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Genetic dissimilarity, genetic diversity, and mate preferences in humans

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Abstract

It is clear that genes at the major histocompatibility complex (MHC) are involved in mate preferences in a range of species, including humans. However, many questions remain regarding the MHC's exact influence on mate preference in humans. Some research suggests that genetic dissimilarity and individual genetic diversity (heterozygosity) at the MHC influence mate preferences, but the evidence is often inconsistent across studies. In addition, it is not known whether apparent preferences for MHC dissimilarity are specific to the MHC or reflect a more general preference for genome-wide dissimilarity, and whether MHC-related preferences are dependent on the context of mate choice (e.g., when choosing a short-term and long-term partner). Here, we investigated whether preferences for genetic dissimilarity are specific to the MHC and also whether preferences for genetic dissimilarity and diversity are context dependent. Genetic dissimilarity (number of alleles shared) influenced male, but not female, partner preferences, with males showing a preference for the faces of MHC-dissimilar females in both mating contexts. Genetic diversity [heterozygosity (H) and standardized mean (d^2)] influenced both male and female preferences, regardless of mating context. Females preferred males with greater diversity at MHC loci (H) and males preferred females with greater diversity at non-MHC loci (d^2) in both contexts. Importantly, these findings provide further support for a special role of the MHC in human sexual selection and suggest that male and female mate preferences may work together to potentially enhance both male and female reproductive success by increasing genetic diversity in offspring.

Keywords: MHC; Mate preferences; Genetic diversity; Genetic similarity; Disassortative mate preferences; Facial attractiveness

1. Introduction

The major histocompatibility complex (MHC, or human leukocyte antigen, HLA, in humans) is found in all jawed vertebrates and contains genes that are implicated in many important biological functions, including immune functioning (Doherty & Zinkernagel, 1975; Lechler & Warrens, 2000) and mate preferences (reviewed in Havlicek & Roberts, 2009; Milinski, 2006). Because MHC genes are important for several aspects of individual fitness, they are particularly good candidates for studying the genetic benefits of mate choice (Apanius, Penn, Slev, Ruff, & Potts, 1997; Schwensow, Fietz, Dausmann, & Sommer, 2008; Tregenza & Wedell, 2000). MHC genes are directly involved in immune functioning, where each allele codes for peptides that can detect a restricted range of antigens derived from pathogens and parasites. MHC alleles are expressed codominantly. Therefore, increased allelic diversity at the MHC should be beneficial as it broadens the range of antigens an individual can detect and present to T cells for destruction (Doherty & Zinkernagel, 1975). There is evidence that greater MHC diversity (heterozygosity) enhances immunocompetence in some cases (e.g., Carrington et al., 1999; Duggal et al., 2004; Froeschke & Sommer, 2005; Hraber, Kuiken, & Yusim, 2007; McClelland, Penn, & Potts, 2003; Oliver, Telfer, & Piertney, 2009; Schwensow, Fietz, Dausmann, & Sommer, 2007; Thursz, Thomas, Greenwood, & Hill, 1997), although not in all (e.g., Hill et al., 1991; Meyer-Lucht & Sommer, 2005).

The exact effects of the MHC on mate preferences in humans are still debated, but are likely to involve preferences for MHC diversity (heterozygosity) and/or compatibility of parental MHC genotypes (e.g., Havlicek & Roberts, 2009; Roberts, Hale, & Petrie, 2006; Tregenza & Wedell, 2000). For example, the disassortative mating hypothesis proposes

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that individuals may prefer mates with dissimilar MHC alleles to avoid inbreeding and to gain indirect benefits in terms of increased genetic diversity and disease resistance in offspring (Brown, 1997, 1999; Freeman-Gallant, Meguerdichian, Wheelwright, & Sollecito, 2003; Penn & Potts, 1998; Potts, Manning, & Wakeland, 1991; Tregenza & Wedell, 2000; Yamazaki et al., 1976; Ziegler, Kentenich, & Uchanska-Ziegler, 2005). Additionally, the good-genes-as-heterozygosity hypothesis (Brown, 1997, 1999) proposes that MHC diversity should be preferred in a mate if it is associated with individual quality. Preferences for MHC-diverse mates could therefore be adaptive because high-quality mates should be able to provide direct benefits, including parental care, resources, and reduced risk of contagion to their partner and offspring (Kirkpatrick & Ryan, 1991; Roberts, Little, Gosling, Perrett, et al., 2005; Sauermann et al., 2001). Moreover, choosing a genetically diverse, or heterozygous, mate could also potentially increase genetic variability in the offspring since heterozygosity is on average heritable (Hoffman, Forcada, Trathan, & Amos, 2007; Mitton, Schuster, Cothran, & De Fries, 1993). Mate preferences for genetic diversity and dissimilarity are not mutually exclusive, and both may contribute to the maintenance of high levels of polymorphism observed at MHC loci (e.g., Apanius et al., 1997; Piertney & Oliver, 2006).

