*, 2001) and female hair growth on the head is more stable than that of males. Indeed hair loss and baldness are a result of male sex hormones (Muscarella & Cunningham, 1996; Anderson, 2001; Choi, Yoo & Chung, 2001). Long hair thus is again sexually dimorphic. The general function of hair (on the head, in the armpits and pubic hair) may be the distribution of human pheromones produced in the apocrine glands. Hair will give a greater surface for its distribution into the air (see also Stoddart, 1990). We will see below that sexual pheromones play a major role in attractiveness. Long female hair thus would be a 'pheromone-distribution organ'.

Body forms also have an inherent signal value: they create regions of high contrast, which in return keep attention. In a study where an eye-mark recorder revealed male fixations on a female body, males tended to fixate the body contours and regions of high contrast like the shadows under the breasts (Santin, 1995).

(2) Theories of feature processing: contra

There are, however, many objections to a simple feature-based approach to the decoding of attractiveness. One of them is methodological. Most researchers measure many features (up to hundreds) and then they correlate them with attractiveness. There is often no correction for a large number of statistical tests, and hence the replication rate of many attractiveness traits from these studies is very low. Other reasons for inconsistent results regarding the attractiveness of exaggerated facial traits may have arisen from differences in samples of perceivers used. For example, Little *et al.* (2001) explored how female self-rated attractiveness influences male face preference by females and found that there is an increased preference for masculinity and

symmetry by women who regard themselves as attractive. Some other studies considered the position in the menstrual cycle when females rated male faces, and this has repeatedly been shown to affect ratings significantly (e.g. Penton-Voak *et al.*, 1999; Johnston *et al.*, 2001). A lot of previous studies did not control for these variables, although this is likely to obscure any relationships due to noise. However, there is a strong demand for consistent research designs in future studies to make results comparable (see Fink & Penton-Voak, 2002).

One of the earliest assumptions in beauty research was that innate templates are involved in recognition of attractiveness, like the one for 'babyness' (Zebrowitz, McArthur & Apatow, 1984). Babyness is normally perceived as positive and females react to babyness with an increase in frequency of smiles (A. J. Friedlund & J. M. Loftis, unpublished observations). This almost automatic reaction has led to the assumption that babyness could also be involved in adult attractiveness perception, because it could signal neoteny or youth. But the main characteristics of babyness like big puffy cheeks are unappreciated by males. High cheekbones, as a sign of maturity, must be added for a female face to be viewed as attractive (Grammer & Atzwanger, 1994).

But it is not this simple. Research finds that babyness in its original expression is not attractive at all, because males attribute to it negative behavioural tendencies: a babyface seems to imply being 'babyish' (Grammer & Atzwanger, 1994). So, if you remove one part of a template (the puffy cheeks) it is not a template any more – there seems to be a completely new 'Gestalt', and thus a new template. We call this template 'sexy-scheme', because it is a combination of parts of the babyness feature (signalling youth) and high and prominent cheekbones (signalling maturity). The prominent cheekbones themselves seem to be a trait developed under the influence of female sex hormones (Symons, 1995) and thus possibly signal an immunocompetence handicap comparable to male jaw size.

Moreover the presence of babyness features in a female face leads to a transfer of personality traits. Personality traits coupled to babyness are positive and negative: babyness can signal 'submission' and 'eliciting parental care' but it also signals 'incompetence', which would be the last trait in a partner one would look for. Raising offspring requires competence. If a female is very young and at the optimal age of reproduction, she is likely to be an incompetent mother. The optimal age of reproduction is reached at age 24 (Buss, 1989). If attractiveness judgments vary with age, 24-year old females should receive the highest scores. This seems to be the case (Grammer & Thornhill, 1994). All features

described as attractiveness features are sex-specific and are also responsible for gender recognition. When one examines how many measures are necessary to discriminate between faces of different sexes we find that a combination of only 16 different measurements reaches sufficient reliability (Bruce *et al.*, 1993). So gender recognition *per se* seems to be more than simple feature analysis.

Comparable ideas relate to the perception of bodies. In most studies we find a curvilinear relation between features and attractiveness. This means that attractive features are neither too small nor too big. Legs should be neither too short, thick, thin or long (Ronzal, 1996). The same applies to attractive breasts. Moreover, what is attractive seems to be gender prototypical, i.e. sexually dimorphic. Rensch (1963) recognized this relation between stimuli and attractiveness quite early, after studying facial attractiveness and he came to the conclusion that those features which are gender-prototypical are those which are rated as attractive.

VIII. THE ATTRACTIVE PROTOTYPE: FACES

What could the 'Gestalt' we use for attractiveness and beauty decoding then be? A basic feature of human cognition is the creation of 'prototypes' (Rosch, 1978). This means that we constantly evaluate stimuli from our social and non-social environment and classify them into categories and concepts, thus reducing the amount of environmental information into 'pieces', which can be used or stored very economically. For a first approach let us assume that prototypes are some kind of average representation of stimuli of one class.

There are some hints that our brain solves the problem of storing faces with the help of prototypes. We seem to build facial prototypes and then simply assess the deviations of a single face from these prototypes. Children build such facial prototypes very early and when confronted with average faces in recognition tests children give false alarms to them (Bruce, 1988). They behave as if they had seen them before, although they have not. Moscovitch, Winocur & Behrmann (1997) put forward the idea that there is a holistic processing involved in face recognition. The spatial relations among its components define the Gestalt but this Gestalt is more than the sum of its parts. From this starting point basically three hypotheses emerge. The first is 'norm-based coding' (Rhodes, Brennan & Carey, 1987), where averaging a large number of faces in the brain derives the norm. The second hypothesis is the 'density alone hypothesis', where the Gestalt is a point-by-point representation in a multidimensional space

(Valentine, 1991). The third hypothesis is the 'template' hypothesis, which suggests that the brain analyses the single parts with templates and then reintegrates them (e.g. Farah, 1990; Corballis, 1991).

Moscovitch, Winocur & Behrmann (1997) analysed the three hypotheses using the performance in face recognition of a patient who suffered from object agnosia after a brain trauma but was able to recognize faces. Interestingly this patient could recognize atypical faces, cartoons, family resemblance, and he had a good memory for unfamiliar faces. However, he was unable to recognize a face when it was inverted, when single features were inverted, when spatial features were distorted and when faces were misaligned. These results suggest that we indeed process faces via norm-based coding: the patient could process faces only as a 'whole'. If this is so, norm-based coding will be one of the main processes involved in the assessment of beauty.

As soon as prototypes are present they can be used for learning. We learn very fast and almost irreversibly to link personality traits with facial prototypes (Henss, 1992). This helps us to decode behavioural tendencies of people we meet, and thus we are able to structure our behaviour accordingly. Indeed, several studies have repeatedly shown that computer-generated prototypical faces are more attractive than the single faces which have been used to generate them (Galton, 1878; Kalkofen, Müller & Strack, 1990; Langlois & Roggman, 1990; Müller, 1993; Grammer & Thornhill, 1994; Perrett, May & Yoshikawa, 1994). But there are two caveats again: this is only replicable for female faces and all researchers find that there are some individual faces which are more attractive than the prototypes.

IX. THE ATTRACTIVE PROTOTYPE: BODIES

Prototyping does not only apply to faces. Comparable results are reported for the attractiveness of averageness for female body features. The waist-to-hip ratio (WHR) has been suggested to be a good predictor of the ability of women to produce male offspring. Thus, an androgynous body shape may be judged as most attractive in cultures that value male children. Several studies have described WHR in women as a single measure linked consistently across studies to bodily attractiveness (Singh, 1993, 1995). There is a curvilinear relationship to attractiveness with a maximum attractiveness at 0.71. Surprisingly this maximum is related to many health features in women. Moreover there is a direct link to fertility: females with an optimal WHR become more often and more quickly pregnant through artificial

insemination. It has been taken for granted for a long time that the preference for body shapes at the population mean is cross-culturally stable. Research in Great Britain and Uganda showed similar results (Furnham & Baguma, 1994). Recent studies, however, found that male preferences for a low WHR is not culturally universal (Yu & Shepard, 1998). Furthermore, Tovèe *et al.* (2001) suggested that differences in attractiveness preferences between different ethnic groups appear to be based on weight scaled for height (the body mass index or BMI) rather than WHR. Although there is a preferred optimal BMI for each ethnic group, which will balance environmental and health factors, this optimal BMI may differ between groups and environments.

One problem of these studies is that women included in the samples do not represent the average of the actual female population at the age of optimal reproduction. German measurements of 10 000 young adult females show a much higher average WHR (Grammer, 1995). Generally, waists have higher measures in the population than perceived as optimal and attractive. For instance, in Playboy centrefolds, breast measurements are around the population mean (population mean = 88.4 cm in Germany; 88.8 cm in Playboy centrefolds), but waist measures are 7.2 cm smaller in Playboy centrefolds than the population mean for German females (see Garner *et al.*, 1980). The conclusion up to this point is that beauty is averageness, but with exceptions.

(1) Theories of prototype processing: pro

If our brain uses prototypes, averageness might well be coupled with being 'prototypical'. Thus there might be a better fit of the stimulus onto the prototypical template. As a result, prototypes are recognized faster and better and thus might create higher nervous excitation. This could be the reason that averageness is preferred. Our brain could accept more willingly better fitting stimuli. Müller (1993) has called this process 'neuroaesthetics'.

