

Communication of mate quality in humans

S. Craig Roberts

9.1 Introduction

Sociality affords individuals with greater opportunity for improving reproductive success through mate choice than will generally be possible for those of habitually solitary or socially monogamous species. Group-living individuals can attract more potential mates from a relatively large number of opposite-sex group members, or choose better ones, following the same principle that appears to drive the evolution of leks in some species, where males form aggregations to attract large numbers of females and females visit the aggregations solely for mating (Bradbury and Gibson 1983). Furthermore, the costs of mate choice, including time or energetic costs of travelling between potential mates, and the risk of injury or predation while doing so, are likely to be substantially lower in larger and mixed-sex groups (Reynolds and Gross 1990). Finally, mate choice within groups allows individuals to compare directly between potential mates and make choices based on relative qualities, which may be a quicker and more efficient mechanism for choice than relying on absolute trait values (Bateson and Healy 2005).

Just as in animal groups, opportunities exist in most human societies for individuals to view, track, and compare an array of potential mates; females are thought to be the choosier sex due to the relatively large costs of reproduction. Shaping of adult-like mate preferences starts well before first sexual encounters (Saxton *et al.* 2006); indeed, early exposure to individuals of the opposite sex can profoundly influence individual variation in preferences, whether it originates in general

inbreeding avoidance mechanisms (Weisfeld *et al.* 2003) or through more subtle imprinting-like effects in which men and women are attracted to potential mates who share specific traits with their opposite-sex parent (Jacob *et al.* 2002; Little *et al.* 2003). Towards adulthood, there is further opportunity to gain experience from a variety of potential partners. For example, in most societies there is usually a considerable interval between first sexual intercourse and first marriage or cohabitation, from a mean of 5–7 years in most African countries to 7.5 and 10.6 years for the UK and USA, respectively (Wellings *et al.* 2006).

But if sociality offers particular opportunities for choice, it also requires individuals to sift through and process an array of available information about the quality or suitability of many different potential partners. Furthermore, the individuals doing the choosing must be sensitive to the vagaries of different kinds of information and to the context in which decisions are made. For example, we might not expect different kinds of information to be equally reliable about the quality of a potential mate, since some could be faked and some may be irrelevant to discrimination of mate quality. How then do males in particular communicate their own quality as a partner to potential mates, and how do females select a suitable partner from so many different males? The attributes used in mate choice are many and diverse, but include intelligence (including correlates like education and sense of humour; Miller 2000), personality (e.g. Buston and Emlen 2003), resources and wealth (Daly and Wilson 1983), and physical traits. Each of these characteristics can be reliable to a considerable degree, certainly

when tracked over time, but physical traits are particularly hard to fake, even in the short term. This quality, coupled with generally high heritability and comparative dissociation from cultural effects, has led to a sustained and intense research effort in the past decade or two to catalogue the ways in which physical attributes influence judgements of attractiveness.

In this chapter I outline some of the recent progress that has been made towards a biological understanding of the communication of mate quality in human interactions, which closely follows and matches the findings of behavioural ecologists working on other animals. Just as in animal studies (e.g. Andersson 1994; Petrie 1994), evolutionary psychologists interested in human mate choice have particularly focused on physical characteristics that potentially indicate underlying good genes. These researchers conventionally use volunteers to rate the attractiveness of stimuli (e.g. face photographs) of other individuals. More recently, the scope of such studies has widened to incorporate behavioural patterns and expressions that may reveal similar information about genetic quality; that is, researchers might present a video, rather than a single photo. Questions remain as to how wide this behavioural scope can stretch and I conclude by exploring the extent to which dynamic cues can reliably reveal mate quality.

9.2 Physical traits and mate quality

Variation in male attractiveness is underpinned by variation in physical traits, most of which can be discerned at a distance and almost instantaneously, and acted upon without intimate contact. It has been hypothesized that at least some of these traits reveal underlying genetic quality. In the following sections, some key evidence to support this idea is described, but the reader is also referred to several recent wide-ranging reviews (Grammer *et al.* 2003; Gangestad and Scheyd 2005; Rhodes 2006; Roberts and Little 2008).

9.2.1 The face

Unsurprisingly, the face is the centrepiece of human attractiveness research. Facial perception

is key to individual recognition, kin recognition, and judgements of mood, intention, and personality in others (Posamentier and Abdi 2003; Zhao *et al.* 2003), in addition to judgements of attractiveness (Thornhill and Gangestad 1999; Rhodes and Zebrowitz 2002). Facial judgements of opposite-sex individuals are also better correlated with overall impressions of their attractiveness than are judgements of body attractiveness (Peters *et al.* 2007). This is despite the fact that independent attractiveness ratings of face and body correlate very well, indicating that both are underpinned by congruent **hormonal** and genetic influence (Thornhill and Grammer 1999).

What facial characteristics are attractive? As Rhodes and Zebrowitz (2002) point out, there is no 'gold standard' in what makes any face attractive, many different factors appear to contribute. One of the most intensively studied aspects is fluctuating asymmetry, building on work in animals such as barn swallows, where males with the most symmetrical tails are preferred by females (Møller 1992). In similar fashion, facial symmetry is positively related to judgements of facial attractiveness (Grammer and Thornhill 1994). Some of the most persuasive studies are able to use elegant experimental designs by employing computer-graphics techniques and composite images to control for potential confounds (see Fig. 9.1) and hence manipulate symmetry to increase attractiveness (e.g. Rhodes *et al.* 1998; Little *et al.* 2001). However, although symmetry is correlated with attractiveness, individuals are not generally adept in assessing symmetry *per se* in faces (Scheib *et al.* 1999) and the ability to detect symmetry is dissociated from preference for it (Little and Jones 2006). Indeed, the symmetry–attractiveness relationship is maintained when attractiveness ratings are based on only the left or right half of a face, such that symmetry cues are withheld (Scheib *et al.* 1999). It would seem, therefore, that symmetry is unlikely to be the proximate mechanism that mediates judgements of attractiveness, rather it may simply correlate with one or more other attractive traits (Scheib *et al.* 1999; Penton-Voak *et al.* 2001). Scheib *et al.* suggest this may be facial masculinity (see also Gangestad and Thornhill 2003), but Penton-Voak *et al.* (2001), suggest facial skin condition would correlate more