Preferences for MHC-dissimilar mates have been found in a range of nonhuman species, including lizards (Olsson et al., 2003), fish (Landry, Garant, Duchesne, & Bernatchez, 2001), birds (Freeman-Gallant et al., 2003; but see Bonneaud, Chastel, Federici, Westerdahl, & Sorci, 2006), and mice (Penn & Potts, 1998; Potts et al., 1991; Yamazaki et al., 1976), while female sticklebacks choose mates to achieve an intermediate level of MHC diversity in their offspring (Aeschlimann, Haberli, Reusch, Boehm, & Milinski, 2003; Milinski, 2003, 2006). In humans, studies of preferences for MHC dissimilarity in mates yield inconsistent results (recently reviewed in Havlicek & Roberts, 2009). Couples were found to be more dissimilar at the MHC than by chance in two reproductively isolated populations, in the Hutterites (Ober et al., 1997) and Mormons (Chaix, Cao, & Donnelly, 2008), but not across the genome (Mormon sample), suggesting that the dissimilarity preference is specific to the MHC (Chaix et al., 2008). However, no evidence of MHC-based mate choice in couples was found in studies across a range of ethnic populations (Chaix et al., 2008; Hedrick & Black, 1997; Ihara, Aoki, Tokunaga, Takahashi, & Juji, 2000; Jin, Speed, & Thompson, 1995; Nordlander et al., 1983; but see Rosenberg, Cooperman, & Payne, 1983). Interestingly, increased MHC similarity in romantic couples has been associated with relationship dissatisfaction and a tendency to seek extra-pair partners for females (Garver-Apgar et al., 2006).

In the laboratory, a female preference for the odor of MHC-dissimilar males was found in two studies (Wedekind & Furi, 1997; Wedekind, Seebeck, Bettens, & Paepke, 1995) but not in two larger studies (Roberts, Gosling, Carter, & Petrie, 2008; Thornhill et al., 2003). Additionally, Jacob, McClintock, Zelano, & Ober (2002) found a female preference for an intermediate level of MHC dissimilarity in males. Of three studies testing male preferences for female odor, two found a preference for MHC dissimilarity (Thornhill et al., 2003; Wedekind & Furi, 1997; see also Santos, Schinemann, Gabardo, & da Graca Bicalho, 2005).

Only one study has directly tested preferences for MHC dissimilarity in faces. Roberts, Little, Gosling, Jones, et al. (2005) conducted a study where each female rater was "prematched" with three MHC-similar and three MHC-dissimilar males. Contrary to past studies where a female preference for the odor of MHC-dissimilar males has been reported, Roberts, Little, Gosling, Jones, et al. (2005) found a female preference for the faces of MHC-similar men (see also Roberts, Little, Gosling, Perrett, et al., 2005). Roberts et al. suggested that the MHC-similarity preference is consistent with familial imprinting studies showing assortative preferences for facial appearance among actual couples (e.g., Bereczkei, Gyuris, Koves, & Bernath, 2002; Bereczkei, Gyuris, & Weisfeld, 2004). Thus, in humans, the current evidence for the MHC-disassortative mating hypothesis is mixed.

Preferences for genetic diversity (heterozygosity) at the MHC have been found in some nonhuman animals (reviewed in Kempenaers, 2007). For example, female fat-tailed dwarf lemurs (*Cheirogaleus medius*) prefer their social and extra-pair mates to be genetically diverse at both MHC and non-MHC loci (Schwensow, Fietz, et al., 2008). MHC diversity also predicted male mating success in rhesus macaques (*Macaca mulatta*, Sauermann et al., 2001). In humans, laboratory studies suggest that females prefer both the odor and the faces of men who have greater genetic diversity at MHC loci compared to less diverse males (Lie, Rhodes, & Simmons, 2008; Roberts, Little, Gosling, Perrett, et al., 2005; Thornhill et al., 2003), even when controlling for diversity at non-MHC loci (Lie et al., 2008). However, males do not show a preference for MHC diversity in female faces (Coetzee et al., 2007; Lie et al., 2008; Thornhill et al., 2003), but may prefer genetic diversity at loci outside the MHC (Lie et al., 2008). Thus, at least female preferences for male MHC diversity appear to be consistent with the good genes as heterozygosity hypothesis in humans.

Although there is evidence for MHC-related influences on mate preferences in many species (Havlicek & Roberts, 2009; Milinski, 2006; Penn, 2002; Penn & Potts, 1999), little is known about the relative importance of the MHC versus genetic background since most studies do not control for the potential influence of non-MHC loci (but see Chaix et al., 2008; Lie et al., 2008; Reusch, Häberli, Aeschlimann, & Milinski, 2001; Schwensow, Fietz, et al., 2008). Moreover, in humans, little is known about whether preferences for MHC dissimilarity or diversity are dependent on the mating context. That is, are they equally preferred in short-term and long-term mates? Roberts, Little, Gosling, Jones, et al.