An ethological theory of attractiveness*

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Abstract

In this chapter we explore the extent to which learning and memory mechanisms can explain variation in facial attractiveness. We suggest that two general mechanisms are in operation, and work together in determining attractiveness. Both can be understood in terms of general principles of learning, memory and generalization. One mechanism is related to the problem of many different stimuli requiring the same response. For instance, faces of babies are all different but all should be recognized as babies. The way the nervous system solves this problem leads to preference for average faces. The second mechanism favors extremes. For example, the discrimination task of telling female and male faces apart may result in extreme male or female faces appearing more attractive (i.e. supernormality, peak-shift, overgeneralization or receiver bias). Adding more aspects to the face discrimination task (e.g. telling individuals of different age apart) may account for the full range of variations in attractiveness. We also introduce an ontogenetic model inspired by ethological theories of imprinting. This model can potentially explain why cultural innovations such as spectacles, clothing and haircuts influence attractiveness. Our conclusion is that we do not need to invoke evolutionary theories linking genetic quality with appearance to explain observed patterns of attractiveness.

1 Introduction

Faces play a very important role in human social life. With our faces we can communicate emotions, species identity and individual identity, sex and age. The ability to read and remember faces is also highly developed. One intriguing fact is that we experience considerable variation in facial attractiveness, and this influences our behavior. We seek sexual partners who are attractive, we are more likely to vote for an attractive politician and beautiful faces make an advertisement more persuasive (Zebrowitz, 1997; Chaiken, 1979; Efran, & Patterson, 1974), to take just a few examples. It is important here to point out that judgements of attractiveness emerge within the person that observes the face stimuli (the "receiver"). Unlike physical features such as shape or size, attractiveness is not a property of the face itself. An extraterrestrial being would not be able to tell what faces we find attractive without knowledge of our nervous systems. On the other hand, the same being could easily measure physical features of faces.

Attempts have been made to explain the variability in perceived attractiveness using evolutionary biology, arguing that reproducing with a more attractive partner will increase an individual's biological fitness (see e.g. Andersson, 1994; Bradbury & Verhencamp 1998 for theory and empirical data in favor or against such views). Choosing, for instance, the right species is crucial for successful reproduction, so that reliable mechanisms of species recognition are favored by evolution. Sex and sexual maturity are also important. Assessment of these characteristics in a potential mate is not necessarily a trivial task, and mistakes occur (Gray, 1958). However, current thinking suggests that mate choice is about finer details of partner quality, making the problems

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of species, sex and age recognition appear simpler than they are. According to this view the genetic and sometimes the phenotypic quality of the partner is assessed during mate choice (Trivers, 1972; Andersson, 1994). The advantage of choosing a mate with high genetic quality is that the offspring inherit these high quality genes. If such a mate-quality hypothesis is correct, we expect a correlation between attractiveness of a face and the person's genetic or phenotypic quality. So far studies of facial attractiveness have not revealed such a relationship (Kalick, Zebrowitz, Langlois, & Johnson, 1998; Shackelford, & Larsen, 1999).

In this paper we present an alternative hypothesis combining theories of signal evolution that emphasizes coevolution between signals and receiver mechanisms (Dawkins & Krebs 1978; Enquist, & Arak, 1993, 1998; Arak, & Enquist, 1995, Jones, & Hill, 1993), ethological theories of sexual imprinting (see e.g. Shettleworth, 1998) and theories of stimulus control (Mackintosh, 1974; Pearce, 1994). The hypothesis recognizes that some basic communication is needed and mechanisms have evolved enabling recognition of, for instance, species, sex and age. On the other hand, the hypothesis does not assume the existence of cues enabling assessment of finer details of mate quality. Variation in attractiveness emerges in our model partly as a byproduct of how recognition mechanisms work. We refer to such byproducts as receiver biases. We will show that this is a viable alternative that can explain a wider range of phenomena than can theories based on communication of mate quality.

The paper is organized according to three levels of causation, following ethological thinking (Tinbergen 1963). At the first level, we consider attractiveness as the response of a behavior mechanism to stimulation from faces. Thus, variation in attractiveness can be investigated using models of stimulus control, which summarize our knowledge about how stimuli are coded into memory and how variation in stimulation influences behavior (Mackintosh 1974, Pearce 1997). We shall see that simple principles of stimulus control can explain many major findings about human facial attractiveness. To understand diversity and uniformity of preferences among people we need to consider the other levels of causation. As the second level we consider developmental mechanisms — how judgments of attractiveness develop during an individual's lifetime. Finally, as the third level, we investigate cultural and genetic evolution of preferences, focusing on the interplay between behavioral mechanisms, development and evolutionary mechanisms.

2 Discrimination and generalization

Communication requires evolution of signals as well as identification and discrimination abilities. Although we do not know the evolutionary history in detail it is fair to assume that many characteristics of faces have evolved for communication. There have been many suggestions of messages that faces might communicate. However, an important aspect of our model is that even if we consider just one or two messages, such as sex and age, several phenomena arise. To see this we must consider how signals are recognized. A signal (in the present context, a face) is first received by a sense organ and then processed by the nervous system, eventually producing a behavioral response. This process has been extensively studied at the behavioral level both in animals and humans and some very general rules have been described (Mackintosh, 1974; Baerends, 1982; Pearce, 1994; Shanks, 1995). Judgements of attractiveness are behavioral responses (choice or ratings by subjects) and may thus follow general rules of stimulus control. Note also that many issues lurk behind the meaning of "attractive", and the reader should be aware that there is no unambiguous definition of attractiveness. Studies of attractiveness have considered sexual and other partner preferences, as well as pure aesthetic judgements and ratings of femininity and/or masculinity. In this paper we will mainly consider sexual preferences.