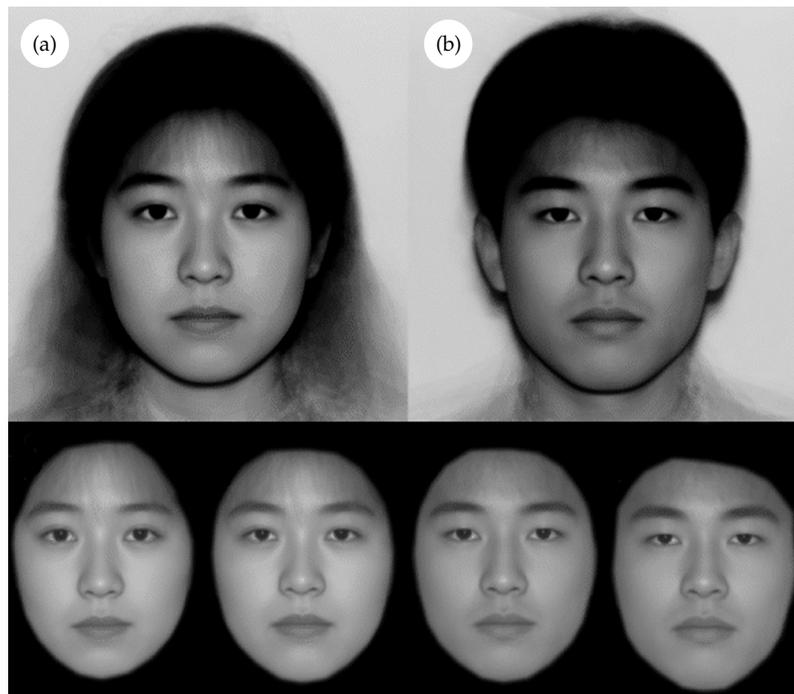


Figure 9.1 Use of facial composites in mate choice research. Progress in study of facial preferences has been facilitated by computer graphics techniques which enable the construction of 'average' or 'composite' faces by digitally blending photographs of individual faces. Here, 28 male and 28 female faces of young Japanese students (from Perrett *et al.* 1998) are used to construct a female composite (a) and male composite (b). In the lower panel, each composite has then been digitally morphed to render the face either feminised (the left-hand image of each pair) or masculinised (the right-hand image of each pair). These faces can then be presented as stimuli to assess preference for sexual dimorphism in faces. The same technique can be used to manipulate or control for other characteristics, such as symmetry. Reprinted by permission from Macmillan Publishers Ltd: Perrett *et al.*, *Nature* 394, 884–887, copyright 1998.

reliably with symmetry because both may be fundamentally linked to health (see also Jones *et al.* 2001). Indeed, in a subsequent study, Jones *et al.* (2004b) showed that symmetrical faces were judged to have healthier-looking skin than asymmetrical faces (whether real faces or composites).

A great deal of research has also focused on the extent to which attractiveness correlates with the degree of sexual dimorphism in the face. Perrett *et al.* (1998) produced composite images of men and women from either the UK or Japan, and morphed these in a masculine–feminine dimension (Fig. 9.1); subjects were then required to indicate the face they most preferred. More feminized versions of female faces were most attractive for men, while women preferred an intermediate level of facial masculinity, apparently because masculinization

was associated with negative personality attributions associated with low paternal investment. Perceptions of facial masculinity are correlated with levels of testosterone (Penton-Voak and Chen 2004) and physical strength (Fink *et al.* 2007a), so it appears to be a reliable cue of physiological differences between men. Furthermore, facial masculinity also appears to be correlated with facial symmetry and thus to carry consistent information regarding genetic quality (Gangestad and Thornhill 2003). In support of this idea, highly dimorphic facial features co-vary with low susceptibility to infection (Thornhill and Gangestad 2006).

The extent to which individual women prefer facial masculinity varies with women's perception of their own attractiveness, in other words how well they perform in the mating marketplace (Little

et al. 2001). In addition, there are systematic temporal changes in preference expression depending on the stage of the woman's menstrual cycle, such that preference shifts towards masculinity occur around ovulation, when women may benefit most in terms of indirect benefits from preferring and choosing males with good genes (Penton-Voak *et al.* 1999; Fig. 9.2).

More recently, the possibility that facial attractiveness could be underpinned by genetic heterozygosity has been investigated. To do this, Roberts *et al.* (2005b) asked women to rate the faces of men who had been genotyped at key loci in the major histocompatibility complex (MHC). Men who were heterozygous for all the genes under study were rated more attractive on average than men who were homozygous at one or more loci. This result is consistent with the general finding that perceived health of potential mates may be a reliable general influence on mate preferences in humans

(Thornhill and Gangestad 1999; Grammer *et al.* 2003, 2005; Rhodes 2006). Indeed, further investigation showed that very similar results were obtained when women assessed the healthiness of small patches of skin excised from the facial photographs and that these healthiness ratings correlated with attractiveness ratings of the whole face. This finding was the first to directly link male genotype with perception of attractiveness, but shows consistent effects with other studies, notably those of Jones *et al.* (2004a,b), that use the healthiness of skin as an indicator of underlying good genes.

9.2.2 Body

Although bodily features have been less intensively studied than faces, similar approaches indicate that putative indicators of good genes are discriminable and considered attractive. Male body attractiveness correlates with higher physical **fitness** (Honekopp

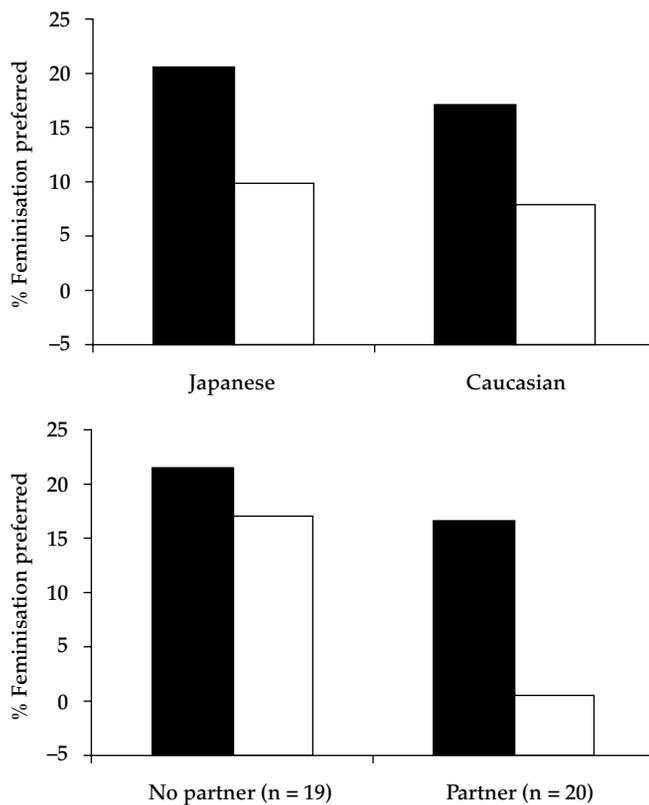


Figure 9.2 Conception risk and its effect on preference for femininity in male faces by Japanese females in Japanese and Caucasian faces (upper; open bars: non-fertile phase, shaded bars: fertile phase). Preferences during high and low conception risk phases for subjects with and without a partner (lower), data for Japanese and Caucasian faces combined. Redrawn from Penton-Voak *et al.*, 1999b.

et al. 2007) as well as with earlier onset of sexual activity and the number of short-term sexual partners (Rhodes *et al.* 2005). Fluctuating asymmetry in body traits correlates negatively with facial attractiveness (Gangestad *et al.* 1994), indicating an underlying connection between the two traits (see also Prokosch *et al.* (2005) for an extension of this principle to intelligence). Levels of fluctuating asymmetry also correlate negatively with weight (Manning, 1995), suggesting that only the most symmetrical males can achieve and maintain large body size. As in faces, low fluctuating body asymmetry correlates with low susceptibility to infection (Thornhill and Gangestad 2006).