The fact that female attractiveness should be the average was predicted by Symons (1979) on completely different grounds. He proposed that males should avoid mating with females who are at the extremes of a population, because these females may carry disadvantageous genes. Prototypes do portray some genetic information. With respect to features with additive genetic variance, homozygous individuals tend to be over-represented at the extreme tails of the distributions. By contrast, heterozygous individuals tend to be over-represented at the middle of such distributions

(Soulé & Cuzin-Roudy, 1982). However, the traits studied by Soulé & Cuzin-Roudy (1982) were not secondary sexual characters, so it remains unclear to which extent their observations can be extended to this category of traits.

By contrast, male gender prototypes are not average (Grammer & Thornhill, 1994). We have seen that large facial traits are attractive for males. The most interesting feature of prototypes is that attractive prototyping allows two things: first, we are able to adjust our beauty standards to the mean of the population. This is nicely demonstrated by the 'Farrah-effect'. Men who see films with beautiful women adjust their beauty standards accordingly as compared to controls (Kenrick & Gutierres, 1980; Kenrick, Gutierres & Goldberg, 1989). They then have higher aspiration to attractiveness in a dating experiment. Media thus can create 'unreal' beauty standards. Second, prototyping opens our possibilities of mate-choice. If we had an innate template for attractiveness, we could run the danger of either never meeting somebody fitting the template, or being frustrated by the non-fitting mates we find. Through prototyping our beauty standard is adjusted to the population in which we live. If the distribution of traits is a normal one, there are simply more average people than extremes. This creates a bigger population of possible mates. In view of this we should expect some learning mechanisms involved in beauty standards, and an almost automatic fitting of these standards to the population in which we live – which again increases our chances of finding a mate.

(2) Theories of prototype processing: contra

One problem for prototyping is created by the fact that we recognize average faces poorly (Bruce, 1988), because they do not deviate from the templates we use to store faces. With individual recognition as the basis for social interaction, attractive people would have a handicap when it comes to pro-social exchange. If this is true, we should expect deviations from averageness in beautiful faces. One has to be recognizable and distinct. Adding an individual touch to averageness could thus make an attractive face beautiful.

There are still more problems with this approach. First, the computer-generated prototypes lack skin blemishes and faces appear much softer than in normal pictures. Second, there are single faces that are not prototypical at all, and they are constantly rated as more attractive (Grammer & Thornhill, 1994; Perrett et al., 1994). Third, symmetry could play a role; composite faces are much more symmetrical than the single faces, which are used to form the prototype. Computed

averageness is symmetrical; thus we have to control for symmetry and determine what role it plays for prototypes and attractiveness.

X. DEVELOPMENTAL STABILITY AND BEAUTY

Developmental stability reflects the ability of individuals to maintain stable development of their morphology under given environmental conditions (Møller & Swaddle, 1997). While developmental noise and various developmental upsets tend to destabilize development, developmental control adaptations have the opposite effects on the phenotype. Measures of developmental instability include fluctuating asymmetry and the frequency of phenodeviants, but also other measurements. A character demonstrates fluctuating asymmetry when symmetry is the norm and deviations from symmetry are randomly distributed with respect to side (Ludwig, 1932). Phenodeviants are relative large deviations from normal phenotypes such as a position of the heart in the right side of the body cavity or the presence of an even number of fingers on a hand.

Fluctuating asymmetry is a particularly useful measure of developmental control ability for several reasons. First, we know the optimal solution *a priori*: it is symmetry. Second, fluctuating asymmetry develops in response to an enormous range of genetic and environmental factors that tend to upset developmental processes (review in Møller & Swaddle, 1997). Third, fluctuating asymmetry can be measured accurately with practice and we can investigate plants, insects, birds and humans using the same simple and uncostly tool, a precise ruler. Fourth, we cannot investigate how plants and animals feel about or perceive their environment, but we can answer this question indirectly by measuring their asymmetry because asymmetry reliably integrates the consequences of many disruptive effects of the environment. Since the optimal phenotype is the symmetric one because it promotes performance, any deviation from perfect symmetry can be considered a sub-optimal solution to a design problem that will result in performance problems in the future. It was probably difficult for a pre-historic human to escape from a lion, but it was even more difficult to escape with two legs of unequal length. Indeed, skeletal remains from pre-historic Indians have shown that individuals that were old had more symmetric bones than individuals that died young (Ruff & Jones, 1981). This finding is particularly interesting because continuous re-modelling of bones during life generally gives rise to increasing asymmetry among older humans.

It is perhaps not surprising that asymmetry has been found to be important for plants and animals including humans when faced with the realities of life, the struggle for survival, mates and reproduction (Møller & Swaddle, 1997). The continuous selection against asymmetry starts already among sperm and eggs within females of species with internal fertilization: developmental selection against deviant gametes and zygotes appears to be a very widespread phenomenon. Fruit and seed abortion is extremely common in plants. Experimental work 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 developmental patterns (Møller, 1996*a*). Interestingly, the abortion frequency is directly related to the symmetry of the flowers of both the pollen donor and the pollen recipient. Similar phenomena have been described among a wide range of organisms spanning invertebrates and vertebrates including humans (Møller, 1997). Infanticide has been and is still a common practice in many human societies mainly directed towards children with deviant phenotypes. This behaviour has obviously been adaptive by avoiding wastage of costly resources on offspring with poor survival prospects. Evolutionary psychological studies of parental reactions to newborns have demonstrated that modern human beings still carry psychological adaptations towards this end by reacting with strongly negative feelings that best can be described as disgust and aggression when confronted with children with increasingly deviant appearances (Daly & Wilson, 1988).

Asymmetry also matters when it comes to the mating game. Developmental stability and sexual selection are closely associated in a wide variety of organisms ranging from plants, flies, grasshoppers and fish to birds and mammals (Møller & Thornhill, 1998; Møller & Cuervo, in press). For example, women prefer men with symmetric faces and bodies (Grammer & Thornhill, 1994; Thornhill & Gangestad, 1994; Jones *et al.*, 2001), and the number of sexual partners during life is directly related to skeletal asymmetry in men (Thornhill & Gangestad, 1994; Gangestad, Bennett & Thornhill, 2001). Since symmetry relates to performance in general, choosy females that prefer symmetric males will obtain mates that are better able to provide resources, but also able to provide genes for developmental health to the offspring. Given the intense developmental selection against asymmetric offspring, females will also benefit in terms of increased fecundity.

Some bodily and facial asymmetries manifest themselves very early in human development and remain stable during lifetime (Thornhill & Gangestad, 1996;

Thornhill & Møller, 1997). These minor physical anomalies (MPAs) seem to be the result of developmental instabilities during early embryonic development. MPAs are formed in the first trimester of gestation, and fluctuating asymmetries develop throughout life. However, several studies have shown positive correlations between the frequency of MPAs and fluctuating asymmetry. At this point we have to distinguish between MPAs and bodily laterality. Usually the sides of the body differ, but the vertical body symmetry line can still be a straight line (despite laterality being present). Asymmetries in the face distort this straight line into a zigzag line.

Thus MPA or fluctuating asymmetry may be a significant negative predictor of attractiveness and used as a negative scale for prototype beauty. Comparable results can be found for the rating of bodily attractiveness in relation to breast asymmetry (Singh, 1995). Symmetrical breasts are more attractive than asymmetrical breasts. Moreover, breast asymmetry is a significant negative predictor of lactation ability and even reproductive success (Møller, Soler & Thornhill, 1995). Thus bodily and facial symmetry seems to be important in ratings of attractiveness.

(1) Theories of symmetry and attractiveness: pro

Host–parasite co-evolutionary cycling predicts that parasite resistance should be a trait that is valued in mate selection (Møller *et al.*, 1999*a*). One defence against parasites is the production of substantial polymorphism: when a parasite adapts to one allele, alternative alleles may be advantageous. Pathogens are a major environmental perturbation underlying developmental instability, and developmental stability may be related to additive genetic variance in disease resistance, which in turn may relate to fitness. Thus symmetry, which cannot be faked, may be an honest signal of mate quality. Symmetry as a mate-selection criterion has been shown in many species, from insects, birds and mammals to humans (reviews in Møller & Thornhill, 1998; Møller & Cuervo, in press). Moreover attractiveness plays a prominent role in mate selection in those human societies where parasites are prominent (Gangestad & Buss, 1993). The basic finding is that if symmetry is present in the face or the body an individual is judged as being relatively attractive, and if the body is asymmetric the face is rated unattractive, even if the rater never sees the body (Thornhill & Gangestad, 1993, 1994; Gangestad, Thornhill & Yeo, 1994).

Although this statement should be qualified, let us simply assume that symmetry seems to be influential in

ratings of attractiveness and thus mate choice. In addition, we note that symmetry may be more salient than averageness (Grammer & Thornhill, 1994).

(2) Theories of symmetry and attractiveness: contra

There are several objections against a theoretical connection between fitness and facial and bodily symmetry. Most of these objections can be subsumed under the term 'sensory exploitation'. Research on the perception and computation of stimuli has shown that symmetry of stimuli is one of the main factors in recognition and reaction to stimuli. Several computer simulations have shown that neural networks, when confronted with stimuli, respond better and easier to symmetrical ones (Johnstone, 1994). Enquist & Arak (1994) have shown that symmetry preferences may arise as a by-product of the need to recognize objects irrespective of their position and orientation in the visual field. Another objection is that templates can only be constructed symmetrically (Eibl-Eibesfeldt, 1997), although this poses the question why such a mechanism came about, if not for the utility of processing information about biological entities. Symmetrical stimuli thus would exploit the sensory system of the receiver. Symmetrical patterns are attractive for humans in contexts unrelated to signalling, although it remains unclear whether such preferences arose before or after the preferences for symmetry of sexual signals. Such general preferences for symmetry serve no obvious function (Rensch, 1963).