A basic principle of stimulus control is that if an organism reacts to a particular stimulus it will also react to stimuli that are similar. This phenomenon is called generalization. It allows organisms to respond consistently to stimuli although they are perceived differently (object or perceptual constancy, see e.g. Walsh, & Kulikowski, 1998). It also allows organisms in novel situations to try out those responses that functioned well in similar situations. However, the rules for generalization are largely independent of context, stemming from basic properties of the nervous systems (Enquist, & Arak, 1998). Because of this, and because old responses are not always appropriate in a new situation, generalization is not perfectly tuned to each situation (Enquist,

Arak, Ghirlanda, & Wachtmeister, in preparation.). Below we show how generalization and discrimination processes can explain general empirical results from studies of face perception.

2.1 Extreme Faces

An important determinant of generalization is the need for discrimination between stimuli. This can shift our preferences towards more exaggerated appearances. There is ample evidence that many animals prefer modifications of familiar stimuli that are outside the natural range of variation (Tinbergen, 1951; Baerends, 1982). These effects can be understood from the results of simple generalization experiments (Mackintosh, 1974). The first step is to train an animal to discriminate between two stimuli along a particular dimension (e.g. frequency of sound). In the second step the generalization gradient is determined by testing the animal's response towards a number of stimuli along the same dimension. This gradient will often show a response bias (Figure 1) resulting from the interaction between the memories of the positive and negative stimuli (we refer to such phenomena as memory interactions). Such bias in responding is known as peak shift or supernormal stimulation and has been shown in humans and animals (Baron, 1973; Mackintosh, 1974; Baerends, 1982).

Several studies have shown that perception of faces is biased in this way — the impact a face has can often be magnified by exaggerating those components that make that face unique among other faces. The studies on recognition of individual faces firmly establish the existence of such biases (Rhodes, Brennan, & Carey, 1987; Rhodes, 1996). Caricatures of faces exploit this principle (Rhodes 1996). Sexual preferences, judgements of beauty, femininity or masculinity seem also biased. Rensch (1963) showed that Europeans' preferences for faces do not match the actual appearance of Europeans. Discrimination between faces may be one factor behind such biases, by favoring characteristics in both sexes that make them more different from each other. In Figure 2 such an effect is demonstrated along the male-female dimension.

Several studies show that femininity is beneficial to female attractiveness (Keating, 1985; Gillen, 1981; Perrett, Lee, Ian, Rowland, Yoshikawa, Burt, Henzi, Castles, & Amakatsu, 1998; Rhodes, Hickford, & Jeffrey, 2000). Data about the effect of masculinity on male attractiveness are less clear. Gillen (1981) reported that attractive males are rated high in masculinity. However, Perrett et al. (1998) and Rhodes et al. (in press) found that a masculinised male face, obtained by moving away the average male face from the average female face, is not preferred to the average male face. Biased responding has also been shown for reactions to infants (i.e. stimuli for parental care in humans). It was noted by Lorenz (1950) that big eyes, rounded head, big forehead and small nose contributed to elicit parental care (for more precise studies see Sternglanz, Gray, & Murakami, 1977; Maier, Holmes, Slaymaker, & Reich, 1984; Gardner, & Wallach, 1965; Zebrowitz, 1997). Some of these findings are consistent with a peak shift in responding resulting from the need of discriminating infants from adults. In reality, recognition of sexual partners is not based on sex only. For instance, age is also important: children and old individuals should not be preferred. The many discriminations involved in partner choice result in a more intricate organization of the memory than explored here, whose effect on preferences remains to be fully understood.

We conclude this section with a technical note concerning the difficulty of predicting reactions to

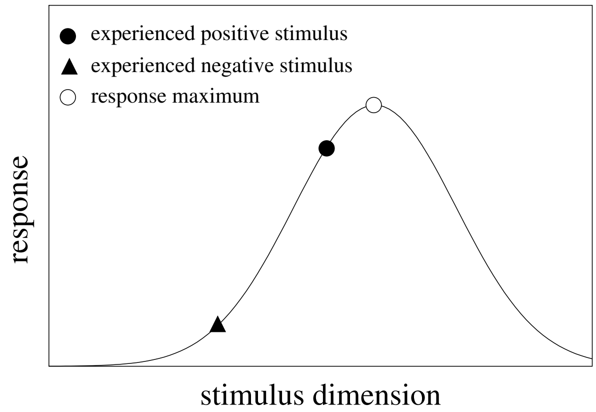

Figure 1: The generalization gradient shows how response strength typically is generalized along a stimulus dimension (e.g. sound frequency) after experiences of two similar stimuli when it is advantageous to react to one of them but not to the other (see e.g. Mackintosh 1974). Observe that the strongest response is not elicited by the positive stimulus. Instead, the response peak is shifted towards the right due to the interaction between the memory of the positive stimuli and the memory of the negative stimulus.

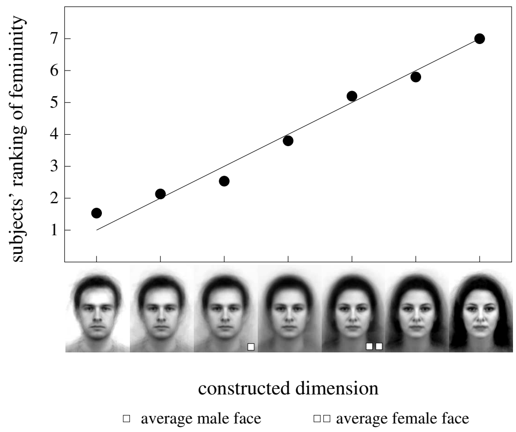

Figure 2: Subjects (17 biology students) were asked to rank 7 faces with respect to femininity. The figure shows average rank for each face (SE varied between 0.0 and 0.2). The pictures were constructed using two composites, one of male faces and one of female faces. Defining the value of each pixel in the figure as a dimension in a space, the positions of the two composites can be located in this space as two points. We construct a new dimension in this space by defining a line that travels through these two points. Five additional faces were picked along this line. One located exactly between the two composites and two located on each side of the composites. The aim is to demonstrate a response bias caused by the interaction between memories of female and male faces: exaggerated faces are rated as more feminine or masculine than average faces. The averages faces used are from the "Averaged Karolinska directed emotional faces" (Lundqvist, & Litton, in preparation).