For body height (Pawlowski *et al.* 2000), muscular body shapes (Barber 1995), and waist to hip ratio (Singh 1995), females tend to prefer intermediate levels and avoid extremes. Several studies demonstrate a general preference for a 'V-shape' torso with wider shoulders than waist (e.g. Hughes and Gallup 2003). Chest and body hair also appear to increase ratings of attractiveness (Dixson *et al.* 2003), perhaps because it **signals** high masculinity, dominance, and levels of testosterone. As in faces, the strength of preference expression for body markers such as height varies depending on the stage of the woman's cycle and the context of the judgements being made, namely her expectations of the length of the relationship (Pawlowski and Jasienska 2005).

A number of studies have examined another putative marker of testosterone, the ratio of the second to fourth digits (2D:4D), which is thought to reflect the level of the hormone experienced *in utero* (Manning 2002). Although this ratio is unlikely to be used as a proximate cue in judgements of mate attractiveness, we might predict that it will correlate with other phenotypic features if it indeed taps the same form of underlying quality. Consistent with this, 2D:4D ratio is correlated with facial asymmetry (Fink *et al.* 2004).

9.2.3 Voice

In one of the first studies that used vocal characteristics to study attractiveness, Collins (2000) found that men with voices characterized by having closely spaced, low-frequency harmonics were

judged as being more attractive, older and heavier, more likely to have a hairy chest, and of a more muscular body type. Although estimates of male characteristics based on their voices were incorrect (with the exception of body weight), she concluded that the preference for deeper voices could be subject to **sexual selection** through female choice. Women agreed over which voices were attractive or unattractive. Subsequently, other studies have found significant correlations between body dimensions and vocal characteristics such as fundamental frequency and formant dispersion (see Evans *et al.* 2006), and these can be manipulated to increase attractiveness ratings (Feinberg *et al.* 2005). Male vocal attractiveness has been shown to be positively correlated with attractiveness of faces (Saxton *et al.* 2006), body shape (Hughes *et al.* 2004), and ratings of social dominance (Puts *et al.* 2006). Studies have also shown that individual women experience cyclical shifts in preference across the menstrual cycle, with preference for lower-pitched male voices around the time of ovulation (Feinberg *et al.* 2006). The attractiveness of women's voices also correlates with their facial attractiveness (Collins and Missing 2003).

9.2.4 Odour

Although humans have been described as microsmatic (having a poor sense of smell compared to other mammalian species), evidence is accumulating to show that odour can influence human behaviour to a greater extent than previously realized (Schaal and Porter 1991). Despite this, odour is perhaps the exception to the traits listed above in that it probably requires more intimate, close-range, and prolonged association in order to fully gauge its effects (for a complementary discussion of odour in rodents see Chapter 6 and for insects see Chapter 5). Nonetheless, in mate choice contexts, attractiveness ratings of body odour are correlated with body symmetry (Rikowski and Grammer 1999), facial attractiveness (Rikowski and Grammer 1999; Thornhill *et al.* 2003), heterozygosity at MHC genes (Thornhill *et al.* 2003), and measures of psychological dominance (Havlicek *et al.* 2005). Once again, these effects may be dependent upon the relationship context of the women judges and the phase of their menstrual

cycle. Additionally, using synthetic steroid chemicals associated with male body odour, Cornwell *et al.* (2004) have demonstrated that the extent to which individual women prefer this masculine odour correlates with their expressed preference for masculinity in faces, indicating a concordant preference for potential good-gene indicators across two different sensory modalities.

9.3 Behavioural attributes

Research into non-physical traits or behaviour in human communication has a long history. Early work was mostly ethological in nature, focusing on general behavioural patterns and conducted by researchers who would describe themselves as anthropologists, psychologists, or ethologists. Notable examples can be found in Eibl-Eibesfeldt (1970), Hinde (1972), Mehrabian (1972), and Kendon *et al.* (1975). Similarly, work on human facial expression was led by psychologists such as Ekman (1982). The field has made enormous progress in the interceding years. Specialists use the terms paralinguage (non-verbal aspects of language, such as voice pitch and volume) and kinesics (facial expressions, postures, gestures, etc.) as the two non-verbal arms of the triune nature of human communication. These are now applied in an interdisciplinary fashion to a wide variety of communication contexts, including language interpretation, business communication, and the dramatic arts (e.g. Poyatos 2002).

Such progress has not been entirely matched by research into human courtship behaviour. Although there are many popular accounts of how to interpret body language, these are based on relatively few rigorous studies (cf. Grammer *et al.* 1999). Evolutionary psychologists who have thrown themselves headlong into the task of revealing the physical traits underlying human attractiveness have, with very few exceptions, appeared to ignore or even avoid these non-physical aspects of attraction and courtship, especially kinesics. This is probably largely due to a pervasive, but not completely accurate, perception that such communicative information can be easily faked and that it is therefore unreliable and unlikely to be used in decisions about mate choice. I will deal with this problem in more detail later in this chapter.

Whatever the reason for it, however, it is clear that this is an area which deserves more enquiry. The kinds of cues reviewed above, which are available almost at first sight, constitute only the foundation of an impression of a potential mate. This initial impression is then developed and refined, sometimes radically altered. Since almost all of the recent research addresses physical traits of unknown individuals—the zero-acquaintance paradigm—a large proportion of the complexity of mate choice may be being missed. Only in the past few years has the apparent reluctance of evolutionary psychologists to engage with kinesics been eroded, and it now receiving growing attention. Gangestad and Scheyd (2005), for example, include non-physical features as one of their five critical topics for future research in human mate choice. In the next section, I review some of the recent research which has begun to explore the contribution of kinesics to our understanding of perceptions of mate quality.

