

Good genes, complementary genes and human mate preferences

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Abstract The past decade has witnessed a rapidly growing interest in the biological basis of human mate choice. Here we review recent studies that demonstrate preferences for traits which might reveal genetic quality to prospective mates, with potential but still largely unknown influence on offspring fitness. These include studies assessing visual, olfactory and auditory preferences for potential good-gene indicator traits, such as dominance or bilateral symmetry. Individual differences in these robust preferences mainly arise through within and between individual variation in condition and reproductive status. Another set of studies have revealed preferences for traits indicating complementary genes, focussing on discrimination of dissimilarity at genes in the major histocompatibility complex (MHC). As in animal studies, we are only just beginning to understand how preferences for specific traits vary and inter-relate, how consideration of good and compatible genes can lead to substantial variability in individual mate choice decisions and how preferences expressed in one sensory modality may reflect those in another. Humans may be an ideal model species in which to explore these interesting complexities.

Keywords HLA · Disassortative · Heterozygosity · Menstrual cycle · Evolutionary psychology · Sexual dimorphism · Masculinity · Compatibility · Fluctuating asymmetry

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Abbreviations

MHC Major Histocompatibility Complex
HLA Human Leukocyte Antigen
FA Fluctuating Asymmetry
2D:4D second to fourth digit ratio

Introduction

The past two or three decades have seen enormous progress in our understanding of mate preferences in animals and the kinds of benefits that accrue to individuals from their mate choice decisions. In a wide variety of taxa, studies have shown, for example, that females in particular attend to phenotypic traits displayed amongst potential mates that indicate their underlying genetic quality (e.g. Petrie 1994). They are also sensitive to the degree of complementarity between their own genes and those of potential mates; often this means choosing from amongst the most genetically dissimilar individuals available (Brown 1997; Jordan and Bruford 1998; Penn and Potts 1999). Furthermore, decisions made at a particular mating event may not necessarily reflect choices on subsequent occasions or opportunities. For example, in mated pairs exhibiting a relatively high degree of genetic similarity, individuals are more likely to seek out extra-pair partners than those that appear to have made a better choice first time round (e.g. Blomqvist et al. 2002; Freeman-Gallant et al. 2003).

Many of these exciting advances have been closely followed by studies in humans. These are often led by zoologists interested in human behaviour as a natural extension to their main or prior research interests, or by psychologists interested in individual differences in mate

preference. The predominant result of this vigorous and flourishing research activity is that, time and again, humans can be shown to express preferences and choices that closely mirror the patterns evident in animal studies.

In this paper, we review some of these recent discoveries with particular reference to those that reveal a predilection for underlying genetic quality. We begin by presenting an outline of research demonstrating attention to potential indicator traits displayed by human males, and discuss the nature and source of individual variation in preferences for these traits amongst females. We then provide an overview of studies investigating sensitivity to phenotypic indicators of genetic similarity, including those that investigate the association between preferences and degree of allele sharing at the major histocompatibility complex, MHC. Finally, we discuss several key directions for future studies, including how preferences for good-gene indicator traits and genetic compatibility are integrated during mate choice decisions, how different sensory modalities may occasionally reveal apparently conflicting preferences, and how idealised preferences measured in the laboratory are reflected in actual mate choice. We argue that human studies may provide a fruitful approach to testing key predictions that apply not only to humans but also across species.

Mate preferences and indicator traits

The monogamous mating system prevalent in many human populations has usually been attributed to the need for a substantial degree of paternal care for extremely altricial young (Lovejoy 1981; Marlowe 2000). For this reason, ideas about mate choice in humans have historically centred on direct benefits. Studies from evolutionary psychology indicate that, while males jealously guard their mate's sexual fidelity, females are more concerned about the loss of resources that might result from a mate's extra-pair relationship rather than the relationship itself (Daly et al. 1982). This is with good reason: in Australian aboriginal families, women in monogamous marriages bear significantly more children, and benefit from improved infant survival, compared to those in polygynous marriages (Chisholm and Burbank 1991), while within monogamous marriages, male wealth predicts reproductive success (e.g. Klindworth and Voland 1995, reviewed in Barrett et al. 2001).

Despite this historic focus, the importance of potential indirect benefits has recently been receiving much attention. While one might expect even monogamous human females to be moderately sensitive to cues of potential indirect benefits, their potential importance is reinforced by evidence from comparative studies of sexual dimorphism

(Harcourt et al. 1981) and Y-chromosomal diversity (Dupanloup et al. 2003) that indicate a moderately polygynous past. Amongst the burgeoning number of studies on human mate preferences, particular interest has focussed on putative 'good gene' indicator traits. Robust generalised preferences have been demonstrated for a variety of traits. These include aspects of body shape that may indicate physical strength (Barber 1995; Maisey et al. 1999; Fan et al. 2005) and body size: height, for example, correlates with reproductive success in large cohorts of Polish and British men (Pawlowski et al. 2000; Nettle 2002) and this appears to be at least partly due to mate choice, since bachelors are shorter than married men of the same age (Pawlowski et al. 2000; Sear 2006).