complex stimuli such as faces. In the simple, one-dimensional case in Figure 1 it was clear that stronger responses should be searched on the right of the positive stimulus. This was in fact the only way of departing from the negative stimulus. In multi-dimensional spaces, such as the various spaces used to represent faces, it is far from trivial to predict in which direction to expect the stronger preferences. If we consider a case with just one positive and one negative stimulus, theories of generalisation (see e.g. Spence, 1937; Ghirlanda, & Enquist, 1999) predict that the strongest preferences lie somewhere on the line joining the positive and negative stimuli. At the simplest level, this result can be applied to pixel patterns representing faces (as in Figure 2). Other techniques such as caricature generation by morphing (Brennan, 1985; Benson, & Perrett, 1991; Rhodes, 1996) can be understood as applications of this result to various abstract spaces. If we have more than one negative stimulus and possibly more than one positive stimulus, we know of no simple method to predict the preference gradient, with one exception. If experiences fall into two well-defined clusters (e.g. male and female faces) we may use the two centers (averages) as a single positive and negative stimuli and study how preferences vary along the line that goes through the two averages (cf. Figure 2). However, if we want to add additional factors to the discrimination this technique does not work because the gradient can no longer be satisfactorily described along a line. For instance, if we want to consider partner preferences based on both sex and age we need to include old and young faces as negative stimuli as well as faces of the same sex. It should be possible, though, to use artificial neural networks to make predictions (Enquist, & Arak, 1998; Ghirlanda, & Enquist, 1998). Such a network would need to be trained not only to recognize individuals but also sex and age.

2.2 Average Faces

In attempts to link appearances of faces with personality traits, Francis Galton developed in 1878 the technique of multi-exposure photography allowing him to blend several faces together. This had a surprising effect: the composite faces turned out to be more attractive than the individual ones used to produce composite (Galton, 1878, 1883). Galton also mentioned that A. L. Austin from Invercargill, New Zealand, had reported the same result using stereoscopic viewing of pairs of faces (Rhodes, 1996). This result has now been confirmed in several studies (Langlois, & Roggman, 1990; Langlois, Roggman, & Musselman, 1994; Rhodes, & Tremewan, 1996; Rhodes, Sumich, & Byatt, 1999).

A preference for the average of many stimuli can be predicted from stimulus control theory (Enquist & Arak, 1994, 1998; Johnstone, 1994; Enquist, & Johnstone, 1997; Swaddle, & Cuthill, 1994; Ghirlanda, & Enquist, 1999). What we have to consider is how subjects generalise among many similar stimuli requiring the same response. For instance, after training pigeons to react in the same way to light of two different wavelengths the resulting generalization gradient is bell shaped with a maximum at the average wavelength (see Figure 3). This finding is relevant to questions about symmetry as well,

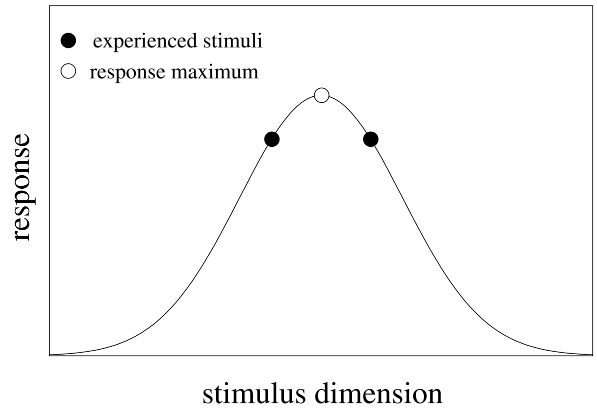

Figure 3: Experience of two similar stimuli requiring the same response can also create a peak shift. In contrast with Figure 1, the response maximum is now located between the two experienced stimuli.

since average stimuli are typically more symmetrical than the stimuli which enter the average (Enquist, & Johnstone, 1997; Enquist, & Arak, 1998; Ghirlanda, & Enquist, 1999). Applied to faces this means that one may tend to prefer the average of those faces requiring similar responses, e.g. adult male faces. One useful interpretation of the *x*-axis in Figure 3 is that it measures some difference between the left and right halves of the face. If there is no difference the face is symmetrical with respect to this measure. Note that our model assumes memory interaction even after extensive experience (Enquist & Arak 1998). Such an interaction is the hallmark many popular memory models such as prototype and exemplar theory (Shanks 1995).

2.3 Averages and extremes combined

The reader may have noted that from the two types of memory interaction described above a contradiction may arise. An extreme face is not an average face, and vice-versa. It is possible to reconcile these two factors and to show that in reality they both affect responding. In Figure 4 we have combined the gradients from Figure 1 and Figure 3 and obtained a gradient that is a function of two dimensions. The first dimension is the male-female dimension. The second dimension is some other dimension along which faces vary. The height of the gradient is the judgement of sexual attractiveness of male and female faces by receivers of one sex. Along the male-female dimension the gradient shows a peak shift in the direction of extreme traits. Along the second dimension a preference for the average is present.