9.3.1 Communicative value of kinesic information

Humans possess the ability to infer critical socially relevant information from body posture, movement, and expression. A good example of this comes from Archer and Akert's (1977) study in which participants watched video clips of social interactions and were later asked questions about the clips, for each of which there was an unambiguously right or wrong answer. One such example was a clip of two women playing with a baby; at the end of the clip, participants were asked to judge which was the mother. A second group of participants were asked to make the same judgements but were shown only a verbal transcript of the encounters; they did not see the clips. While the second group actually performed worse than expected by chance, the group who both heard the conversations and observed the interactions did significantly better.

The potential for kinesic information to similarly provide useful information concerning mate value can be illustrated by a number of studies. A notable example is that of Brown *et al.* (2005), who set out to test whether dance, a dynamic display used in

human courtship, might reveal information about mate quality. They specifically tested whether the dancing ability of men and women, as judged by participants from the same Jamaican population, correlated with body asymmetry. The results indicated a significant association between dancing ability and asymmetry, particularly in men, consistent with the idea that dance could be used as a reliable indicator of mate quality. Importantly, they employed in their study a form of motion-capture technology that enabled them to control for other visual cues such as attractiveness, symmetry, and height (Fig. 9.3), thus demonstrating a specific effect of motion and rhythm on the rater's perception of the video clips. A subsequent study which used simple video clips of dancers has also shown that men with low 2D:4D ratios (i.e. masculine ratios) were also judged more attractive than men with more feminized ratios (Fink *et al.* 2007b).

If non-physical cues such as movement are used in assessing mate quality in a way similar to that described for physical cues, then we might expect some degree of plasticity in judgements according to the context in which the cues are judged. Very little work has been done in this area, but Gangestad *et al.* (2004) have found just such an effect. Male participants in an experiment ostensibly about relationship formation, in which they were led to believe they were competing with another male for a date with an attractive female, were videoed responding to questions by the 'potential date' and then by the 'competitor' (both were confederates). Trained raters then coded responses in the two conditions for the number of certain non-verbal displays and behavioural tactics in order to obtain scores for each man

on dimensions of 'social presence' (from interaction with the 'date') and 'direct intrasexual competitiveness' (interaction with the 'competitor'). A panel of independent female raters then observed segments of these video clips and made attractiveness judgements of the males as either a potential short-term or long-term partner. Gangestad *et al.* correlated the preference for men with high social presence and competitiveness with the menstrual cycle phase of the women raters, revealing that predilection for these male cues increased on high-fertility days, and only in the short-term relationship context. This result is reminiscent of those previously described for physical traits.

Very little research has examined the effect of male behavioural patterns on actual success in attracting female attention. However, Renninger *et al.* (2004) aimed to do just that in an observational study in a bar. They hypothesized that six specific behavioural patterns might be important in eliciting female attention: intrasexual touch, space-maximization movements, open body positioning, glancing, gesticulation, and automanipulation. Their study indicated that most of these behavioural patterns did indeed differ between men who were successful or not in establishing conversational contact with at least one woman, and that some of these were expressed at higher frequencies when women were present than when they were not.

9.3.2 Dynamic versus static stimuli

The previous section suggests that information available in dynamic, non-physical cues could potentially influence mate preferences in similar

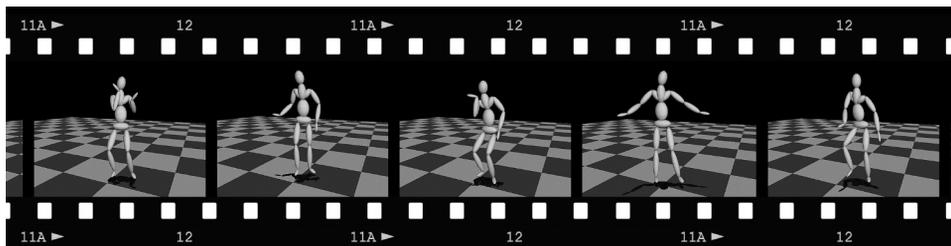


Figure 9.3 Example frames from video clips used by Brown *et al.* (2005) to show that dancing ability is correlated with body symmetry. The clips are manipulated from actual footage of dancers such that other physical cues (e.g. gender, identity, attractiveness) are removed. Image reproduced with permission of William M. Brown, Keith Grochow, Karen Liu, Zoran Popović and Robert Trivers.

fashion to purely physical traits. Is there then any advantage to using dynamic stimuli, which will usually be a more challenging logistical task? The answer would appear to be 'yes'. In a study which compared the contributions to judgements of overall attractiveness, Riggio *et al.* (1991) found that facial attractiveness (judged from static images) and expressive behaviour/style (gleaned from video clips) both independently explained overall judgements. Furthermore, Rubenstein (2005) reported a surprisingly low correlation between judgements of attractiveness based on video clips of participants reading from a card and judgements based on a single, standardized frame taken from the same clip. He concludes that the two types of presentation are evaluated in different ways and that dynamic displays in particular yield emotional content that is unavailable from static images. However, while these conclusions may well be true, the surprisingly low correlation between dynamic and static judgements may be an artefact of the between-subject design of this experiment: raters saw each face in only one format. In contrast, within-subject judgements are highly correlated (S. C. Roberts, unpublished data).

Although the dynamic stimulus studies potentially go further than those based on static stimuli, those of Riggio *et al.* and Rubenstein are based on the zero-acquaintance paradigm; in other words, they deal with the effects of kinesics over a very short period. This is entirely appropriate as an experimental design, but does little to tell us how these dynamic cues add or subtract to the initial judgement. This is certainly a question for the future, but an interesting study using actual acquaintances and attractiveness judgements neatly demonstrates the potential for describing longer-term development of initial impressions. Kniffin and Wilson (2004) explored the extent to which zero-acquaintance attractiveness ratings (e.g. from high-school yearbook photographs) compared with the attractiveness ratings of former classmates, who had obviously assimilated additional information about the people being judged. Although ratings by strangers accounted for a large proportion of the variance in the classmate ratings (60% for males rating females and 38% for females rating males), there was a proportion that remained unexplained,

and this varied a great deal from person to person. In a separate experiment, they asked participants, who were unfamiliar with each other, to judge each other's attractiveness and other attributes at the beginning and end of a 6-week field course. Initial judgements of physical attractiveness accounted for a relatively small proportion of the variance in final judgements for females judging males, but a large proportion for males judging females.