Furthermore, just as in animal studies, preference for symmetrical features has been a significant focus for laboratory studies on human mate preferences. Levels of fluctuating asymmetry (FA), a potential measure of developmental stability (Møller and Swaddle 1997), are inversely correlated with height (Manning 1995), suggesting an underlying connection between the two traits. FA is also inversely correlated with measures of physical prowess (Manning and Pickup 1998), sexual displays (Brown et al. 2005) and attractiveness ratings of body odour (Rikowski and Grammer 1999). In a similar vein, negative correlations are found between body FA and facial attractiveness (Gangestad et al. 1994), and between facial FA and judgements of attractiveness (Penton-Voak et al. 2001). Controlling for potential confounds, computer graphic studies have shown preferences for faces manipulated to increase symmetry (Rhodes et al. 1998; Perrett et al. 1999; Little et al. 2001). However, in a clever experiment, Scheib et al. (1999) showed that although participants' ratings of male facial attractiveness correlated with facialmetric symmetry (i.e. directly measured from a subset of facial features), they were not especially adept in rating symmetry per se in faces. Furthermore, the correlation between symmetry and attractiveness persisted even when attractiveness judgments were based on assessments of only half a face (divided vertically so that symmetry cues were unavailable, or at least markedly reduced). Scheib et al. suggest that FA correlates with other good-gene indicators that are proximally involved in expression of preference, such as facial masculinity (see also Gangestad and Thornhill 2003) and skin health (Jones et al. 2004b).

Sexual dimorphism in face shape certainly plays an important role in perception of attractiveness (Perrett et al. 1998). As with height (Pawlowski et al. 2000) and muscular body shapes (Barber 1995), very extreme values of dimorphism appear to be avoided. Women tend to prefer an intermediate level of facial masculinity (Perrett et al. 1998; Rhodes et al. 2000), suggesting these traits are not subject to runaway selection. Nonetheless, preferences are robust

across different women and across cultures (Perrett et al. 1998; Rhodes et al. 2000). Perceived facial masculinity and dominance is correlated with measures of physical strength (Fink et al. 2007) and the ratio of the second to fourth digits (2D:4D), a putative marker of prenatal exposure to testosterone (Fink et al. 2004; but see Koehler et al. 2004). The 2D:4D ratio also appears to be associated with attractiveness judged by short interactive conversations (Roney and Maestriperi 2004), even though Neave et al. (2003) did not find a significant correlation between 2D:4D ratio and facial attractiveness using male photographs. However, despite this evidence, the link proposed by Scheib et al. between symmetry and dimorphic features has been disputed by Penton-Voak et al. (2001), who hypothesised that a more likely reliable correlate of symmetry would be facial skin condition, since they would both reflect underlying healthiness (see also Jones et al. 2001).

Subsequent research has verified that skin condition may well be the perceptual cue that can explain the symmetry–attractiveness relationship in the human face. Jones et al. (2004b) showed that men with more symmetrical faces were perceived as having more healthy skin than those with asymmetric faces, and that the influence on judgments of skin colour and texture appear independent of face shape (see also Jones et al. 2004a). Indeed, judgments about perceived health of potential mates may be a reliable general influence on mate preferences in humans that has links to a number of other traits (Thornhill and Gangestad 1999; Fink and Penton-Voak 2002; Grammer et al. 2003, 2005; Shackelford et al. 2005; Zaidel et al. 2005; Rhodes 2006), including sexual dimorphism (Rhodes et al. 2003) and heterozygosity (Roberts et al. 2005b).

If these preferred traits do indeed indicate underlying good-genes, a key prediction is that there should be significant co-variation in attractiveness of different phenotypic characters within individuals. An increasing body of evidence suggests this is so. Ratings of attractiveness of male axillary body odour correlate with ratings of the same men's facial attractiveness (Rikowski and Grammer 1999; Thornhill et al. 2003) and psychometric dominance (Havlicek et al. 2005). Similarly, male voice attractiveness is positively correlated with attractiveness of faces (Saxton et al. 2006), body shape (Hughes et al. 2004) and with ratings of social dominance (Puts et al. 2006). Although not considered in detail here, it is interesting to note that these inter-trait correlations are also often evident in women (Thornhill and Grammer 1999; Feinberg et al. 2005).