Preferences for symmetry might have evolved for completely different reasons, but independent from this, they have an effect on mate choice, related to reproductive success. Using photographs of men's faces, for which facial symmetry had been measured, Scheib, Gangestad & Thornhill (1999) found a relationship between women's attractiveness ratings of these faces and symmetry. Interestingly, subjects could not rate facial symmetry accurately. Moreover, the relationship between facial attractiveness and symmetry was still observed, even when symmetry cues were removed by presenting only the left or right half of faces. These results suggest that attractive features other than symmetry can be used to assess phenotypic condition. The authors identified one such cue, facial masculinity.

Further empirical results are also strongly contrary to this incidental effect hypothesis for the human facial symmetry preference and strongly consistent with the good genes hypothesis for the preference (i.e. the preference favours healthy individuals). Little et al. (2001) found that experimental manipulations of facial symmetry have a greater influence on opposite-sex facial attractiveness ratings than on same-sex ratings. In their study comparing females who did and did not consider themselves to be physically attractive, those who considered themselves physically attractive showed a greater preference for two proposed markers of quality in male faces: masculinity and symmetry. Little et al. (2001) consider this a condition-dependent mating strategy analogous to behaviours found in other species. In other words, 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. This was repeated by Jones et al. (2001). The latter study also found the same bias when judging apparent health: facial symmetry variation affects opposite-sex health ratings more than same-sex ratings, and symmetry is rated as healthy. These sex-specific patterns are inconsistent with the claim that symmetry is found attractive as a by-product of the ease with which the recognition system can process symmetric stimuli. As strongly inconsistent with this suggestion was Jones et al.'s (2001) report that the relationship between facial attractiveness and facial symmetry is mediated by a link between judgments of apparent health and symmetry. When the effect of attractiveness ratings was controlled statistically, the positive relationship between facial symmetry ratings and health remained significant. This negates the view that the relationship between facial symmetry and rated health may be caused by an attractiveness halo effect. But when the effect of judgments of apparent health was controlled, the relationship between facial symmetry and attractiveness disappeared. This latter result establishes that the facial attractiveness–symmetry relationship is mediated by the link between facial symmetry and judgments of health.

Another feature which should be mentioned here is the role of skin texture because blemishes in the skin can also be related to the perception of symmetry. Blemishes can appear and disappear and distort symmetry. The role of skin texture and facial symmetry has not been subject to much scientific research. No research has been done to solve the problem of what causes the higher attractiveness of some faces compared with a symmetric composite. Both average faces and more symmetrical faces could be recognized simply by texture. In a recent study, Fink et al. (2001) used the co-occurrence-matrix (Haralick, Shanmugam & Dinstein, 1973) to classify female facial skin texture. With this image segmentation method, Fink et al. (2001) showed that human skin provides reliable cues of its health condition. Skin texture plays a role in normal faces – the more homogenous these faces, the more attractive they

are. But this could be due to a correlation between symmetry, averageness and texture. Symmetry was controlled to ensure that a significant correlation between attractiveness and texture was not caused by the influence of symmetry. For this purpose, Fink *et al.* (2001) used the techniques of 'morphing' and 'warping' the original faces to remove their individual shape and thus standardize them. Skin texture still had a significant influence on the judgment of female facial attractiveness: a homogeneous skin texture was considered more attractive. This effect might be caused by cues of immune function that we derive from skin condition. There is a relationship between dermatoses and elevated levels of sex hormones (testosterone, oestrogens), and this is often correlated with ovarian dysfunction (e.g. 'polycystic ovary syndrome'; Steinberger *et al.*, 1981; Schiavone *et al.*, 1983). Accordingly, Mackintosh (2001) evaluated the antimicrobial properties of melanocyctes. He presented evidence that melanization of skin and other tissues forms an important component of the innate immune defence system following previous findings by Duke-Cohan *et al.* (1998) and Duke-Cohen, Tang & Schlossman (2000) on attractin, a protein that seems to have regulating functions on melanization and immunity. Melanization and the innate immune response are likely to be functionally, biochemically and genetically linked. Mackintosh (2001) suggested that melanized tissue acts to seal off vulnerable nutrient-rich tissues from microbial attack. Consequently, the greater the melanosome and melanin content, the more protective will be the effect. This may underlie the finding by Fink *et al.* (2001) who showed that among Caucasian females, a darker skin complexion is considered more attractive than a light one.

XI. CROSS-SENSORY MODALITIES: BODY ODOUR, VOICES, DECORATION AND MOVEMENT

A pheromone is a chemical signal emitted by one individual that alters either the behaviour or physiology of another individual (Luscher & Karlson, 1959). Several investigations on human body odour revealed the relevance of olfactory communication in humans and its implications for sexual behaviour (Schaal & Porter, 1991). Human body odour has been reported to influence female mate choice and may allow finding a partner who possesses complementary immune responses (Wedekind *et al.*, 1995). Females find the body odour of those males attractive whose major-histocompatibility complex (MHC) is different from their own. In this case sexual attractiveness of body odour would lead to heterozygotic offspring. Moreover, as suggested by Grammer (1993), an important possible function of a pheromone would be the induction of effects, because emotions may change information processing in the receiver. Via a pathway to the limbic areas of the brain, the chemical signals carried by odours have a direct influence on emotions. Odours induce negative or positive moods and feelings. Thus, odours allow direct manipulation of cognition. Indeed, odours modify the social perception of other persons (Cowley, Johnson & Brooksbank, 1977). Emotions and moods again drastically change social perception and information processing (Forgas & Moylan, 1991). Isen (1984) found that people who are in a positive mood often use more heuristic, truncated processing, use larger and more inclusive categories, and are more likely to take risks, provided that such risks do not threaten their positive mood state. These people seem to use an effort-minimizing, simplifying processing style. The possible effect of pheromones on mood makes pheromones a highly likely candidate for the alteration of attractiveness assessments. In humans, we have seen that sexually asymmetric parental investment leads to gender-specific mate-selection criteria. If those criteria are part of the adapted mind, they become prone to exploitation. This is the case especially for male mate-selection criteria, because males rely so importantly on a single optical stimulus: female attractiveness.

In their vaginal secretions females produce a sample of fatty acids with behavioural effects, referred to as 'copulins' (Curtis *et al.*, 1971). They were originally discovered by Michael & Keverne (1968) in rhesus monkeys (*Macaca mulatta*). Although normally motivated to copulate, when sexually inexperienced rhesus males were made anosmic, they showed no further sexual motivation despite a powerful visual cue: the female's sexual swellings (Michael & Keverne, 1968). Furthermore, rhesus males show no interest in ovariectomized rhesus females, presumably because ovariectomized rhesus females lose the odour characteristic of ovulation. Rhesus males regained interest in copulation when the vaginal secretions from non-ovariectomized females were applied to ovariectomized females. Studies on menstrual cycle fluctuations in the fatty-acid composition of women's vaginal fluids indicated that a similar type of signalling system might also exist in humans (Waltman *et al.*, 1973; Michael, Bonsall & Warner, 1974; Michael, Bonsall & Kutner, 1975; Preti & Huggins, 1975). Further investigation on the function of copulins in humans remain to be conducted, but we may assume that ovulation is not concealed, and that men could use ovulation-linked

odours in their mate selection. This has now been shown in four separate studies (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999; R. Thornhill, S. W. Gangestad, R. Miller, G. Scheyd, J. Knight & M. Franklin, in preparation).

The strongest pattern in human sex pheromone research pertains to the body scent of symmetric men. Such men's body scent is attractive to women, especially women at peak of fertility in their menstrual cycles. Although men do not show a consistent preference for the body scent of symmetric women, two studies have found that men prefer the body scent of women at ovulatory menstrual cycle phases (Singh & Bronstad, 2001; R. Thornhill, S. W. Gangestad, R. Miller, G. Scheyd, J. Knight & M. Franklin, in preparation).

In addition to smell many other signals might contribute to attractiveness. Voice quality is another candidate. Unfortunately there is not much research in this direction. Zuckerman & Driver (1989) found attractiveness prototypes in voices. People tend to agree what an attractive voice is. They tried to disentangle the physical qualities of voices in relation to attractiveness. The only variable found is frequency: deep male voices are rated attractive. The biological background for such an attractiveness rating might lie in the fact that usually the size of the voice-producing apparatus (the larynx and the oral cavity) correlate with body size, which is sexually dimorphic and thus again prototypical for males. Vocalizations may also provide reliable information about health status as is shown by evidence from studies of bird song reflecting current health status (Saino *et al.*, 1997) and the calls of nestling birds reflecting their current health status (Sacchi, Saino & Galeotti, 2002). Hertrich & Ziegelmayer (1988) have examined to what extent the speaker's body size and shape are betrayed in his speech signal and thus can be recognized by listeners. Contrary to earlier constitutional studies only size and not shape correlates with acoustical parameters of speech; comparing listening experiments with acoustical analysis gives some evidence that the average sound spectrum is used by listeners to judge the speaker's body size. This effect may be direct, or it may be an indirect signal of symmetry since symmetric males tend to have more attractive calls in jungle fowl *Gallus gallus* (Furlow, Kimball & Marshall, 1998). Furthermore, large men are more symmetric than small men (Manning, 1995).