Does dynamic information then provide better and more reliable estimates of underlying genetic quality than simple static cues that have been so widely used in recent research? This question may be difficult to answer, but one way might be to look for clearer relationships between attractiveness judgements and putative good-gene indicator traits when the judgements are made using dynamic stimuli. One such example is the relationship between 2D:4D ratio and attractiveness, which was positively correlated when attractiveness was judged from clips of short interactive conversations (Roney and Maestriperi 2004) but not in another study which used photographs (Neave *et al.* 2003). Alternatively, the answer may lie in the congruency of different categories of basic information, including that between statically and dynamically communicated cues (Johnson and Tassinary 2007).

9.3.3 The problem of honesty

It is clear that for most physical cues we have to make do with what we have. We cannot change the shape of our face or our body size, the sound of our voice, or the smell of our armpits. Modern cultural practices such as platform shoes, shoulder pads, facial cosmetics, perfumes, and cosmetic surgery allow us to tinker at the edges of our phenotypic inheritance, and the wide use of such practices certainly provides interesting insight into the design features of attractive bodies. However, these manipulations usually have relatively minor effect beyond very initial impressions and may often be rapidly 'discovered'. (Note that most studies of human indicator traits attempt to rigorously control for most of these cultural confounds.) The physical traits reviewed earlier in this chapter can thus be seen as providing reliable information about the underlying genetic quality of a potential

partner, in the same way as the train of a peacock or odour of a mouse (Petrie 1994; Roberts and Gosling 2003).

But, as I have already touched upon, it is somewhat less clear that the information carried in dynamic displays can be considered reliable in this sense. This is probably the principal reason why approaches incorporating kinesis information have been so neglected in evolutionary psychology research (although to a lesser extent this may also be explained by differences in technological prerequisites). Although the relative imbalance in focus on static and dynamic cues is beginning to change, there remains engrained a sense that kinesis does not fully belong as a legitimate approach to the study of mate choice, or at best it can be relevant only in a narrowly defined subset of behavioural patterns. Neither a clear understanding of the limits to which kinesis cues can be used in reliable mate assessment, nor a conceptual framework which defines the conditions under which such cues can be reliable, currently exists.

Signalling theory proposes several mechanisms through which biological **signals** can be reliable (Maynard Smith and Harper 2003; see also Chapter 1). These include the ideas that signals are inherently costly to produce (the handicap principle), that a signal (costly or otherwise) which does not accurately reflect the quality of the signaller will invoke socially imposed costs, and that the very nature of some signals cannot possibly be faked (index signals: Maynard Smith and Harper 2003). Any example of kinesis or paralinguistic information being used as reliable information about mate quality would in all likelihood need to fulfil one of these three criteria. However, attributing an observed signal to a particular kind of cost is not straightforward: see, for example, the discussion concerning symmetry and ornaments in Maynard Smith and Harper (2003). If we take the example of the recently described link between fluctuating asymmetry and dancing ability of young men (Brown *et al.* 2005), it could be that dancing is a handicap, if the ability to dance well is energetically dependent and only the best males can afford to invest energy in sufficient quantity to produce a pleasing dance; or, perhaps more likely, it could be an index signal, if dancing ability is directly

linked to symmetry or health. Thus, while costs are certainly important, it is evident that an understanding of signalling reliability at this level is not especially useful for defining behavioural patterns that can be used reliably in mate choice decisions.

I propose that an alternative, more productive and accessible, approach can be formulated by drawing on several emergent themes from the literature on the attractiveness of physical traits, which I reviewed earlier in this chapter (see also Roberts and Little 2008). If these themes were generalized to non-physical traits, we could make the following predictions:

1. Expression of reliable non-physical traits will correlate with attractive physical traits. The basis for this prediction is that if there is some variability between individuals in underlying genetic quality, and this quality is manifest in more than one phenotypic characteristic, then variability in the attractiveness dimension for the different traits should be intercorrelated. For example, ratings of male body odour (Rikowski and Grammer 1999; Thornhill *et al.* 2003) and voices (Saxton *et al.* 2006) co-vary with facial attractiveness ratings. Similar cross-correlations also occur between body (Thornhill and Grammer 1999) or voice attractiveness (Collins and Missing 2003) and women's faces. The same principle should apply to non-verbal behaviours if they indicate genetic quality: they should correlate with both attractive physical traits and also with other attractive non-physical traits.
2. Relative to same-sex individuals, trait expression should be temporally consistent. As we have discussed, physical cues such as masculine facial shape are, by their very nature, consistent over time. They may vary in the long-term, because of ageing or onset of disease for example, but on a day-to-day basis they are relatively constant. In contrast, non-verbal cues can alter much more fluidly, thus allowing the possibility of deception. If a non-verbal trait is to be potentially reliable, we would expect it to be consistently expressed over several independent occasions with similar social relevance. Patterns of expression of the trait may very likely vary with different social contexts (e.g. flirtatious behaviours will be more common in certain situations than others), but within these contexts the degree of

expression relative to that of other males should be relatively consistent. This will be especially true where a degree of social policing or comparison is possible, as for example where potential competitors are present who are of both higher and lower mate value. Individual females do not necessarily need to observe specific males over this period of time for the trait to be reliable, since the premise of reliability in the sense of good genes is that it is relatively fixed. Furthermore it could be enforced by intrasexual selection.

3. Preference for the trait should be condition-dependent. Studies of physical traits repeatedly demonstrate that between-individual variation in the strength of preference for specific indicator traits correlates with measures of individual condition. For example, expression of preferences of facial traits such as masculinity, symmetry, and healthiness in male faces is predicted by the self-rated attractiveness or body attractiveness of female raters (Little *et al.* 2001; Penton-Voak *et al.* 2003; Jones *et al.* 2005). This makes sense if we visualize mate choice as a biological market, where differences in mate value dictate the range of choice open to individuals (e.g. Pawlowski and Dunbar 1999). In the same way, preferences for reliable non-verbal traits should also be expected to be condition-dependent.

4. Preference should be context-dependent. Within-individual shifts in preference for physical traits occur depending on the relationship context under which judgements are made, that is, whether raters are asked to make attractiveness judgements for short-term or long-term partners (e.g. Little *et al.* 2002; Roberts *et al.* 2005a). In addition, for females only, the raters' stage of menstrual cycle is also important (e.g. Penton-Voak *et al.* 1999; Havlicek *et al.* 2005). The theoretical basis for this is that preference shifts reflect the balance of indirect and direct benefits of choice (Gangestad and Simpson 2000). In the same way, if non-verbal cues reliably signal either genetic quality or some aspect of likely paternal investment, the same kinds of shifts in attention should be observed. Indeed, there is already some evidence for variation in preference shifts for non-verbal behaviour depending on the stage of the menstrual cycle (Gangestad *et al.* 2004).