This brief summary of an extensive and rapidly expanding literature serves to illustrate that a number of male traits may be used as phenotypic indicators of underlying good genes, and that females both detect and attend to these markers when expressing mate preferences. What is less clear is whether these preferences are in fact

related to indirect benefits gained for example through offspring viability, or whether they are primarily related to potential direct benefits. These could include the possibility of enhanced resource acquisition and paternal care, or reduced likelihood of contracting disease for both female and offspring. On face value, it is difficult to distinguish between the effects of these two kinds of benefits, but consideration of condition- and context-dependent shifts in preference can help to tease them apart.

Individual variation: relative mate value and adaptive preference shifts

Preferences for the good-gene indicator traits described above have been almost always shown, whenever tested, to be relatively robust and consistent across cultures (Feingold 1992; Perrett et al. 1994; Penton-Voak et al. 1999b; Langlois et al. 2000; Penton-Voak et al. 2004). Within populations, however, there remains substantial individual variation in both sexually-selected traits and in the preferences expressed for these traits. Efforts to explain the source of this variation converge around at least two major effects: (i) variation resulting from between-subject differences in relative mate value and (ii) that brought about through within-subject hormonally-mediated shifts associated with menstrual cycle phase.

The idea that individuals vary in mate value stems from the depiction of mate choice as taking place within a biological marketplace, in which mate value is determined by the laws of supply and demand (e.g. Pawlowski and Dunbar 1999). Differences in relative mate value are normally evaluated by evolutionary psychologists through assessments of the attractiveness of individual judges. This is achieved by asking the participants to rate themselves (on a Likert scale of say, 1–10, where high scores indicate high attractiveness) or by a panel of independent assessors viewing photographs taken of the judges under standard conditions. Comparisons indicate that self-judgments correlate highly with other-rated judgments (Feingold 1988) and non-facial correlates of attractiveness (Wade et al. 2004), indicating that the former are an easily-measured estimate of a meaningful biological attribute (c.f. Little et al. 2001). Under these conditions, relative mate value predicts individual differences in expressed preferences for several of the traits described above, including facial masculinity and symmetry in male faces (Little et al. 2001). Preferences for facially-mediated indicator traits may also correlate with alternative measures of female mate value such as waist:hip ratio (Penton-Voak et al. 2003; Jones et al. 2005b). Finally, Little and Mannion (2006) show that these mate value-linked preferences are fluid and sensitive to change in market forces. They

manipulated self-perceptions of attractiveness by exposing experimental participants to very attractive or unattractive same-sex images, and this manipulation induced shifts in preference expression for sexually dimorphic faces, such that changes in the judges' self-perceived market value led to a corresponding change in their degree of choosiness. Figure 1 illustrates some examples of masculinised and feminised composite faces used in such experiments.

Research into preference shifts for putative good-gene marker traits has gathered pace in the years following Gangestad and Thornhill's (1998; see also Penton-Voak et al. 1999b) study showing that women in the fertile phase of their cycle (but not those in non-fertile cycle phases nor those using hormonal contraception) expressed preferences for the body odours of relatively symmetrical men and that the strength of this preference correlated with conception probability. The authors suggested that stronger preference for indicator traits at conception than elsewhere within the cycle suggests the possibility that these shifts may reflect a



Fig. 1 Examples of masculinised (left) and feminised (right) composite female and male faces. To make each composite face, individual faces had salient points marked on them and were then blended together to make the single identity and the average face shape. Images were transformed using the difference between a composite of 50 men and a composite of 50 women

selected mechanism by which females maximise the genetic quality of a mating partner, and hence reap maximal indirect benefits (and perhaps also direct ones). Consistent with this idea, cyclic shifts have been demonstrated with regard to preferences as varied as facial masculinity (Fig. 2; Penton-Voak et al. 1999b; Penton-Voak and Perrett 2000) and facialmetrics (Danel and Pawlowski 2006), body masculinity (Little et al. 2007) and height (Pawlowski and Jasienska 2005), behavioural displays (through rating of video clips: Gangestad et al. 2004), axillary body odour of dominant men (Havlicek et al. 2005) and vocal characteristics related to male dominance (Puts 2005; Feinberg et al. 2006). One should note that there are occasional exceptions: Koehler et al. (2002) and Cárdenas and Harris (2007) find no evidence for cyclic shifts related to male facial symmetry, while Jones et al. (2005a) show that preferences for health are conversely stronger in non-fertile stages when progesterone levels are highest, an intriguing result perhaps related to sensitivities to health in pregnancy or differences in signals of current versus long-term health.