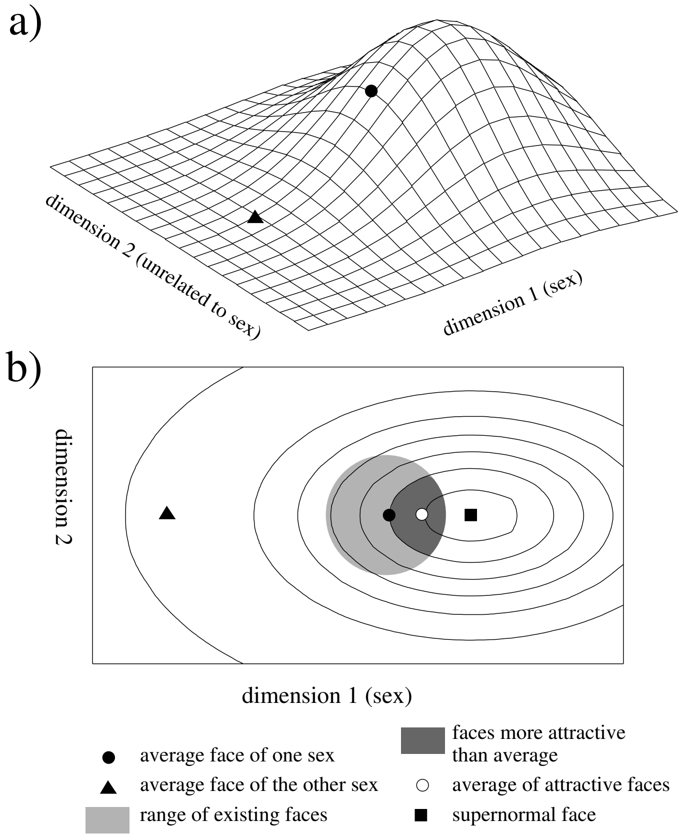

Figure 4: A simplified model of judgement of the sexual attractiveness of faces judged by one sex. The model combines the need for discriminating between sexes (see Figure 1) and responding similarly to variation within a sex (see Figure 3). It can be applied to either male or female preferences. Dimension 1 is the male-female dimension (see Figure 2) and dimension 2 is a trait that varies independently of sex. Part a) shows the gradient in a three dimensional plot with the height of the surface describing the strength of the response to the face (attractiveness). Part b) shows contours of equal attractiveness of the gradient in a). In the right half the existing variation in faces for one sex is indicated. The average face is more attractive than most faces but even more attractive faces exist. These faces are located near the average but further away from faces of the opposite sex. Supernormal (exceptionally attractive) faces may occur outside the range of existing faces.

Note that Figure 4 is idealized. In reality, faces vary along many more dimensions, and indeed we do not know how the brain represents faces. The two-dimensional model, however, allows us to make some detailed predictions (see Figure 4b). First, a minority of faces will be more attractive than the av-

erage face. This has been shown by Alley & Cunningham (1991). Another prediction is that an average of attractive faces of one sex will be more attractive than the average of all faces of the same sex. This has been empirically demonstrated by Perrett, May, and Yoshikawa (1994) for female faces. The model also predicts that making a face more extreme in the male-female dimension does often make the face more attractive, but not always. It can be seen in gradient in Figure 4 that attractiveness eventually decreases when faces become very extreme.

Figure 5: An example of a symmetrical but unattractive face

2.4 Symmetry

Symmetry has often been considered an important aspect of beauty in general as well as for faces (Gombrich, 1984; Zebrowitz, 1997). Before we deal with preferences for symmetry let us consider why faces are bilaterally symmetrical (viewed from the front). Symmetries can usually be traced back to fundamental physical phenomena such as gravitation and the three dimensions of space (Stewart, & Golubitsky, 1992). For land-living animals balance with respect to gravitation is necessary, and this will favor symmetry in form. As a further example, if one wants to minimize the surface to volume ratio in a three-dimensional world a sphere (possessing complete rotational symmetry) is the solution. In addition, in many organisms the developmental process is based on a bilateral development plan established very early in embryonic life. Communication as well may favor symmetries. For instance, a signal may gain by looking the same from different directions, meaning that it must have the corresponding symmetries (Enquist, & Arak, 1993). The latter may be less important for faces since we usually interact face to face.

An important point is that average faces are typically more symmetrical than individual ones. Even if a high degree of symmetry is present in all individual faces (and possibly maintained by selection), we see some random deviations (fluctuating asymmetry) possibly due to stress during development (Ludwig, 1932; van Valen, 1962; Parsons, 1990; Møller, & Swaddle, 1997). What is important here is that such fluctuations are random in size and direction. By combining many faces these random asymmetries cancel out each other and the composite face is more symmetrical. Thus, a preference for an average, thereby symmetrical face does not reveal a general preference for symmetry. A fair question is whether symmetry per se is an aspect of facial attractiveness independent of preference for the average. If we make a face more symmetrical will it be more attractive? Our simple model does not predict this. It seems also intuitively clear that faces can be symmetrical but at the same time unattractive (see Figure 5 for an example).

At the heart of the problem lies the fact that a face can be made symmetrical in an infinite number of ways whereas "averaging" is a unique operation. If symmetry is not an independent component of attractiveness it can be conceived that a particular symmetrization will enhance the sexual attractiveness of a face only insofar as it brings the face closer to the average or away from other faces of the subject's own sex. To understand the predictions of our model with respect to symmetry, note first that all faces that lie on the line joining the averages of the two sexes are perfectly symmetrical. Any modification that brings a face closer to this line increases its symmetry but not necessarily its attractiveness (see Figure 6). However, the most attractive faces lie close to the line and are thus highly symmetrical. We arrive at this result without any assumptions about symmetry. Instead the result arises from combining stimulus-control theory with the fact that faces are on average symmetrical.