5. Preferences should normally be culturally independent. There is more agreement regarding the attractiveness of physical traits across cultures and ethnicities than there is disagreement (Perrett *et al.* 1998; Langlois *et al.* 2000). While non-verbal behaviours may very well be more labile with respect to cultural influences, reliable components should be among the most robustly conserved across cultural and ethnic groups.

These five predictions provide a basis for extending the scope of investigation into phenotypic indicator traits from purely physical cues to include non-physical traits and behavioural patterns. Note that some of these predictions may also apply to other important aspects of mate choice which do not involve good-gene indicators, including preference for genetic dissimilarity or assortative preferences for traits such as personality. Thus, if a particular behavioural pattern does not fulfil most or all of these predictions, it remains possible that they could nonetheless reflect some important attribute other than good genes that may still be attractive and used in the formation of preferences. In this chapter I have not addressed assortative preferences because, although this is an important and emerging genetically based component of individual decisions (see for example Wedekind *et al.* 1995; Roberts and Gosling 2003; Mays and Hill 2004), the interpretation of mate quality is then specific to the individual. A review of this aspect of mate choice as it applies to humans has recently been published elsewhere (Roberts and Little 2008). The development of a set of predictions that pertains to such alternative considerations within mate choice is beyond the scope of this chapter but remains a challenging task for the future.

Finally, how should females behave in order to benefit from judicious choice based on non-physical traits? The reliability of any trait can be increased in three key ways. First, duration of observation of a particular male will be an important factor allowing ongoing adjustment of the estimate of mate quality. Second, the precision of this estimate is likely to be markedly increased if the target male(s) is unaware he is being observed (Locke 2005). Third, during the early stages of any

initiated contact, females may probe the male to check whether their estimate appears reliable. Indeed this will be an ongoing process throughout courtship and beyond.

9.4 Conclusion

There is a huge diversity of approaches and volume of research that addresses the possibility in humans that underlying genetic quality can be perceived and acted upon. Physical characteristics, such as facial or bodily appearance, are generally accepted to be as useful proximate indicators of quality in humans as ornaments and weaponry are in animals. The influence of dynamic, non-physical traits is much more controversial, but the attention of researchers is gradually turning to this interesting area. Defining the limits of such enquiry, in terms of what kinds of behavioural traits can be useful and reliable cues of mate quality, is a key step. It is hoped that the predictions generated here will stimulate further progress.

Summary

In most human societies, individuals make comparisons between numerous potential mates. Recent research on the biological determinants of mate preferences explores the idea that attractive physical characteristics might be cues of underlying good genes. The first half of this chapter summarizes this work on physical cues of mate quality, including facial, bodily, vocal, and olfactory traits. In the second half, I speculate on how broad principles that arise out of this research might be directly transposed to help us understand the potential effects of good genes on behaviour and 'body language'. The reliability of behavioural cues betraying mate quality is likely to determine how far we can apply biological interpretations on behaviour, and an outline for how researchers might tackle this issue is proposed.

Acknowledgements

I was stimulated to think about reliability of non-physical traits by staff and students at the Evolutionary Biology of Communication PhD

course in June 2007 at the University of Copenhagen. I thank them all. I also thank John Lycett for helpful discussions.

References

- Andersson, M. (1994). *Sexual Selection*. Princeton University Press, Princeton, NJ.
- Archer, D. and Akert, R.M. (1977). Words and everything else: verbal and nonverbal cues in social interpretation. *Journal of Personality and Social Psychology*, **35**, 443–449.
- Barber, N. (1995). The evolutionary psychology of physical attractiveness: asexual selection and human morphology. *Ethology and Sociobiology*, **16**, 395–424.
- Bateson, M. and Healy, S.D. (2005). Comparative evaluation and its implications for mate choice. *Trends in Ecology and Evolution*, **20**, 659–664.
- Bradbury, J. and Gibson, R. (1983). Leks and mate choice. In: P. Bateson (ed.), *Mate Choice*, pp. 109–138. Cambridge University Press, Cambridge.
- Brown, W.M., Cronk, L., Grochow, K., Jacobson, A., Liu, C.K., Popovic, Z., and Trivers, R. (2005). Dance reveals symmetry especially in young men. *Nature*, **438**, 1148–1150.
- Buston, P.M. and Emlen, S.T. (2003). Cognitive processes underlying human mate choice: the relationship between self-perception and mate preference in Western society. *Proceedings of the National Academy of Sciences of the USA*, **100**, 8805–8810.
- Collins, S.A. (2000). Men's voices and women's choices. *Animal Behaviour*, **60**, 773–780.
- Collins, S.A. and Missing, C. (2003). Vocal and visual attractiveness are related in women. *Animal Behaviour*, **65**, 997–1004.
- Cornwell, R.E., Boothroyd, L., Burt, D.M. et al. (2004). Concordant preferences for opposite-sex signals? Human pheromones and facial characteristics. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 635–640.
- Daly, M. and Wilson, M. (1983). *Sex, Evolution and Behavior*. PWS Publishers, Boston, MA.
- Dixon, A.F., Halliwell, G., East, R., Wignarajah, P., and Anderson, M.J. (2003). Masculine somatotype and hirsuteness as determinants of sexual attractiveness to women. *Archives of Sexual Behavior*, **32**, 29–39.
- Eibl-Eibesfeldt, I. (1970). *Ethology, the Biology of Behaviour*. Holt, Rinehart, and Wilson, New York.
- Ekman, P. (1982). *Emotion in the Human Face*. Cambridge University Press, Cambridge.
- Evans, S., Neave, N., and Wakelin, D. (2006). Relationships between vocal characteristics and body size and shape