It seems likely that these cycle-contingent adaptive shifts play a significant role in primary mate selection, given that courtship often lasts for more than one cycle. However, it has also been hypothesised that they may play

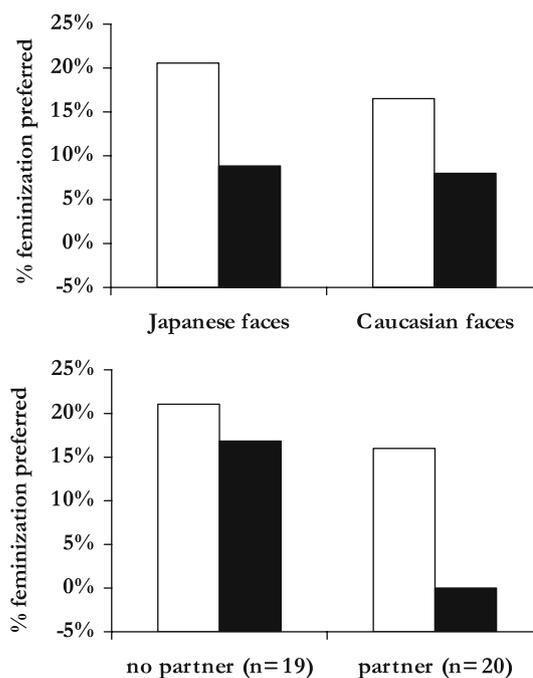


Fig. 2 Effects of conception risk on femininity preferred in male faces by Japanese females in Japanese and Caucasian faces (upper; open bars: non-fertile phase, shaded bars: fertile phase). Preferences during high and low conception risk phases for subjects with and without a partner (lower), data for Japanese and Caucasian faces combined. Redrawn from Penton-Voak et al. (1999b)

a role in choice of extra-pair partners (Gangestad and Thornhill 1998), since they are coincident with reported likelihood of extra-pair matings (Bellis and Baker 1990). This is supported by recent within-subject experiments showing that females are more attractive to males around ovulation than at other times, whether assessed by males on the basis of their odour (Singh and Bronstad 2001), faces (Roberts et al. 2004) or integral appearance (including clothing differences, Haselton et al. 2007) and that females show reduced commitment to their primary relationship in fertile cycle phases (Jones et al. 2005a). Whether these adaptive shifts function primarily in choice of primary or extra-pair partners need not be mutually exclusive, but the latter would emphasise indirect benefits. Indeed, Gangestad and Simpson (2000) argue that women trade-off paternal investment and genetic quality offered by primary and potential extra-pair partners, what they term 'strategic pluralism'. Consistent with this, women are found to prefer more masculine male faces for short-term relationships and relatively feminine faces for long-term relationships (Little et al. 2002), suggestive that women are sensitive to the context of mating. While strategic pluralism was initially framed as a generalised mixed-mating strategy, cyclic adaptive shifts can be seen to be at least symptomatic of such a strategy, if not a critical component. Thus, initial partner choice could secure direct benefits through paternal care while extra-pair matings could serve, amongst other possible factors, to enhance indirect benefits (Gangestad and Simpson 2000; Gangestad et al. 2005a, 2007).

Two corollaries of this are that (i) women who are in established partnerships, who have thus secured investment in offspring, should be particularly sensitive to good-gene indicator traits, but relatively insensitive to cues of paternal investment, in potential extra-pair partners, and (ii) that females exhibiting lower mate value should be more likely to seek extra-pair partners than those of relatively high value. Recent evidence supports both these predictions. First, women in established relationships express greater preference for male facial masculinity than single women (Little et al. 2002). It is worth noting an important underpinning of this result: that personality attribution studies show that individuals associate high facial masculinity with perception of high mating and low parenting effort (e.g. Kruger 2006). Cyclical preference shifts for dominant male odours are also more marked among women in established partnerships than single women (Havlicek et al. 2005), as are changes in flirtatiousness (Haselton and Gangestad 2006). Second, shifts in preferences toward lower-pitch male voices (Feinberg et al. 2006) and more dominant faces (Johnston et al. 2001) are especially evident in less-feminine, and therefore potentially less attractive women who may be less likely to be able to maintain a long-term relationship with a high quality male. Shifts in flirtatious-

ness and motivation to seek extra-pair partners, and corresponding reported attentiveness by primary partners, are also greater for women who are of relatively low mate value (Haselton and Gangestad 2006; Pillsworth and Haselton 2006), such as those having high levels of FA (Gangestad et al. 2005b).