Another point often put forward in attractiveness research is the role of decoration and subsequent body changes. Decoration allows primarily two things: first decoration can alter perception of attractiveness and second, decoration can be used for in-group identification. Grammer (1998) showed that advertisement by females is mostly about body improvement and decoration. Here culturally determined ways of body improvement operate on a biological theme. Grammer (1995) showed that although body decoration may significantly change ratings of attractiveness and personality, it cannot change the overall perception of a person. For instance, if a female is rated as dominant and not romantic, only the overall perception of the magnitude of the rating changes, but the female will not be rated subordinate and romantic. Low's (1979) research suggests an interesting link to decoration and parasite resistance. Decoration may be most prevalent in those societies where parasite load is high. In this view decoration would follow a handicap principle and it would signal that the decorated person is able to spend time on decoration. Recent studies of perfume use in western society have suggested that perfume is a means of enhancing or exaggerating differences in natural odour related to MHC genotype, again suggesting a clear link to parasite-mediated sexual selection (Milinski & Wedekind, 2001).

Last but not least we will look at the beauty of human movement. It is obvious that movement plays a role in person perception. In German expression psychology the assessment of movement quality played an important role as early as at the beginning of the 20th century. Fischer (1911) introduced an objective method for the analysis of movements from films by measuring the co-ordinates of joints in every film picture. Consequently, Flach (1928) postulated: 'a symbol alone, a gesture … is ambiguous. In contrast, the dynamics of a movement are unambiguous and convincing' (p. 461, authors' translation).

Unfortunately, this objective approach was dropped in favour of subjective interpretations of the objective measurement data. Fifty years later, Johansson (1973, 1976) fixed point-light displays to the joints of participants and filmed their movements in the dark. If such point-light films were shown to raters, they would recognize sex, age and movement patterns (e.g. walking), but if presented as a fixed image, the points would appear randomly distributed (Cutting & Proffitt, 1981; Runeson & Frykholm, 1983). Observers are able to detect effort, intention and deception from body movements. Berry *et al.* (1991) used quantized videos, which obscured the individual information and left only the movement visible for rating. In this approach the constraints of point-light displays are not present. The new method allowed the above results to be replicated. In neither approach was an empirical description of movement quality carried out. A substantial

gap therefore exists between the fact that we know that participants are able to deduce information from movement and the description of the kind of information the participants use. Nonetheless, the results of the above work also suggest that movement alone can carry a meaning.

Thus movement carries at least one type of information for certain: gender identification, which is one source for attractiveness ratings. But there are two more likely candidates we have to look at: symmetry and hormone profiles. Møller, Sanotra & Vestergaard (1999*b*) showed that symmetric chickens show more coordinated and more efficient walking behaviour. Thus symmetry could not only be an indicator of developmental stability; it could also be an indicator of movement efficiency and thus bodily efficiency of an individual. However, since external developmental instability only reflects one part of developmental instability, effects of stress on the neural system might just as well account for the development and the expression of external asymmetries. Studies of animal behaviour have indicated that the fractal dimension of repeated behaviour such as movement differs between healthy and sick individuals (Escós, Alados & Emlen, 1995). Thus, the ability to repeat behaviour in a consistent way may provide important information about condition and represent a behavioural equivalent of morphological developmental instability (Møller, 1998). The same also holds for faces: on symmetrical faces for instance it could be easier to detect and see emotions. Moreover, asymmetric movement in facial expression is one indicator of deception (Ekman & Friesen, 1969). Thus facial and bodily symmetry are not only indicators of developmental stability, they might also guarantee honesty (even if this is not functionally related to it).

In recent years, although there is still controversy about the findings, some studies have shown that female movement might be related to sex-hormone profiles. Self-reports of Olympic women athletes and other sportswomen indicate a pre-menstrual decline in athletic performance. Hampson & Kimura (1988) showed that there is a significantly better mid-luteal than menstrual performance on several measures of manual speed and co-ordination. Grammer, Fieder & Filova (1997) have also shown that a neural network, which was fed with digitally analysed movement data, was able to discriminate between women at high and low oestrogen levels in relation to menstrual cycle point. Thus we can speculate that the beauty of movement could be related to signalling optimal oestrogen levels, but also that oestrogen could affect asymmetry, which in turn might affect attractiveness.

XII. THE BEAUTY OF BOUNDARIES AND BOUNDARIES OF BEAUTY

What we find in research on attractiveness is a differential reaction to humans according to their appearance, which is biologically based. Yet it remains unclear how attractiveness itself is decoded. We have discussed many variables which may influence the decoding of attractiveness: form of faces and bodies, structure, skin texture, gender prototypicality, body movements, voices, age, decoration, cosmetics, body scent, hair colour, hair style, cultural dynamics, normative comparisons and finally temporal dynamics. Considerable evidence has accumulated in recent years supporting the hypothesis that both facial and bodily physical attractiveness are health certifications and thus represent honest signals of phenotypic and genetic quality. The hypothesis that beauty connotes health was first proposed by Westermarck (1921) and later by Ellis (1926) and Symons (1979, 1995). There is no doubt, regarding all these variables, that beauty or attractiveness, are cognitive constructs in the eye of the beholder. Thus beauty, its signal values and cognitive processes are interlinked to a high degree.

An approach to solve the problem of integration of many features of signals into one meaning was suggested by Schleidt & Crawley (1980) as an *n*-dimensional vector approach to communication. They assumed that meaning could be encoded in the form of pulse rate modulation. Here the sender sends a signal of uniform height and duration repeatedly at distinct intervals. The receiver then applies some kind of low-pass filter in order to integrate the signals over time. The effect on the receiver then is a slowly accumulating tonic one. Schleidt & Crawley (1980) suggested describing behaviour as a change of an organism over time, which can be done by describing the momentary states of organisms at any point in time. This approach demands an evaluation of features of the individual at its surface, the orientation of the individual and its location. The result would be data in an *n*-dimensional feature space, which can include information on the internal features of an organism, i.e. physiological state, motivation, emotions, etc.

Grammer *et al.* (2001) analysed attractiveness ratings on 92 American females and developed a list of 36 features. These features range from simple measured traits (e.g. lip size, breast size or eye size, body height, body mass index, waist-to-hip ratio) to digitally analysed descriptors (e.g. body colour, hair structure, skin colour) to more sophisticated digitally analysed measures (symmetry, skin texture and averageness). This multidimensional vector room was then transformed

with principal component analysis to four factors explaining 56 % of the variance in the population. The basic factors are: a body mass index factor which is related negatively to attractiveness, a nubile factor which is related positively, a positively related symmetry and skin colour factor, and a babyness-androgynous factor which is related negatively to attractiveness. This shows that it is possible to extract basic features.

If such a multidimensional feature space is linked to the perception of beauty, and if beauty is an honest signal, this feature space needs to have a specific internal structure. Each feature could also be a prototype. In order to reach its communicative purpose, all features have to point in the same direction because otherwise the receiver would be unable to decode the signal clearly and unmistakably. Møller & Pomiankowski (1993) come to a comparable conclusion in their analysis of why birds have multiple sexual ornaments. Thornhill & Grammer (1999) showed that independent ratings of faces in Austria and the USA, body fronts with faces covered, and backs of the same women are significantly positively correlated, as predicted by the health certification hypothesis and the n-dimensional feature approach. The correlation between the ratings of different pictures implies that women's faces and bodies comprise a single ornament of honest mate value, apparently developed during puberty under the influence of oestrogens.

This is not a single piece of evidence. If we are right, features from different communicative channels also have to point in the same direction. In order to study this, Rikowski & Grammer (1999) investigated whether smell could signal general mate quality like other cues in sexual selection. They compared ratings of attractiveness and measurements of bodily asymmetry with the evaluated attractiveness of body odour from male and female subjects. Each subject wore a T-shirt on three consecutive nights under controlled conditions. Immediately after use the T-shirts were deep frozen and heated up to 37 °C just before the evaluation of odour, then 15 subjects of the opposite sex rated the smell of each T-shirt on intensity, pleasantness and sexiness on a seven-point scale.

Another 22 men and women evaluated portraits of the subjects on attractiveness. For the assessment of bodily asymmetry seven bilateral traits of each subject's body were measured. The results showed significant positive correlations between facial attractiveness and sexiness of body odour for female subjects. Moreover, the more symmetric the body of a woman, the more sexy her smell. Men rated the smell of women as more erotic, the more attractive their faces had been

evaluated. Positive relations were found between body odour and attractiveness for males only when female odour raters were in their most fertile phase of their menstrual cycle. In other words, these fertile women tend to prefer the odour of physically attractive and symmetric men. As mentioned above, the finding that symmetric men's scent is attractive to fertile women has been reported in four separate studies.