- in human males: an evolutionary explanation for a deep male voice. *Biological Psychology*, **72**, 160–163.
- Feinberg, D.R., Jones, B.C., Little, A.C., Burt, D.M., and Perrett, D.I. (2005). Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices *Animal Behaviour*, **69**, 561–568.
- Feinberg, D.R., Jones, B.C., Law-Smith, M.J. *et al.* (2006). Menstrual cycle, trait estrogen level, and masculinity preferences in the human voice. *Hormones and Behavior*, **49**, 215–222.
- Fink, B., Manning, J.T., Neave, N., and Grammer, K. (2004). Second to fourth digit ratio and facial asymmetry. *Evolution and Human Behavior*, **25**, 125–132.
- Fink, B., Neave, N., and Seydel, H. (2007a). Male facial appearance signals physical strength to women. *American Journal of Human Biology*, **19**, 82–87.
- Fink, B., Seydel, H., Manning, J.T., and Kappeler, P.M. (2007b). A preliminary investigation of the associations between digit ratio and women's perception of men's dance. *Personality and Individual Differences*, **42**, 381–390.
- Gangestad, S.W. and Scheyd, G.J. (2005). The evolution of human physical attractiveness. *Annual Review of Anthropology*, **34**, 523–548.
- Gangestad, S.W. and Simpson, J.A. (2000). The evolution of human mating: trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, **23**, 573–587.
- Gangestad, S.W. and Thornhill, R. (2003). Facial masculinity and fluctuating asymmetry. *Evolution and Human Behavior*, **24**, 231–241.
- Gangestad, S.W., Thornhill, R., and Yeo, R.A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology*, **15**, 73–85.
- Gangestad, S.W., Simpson, J.A., Cousins, A.J., Garver-Apgar, C.E., and Christensen, P.N. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science*, **15**, 203–207.
- Grammer, K. and Thornhill, R. (1994). Human (*Homo sapiens*) facial attractiveness and sexual selection: the role of symmetry and averageness. *Journal of Comparative Psychology*, **108**, 233–242.
- Grammer, K., Honda, M., Jütte, A., and Schmitt, A. (1999). Fuzziness of nonverbal courtship communication unblurred by motion energy detection. *Journal of Personality and Social Psychology*, **77**, 487–508.
- Grammer, K., Fink, B., Möller, A.P., and Thornhill, R. (2003). Darwinian aesthetics: sexual selection and the biology of beauty. *Biological Reviews*, **78**, 385–407.
- Grammer, K., Fink, B., Möller, A.P., and Manning, J.T. (2005). Physical attractiveness and health: comment on Weeden and Sabini (2005). *Psychological Bulletin*, **131**, 658–661.
- Havlicek, J., Roberts, S.C., and Flegr, J. (2005). Women's preference for dominant male odour: effects of menstrual cycle and relationship status. *Biology Letters*, **1**, 256–259.
- Hinde, R.A. (1972). *Nonverbal Communication*. Cambridge University Press, Cambridge.
- Honekopp, J., Rudolph, U., Beier, L., Liebert, A., and Müller, C. (2007). Physical attractiveness of face and body as indicators of physical fitness in men. *Evolution and Human Behavior*, **28**, 106–111.
- Hughes, S.M. and Gallup, G.G. (2003). Sex differences in morphological predictors of sexual behavior—Shoulder to hip and waist to hip ratios. *Evolution and Human Behavior*, **24**, 173–178.
- Hughes, S.M., Dispenza, F., and Gallup, G.G. (2004). Ratings of voice attractiveness predict sexual behavior and body configuration. *Evolution and Human Behavior*, **25**, 295–304.
- Jacob, S., McClintock, M.K., Zelano, B., and Ober, C. (2002). Paternally inherited HLA alleles are associated with women's choice of male odor. *Nature Genetics*, **30**, 175–179.
- Johnson, K.L. and Tassinari, L.G. (2007). Compatibility of basic social perceptions determines perceived attractiveness. *Proceedings of the National Academy of Sciences of the USA*, **104**, 5246–5251.
- Jones, B.C., Little, A.C., Penton-Voak, I.S., Tiddeman, B.P., Burt, D.M., and Perrett, D.I. (2001). Facial symmetry and judgements of apparent health – support for a 'good genes' explanation of the attractiveness–symmetry relationship. *Evolution and Human Behavior*, **22**, 417–29.
- Jones, B.C., Little, A.C., Burt, D.M., and Perrett, D.I. (2004a). When facial attractiveness is only skin deep. *Perception*, **33**, 569–576.
- Jones, B.C., Little, A.C., Feinberg, D.R., Penton-Voak, I.S., Tiddeman, B.P., and Perrett, D.I. (2004b). The relationship between shape symmetry and perceived skin condition in male facial attractiveness. *Evolution and Human Behavior*, **25**, 24–30.
- Jones, B.C., Little, A.C., Boothroyd, L. *et al.* (2005). Women's physical and psychological condition independently predict their preference for apparent health in faces. *Evolution and Human Behavior*, **26**, 451–457.
- Kendon, A., Harris, R.M., and Key, M.R. (eds) (1975). *The Organization of Behavior in Face-to-face Interaction* Mouton, The Hague.
- Kniffin, K.M. and Wilson, D.S. (2004). The effect of non-physical traits on the perception of physical attractiveness – three naturalistic studies. *Evolution and Human Behavior*, **25**, 88–101.
- Langlois, J.H., Kalakanis, L., Rubenstein, A.J., Larson, A., Hallamm, M., and Smoot, M. (2000). Maxims or myths