Mate preferences, complementary genes and heterozygosity

In a landmark paper, Brown (1997; see also Brown 1999) argued that heterozygosity could be an influential factor underlying female mate choice decisions, primarily with regard to offspring but also through direct benefits resulting from choice of heterozygous mates. This idea has spawned a flurry of empirical tests in animals and humans alike. The human studies have focussed on MHC genes (known in humans as human leukocyte antigen, HLA), which code for the body's immune response. Following previous mouse studies (e.g. Yamazaki et al. 1976; Yamaguchi et al. 1981; Potts et al. 1991), initial research focussed on body odour perception and the degree of allele-sharing between individuals producing the odour and those smelling it. At least for most studies to date (Table 1), it appears that HLA-haplotype can be discriminated solely through odour, and that human females prefer the odours of HLA-dissimilar over those of HLA-similar males. Although the results show different levels of effect and have often proved controversial (Hedrick and Loeschke 1996; Wedekind and Seebeck 1996; McClintock et al. 2002; Wedekind 2002), they are consistent with most rodent studies (Yamazaki et al. 1976; Potts et al. 1991; Jordan and Bruford 1998; Roberts and Gosling 2003), and suggest a mechanism for increasing offspring heterozygosity at the

Table 1 Summary of MHC similarity results in human mate preferences

Stimulus	Females	Males	Study
<i>Dissimilarity tests</i>			
Odour	Dissimilar	–	Wedekind et al. (1995)
Odour	Dissimilar	Dissimilar	Wedekind and Furi (1997)
Odour	Intermediate	–	Jacob et al. (2002)
Odour	No preference	Dissimilar	Thornhill et al. (2003)
Odour	Dissimilar	No preference	Santos et al. (2005)
Face	No preference	No preference	Thornhill et al. (2003)
Face	Similar	–	Roberts et al. (2005a)
<i>Heterozygosity tests</i>			
Odour	Heterozygous	No preference	Thornhill et al. (2003)
Face	No preference	No preference	Thornhill et al. (2003)
Face	Heterozygous	–	Roberts et al. (2005b)

MHC. This is reinforced by the finding of Wedekind and colleagues (1995; Wedekind and Furi 1997) that HLA-dissimilar odours reminded sniffers of their partners or ex-partners more often than did HLA-similar odours. In common with the previously-described menstrual effects on preferences, there is also some evidence that hormonal status may play a part in preference expression, as use of hormonally-based oral contraceptives might reverse or nullify preferences for HLA-dissimilarity (Wedekind et al. 1995); however, no effect of cycle phase was found in Thornhill et al.'s (2003) study.

More recently, research into MHC-correlated effects has diversified to investigate whether they might also extend to preferences for heterozygosity in mates, and whether they might be expressed in other sensory modalities, such as visual cues available in the human face. Direct benefits accruing to females from choosing MHC-heterozygous mates potentially include reduced risk of contracting disease for both female and offspring, since such mates would more likely be healthy (Thursz et al. 1997; Carrington et al. 1999; McClelland et al. 2003), and in consequence they should also benefit from a more protracted period of high quality paternal care (Kirkpatrick and Ryan 1991; Roberts et al. 2005b). Consistent with Brown's (1997, 1999) 'good-genes as heterozygosity' hypothesis, Thornhill et al. (2003) found a relationship between heterozygosity of male axillary odour and odour attractiveness (although the effect appeared stronger in the luteal phase). The chemical nature of the odour difference which reveals heterozygosity is unknown but might be related to odour intensity (Wedekind et al. 2006). In the same sample, Thornhill et al. found no correlation between heterozygosity and facial appearance. However, another study did report this effect (Roberts et al. 2005b): as predicted, increasing heterozygosity across three MHC loci correlated positively with perceived attractiveness and this appeared to be determined by perceived healthiness of skin derived from the cheek area. Furthermore, this effect appeared robust to changes in the degree of similarity at the same loci between stimulus and rater. This is an important point, because male facial attractiveness appears also to be independently and positively related to MHC allele-sharing (Roberts et al. 2005a), the reverse effect to that found using body odour. In an experiment designed as a visual analogue of Wedekind et al.'s (1995) odour study, where women judged attractiveness of 3 MHC-similar and 3 MHC-dissimilar male faces, women preferred faces of the former, particularly when asked to rate faces within the context of choosing a long-term partner (Roberts et al. 2005a).

The commonality between the studies summarised in Table 1 are that they are laboratory-based. Wedekind's studies (Wedekind et al. 1995; Wedekind and Furi 1997) go some way to bridging the gap between laboratory

preference and real behaviour, through the reported memory associations between odours perceived in the lab and those of current or former partners. However, the ultimate influence of HLA on mate choice can only be reliably measured by genotyping actual, established partners. Like laboratory preferences, results from a small number of previous studies are equivocal, with one (in North American Hutterites) suggesting negative assortative mating (Ober et al. 1997) and others finding no significant trends (Japan, Ihara et al. 2000; Amazon basin, Hedrick and Black 1997) or even slight positive assortative mating (USA, Rosenberg et al. 1983). The differences in these studies may be at least partly attributable to underlying differences in genetic heterogeneity within the sample and in differences in representations of ethnic groups. In the study by Ober et al., for example, the tightly-knit Hutterite community may have lower overall heterogeneity than many other human populations, while Rosenberg et al. did not control for the potentially confounding effects of ethnicity. MHC allele frequencies vary across ethnic groups (Cao et al. 2001), so assortative mating within ethnic group could suggest spurious links to MHC-correlated mating patterns. Although they do not specify the ethnic composition of their sample, Garver-Apgar et al. (2006) have carried out arguably the most sensitive analysis, showing that, within a sample of 48 American couples, MHC allele-sharing correlated positively with women's lower sexual interest toward primary partners, especially mid-cycle, as well as with their interest in extra-pair partners.