Empirically, symmetrical faces have been produced chiefly with two different techniques. One consists of mirror imaging one half of the face along the central vertical axis of the face. Using the left and right halves, two symmetrical faces can thus be

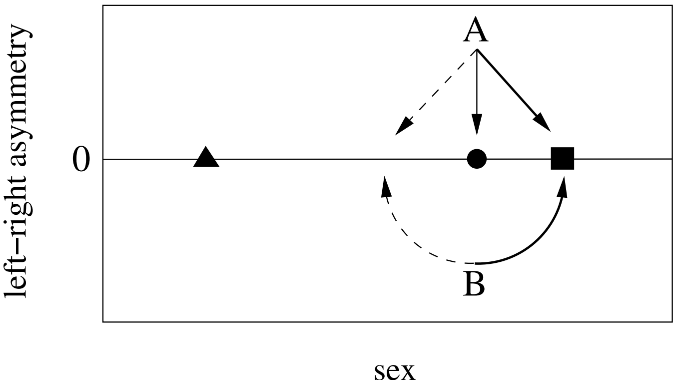

Figure 6: Examples of face modifications that increase symmetry but have different effects on sexual attractiveness (recall the model outlined in Figure 4). The first dimension is sex and the second dimension is some measure of the difference between the left and the right halves of a face. Zero difference means that the face is bilaterally symmetric with respect to this measure. The averages of the two sexes are indicated with ▲ and • (■ is the peak of the gradient in Figure 4). Faces A and B are somewhat asymmetric faces. For face A three modifications are indicated that all give rise to more symmetrical faces, but with different effects on sexual attractiveness according to the model in Figure 4. Dashed lines indicate a decrease in attractiveness whereas continuous lines indicate an increase in attractiveness (the thicker, the bigger the increase). For face B two modifications are shown that both increase symmetry while keeping constant the distance from the same-sex average.

constructed (so called "chimeras"). The second technique yields a single symmetrical face by averaging the two (already symmetrical) faces obtained with the first method. The same face can also be obtained by first averaging the original face and its mirror image. The first technique produces faces that in comparison with the original are not closer (on average) to the average face. In contrast, the face obtained with the second technique is closer to the average face. Thus, we predict that the second technique but not the first should produce more attractive faces. Indeed, experiments indicate that symmetrical faces obtained with the first technique are not on average rated more attractive (Kowner, 1996; Langlois, Roggman, & Musselman, 1994; Samuels, Butterworth, Rogerts, Graupner, & Hole, 1994), while faces obtained with the second technique are perceived as more beautiful than the original faces (Langlois, Roggman, & Musselman, 1994; Rhodes, Proffitt, Grady, & Sumich, 1998; Rhodes, Roberts, & Simmons, in press; but see also Swaddle and Cuthill, 1995).

The impact of facial symmetry per se on attractiveness can also be studied using individual faces directly. When both symmetry and attractiveness were rated by subjects significant correlations have been found. (Zebrowitz, Voinescu, & Collins, 1996; Rhodes, Proffitt, Grady, & Sumich, 1998; Mealey, & Townsend, 1999; Rhodes et al, 1999). However, when face symmetry is measured objectively rather than judged significant correlations have not been obtained. Shackelford and Larsen (1997) report overall correlations of -0.01 and -0.02 in two studies. Jones and Hill (1993) report only two significant correlations out of 28 in samples of faces of Ache Indians, Brazilians and people from the United States. These results may suggest that attractiveness enhances perceived symmetry, rather than vice versa.

Existing studies are thus consistent with the view that symmetry per se is not a powerful determinant of attractiveness. However, it is also possible that experiences of symmetries in general could interact with particular memories and produce preferences for symmetries (Enquist, & Arak, 1994). Also, special cognitive abilities to deal with symmetries may exist that could produce preferences for symmetry in general. A greater understanding of how symmetrical faces, and perhaps symmetries in general, are represented in the brain is needed to settle these questions.

3 Diversity and uniformity of preferences

By considering how recognition mechanisms operate it seems possible to explain biases in judgement of attractiveness within an individual, but what about patterns of variation within and between societies or populations? To answer this we have to consider developmental (ontogenetic) and evolutionary processes. We start with development.

3.1 Development

In principle, we are faced with three possibilities for development. The first is that judgements of attractiveness are mainly under genetic control. This would fit with the view that sexual preferences have been fine tuned by genetic evolution to allow an individual to choose a mate of high genetic quality. This

view is also consistent with empirical studies showing that such judgements agree among individuals to a considerable extent (but not completely), both within and between populations (see e.g. Buss 1989; Cunningham, Roberts, Barbee, Druen, & Wu, 1995; Rhodes, Harwood, & Clark, this volume; Cunningham et al, this volume; Dion, this volume).

If genetic control dominates, variation between individuals must be due to genetic variation. However, it seems to us that it is difficult to explain in this way all diversity that we see. That variations in preferences for "natural" features such as skin, eye and hair color or facial form have a genetic background may not pose any logical problems, but it seems implausible that preferences for recent cultural innovations can be explained in this way. Humans have been very creative when it comes to manipulating facial appearance in order to increase their attractiveness or status. Innovations include makeup, jewelry, haircut, tattoos, piercing, scarves and hats. Some of these alterations simply exaggerate natural features such as eyebrows and lips. Other modifications are more remote from natural appearance and thus particularly difficult to reconcile with the idea of genetically coded recognition. Preference for individuals wearing eyeglasses is an interesting example. Glasses were originally designed not to enhance attractiveness but once they were used they became a part of faces and thus experienced by observers. As a consequence we now have some people who prefer partners with glasses and in some individuals this preference has reached the level of fetishism (self-reports from individuals on the internet). Note also that glasses could be considered an indicator of bad quality. For similar reasons the hypothesis that preferences are under genetic control is difficult to reconcile with cultural diversity. It is not uncommon to find facial adornment from a different culture funny and unattractive (Zebrowitz, 1997). A classic example is lip enlargement occurring in some African and South American tribes (Zebrowitz, 1997). We guess that within these cultures these features are very sexy although this is hard to imagine for people from other cultures. Another reason why the genetic hypothesis seems less likely is the fact that we learn to recognize individual faces. If judgements of face attractiveness were under genetic control that would mean that these two systems need to be independent.