One point we want to emphasize is that every theory in this field has to take the construction of the cognitive apparatus into account. We have shown that the decoding of attractiveness depends on our abilities to create prototypes. Humans seem to use single cues, prototypical cues and overall constructive features of the body. Our brain combines these n-features; their common direction makes decoding a little easier. Now we can also suggest a possible method for the decoding procedure itself. If, and when, the features have the same orientation, only their size needs to be compared. Gigerenzer & Goldstein (1996) suggests that people use fast and frugal algorithms, which produce the same results as more complex decision-making algorithms in many every-day decision-making problems. Such a simple algorithm would be 'the worst (or best) feature approach'. This means that signal receivers simply compare the size of the best or worst feature in an n-dimensional feature space (regardless of the feature content) in order to come to a decision that one person is more attractive than another. Grammer *et al.* (2001) showed that when the lowest value of the regressed factor scores on the above mentioned four principal component analysis factors is used as an attractiveness descriptor, the correlation between attractiveness rating and factor size exceeds 0.60. Note that this method only takes the size of the factor into account, not the content. This also suggests that beauty perception is not a positive concept – it could be that it is reversed: avoid ugliness. Yet even more simple methods are possible. When there is no direct comparison available a simple threshold model could be used; the worst feature then has to be over a certain threshold before the whole person is rated as attractive. Other models might be parallel-distributed models of cognitive processing as suggested by Haken (1996) through synergetics, where one feature might strongly affect the perception of other features and then create a coherent signal value.

The main feature is that although different people might have different templates for beauty, these templates underlie common construction principles. This also explains the high cultural and temporal variability of beauty standards. What we know is that mate-selection criteria play a role in attractiveness

ratings: females rate males as attractive when they are dominant and healthy, males rate females as attractive when they are healthy, receptive at the optimal age of reproduction, and when they promise high-quality off-spring. The question of what exactly is communicated is still open. For the time being we suggest that it is mainly 'gender identification': appearing as a 'typical' male or a 'typical' female in a certain environment will cause attractive ratings. This means that sexually dimorphic traits that signal youth are valued. These traits then form the respective prototypes for the cognitive evaluation of attractiveness.

In addition, each theory of attractiveness has to take into account that a great deal of learning is involved. Different cultures indeed have different standards, if we look at the content of these standards (although they might agree on faces of a single population). The effect of learning is that we adapt our standards to our population and ecological niche. This changes as soon as we look at the construction rules: features, averageness and symmetry. Thus the concept of attractiveness can be filled with different contents, as long as these contents follow the given rules.

One condition posed at the beginning of this review is the fact that 'attractiveness' and 'beauty' should be linked to reproductive success. If this is so, why do people not become more and more attractive and beautiful? This question leads to Van Valen's (1973) 'Red-Queen-Hypothesis' based on an experience Alice had in the novel *Alice Through the Looking Glass* by Lewis Caroll. In this experience, Alice proposes to race against the red queen on the chessboard in order to become queen herself. Unfortunately, one of the principles behind the mirrors is that you have to be twice as fast as you can simply in order to move and leave your place. One such race is host–parasite co-evolution. In this view only rare genotypes have a selective advantage in terms of survival and reproductive success. Genotypes that are attractive today may not be so for a long time because their increase in abundance will cause evolution by parasites towards efficient exploitation of this increasingly more common host genotype.

We see that Darwin was wrong, but he was also right. We saw that cultures and their media might change beauty standards, but these standards are biologically based, not their actual content but the rules which determine these standards. If we assume that beauty brings a certain amount of status in a society, we have started another race behind the mirrors. This time people will race against the media and surely also against other people. The future of the adapted mind is the creation of artificial people.

XIII. THE FUTURE OF THE ADAPTED MIND

A feature of the adapted mind which is rarely addressed is the fact that adaptation is prone to exploitation, and to what extent this exploitation occurs in the modern society. This does not mean that we are ill- or maladapted to the modern environment. It may simply be the case that, for instance, new cultural developments can out-run biological adaptations. One example is the speed of information transfer. Many of our adaptations are possibly tuned to slow and small information changes in our environment, and the invention of modern media has created a completely new situation. The literature shows that beauty brings status and success (and naturally, reproductive success, at least in the evolutionary past). If so, artificial body enhancement, which amplifies beauty perception will be widespread. In fact, almost all cultures use such measures. Yet beauty is limited – through evolution we cannot become more beautiful. In the future, if a certain beauty enhancement generates status, this enhancement will lose its advantage when used by too many people, and new enhancements will be made. This is the eternal circle of new fashion and beauty product inventions. Now this trickle-down mechanism meets prototyping. If beauty standards are a result of what people perceive in the average media, exposure to media will change the prototypes. As the media themselves will use beauty for the status quest among different types of media, beauty standards will automatically trickle down in the media and then a quest for more beauty will start. As human beauty is limited, it is plastic surgery and hormonal treatments which come into play.

Beauty surgery, especially breast augmentation, is increasingly common. Surveys suggest that more than 800 000 American women have breast implants. The majority is not done for medical reasons. Surveys suggest that women desiring surgical breast augmentation are as psychologically stable as other women. They differ from other women only in limited areas – primarily in their negative evaluation of their breasts and their greater emphasis on dress and physical attractiveness (Shipley, O'Donnell & Bader, 1977); increase in desire for attractiveness is the reason for plastic surgery. Indeed in very young (pubescent) girls who have breast surgery, the removal of asymmetries make up more than 60 % of the cases (Grolleau *et al.*, 1999). This correction would be expected if we take the role of symmetry in beauty detection into account. In a study of women who had received augmentation mammaplasty an interesting pattern occurred (Cook *et al.*, 1997). Women with breast implants were more likely to drink a greater average number of alcoholic drinks, be younger

at first pregnancy, be younger at first birth, have a history of terminated pregnancies, have used hair dyes, and have had a greater lifetime number of sexual partners than women without implants. This difference between women with and without breast implants suggest that breast augmentation may lead to higher attractiveness for males, a larger number of possible choices of high status males, and finally possibly higher reproductive success. But as soon as this circle is started and success comes by surgery, its use will spread and trickle down to more and more surgery, until plastic people emerge. But there is also a down side to this game. When the media raise attractiveness standards by prototyping beauty, then unreal expectations to mate quality (beauty) will emerge. If the mean is more beautiful than reality, no mate selection can occur on realistic grounds leading to a high proportion of singles.

The second even more problematic development is coupled to the emergence of relatively new diseases like anorexia and similar conditions. Feminist approaches (Crogan, 1999) to understanding women's dissatisfaction with their bodies claim that social pressure on women causes them to strive for the slender, toned body shape which is associated with youth, leading in its extreme form to such diseases. Actually, this social pressure is caused by other women who compete for resources, and not by the beauty industry. It can be viewed as a trickle-down phenomenon with a biological basis, which with the help of fast information transfer causes a beauty rat-race. However, independent of any artificial changes we may still infer that such modifications generally will not have the desired effects. The reason is that the various dimensions of attractiveness tend to signal the same qualities. Although external phenotype can be modified, the message arising from such a signal will prove to be incongruent with other signals such as movement, vocalizations, and pheromones. Hence, we predict that 'experimentally' manipulated phenotypes will prove unsatisfactory, even for the individuals themselves because of being incongruently perceived by others. There are some hints consistent with such effects in the studies of consequences of plastic surgery (e.g. Simis, Verhulst & Koot, 2001; Muzaffar & Rohrich, 2002).

XIV. DIRECTIONS FOR FUTURE RESEARCH

Although the field of sexual selection and studies of attractiveness in humans has made tremendous strides forward during the last decade, there is still much that needs to be done. We have emphasized the large number of different categories of traits that play a role in

sexual selection but it is a salient question how these different kinds of traits are related to each other. Do they reflect different aspects of quality, are they providing redundant information, or are some signals simply not providing any information (Møller & Pomiankowski, 1993)? How are these different traits related to each other when fully developed? What is their order of ontogeny? What determines their development? And how are they integrated? We have described the apparent links between human beauty and parasites and disease. We still need to know which kinds of diseases are reflected by signals of beauty? How well do different signals predict risks of disease and parasitism? These are important questions of potentially great medical importance. Numerous studies of animals have already addressed how sexual selection relates to immune function (review in Møller *et al.*, 1999*a*). However, we know virtually nothing about the links between beauty and immunity in humans. Again, such knowledge could potentially have important implications for medicine and public health.

Finally, while almost all studies of animals have tied research on sexual signals to components of fitness, that has rarely if ever been done in humans. How does attractiveness relate to reproductive success? We need many more studies that investigate the benefits of mate choice in terms of reproductive success measured as the number of reproductive offspring in the next generation, and even in the grand-parental generation. Before such estimates have been obtained, conclusions still remain extremely tentative.

XV. CONCLUSIONS

(1) Sexual selection is the study of what might be called beauty perception and its role in mating competition in plants and animals.

(2) Human obsession with beauty is no different from similar obsessions in other organisms.

(3) Humans are sexually size dimorphic with males on average being larger than females, females usually limiting male reproductive success, and male resources being a primary goal for female mate preferences. The basic features of human beauty in faces and bodies are symmetry, averageness, and sex-hormone markers. These features reflect sex-prototypical design of traits, developmental stability and immuno-handicaps and are linked directly to optimal reproduction. The basic processes are biological universals for humans, animals and even plants.

(4) Single features from these three categories can be placed in two groups. The first group gives information

about the general reproductive capabilities of an individual, while the second group consists of transient features which give information about the current physiological state of an individual.

(5) Features that comprise the attractiveness complex are intricate parts of an *n*-dimensional feature space. This feature space is organized such that all features point in the same direction. Attractiveness thus follows the redundant signalling hypothesis.

(6) The features themselves are cross culturally universal but their importance can be modified culturally depending on socio-economic factors.