The future: integration of traits in decision-making

So far, we have outlined some of the main areas of focus in research on potential genetic underpinning of human mate preferences. This is a vigorous and bustling field; consequently, this is not a comprehensive review but a snapshot of some important findings. It seems that, with these and other findings, we have now acquired most of the pieces of the jigsaw, but have yet to construct the picture of how mate choice decisions are reached. In this section, we explore three key outstanding questions which have emerged from the plethora of studies over the past decade or so, together with new insights gained by studies in other species, which we believe will take us some way towards this objective.

How do compatibility cues interact with other good gene indicators?

The recent finding that expression of genetic compatibility-based preferences are modulated by simultaneous preferences for good gene indicator traits in mice (Roberts and

Gosling 2003) suggests that both additive and non-additive components to mate choice need to be considered for a fuller understanding of genetic effects on individual mate choice decisions. Two replete but largely separate literatures exist, one recounting how female mice are attuned to cues of quality and dominance signalled by specific odorous compounds within male mouse urine, the second describing how females attend to cues of genetic dissimilarity that are also available in male urine via a set of different aromatic compounds. Roberts and Gosling showed that both kinds of information simultaneously influenced mate preferences and explored how these cues were differentially weighted. The coalescence of these very different influences on mate choice has since been thoroughly reviewed by Mays and Hill (2004) and Neff and Pitcher (2005), and has been modelled by Colegrave et al. (2002).

Understanding the nature of the interaction between preferences for good-gene indicator traits and those revealing genetic compatibility is as much required in human studies as in animals. Based on existing evidence, much of this research in humans is likely to focus on these effects in terms of odour and facial preferences, and at least with regard to genetic compatibility, on the MHC.

While the polymorphic nature of the MHC makes it relatively difficult to design experiments with humans compared with, for example, those using MHC-congenic mouse strains (Roberts and Gosling 2003), it is certainly possible to draw interesting and insightful conclusions using the degree of allele-sharing (e.g. Wedekind et al. 1995; Jacob et al. 2002; Thornhill et al. 2003; Roberts et al. 2005a) or the rarity of alleles, relative to the remainder of the participant sample (Thornhill et al. 2003).

Furthermore, at least with regard to facial preference studies, it may be possible to design experiments based on a qualitative proxy for the degree of genetic compatibility, without the need for invasive blood sampling of participants or expensive genotyping. The finding that women judge as more attractive the faces of men who share several MHC alleles with themselves compared with faces of men with whom they share few or no alleles (Roberts et al. 2005a) indicates that degree of MHC-similarity (at least) is somehow perceived through facial shape. Given this, computerised face-morphing techniques bestow on experimenters the opportunity to manipulate facial appearance with the assumption that the degree of facial similarity is indicative of genetic similarity. Figure 3 shows an example of how one neutral face can be manipulated to appear more or less similar to a target face (here, the actress Uma Thurman, but normally this would be the face of the experimental participant). Experimenters could then measure preferences of participants in response to stimulus sets that co-vary facial self-resemblance with the expression of

putative indicator traits. Several experiments have been carried out using these techniques to study face perception in relation to facial similarity (Penton-Voak et al. 1999a; DeBruine 2002, 2005), including one that demonstrates menstrual cycle shifts (DeBruine et al. 2005), so the stage is now set to combine these resemblance effects with indicator traits.

Finally, studies that specifically aim to investigate possible correlations between heterozygosity and mate quality should be careful to also take compatibility effects into account. Using 441 humans genotyped at 3 MHC loci, and 281 peafowl (*Pavo cristatus*) typed at 13 microsatellite loci, Roberts et al. (2006) showed that simple allele-sharing correlated positively with heterozygosity, at least under conditions of moderate to high polymorphism. Furthermore, the nature of this correlation between heterozygosity and similarity altered qualitatively when an alternative index of genetic similarity was used: Queller and Goodnight's (1989) relatedness measure, commonly used in behavioural genetics studies. One implication of these correlations is that, in tests of either simple (dis)assortative mating preferences or the good-genes-as-heterozygosity hypothesis, it may be premature to draw firm conclusions without taking both heterozygosity and similarity into account.

How do individuals integrate cues in different sensory modalities?