The second hypothesis is that preferences are under no or little genetic control. While this could explain diversity it leaves us with problems of a different kind. Without genetic guidance it would be impossible to know what to pay attention to and what to learn. A completely naïve individual surrounded by massive amounts of more or less biologically relevant stimuli would not be able to know that it should learn about such things as sex and age.

The third hypothesis is that both genes and learning are important. Indeed, in reality most behavioral systems often seem to develop in a complex interaction between genes and learning (see e.g. Hogan, & Bolhuis, 1994). The process we envision most likely for reading faces is a learning process that is guided by genetic predispositions (Hogan, & Bolhuis, 1994). Such guided learning is consistent both with the observation of individual and cultural diversity and the fact that we need to pay attention to certain properties such as age and sex. It is also consistent with patterns of generalization and discrimination as discussed above. Since experiences will differ individuals will learn different things. This may lead to more extreme preferences that in some contexts are called fetishes (Steele, 1996). Guided learning can also, perhaps surprisingly, explain why some preferences are shared by many human societies (Buss, 1989; Jones, & Hill, 1993; Cunningham et al. 1995; Rhodes, Harwood & Clark in this book). Such universalities in general are often regarded as genetic, adaptive and due to common ancestry, but this may not always be the case. We can distinguish between universalities that stem from sharing the same genes and those stemming from other shared factors. For faces, such a shared factor may be that faces look alike in different populations, due to shared genes responsible for face morphology. Thus, universal preferences may derive from learning based on the faces we see and not from genetic control of preferences. It would be illuminating here to know more about differences between societies or populations. According to our theory a bias towards experienced faces is often expected due to a preference for the average. In a comparison of several human populations Jones and Hill (1993) showed that subjects within a population agree to a larger extent when rating familiar faces (from the same population) than unfamiliar ones (from different populations). They also showed that different populations may have different standards of attractiveness. For example, Ache and Hiwi Indians did not agree with people from U.S. and Russia when rating faces of

females from Brazil, U.S. and the Ache tribe (correlations varied between -0.04 and 0.13).

Insight about development of facial preferences may be gained by considering how perceptual mechanisms develop in some animals. Ethologists have studied how animals learn sexual preferences through imprinting (see reviews by Krujt, 1985; Bolhuis, 1991; Clayton, 1994; ten Cate 1994). In the beginning this developmental process was considered as a very unique and stable form of learning of species-specific characteristics, occurring only during a short and restricted period early in life (Lorenz, 1935; Eibl-Eibesfeldt, 1975). Recent studies have provided a more dynamic picture and demonstrated similarities with other forms of learning (e.g. Bolhuis, 1991; Shettleworth, 1994). Still, imprinting-like processes are characterized by preprogrammed sensitive periods in which learning occurs more easily, often independent of the contexts in which it is later to be used. Modifications later in life are however possible (Bolhuis, 1991). In sexual imprinting, information about which stimuli sexual behavior will be directed to is learnt. This has been studied in male zebra finches using cross-fostering experiments, in which Bengalese finches acted as foster parents. These experiments reveal the importance of experience in the development of partner preferences: zebra finches that have been raised by Bengalese finches develop a preference for Bengalese finches (ten Cate, 1994). An important finding is that social interactions and attention are decisive factors in these learning processes, that is young are particularly prone to be imprinted on adults that interact with them (see e.g. Bolhuis, 1991; ten Cate, 1994; Kraemer, 1992; Hofer, 1987). Observing the actions of others might also influence preferences. Recently, it has been shown that females of some bird species copy the mate preferences of other females (e.g. Gibson, Bradbury, & Vehrencamp, 1991; Andersson, 1994).

We suggest that learning processes similar to those observed in birds occur in humans as well. Unfortunately, our knowledge about ourselves is less precise than that we have for birds. Note however that many theories of human behavior and personality consider, in one way or the other, early experiences as important or fundamental to the ontogeny of perceptual mechanisms (see e.g. Bowlby, 1969; Bandura, 1977; Money, 1986). Empirical studies of face reading in infants seem to suggest that we are born with coarse information about faces and a mechanism that guides development through learning (see e.g. Johnson, 1994, Johnson, & Morton, 1991). With increasing experience the child pays more and more attention to both details and real faces (Johnson, 1992). However, exactly when sexual preferences become established and how genetic factors and individual experiences interact is poorly known. We are not aware of any studies that have tried to correlate mate preferences with appearance of parents or peers of the opposite sex. For instance, will a man with an older mother prefer older women than a man with a younger mother? Studies of this kind, relating childhood experiences with adult preferences would be very enlightening.

3.2 Coevolution

We shall now turn to coevolution between facial appearances (regarding faces as signals or signaling devices) and receivers' preferences. By considering evolution we should be able to understand why preferences and appearances vary among populations and in time. Both genetic and cultural evolution are important in shaping the appearance of faces. Face morphology (form and position of facial features) is primarily under genetic control. On top of this an individual may add things in a diversity of ways using makeup, jewelry, haircut, tattoos or other means.

Let us first consider facial attributes that are under genetic control. Genetic evolution promotes those recognition mechanisms and those faces that produce most offspring. Over the last million years we can observe some significant changes in the skull of hominids (see e.g. Boyd, & Silk, 1997). This evolution may to some degree have been caused by receivers' preferences favoring certain appearances. Due to a combination of isolation and genetic evolution we also see variation in facial appearance between populations in different parts of the world today.