(7) We do not assume innate beauty detectors; we rather propose that the brain has an innate tendency and basic rules on how to create beauty templates, which then are filled up during ontogeny.

XVI. ACKNOWLEDGMENTS

XVII. REFERENCES

ANDERSON, J. L., CRAWFORD, C. B., NADEAN, J. & LINDBERG, T. (1992). Was the Duchess of Windsor right? A cross-cultural review of the sociobiology of ideals of female body shape. *Ethology and Sociobiology* **13**, 197–227.

ANDERSSON, M. (1994). *Sexual Selection*. Princeton University Press, Princeton.

ANDERSSON, S. (2001). Steroidogenic enzymes in skin. *European Journal of Dermatology* **11**, 293–295.

BAUGH, S. G. & PARRY, L. E. (1991). The relationship between physical attractiveness and grade point average among college women. *Journal of Social Behavior and Personality* **6**, 219–228.

BERRY, D. S., KEAN, K. J., MISOVICH, S. J. & BARON, R. M. (1991). Quantized displays of human movement: a methodological alternative to the point light display. *Journal of Nonverbal Behavior* **15**, 81–97.

BRUCE, V. (1988). *Recognizing Faces*. Erlbaum, London.

BRUCE, V., BURTON, A. M., HANNA, E., HEALEY, P., MASON, O., COOMBES, A., FRIGHT, R. & LINNEY, A. (1993). Sex discrimination: how do we tell the difference between male and female faces? *Perception* **22**, 131–152.

BUSS, D. M. (1989). Sex differences in human mate preferences – evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences* **14**, 519.

BUSS, D. M. (1994). *The Evolution of Desire: Strategies of Human Mating*. Basic Books, New York.

BUSS, D. M. & SCHMITT, D. P. (1993). Sexual strategies theory – an evolutionary perspective on human mating. *Psychological Review* **100**, 204–232.

CHOI, M. H., YOO, Y. S. & CHUNG, B. C. (2001). Biochemical roles of testosterone and epitestosterone to 5 alpha-reductase as indicators of male-pattern baldness. *Journal of Investigative Dermatology* **116**, 57–61.

COLLINS, M. & ZEBROWITZ, L. (1995). The contributions of appearance to occupational outcomes on civilian and military settings. *Journal of Comparative Psychology* **25**, 129–163.

COOK, L. S., DALING, R., VOIGT, L. F., deHART, P., MALONE, K. E., STANFORD, J. L., WEISS, N. S., BRINTON, L. A., GAMMON, M. D. & BROGAN, D. (1997). Characteristics of women with and without breast augmentation. *Journal of the American Medical Association* **277**, 1612–1617.

CORBALLIS, M. C. (1991). *The Lopsided Ape: The Evolution of the Generative Mind*. Oxford University Press, New York.

COSMIDES, L., TOOBY, J. & BARKOW, J. H. (1992). Introduction: evolutionary psychology and conceptual integration. In *The Adapted Mind. Evolutionary Psychology and the Generation of Culture* (eds. J. Barkow, L. Cosmides and J. Tooby), pp. 3–15. Oxford University Press, New York, Oxford.

COWLEY, J. J., JOHNSON, A. L. & BROOKSBANK, B. W. L. (1977). The effect of two odorous compounds on performance in an assessment-of-people test. *Psychoneuroendocrinology* **2**, 159–172.

CROGAN, S. (1999). *Body Image. Understanding Body Dissatisfaction in Men, Women and Children*. Routledge, London.

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

CUNNINGHAM, M. R., ROBERTS, A. R., WU, C.-H., 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**, 261–279.

CURTIS, R. F., BALLANTINE, J. A., KEVERNE, E. B., BONSALL, R. W. & MICHAEL, R. P. (1971). Identification of primate sexual pheromones and the properties of synthetic attractants. *Nature* **232**, 396–398.

CUTTING, J. E. & PROFFITT, D. E. (1981). Gait perception as an example of how we may perceive events. In *Intersensory Perception and Sensory Integration* (eds. R. D. Walk and D. E. Proffitt), pp. 249–273. Plenum, New York.

DALY, M. & WILSON, M. (1988). *Homicide*. Aldine de Gruyter, Hawthorne.

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

DION, K. K., BERSCHEID, E. & WALSTER, E. (1972). What is beautiful is good. *Journal of Personality and Social Psychology* **24**, 285–322.

DUKE-COHAN, J. S., GU, J., McLAUGHLIN, D. F., XU, Y., FREEMAN, G. J. & SCHLOSSMAN, S. F. (1998). Attractin (DPPT-L), a member of the CUB family of cell adhesion and guidance proteins, is secreted by activated human T lymphocytes and modulates immune cell interactions. *Proceedings of the National Academy of Sciences USA* **95**, 11336–13341.

DUKE-COHAN, J. S., TANG, W. & SCHLOSSMAN, S. F. (2000). Attractin: a cub-family protease involved in T cell-monocyte/macrophage interactions. *Advances in Experimental Medicine and Biology* **477**, 173–185.

EATON, W. B., PIKE, M. S., SHORT, R. V., LEE, N. C., TRUSSELL, J., HATCHER, R. A., WOOD, J. W., WORTHMAN, C. M., BLURTON JONES, N. G., KONNER, M. J., HILL, K. R., BAILEY, R. & HURTADO, A. M. (1994). Women's reproductive cancers in evolutionary perspective. *Quarterly Review of Biology* **69**, 353–367.

EIBL-EIBESFELDT, I. (1997). *Die Biologie des menschliche Verhaltens*. Seehamer Verlag, Weyarn.

EKMAN, P. & FRIESEN, W. (1969). Nonverbal leakage and clues to deception. *Psychiatry* **32**, 88–106.

ELLIS, H. (1926). *Studies in the Psychology of Sex, Vol. IV*. F. A. Davis, Philadelphia.

ENQUIST, M. & ARAK, A. (1994). Symmetry, beauty and evolution. *Nature* **372**, 169–172.

ESCÓS, J. M., ALADOS, C. L. & EMLEN, J. M. (1995). Fractal structures and fractal functions as disease indicators. *Oikos* **74**, 310–314.

FARAH, M. J. (1990). *Visual Agnosia: Disorders of Object Recognition and What They Tell Us About Normal Vision*. MIT Press, Cambridge, MA.

FINK, B., GRAMMER, K. & THORNHILL, R. (2001). Human (*Homo sapiens*) facial attractiveness in relation to skin texture and color. *Journal of Comparative Psychology* **115**, 92–99.

FINK, B. & PENTON-VOAK, I. S. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science* **11**, 154–158.

FISCHER, O. (1911). Methodik der speziellen Bewegungslehre. In *Handbuch der physiologischen Methodik* (ed. R. Tigerstedt), pp. 120–316. Hirzel, Leipzig.

FISHER, R. A. (1930). *The Genetical Theory of Natural Selection*. Oxford University Press, London, Oxford.

FLACH, A. (1928). Die Psychologie der Ausdrucksbewegung. *Archiv für die gesamte Psychologie* **65**, 435–534.

FOLSTAD, I. & KARTER, A. J. (1992). Parasites, bright males and the immunocompetence handicap. *American Naturalist* **139**, 603–622.

FORGAS, J. P. & MOYLAN, S. J. (1991). Affective influences on stereotype judgements. *Cognition and Emotion* **5**, 379–395.

FRISCH, R. E. (1975). Critical weights, a critical body composition, menarche and the maintainance of menstrual cycles. In *Biosocial Interrelations in Population Adaption* (ed. E. S. Watts). Mouton, The Hague.

FURLOW, F. B., KIMBALL, R. T. & MARSHALL, M. C. (1998). Are rooster crows honest signals of fighting ability? *Auk* **115**, 763–766.

FURNHAM, A. & BAGUMA, P. (1994). Cross-cultural differences in the evaluation of male and female body shapes. *International Journal of Eating Disorders* **15**, 81–89.

GALTON, F. (1878). Composite portraits, made by combining those of many different persons in a single resultant figure. *Journal of the Anthropological Institute* **8**, 132–144.

GANGESTAD, S. W., BENNETT, K. L. & THORNHILL, R. (2001). A latent variable model of developmental instability in relation to men's sexual behaviour. *Proceedings of the Royal Society of London B* **268**, 1677–1684.

GANGESTAD, S. W. & BUSS, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology* **14**, 89–96.

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.

GANGESTAD, S. W., THORNHILL, R. & YEO, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology* **15**, 73–85.

GARNER, D. M., GARFINKEL, P. E., SCHWARZ, D. & THOMPSON, M. (1980). Cultural expectations of thinness in women. *Psychiatric Research Reports* **47**, 483–491.

GIGERENZER, G. & GOLDSTEIN, D. G. (1996). Reasoning the fast and frugal way: models of bounded rationality. *Psychological Review* **103**, 650–669.

GRAMMER, K. (1993). 5-a-Androst-16en-3a-on: a male pheromone? A brief report. *Ethology and Sociobiology* **14**, 201–208.

GRAMMER, K. (1995). *Signale der Liebe: Die Biologischen Gesetze der Partnerschaft*. Deutscher Taschenbuch Verlag, Munich.

GRAMMER, K. (1998). Sex and gender in advertisements: indoctrination and exploitation. In *Indoctrinability, ideology, and warfare:*

Evolutionary Perspectives (eds. I. Eibl-Eibesfeldt and F. Salter), pp. 219–240. Berghahn, New York, London.