Where several different cues are available to potential mates and reliably signal good genes, it seems reasonable to suppose that these should usually be congruent in their direction and size of effect. This prediction has been met, for example, in the reported correlations between facial attractiveness and both odour (Rikowski and Grammer 1999) and voice perception (Saxton et al. 2006). In similar vein, if preferences themselves represent biologically meaningful choices, then the patterns of preference expression should also be concordant within individuals. This has been illustrated in an experiment showing that the strength of preference by individual judges for markers of dominance in faces is matched by their preference strength for markers of dominance in the odour domain (Cornwell et al. 2004).

However, a notable exception to this rule appears to lie in preferences related to choice of complementary mates when tested using either odour or faces. Most studies that have investigated relationships between MHC-correlated odour perception have found disassortative preferences (Table 1), in common with studies in rodents, birds, reptiles and fish (Yamazaki et al. 1976; Landry et al. 2001; Freeman-Gallant et al. 2003; Olsson et al. 2003). In contrast, where an effect has been shown, MHC-correlated

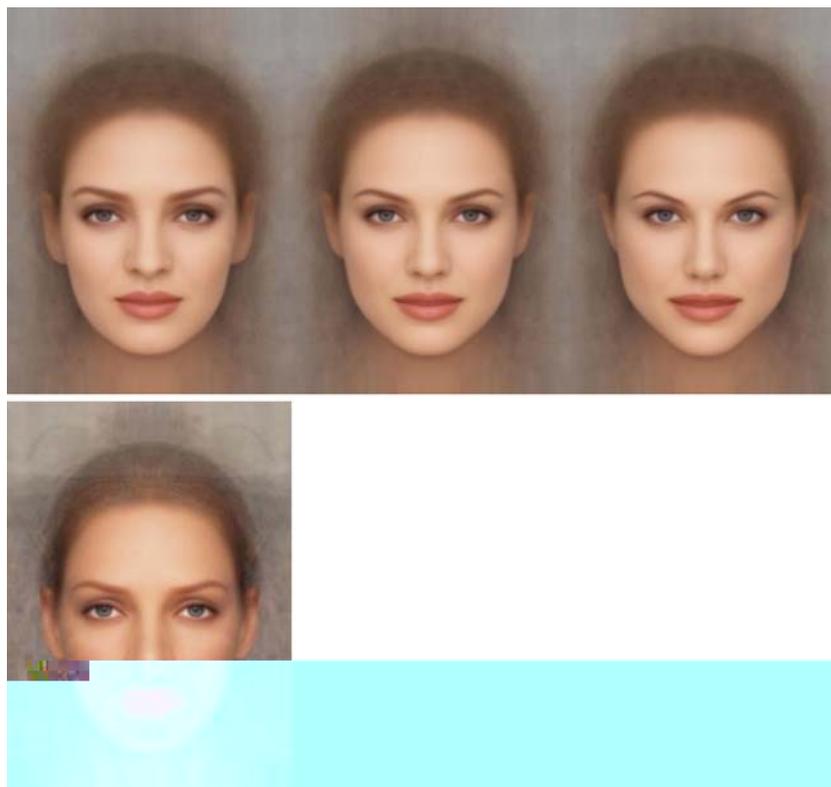


Fig. 3 Examples of transformed face images manipulating self-similarity. Here we use a female celebrity, Uma Thurman (lower), compared against an average female celebrity (the middle face in the panel). To create these two images a composite image was made from 5 different pictures of Uma Thurman (lower image), and five different celebrity composites made in the same way (top centre image), respectively. Similarity was manipulated by using the difference in

shape between Uma's face shape and the average female celebrity image to move the same prescribed distance (plus or anti) away from the mean. This shape change was applied to the average face so that only shape was evident in the images. The 50% anti-transform is the face on the right of the panel, and the 50% plus-transform is on the left of the panel. Preferences for self similarity can be assessed by showing participants a variety of such transformed pairs of images

facial preferences appear to be assortative (Roberts et al. 2005a). While this surprising result would doubtless benefit from replication, its robustness might be attested for by its consistency with a large psychological literature on facially-assortative mate selection in humans. For example, there is assortative mating for facial attractiveness (Berscheid et al. 1973) and actual couples are perceived as being more facially similar than expected by chance (Griffiths and Kunz 1973; Hinsz 1989). Face-morphing studies demonstrate consistent results in the lab, particularly for long-term partners (DeBruine 2005). Studies testing these effects further suggest that these preferences develop through sexual imprinting-like effects on opposite-sex parents (Berezkei et al. 2002; Little et al. 2003; Berezkei et al. 2004), as indeed has been suggested for development of odour preferences (Jacob et al. 2002). If, then, assortative facial preferences appear robust, how can we explain the discrepancy in preference for similarity when assessed in odours and faces? One explanation is that the combination of two preferences could effectively screen out opposite extremes of a continuum of similarity

(Roberts et al. 2005a), thereby potentially achieving a degree of intermediate genetic similarity in mates, consonant with the idea of optimal outbreeding (Bateson 1978). This filtering effect may well be asymmetric with respect to the two modalities and its stringency may vary depending on individual condition and other effects described previously, but further tests are needed to investigate these possibilities.