- of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, **126**, 390–423.
- Little, A.C. and Jones, B.C. (2006). Attraction independent of detection suggests special mechanisms for symmetry preferences in human face perception. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 3093–3099.
- Little, A.C., Burt, D.M., Penton-Voak, I.S., and Perrett, D.I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 39–44.
- Little, A.C., Jones, B.C., Penton-Voak, I.S., Burt, D.M., and Perrett, D.I. (2002). Partnership status and the temporal context of relationships influence human female preferences for sexual dimorphism in male face shape. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1095–1100.
- Little, A.C., Penton-Voak, I.S., Burt, D.M., and Perrett, D.I. (2003). Investigating an imprinting-like phenomenon in humans: partners and opposite-sex parents have similar hair and eye colour. *Evolution and Human Behavior*, **24**, 43–51.
- Locke, J.L. (2005). Looking for, looking at: social control, honest signals and intimate experience in human evolution and history. In: P.K. McGregor (ed.), *Animal Communication Networks*, pp. 416–441. Cambridge University Press Cambridge.
- Manning, J.T. (1995). Fluctuating asymmetry and body weight in men and women: implications for sexual selection. *Ethology and Sociobiology*, **16**, 145–153.
- Manning, J.T. (2002). *Digit Ratio: a Pointer to Fertility, Behaviour and Health*. Rutgers University Press, New Brunswick, NJ.
- Maynard Smith, J. and Harper, D. (2003). *Animal Signals*. Oxford University Press, Oxford.
- Mays, H.L.J. and Hill, G.E. (2004). Choosing mates: good genes versus genes that are a good fit. *Trends in Ecology and Evolution*, **19**, 555–559.
- Mehrabian, A. (1972). *Nonverbal Communication*. Aldine, Chicago.
- Miller, G. (2000). *The Mating Mind*. William Heinemann, London.
- Møller, AP (1992). Female swallow preference for symmetrical male sexual ornaments. *Nature*, **357**, 238–240.
- Neave, N., Laing, S., Fink, B., and Manning, J.T. (2003). Second to fourth digit ratio, testosterone and perceived male dominance. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2167–2172.
- Pawlowski, B. and Dunbar, R.I.M. (1999). Impact of market value on human mate choice decisions. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 281–285.
- Pawlowski, B. and Jasienska, G. (2005). Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biological Psychology*, **70**, 38–43.
- Pawlowski, B., Dunbar, R.I.M., and Lipowicz, A. (2000). Evolutionary fitness—tall men have more reproductive success. *Nature*, **403**, 156.
- Penton-Voak, I.S. and Chen, J.Y. (2004). High salivary testosterone is linked to masculine male facial appearance in humans. *Evolution And Human Behavior*, **25**, 229–241.
- Penton-Voak, I.S., Perrett, D.I., Castles, D.L., Kobayashi, T., Burt, D.M., Murray, L.K., and Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature*, **399**, 741–742.
- Penton-Voak, I.S., Jones, B.C., Little, A.C., Baker, S., Tiddeman, B.P., Burt, D.M., and Perrett, D.I. (2001). Symmetry, sexual dimorphism in facial proportions and male facial attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 1617–1623.
- Penton-Voak, I.S., Little, A.C., Jones, B.C., Burt, D.M., Tiddeman, B.P., and Perrett, D.I. (2003). Female condition influences preferences for sexual dimorphism in faces of male humans (*Homo sapiens*). *Journal of Comparative Psychology*, **117**, 264–271.
- Perrett, D.I., Lee, K.J., Penton-Voak, I.S. et al. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, **394**, 884–887.
- Peters, M., Rhodes, G., and Simmons, L.W. (2007). Contributions of the face and body to overall attractiveness. *Animal Behaviour*, **73**, 937–942.
- Petrie, M. (1994). Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, **371**, 598–599.
- Posamentier, M.T. and Abdi, H. (2003). Processing faces and facial expressions. *Neuropsychology Review*, **13**, 113–143.
- Poyatos, F. (2002). *Nonverbal Communication across Disciplines*. John Benjamins Publishing Company, Philadelphia, PA.
- Prokosch, M.D., Yeo, R.A., and Miller, G.F. (2005). Intelligence tests with higher g-loadings show higher correlations with body symmetry: evidence for a general fitness factor mediated by developmental stability. *Intelligence*, **33**, 203–213.
- Puts, D.A., Gaulin, S.J.C., and Verdolini, K. (2006). Dominance and the evolution of sexual dimorphism in human voice pitch. *Evolution and Human Behavior*, **27**, 283–296.
- Renninger, L.A., Wade, T.J., and Grammer, K. (2004). Getting that female glance: patterns and consequences of male nonverbal behavior in courtship contexts. *Evolution and Human Behavior*, **25**, 416–431.

- Reynolds, J.D. and Gross, M.R. (1990). Costs and benefits of female mate choice—is there a lek paradox? *The American Naturalist*, **136**, 230–243.
- Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, **57**, 199–226.
- Rhodes, G. and Zebrowitz, L.A. (2002). *Facial Attractiveness*. Ablex, Westport, CT.
- Rhodes, G., Proffitt, F., Grady, J., and Sumich, A. (1998). Facial symmetry and the perception of beauty. *Psychonomic Bulletin and Review*, **5**, 659–669.
- Rhodes, G., Simmons, L.W. and Peters, M. (2005). Attractiveness and sexual behavior: does attractiveness enhance mating success? *Evolution and Human Behavior*, **26**, 186–201.
- Riggio, R.E., Widaman, K.F., Tucker, J.S., and Salinas, C. (1991). Beauty is more than skin deep—components of attractiveness. *Basic and Applied Social Psychology*, **12**, 423–439.
- Rikowski, A. and Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 869–874.
- Roberts, S.C. and Gosling, L.M. (2003). Genetic similarity and quality interact in mate choice decisions by female mice. *Nature Genetics*, **35**, 103–106.
- Roberts, S.C. and Little, A.C. (2008). Good genes, complementary genes and human mate preference. *Genetica*, **132**, 309–321.
- Roberts, S.C., Little, A.C., Gosling, L.M. *et al.* (2005a). MHC-assortative facial preferences in humans. *Biology Letters*, **1**, 400–403.
- Roberts, S.C., Little, A.C., Gosling, L.M. *et al.* (2005b). MHC-heterozygosity and human facial attractiveness. *Evolution and Human Behavior*, **26**, 213–226.
- Roney, J.R. and Maestripieri, D. (2004). Relative digit lengths predict men's behavior and attractiveness during social interactions with women. *Human Nature*, **15**, 271–282.
- Rubenstein, A.J. (2005). Variation in perceived attractiveness—differences between dynamic and static faces. *Psychological Science*, **16**, 759–762.
- Saxton, T.K., Caryl, P.G., and Roberts, S.C. (2006). Vocal and facial attractiveness judgments of children, adolescents and adults: the ontogeny of mate choice. *Ethology*, **112**, 1179–1185.
- Schaal, B. and Porter, R.H. (1991). Microsmatic humans revisited—the generation and perception of chemical signals. *Advances in the Study of Behavior*, **20**, 135–199.
- Scheib, J.E., Gangestad, S.W., and Thornhill, R. (1999). Facial attractiveness, symmetry, and cues to good genes. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1913–1917.
- Singh, D. (1995). Female judgment of male attractiveness and desirability for relationships—role of waist-to-hip ratio and financial status. *Journal of Personality and Social Psychology*, **69**, 1089–1101.
- Thornhill, R. and Gangestad, S.W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, **3**, 452–460.
- Thornhill, R. and Gangestad, S.W. (2006). Facial sexual dimorphism, developmental stability, and susceptibility to disease in men and women. *Evolution and Human Behavior*, **27**, 131–144.
- Thornhill, R., Gangestad, S.W., Miller, R., Scheyd, G., McCullough, J.K., and Franklin, M. (2003). Major histocompatibility genes, symmetry and body scent attractiveness in men and women. *Behavioral Ecology*, **14**, 668–678.
- Thornhill, R. and Grammer, K. (1999). The body and face of woman: one ornament that signals quality? *Evolution and Human Behavior*, **20**, 105–120.
- Wedekind, C., Seebeck, T., Bettens, F., and Paepke, A.J. (1995). MHC-dependent mate preferences in humans. *Proceedings of the Royal Society B: Biological Sciences*, **260**, 245–249.
- Weisfeld, G.E., Czilli, T., Phillips, K.A., Gall, J.A., and Lichtman, C.M. (2003). Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *Journal of Experimental Child Psychology*, **85**, 279–295.
- Wellings, K., Collumbien, M., Slaymaker, E. *et al.* (2006). Sexual behaviour in context: a global perspective. *The Lancet*, **368**, 1706–1728.
- Zhao, W., Chellappa, R., Phillips, P.J., and Rosenfeld, A. (2003). Face recognition: a literature survey. *ACM Computing Surveys*, **35**, 399–459.