Sexual selection and the biology of beauty

Karl Grammer (Bernhard Fink, Anders P. Møller, Randy Thornhill)

Resumé:

Ze současných teoretických a empirických poznatků vyplývá, že partnerské preference jsou podněcovány především vizuálními, vokálními a chemickými podněty, které signalizují stav zdraví, včetně zdraví vývojového. Krásné a neodolatelné znaky se v souvislosti se sexuální selekcí vyvinuly nesčetněkrát jak u rostlin tak u živočichů. Takové standardy pro preference a krásu poskytují důkazy pro tvrzení, že lidská krása a posedlost tělesným krásnem se odrážejí v analogických znacích v celých říších rostlin a živočichů. Standardy lidské krásy odrážejí evoluční minulost i současnost a zdůrazňují roli stanovení stavu zdraví ve volbě partnera tak jak je odrážen analýzou přitažlivosti visuálních charakteristik tváře a těla, ale také vokálními a pachovými signály. Ačkoliv standardy lidské krásy mohou být různé u různých kultur, a také se mohou měnit v čase, naše analýza ukazuje, že příslušné selekční tlaky, které standardy utvářejí, jsou stejné. Vedle toho prokazujeme, že nikoliv obsah standardů, které jsou prokazatelně konvergentní, ale pravidla, nebo konstrukce ideálů krásy, jsou universální napříč kulturami. Tato zjištění mají dopad do lékařských, biologických i sociálních věd.

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 386 Karl Grammer and others 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.

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).

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 maleinitiated 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.

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 metatheoretical 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 shortterm 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.

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., 1999a). There is considerable evidence for secondary sexual characters in a wide variety of organisms reliably re-flecting levels of parasite infections (Møller et al., 1999a). 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, 1996b). 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., 1999a). 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., 1999a).

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 Darwinian aesthetics 389 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).

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 392 Karl Grammer and others (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, Muller & 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.

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, Tove`e 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.

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 dificult for a pre-historic human to escape from a lion, but it was even more dificult to escape with two legs of unequal length. Indeed, skeletal remains from prehistoric 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, 1996a). 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.

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 in-fluence 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 mateselection 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 nonovariectomized 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 re- flecting 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 (1999b) showed that symmetric chickens show more coordinated and more effiient 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 (Esco's, 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.

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 certi- fication 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 xC 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 ndimensional 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.

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.

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