How do mate preferences relate to actual mate choice?

With a few notable exceptions, the studies described in this review examine mate preferences, not mate choice. Most examine preferences in a laboratory setting, with a sample of participants judging and rating stimulus sets under tightly controlled conditions, often within the context of an imaginary choice situation. Participants are usually drawn from an age-restricted sample of young adults, commonly university students around 18–22 years old, using age-matched stimulus sets. Such studies measure idealised preferences, an estimate of the kinds of choices an individual would

make were s/he unshackled from the constraints of the real-world mating market. This approach has logistical advantages and is necessary to establish the veracity of specific effects. In view of these advantages, it is of course not unique to human mate choice studies. Memory associations with or comparisons between laboratory-presented stimuli and current or former partners (Wedekind et al. 1995; Wedekind and Furi 1997) are an intermediate step towards actual behaviour. However, there remains a palpable need for more work in real couples to demonstrate that sometimes subtle preferences survive in reality, to estimate their magnitude, and to explore interactions with other effects.

Two examples illustrate the kind of approaches that may prove profitable, one relating to a good-gene effect, the other investigating compatibility among partnerships. In DeBruine et al.'s (2006) study, women's strength of preference for male facial masculinity was measured in the laboratory using idealised preference tests. This was assessed by measuring the percentage of choices for the more masculine version within pairs of images of the same face manipulated along a masculine–feminine shape dimension (Fig. 1). The masculinity of partners was then assessed by asking female participants to rate their partners on a 1–7 Likert scale, where a score of 4 indicates that partners were of approximately average masculinity compared to most men. After controlling for the age of participant and partner (because perception of facial masculinity can be confounded with age), partner masculinity was shown to be significantly related to measured idealised preference.

In the study by Garver-Apgar et al. (2006), the investigators elegantly combined the advantages and subtleties afforded by human studies with a field-based approach similar to that used in avian studies which examine within-pair compatibility and incidence of extra-pair partnerships. In 48 actual couples with a median relationship length of 17 months, the proportion of allele sharing at 3 MHC loci (the same used by other studies described in Table 1) predicted not only women's self-reported desire for extra-pair relationships (particularly expressed during the fertile phase of the menstrual cycle) but also the number of her extra-pair partners within the current relationship. This pattern of results is reminiscent of and consistent with the discovery that allele-sharing within social pairs of several bird species predicts levels of extra-pair paternity and copulations (e.g. Blomqvist et al. 2002; Foerster et al. 2003; Freeman-Gallant et al. 2006), including at the MHC (Freeman-Gallant et al. 2003).

A final point worthy of consideration in this context is how the benefits to be gained by judicious choice of mates can be demonstrated in humans. In societies that have undergone the demographic transition to lower birth rates and mortality (particularly of infants), it seems unlikely

that this can be achieved by the use of gross measures of reproductive success, such as number of surviving offspring, that might be adequate for some animal studies. A more sensitive approach is required. In terms of indirect benefits through offspring fitness, and correlating with choice for compatible genes, variables that might be illuminating in future work could include difficulties in conception, incidence of miscarriage, infant birth weight and infant health. Indeed, the degree of HLA-similarity within couples (either at specific loci such as HLA-B and HLA-C, or across the HLA region) has been linked to elevated incidence of fetal loss (Ober et al. 1985, 1988) and longer inter-birth intervals (Ober et al. 1985). Other factors which could be linked to either direct or indirect benefits from choice, in addition to those already described from Garver-Apgar et al. (2006), might include measures of relationship satisfaction, relationship length and incidence of divorce (c.f. Vollrath and Milinski 1996).

Conclusions

When it comes to general principles governing mate preferences, what we find in animals to be true will be customarily echoed in humans when the appropriate study is done. Although they sometimes use different methodologies to those employed in animal research, studies in evolutionary psychology such as those described here address very similar questions; in fact they are often indistinguishable. The fact that many of these studies are conducted by researchers who have either a background in zoology or related research programmes on other species is arguably symptomatic of the utility and interest in understanding human preferences and decisions, despite not a little scepticism from some of those who focus on other taxa. There are, of course, limitations to what questions can be asked in any system, but humans have proved an interesting model to test ideas developed in non-human animals. Perhaps there is also potential in the future for ideas generated in human work to inform that done more widely in other species.

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