To the extent that faces are signals these changes and differences must have some meaning in a communication context. There are two major determinants of genetically coded signals. One is related to the problem of transmitting the signal to the receiver. This is an important problem for many signals but faces are signaling devices used mainly for short-range communications so we ignore this problem here. The other main factor is related to the

impact the signal has on the receiver. One idea is that receivers respond to sexual signals in a "rational way" reflecting the information they contain (see e.g. Zahavi, 1975; Grafen, 1990; Andersson, 1994; Bradbury, & Vehrencamp, 1998). Thus, if one sex prefers certain individuals of the opposite sex this would indicate that potential partners vary in mate quality and that the preferences allow individuals to make adaptive choices.

The second hypothesis maintains that signals sometimes get their form because of their ability to manipulate the receivers by exploiting receiver biases (Staddon, 1975; Dawkins, & Krebs, 1978; Ryan, 1998, Enquist, & Arak, 1998). By manipulation we mean that the receiver can be persuaded, to its disadvantage, to respond in a way beneficial to the sender. That is, judging one face more attractive than another may just mean that the preferred face is a stronger stimulus for the receiver, without any associated benefits. Indeed, the analysis of attractiveness presented above reveal that significant selection pressures could emerge directly from mechanisms responsible for generalization and discrimination of faces (see "Discrimination and Generalization" above). In the course of evolution biases can act both as a "repulsion force" (making signals more different) and "attraction force" (making signals more similar). Repulsion occurs in connection with discrimination (see Figure 1), attraction when different stimuli require the same response (Figure 3). Thus, biases in the nervous system could be directly responsible for the evolution of signal form, in particular if there are conflicts between senders and receivers which give an incentive for manipulation (Enquist, & Arak, 1998). Note that even in the presence of manipulation signals may contain some important information (e.g. about the age and sex of the person).

Both hypotheses predict that receivers are influenced by senders. To evaluate these two hypotheses with respect to human faces we need to know how the variation in facial attractiveness influences responses. Some support for the manipulation hypothesis comes from studies showing that attractive individuals of all ages are attributed more positive traits, by adults as well as children (e.g. Zebrowitz, 1997). For instance, attractive infants are judged by adults as easier and more rewarding to care for, as causing less trouble, and as being more competent, at the same time that expectations of competence are lower (Stephan, & Langlois, 1984; Ritter, Casey, & Langlois, 1991). Attitudes influence behavior and mothers of attractive infants are shown to be more attentive, affectionate and playful with their children (Langlois, Ritter, Casey, & Sawin, 1995). Although this may be interpreted as the mother caring more for offspring of higher quality (under the hypothesis that attractiveness signals quality), this can only explain variable investment within a family. Responses to attractiveness in some other situations are even more difficult to understand as reflecting some quality. For instance, attractiveness is advantageous when applying for a job, in communication and persuasion, when in trouble with the law and when in need of aid (see references in Zebrowitz, 1997). People with attractive faces are also perceived as having higher socioeconomic status (Kalick, 1988).

To distinguish between the two hypotheses we must consider whether the receiver benefits from her or his reactions. One possibility is that these reactions to attractive faces are advantageous to the receiver, the other that they are not. Thus, we need to ask whether there are any indications that receivers actually benefit from their preferences. Particularly important for evolution is whether choosing attractive partners increases reproductive success. In the only study we are aware of Kalick, Zebrowitz, Langlois, & Johnson (1998) find no significant correlations between number of children and attractiveness of partner ($r = 0.03$ for males, $n = 116$ and $r = 0.11$ for females, $n = 127$). In the same study, the authors correlated adolescent attractiveness with individual health, an important aspect of mate quality. The sample consisted of 169 females and 164 males, whose health was assessed in adolescence, middle adulthood and late adulthood. No significant correlations were found (r scores varying from -0.10 to 0.10). Shackelford and Larsen (1999), based on health reports from 100 subjects over 4 weeks, report similar results. For men and woman combined the r scores varied between 0.02 and 0.17. Only one of eight health variables considered was significant. In summary, these two studies suggest that at most a few percent of the variation in attractiveness (estimated by r^2) can be explained by variation in health, or vice versa.

Some recent evolutionary thinking about mate preferences both in humans and in other animals have centered on symmetry (see "Symmetry" above). It is hypothesized that symmetry is a honest

signal of mate quality (Møller, & Swaddle, 1997). In particular, this idea has been embraced in studies on humans (Buss 1999) whereas it remains controversial among biologists studying other species (see e.g. Palmer, & Strobeck, 1997). Shackelford and Larsen (1997) studied correlations between facial asymmetry and a number of psychological and physiological measures in two samples (see also above). How these relate to mate quality is in many cases uncertain. However, most of the measures do not correlate with degree of symmetry. In one sample 5 out of 48 correlations are significant and in the other sample 4 out 54. In both samples there is no correlation between symmetry and reports of health parameters (referred to as "physiological complaints and events" in the paper).

In summary, while being attractive clearly has advantages it is unclear whether there are any benefits associated with being sensitive to facial attractiveness when reacting to people. Our preferences may not be perfectly tuned to always choose high-quality partners. Instead, facial attributes under genetic control may have evolved partly to manipulate rather than to provide accurate information to the receiver.

When studying human evolution we cannot avoid cultural processes, and it is possible that findings about attractiveness need such considerations to be fully understood. The same might apply to preferences. To end the discussion about coevolution we shall consider what culture can tell us. As we have already mentioned, facial appearance has been subject to significant cultural evolution. In almost all human societies considerable amounts of time and effort are used to change facial appearance, including hair cuts, colors, cosmetic surgery, and use of artifacts such as jewelry, hats, masks (Alford, 1996; Gröning, 1997). Humans long ago discovered the power of appearance (see e.g. Zebrowitz, 1997) and it seems clear that one purpose of these manipulations is to enhance sexual attractiveness and social status. However, what drives cultural evolution is not always clear (e.g. Boyd, & Richerson, 1985) and other factors may also be important.