GRAMMER, K. & ATZWANGER, K. (1994). Der Lolita-Komplex: sexuelle Attraktivität und Kindchenschema. In *Kommunikation und Humanontogenese* (ed. F. Naumann), pp. 77–99. Kleine Verlag, Bielefeld.

GRAMMER, K., FIEDER, M. & FILOVA, V. (1997). The communication paradox and possible solutions. In *New Aspects of Human Ethology* (eds. A. Schmitt, K. Atzwanger, K. Grammer and K. Schäfer), pp. 91–120. Plenum Press, New York.

GRAMMER, K., FINK, B., JUETTE, A., RONZAL, G. & THORNHILL, R. (2001). Female faces and bodies: n-dimensional feature space and attractiveness. In *Advances in Visual Cognition. Volume I: Facial Attractiveness* (eds. G. Rhodes and L. Zebrowitz), pp. 91–125. Ablex Publishing.

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.

GROLLEAU, J. L., LANFREY, E., LAVIGNE, B., CHAVOIN, J. P. & COSTAGLIOLA, M. (1999). Breast base anomalies: treatment strategy for tuberous breasts, minor deformities, and asymmetry. *Plastic and Reconstructive Surgery* **104**, 2040–2048.

HAKEN, H. (1996). *Principles of Brain Functioning*. Springer Verlag, Berlin.

HAMILTON, W. D. & ZUK, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.

HAMPSON, E. & KIMURA, D. (1988). Reciprocal effects of hormonal fluctuations on human motor and perceptual-spatial skills. *Behavioral Neurosciences* **102**, 456–459.

HARALICK, R. M., SHANMUGAM, K. & DINSTEIN, I. (1973). Textural features for image classification. *IEEE Transactions on Systems, Man, and Cybernetics*, SMC-3 **6**, 610–621.

HATFIELD, E. & SPRECHER, S. (1986). *Mirror, Mirror … : The Importance of Looks in Everyday Life*. State University of New York Press, Albany.

HENSS, R. (1987). Zur Beurteilerübereinstimmung bei der Einschätzung der physischen Attraktivität junger und alter Menschen. *Zeitschrift für Sozialpsychologie* **18**, 118–130.

HENSS, R. (1988). '… wer ist der/die Schönste im ganzen Land?' Zur Beurteilerübereinstimmung bei der Einschätzung der physischen Attraktivität. *Annales – Forschungsmagazin der Universität des Saarlandes* **1**, 54–58.

HENSS, R. (1992). '*Spieglein, Spieglein an der Wand*'. *Geschlecht, Alter und physische Attraktivität*. Psychologie Verlags Union, Weinheim.

HERTRICH, I. & ZIEGELMAYER, G. (1998). The voice as an anthropologic marker system, its constitutional correlates and characteristics. *Anthropologischer Anzeiger* **46**, 185–193.

HESS, E. H., SELTZER, A. L. & SHLIEN, J. M. (1965). Pupil response of hetero- and homosexual males to pictures of man and women. *Journal of Abnormal Psychology* **70**, 165–168.

HORVATH, T. (1979). Correlates of physical beauty in men and women. *Social Behavior and Personality* **7**, 145–151.

HORVATH, T. (1981). Physical attractiveness: the influence of selected torso-parameters. *Archives of Sexual Behavior* **10**, 21–24.

ILIFFE, A. H. (1960). A study of preferences in feminine beauty. *British Journal of Psychology* **51**, 267–273.

ISEN, A. (1984). Toward understanding the role of affect in cognition. In *Handbook of Social Cognition* (eds. R. Wyer and T. Strull), pp. 179–235. Erlbaum, Hillsdale, NY.

JOHANSSON, G. (1973). Visual perception of biological motion and a model of its analysis. *Perception and Psychophysics* **14**, 201–211.

JOHANSSON, G. (1976). Spatio-temporal differentiaion and integration in visual motion perception. *Psychological Research* **38**, 379–393.

JOHNSTON, V. S. & FRANKLIN, M. (1993). Is beauty in the eye of the beholder? *Ethology and Sociobiology* **14**, 183–199.

JOHNSTON, V. S., HAGEL, R., FRANKLIN, M., FINK, B. & GRAMMER, K. (2001). Male facial attractiveness: evidence for hormone mediated adaptive design. *Evolution and Human Behavior* **22**, 251–267.

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

JONES, B. C., LITTLE, A. C., PENTON-VOAK, I. S., TIDDEMAN, B. P., BURT, D. M. & PERRETT, D. I. (2001). Facial symmetry and judgments of apparent health: support for a 'good genes' explanation of the attractiveness–symmetry relationship. *Evolution and Human Behavior* **22**, 417–429.

JONES, D. (1996). *Physical Attractiveness and The Theory of Sexual Selection*. Museum of Anthropology, University of Michigan, Ann Arbor, MI.

KALKOFEN, H., MÜLLER, A. & STRACK, M. (1990). Kant's facial aesthetics and Galton's composite portraiture – are prototypes more beautiful? In *Proceedings of the 11th International Congress on Empirical Aesthetics* (ed. L. Halasz), pp. 151–154. International Association for Empirical Aesthetics, Budapest.

KEATING, C. F., MAZUR, A. & SEGALL, M. H. (1981). A cross cultural exploration of physiognomic traits of dominance and happiness. *Ethology and Sociobiology* **2**, 41–48.

KENRICK, D. T. & GUTIERRES, S. E. (1980). Contrast effects and judgements of physical attractiveness: when beauty becomes a social problem. *Journal of Personality and Social Psychology* **38**, 131–140.

KENRICK, D. T., GUTIERRES, S. E. & GOLDBERG, L. (1989). Influence of erotica on ratings of strangers and mates. *Journal of Experimental Social Psychology* **25**, 159–167.

LANGLOIS, J. H. & ROGGMAN, L. A. (1990). Attractive faces are only average. *Psychological Science* **1**, 115–121.

LANGLOIS, J. H., ROGGMAN, L. A. & REISER-DANNER, L. A. (1990). Infant's differential social responses to attractive and unattractive faces. *Developmental Psychology* **26**, 153–159.

LITTLE, A. C., BURT, D. M., PENTON-VOAK, I. S. & PERRETT, D. I. (2001). Self-perceived attractiveness influences human preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London B* **268**, 39–44.

LOW, B. (1979). Sexual selection and human ornamentation. In *Evolutionary Biology and Human Social Behavior* (eds. N. A. Cagnon and W. Irons). Duxbury Press, Boston.

LUDWIG, W. (1932). *Das Rechts-Links Problem im Tierreich und beim Menschen*. Springer-Verlag, Berlin.

LUSCHER, M. & KARLSON, P. (1959). 'Pheromones': a new term for a class of biologically active substances. *Nature* **183**, 55–56.

MACKINTOSH, J. A. (2001). The antimicrobial properties of melanocytes, melanosomes and melanin and the evolution of black skin. *Journal of Theoretical Biology* **211**, 101–113.

MANNING, J. T. (1995). Fluctuating asymmetry and body weight in men and women: implications for sexual selection. *Ethology and Sociobiology* **16**, 145–153.

MAZUR, A. & BOOTH, A. (1998). Testosterone and dominance in men. *Behavioral and Brain Sciences* **21**, 353–363.

MAZUR, A., MAZUR, J. & KEATING, C. F. (1984). Military rank attainment of a West-Point class effects of cadet's physical features. *American Journal of Sociology* **90**, 125–150.

MICHAEL, R. P., BONSALL, R. W. & KUTNER, M. (1975). Volatile fatty acids, 'Copulins', in human vaginal secretions. *Psychoneuroendocrinology* **1**, 153–163.

MICHAEL, R. P., BONSALL, R. W. & WARNER, P. (1974). Human vaginal secretions: volatile fatty acid content. *Science* **186**, 1217–1219.

MICHAEL, R. P. & KEVERNE, E. B. (1968). Pheromones in the communication of sexual status in primates. *Nature* **218**, 746–749.

MILINSKI, M. & WEDEKIND, C. (2001). Evidence for MHC-correlated perfume preferences in humans. *Behavioral Ecology* **12**, 140–149.

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

MØLLER, A. P. (1996a). 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. (1996b). Effects of host sexual selection on the population biology of parasites. *Oikos* **75**, 340–344.

MØLLER, A. P. (1997). Developmental selection against developmentally unstable offspring and sexual selection. *Journal of Theoretical Biology* **185**, 415–422.

MØLLER, A. P. (1998). Developmental instability as a general measure of stress. *Advances in the Study of Behavior* **27**, 181–213.

MØLLER, A. P. & ALATALO, R. V. (1999). Good genes effects in sexual selection. *Proceedings of the Royal Society of London B* **266**, 85–91.

MØLLER, A. P., CHRISTE, P. & LUX, E. (1999a). Parasite-mediated sexual selection: effects of parasites and host immune function. *Quarterly Review of Biology* **74**, 3–20.

MØLLER, A. P. & CUERVO, J. J. (in press). Asymmetry, size and sexual selection: meta-analysis, publication bias and factors affecting variation in relationships. In *Developmental instability* (ed. M. Polak). Oxford University Press, New York.

MØLLER, A. P. & JENNIONS, M. D. (2001). How important are direct fitness benefits of sexual selection? *Naturwissenschaften* **88**, 401–415.

MØLLER, A. P. & POMIANKOWSKI, A. (1993). Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology* **32**, 167–176.

MØLLER, A. P., SANOTRA, G. S. & VESTERGAARD, K. S. (1999b). Developmental instability and light regime in chickens (*Gallus gallus*). *Applied Animal Behavioral Sciences* **62**, 57–71.

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 University Press, Oxford, London.

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

MOSCOVITCH, M., WINOCUR, G. & BEHRMANN, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience* **9**, 555–604.

MUELLER, U. & MAZUR, A. (1997). Facial dominance in *Homo sapiens* as honest signaling of male quality. *Behavioral Ecology* **8**, 569–579.

MÜLLER, A. (1993). Visuelle Prototypen und die physikalischen Dimensionen von Attraktivität. In *Physische Attraktivität* (eds. R. Niketta and M. Hassebrauck). Hogrefe, Göttingen.

MUSCARELLA, F. & CUNNINGHAM, M. R. (1996). The evolutionary significance and social perception of male pattern baldness and facial hair. *Ethology and Sociobiology* **17**, 99–117.

Muzaffar, A. R. & Rohrich, R. J. (2002). The silicone gel-filled breast implant controversy: an update. *Plastic and Reconstructive Surgery* **109**, 742–747.

Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K. & Minamisawa, R. (1999). Female preference for male faces changes cyclically. *Nature* **399**, 741–742.

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

Perrett, D. I., May, K. A. & Yoshikawa, S. (1994). Facial shape and judgement of female attractiveness. *Nature* **386**, 239–242.

Preti, G. & Huggins, G. R. (1975). Cyclical changes in volatile acidic metabolites of human vaginal secretions and their relation to ovulation. *Journal of Chemical Ecology* **1**, 361–376.

Rensch, B. (1963). Versuche über menschliche Auslösermerkmale beider Geschlechter. *Zeitschrift für Morphologische Anthropologie* **53**, 139–164.

Rhodes, G., Brennan, S. & Carey, S. (1987). Identification and ratings of caricatures: implications for mental representation of faces. *Cognitive Psychology* **1**, 473–497.

Rich, M. K. & Cash, T. F. (1993). The American image of beauty – media representations of hair color for 4 decades. *Sex Roles* **29**, 113–124.

Rikowski, A. & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society London B* **266**, 869–874.

Ronzal, G. I. (1996). *Physische Charakteristika weiblicher Schönheit.* MA Natural Sciences, University of Vienna, Austria.

Rosch, E. H. (1978). Principles of categorization. In *Cognition and Categorization* (eds. E. Rosch & B. B. Lloyd), pp. 27–47. Erlbaum, Hillsdale.

Ruff, C. B. & Jones, H. H. (1981). Bilateral asymmetry in cortical bone of the humerus and tibia-sex and age factors. *Human Biology* **53**, 69–86.

Runeson, S. & Frykholm, G. (1983). Kinematic specification of dynamics as an informational basis for person-and-action perception: expectation, gender recognition, and deceptive intention. *Journal of Experimental Psychology* **112**, 585–615.

Saino, N., Galeotti, P., Sacchi, R. & Møller, A. P. (1997). Song and immunological condition in male barn swallows (*Hirundo rustica*). *Behavioral Ecology* **8**, 364–371.

Sacchi, R., Saino, N. & Galeotti, P. (2002). Features of begging calls reveal general condition and need of food of barn swallow (*Hirundo rustica*) nestlings. *Behavioral Ecology* **13**, 268–273.

Salusso-Deonier, C. J., Markee, N. L. & Pedersen, E. L. (1991). Developing realistic stimuli for assessing observers' perceptions of male and female body types. *Perceptual and Motor Skills* **72**, 603–610.

Santin, E. (1995). *Impression-Management: Die Wirkung von Kleidung.* MA Psychology/Dept. Psychology/Faculty of Philosophical Sciences/University of Vienna.

Schaal, B. & Porter, R. H. (1991). 'Microsmatic humans' revisited: the generation and perception of chemical signals. *Advances in the Study of Behavior* **20**, 474–482.

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

Schiavone, F. E., Rietschel, R. L., Sgoutas, D. & Harris, R. (1983). Elevated free testosterone levels in women with acne. *Archives of Dermatology* **119**, 799–802.

Schleidt, W. M. & Crawley, J. N. (1980). Patterns in the behaviour of organisms. *Journal of Social Biological Structures* **3**, 1–15.

Service, R. (1998). New role of estrogen in cancer. *Science* **279**, 1631–1632.

Shipley, R. H., O'Donnell, J. M. & Bader, K. F. (1977). Personality characteristics of women seeking breast augmentation. Comparison to small-busted and average-busted controls. *Plastic and Reconstructive Surgery* **60**, 369–376.

Simis, K. J., Verhulst, F. C. & Koot, H. M. (2001). Body image, psychosocial functioning, and personality: how different are adolescents and young adults applying for plastic surgery? *Journal of Child Psychology and Psychiatry* **42**, 669–678.

Singh, D. (1993). Adaptive significance of female physical attractiveness: role of waist-to-hip ratio. *Journal of Personality and Social Psychology* **59**, 1191–1201.

Singh, D. (1995). Female health, attractiveness and desirability for relationships: role of breast asymmetry and waist-to-hip ratio. *Ethology and Sociobiology* **16**, 465–481.

Singh, D. & Bronstad, P. M. (2001). Female body odour is a potential cue to ovulation. *Proceedings of the Royal Society of London B* **268**, 797–801.

Singh, D. & Zambarano, R. J. (1997). Offspring sex ratio in women with android body fat distribution. *Human Biology* **69**, 545–556.

Slater, A. M., Von der Schulenburg, Ch., Brown, E., Badenoch, M., Butterworth, G., Parsons, S. & Samuals, C. (1998). Newborn infants prefer attractive faces. *Infant Behavior & Development* **21**, 345–354.

Soulé, M. & Cuzin-Roudy, J. (1982). Allometric variation: 2. Developmental instability of extreme phenotypes. *American Naturalist* **120**, 765–786.

Steinberger, E., Rodriguez-Rigau, L. J., Smith, K. D. & Held, B. (1981). The menstrual cycle and plasma testosterone level in women with acne. *Journal of the American Academy of Dermatology* **4**, 54–58.

Stoddart, D. M. (1990). *The Scented Ape: The Biology and Culture of Human Odor.* Cambridge University Press, Cambridge, UK.

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

Symons, D. (1995). Beauty is in the adaptations of the beholder: the evolutionary psychology of human female sexual attractiveness. In *Sexual Nature/Sexual Culture* (eds. P. R. Abramson and S. D. Pinker), pp. 80–118. University of Chicago Press, Chicago.

Thelen, T. H. (1983). Minority type human mate preference. *Social Biology* **30**, 162–180.

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

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

Thornhill, R. & Gangestad, S. W. (1996). The evolution of human sexuality. *Trends in Ecology and Evolution* **11**, 98–102.

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

Thornhill, R. & Grammer, K. (1999). The body and face of woman: one ornament that signals quality? *Evolution and Human Behavior* **20**, 105–120.

Thornhill, R. & Møller, A. P. (1997). Developmental stability, disease and medicine. *Biological Reviews* **72**, 497–548.

Tovee, M. J., Brown, J. E. & Jacobs, D. (2001). Maternal waist-to-hip ratio does not predict child gender. *Proceedings of the Royal Society of London B* **268**, 1007–1010.

Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual Selection and the Descent of Man* (ed. B. Campbell), pp. 136–179. Heinemann, London.

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

VAN VALEN, L. (1973). A new evolutionary law. *Evolutionary Theory* **1**, 1–30.

WALTMAN, R., TRICOM, V., WILSON, G. E. JR., LEWIN, A. H., GOLDBERG, N. L. & CHANG, M. M. Y. (1973). Volatile fatty acids in vaginal secretions: human pheromones? *The Lancet* **2**, 496.

WEDEKIND, C., SEEBECK, T., BETTENS, F. & PAEPKE, A. J. (1995). MHC-dependent mate preferences in humans. *Proceedings of the Royal Society of London B* **260**, 245–249.

WEISFELD, G. E., BLOCH, S. A. & IVERS, J. W. (1984). Possible determinants of social dominance among adolescent girls. *The Journal of Genetic Psychology* **144**, 115–129.

WESTERMARCK, E. (1921). *The History of Human Marriage*. Macmillan, London.

WINKLER, E. M. & KIRCHENGAST, S. (1994). Body dimensions and differential fertility in !Kung San males from Namibia. *American Journal of Human Biology* **6**, 203–213.

WOLF, N. (1992). *The Beauty Myth: How Images of Beauty Are Used Against Women*. Anchor.

YU, D. W. & SHEPARD, G. H. JR. (1998). Is beauty in the eye of the beholder? *Nature* **396**, 321–322.

ZAHAVI, A. (1975). Mate selection – a selection for a handicap. *Journal of Theoretical Biology* **53**, 205–214.

ZAHAVI, A. & ZAHAVI, A. (1997). *The Handicap Principle*. Oxford University Press, Oxford, London.

ZEBROWITZ, L. & APATOW, K. (1984). Impression of baby-faced adults. *Social Cognition* **2**, 315–342.

ZUCKERMAN, M. & DRIVER, R. E. (1989). What sounds beautiful is good: the vocal attractiveness stereotype. *Journal of Nonverbal Behavior* **13**, 67–82.