In cultural evolution as in genetic evolution we need to understand how a trait spreads and how innovations arise. Cultural traits spread when individuals mimic others. Such processes are often biased (Boyd, & Richerson, 1985), i.e. certain traits are more likely to be copied than others. For instance, it seems possible that receiver biases similar to those influencing judgement of attractiveness also influence what is copied from other individuals, but many other biases are certainly also important. Innovations are due to our creativity; people inventing new ways of modifying the face will supply the raw material for cultural evolution. Some innovations may primarily have another purpose. Hats were invented for protection but once they used they become a part of faces and stored in memory and thus affect judgement of faces. Soon it was discovered that hats in addition to protection also could have some impact on how a person is perceived by others. Such processes are referred to as ritualisation. The exact direction evolution will take depends on preferences, and here signal repulsion and attraction are potentially very important. In addition, preferences may be transferred by imitation from one individual to another.

It is easy to see that cultural evolution can produce a lot of diversity between cultures. Innovations are partly random and depend also on local circumstances such as availability of artifacts. Two isolated groups of people will quickly enter different tracks that will be self-reinforcing as new receiver biases emerge partly caused by the particular innovations that occur. This process will lead to considerable change over time. That standards of beauty have varied considerably with respect to body adornment is well documented in the case of fashion. In contrast, we expect beauty standards for facial features that are under genetic control to be much more stable (see above).

Culture may also give rise to considerable variation within a particular society. Subgroups may want to look different. Young may want to look different from the older generation. Many different innovations may occur at the same time. All this may reinforce individual differences in preferences, because young individuals will have partly different experiences when preferences are established.

4 Discussion

In this paper we have suggested an alternative theory for why we experience faces (and possibly many other things) as varying in attractiveness. First we presented a model of recognition, based on basic mechanisms for generalization and discrimination. This model seems to be able to explain major empirical findings about judgement of attractiveness (See

Table 1). The model we applied is not particular to faces or humans, suggesting that judgments of attractiveness emerge by mechanisms similar to those controlling reactions to other stimuli. Thus, there may be nothing particular about reading faces, with the possible exception of resolution and memory capacity (see e.g. Young 1998). We continued by suggesting that individual learning plays an important role in the formation of our preferences, although this process must to some extent be genetically guided. We discussed the relevance of ethological models. The hypothesis of guided learning is consistent with variation observed within societies and including extreme or unusual preferences. Combined with evolution, this hypothesis can also explain diversity between societies.

Evolution of genetically determined facial attributes as well as cultural traits is likely to be influenced by receiver bias. Two scenarios are particularly important (Enquist & Arak 1998). One mechanism, signal attraction, is related to the problem of many different stimuli (for example, all individuals of one sex) requiring the same behavioral response. This favors average appearance. Our opinion about preferences for certain symmetries is that they are just a byproduct of preference for the average. We suspect that many correlations obtained with symmetry would also be obtained by correlating with degree of deviation from the average appearance. In fact, this variable is probably much more informative. The second mechanism favors extremes and is related to discrimination (different behavior to different stimuli, e.g. individuals of different sex). Due to learning, any changes in the appearance of senders will directly affect receiver preferences and biases, and thus influence further evolution. This can lead to substantial diversity between societies with respect to preferences for facial attributes that are culturally inherited.

How does the theory that has been suggested here compare to a mate-quality hypothesis? Remember that both theories agree that sexual signals contain information about things like sex and species identity. However, mate-quality hypotheses continue further and predict that even details of the signal are informative and that the receiver responses are fine tuned to this information; hence the receiver responses are rational in all details (rational choice). In table 1 we have tried to compare the two hypotheses based on the discussion in this chapter. Two variants of the "receiver bias" hypothesis are considered: one in which receiver preferences are due to genetically guided learning and the other in which preferences are genetically determined. As the table shows, the existence of culture in humans provides us with additional possibilities for distinguishing between hypotheses. Judging from the table, the hypothesis of biased receivers in combination with guided learning has most support.

We would like to end the chapter by pointing out that it is not possible to rule out the possibility that faces or other sexual signals actually contain more information about partner quality than just species, sex and age. However, we have presented a model that is a viable alternative hypothesis to theories based on rational choice. It is the task of future research to evaluate what is the exact mix of information and manipulation in sexual signals, and in particular in faces. Two kinds of empirical studies could be particularly illuminating. One is to explore individuals' ratings of attractiveness and compare them to the gradient in Fig 4. A possibility is to produce faces that vary in the male-female dimension and in an independent dimension in which the degree of asymmetry varies (note that there are many such dimensions, but it should be possible to chose one for which attractiveness varies considerably). The second kind of studies would investigate whether experiences of evolutionarily novel facial attributes such as earrings and haircuts could be encoded in an individual's preferences. Such studies would be important in determining how much of our preferences are genetically coded.

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Table 1: Comparison of hypotheses for why faces vary in attractiveness

Prediction	Hypothesis		
	Receiver bias		Rational choice
	Guided learning	Genetic determination	Genetic determination
Existence of preferences	Yes*	Yes*	Yes*
Correlation between mate quality and attractiveness	-	-	Yes†
Receivers may respond not to their own advantage (manipulation)	Yes	Yes	No
Universality (not necessarily complete)	Yes*	Yes*	Yes*
Preferences for cultural innovations	Yes*	No†	No†
Individual variation in preferences	Yes*	-	-
Unusual preferences (e.g. feticism)	Yes*	No†	No†
Geographical variation in preferences	Yes*	-	-
Preferences change during lifetime	Yes	No	No
Direction of bias predicted by stimulus-control theory	Yes*	Yes*	-

Legend: * agrees with empirical data; † does not agree with empirical data; - prediction unknown or may go in any direction. If empirical data are lacking or unclear no symbol is given.

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