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MHC-heterozygosity and human facial attractiveness

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Abstract

Females gain direct or indirect fitness benefits by choosing between males with traits indicating "good genes," but we usually know very little about the nature of these genes. However, it has been suggested that genetic quality may often be defined as heterozygosity at certain loci. Here, we show that heterozygosity at three key loci in the major histocompatibility complex (MHC) is associated with facial attractiveness: Faces of men who are heterozygous at all three loci are judged more attractive by women than faces of men who are homozygous at one or more of these loci. MHC genes code for proteins involved in immune response. Consistent with this function, faces of MHC heterozygotes are also perceived to be healthier. In a separate test, in the absence of any other cues, patches of skin from the cheeks of heterozygotes are judged healthier than skin of homozygotes, and these ratings correlate with attractiveness judgements for the whole face. Because levels of MHC similarity can influence mate preferences in animals and humans, we conducted a second experiment with genotyped women raters, finding that preferences for heterozygosity are independent of the degree of MHC similarity between the men and the female raters. Our results are the first to directly link facial attractiveness and a measure of genetic quality and suggest a mechanism to help explain common consensus concerning individual attractiveness.

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In a relatively monogamous species like humans, evolutionary benefits from choosing heterozygous mates could include prolonged parental care and reduced risk of contracting disease for females and their offspring.
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1. Introduction

Sexual selection theory asserts that males maximise reproductive success through seeking multiple matings, while females achieve this goal through discrimination of mate quality, or choosiness (Bateman, 1948; Trivers, 1972). Through mate choice, females gain direct and indirect benefits, where direct benefits include resources provided by males to females or offspring, and indirect benefits refer to genetic properties that enhance fitness of resulting progeny (Andersson, 1994; Kirkpatrick & Ryan, 1991). Females may base their discrimination on phenotypic or behavioural variation among candidate males in traits that signal genetic quality (Hasselquist, Bensch, & Schantz, 1996; Petrie, 1994) or genetic complementarity (usually dissimilar genotype: Potts, Manning, & Wakeland, 1991; Yamaguchi et al., 1981), or both (Colegrave, Kotiaho, & Tomkins, 2002; Roberts & Gosling, 2003).

In most cases, we know little about the exact nature of the good genes involved, although Brown (1997, 1999) has recently suggested that genetic quality, in this sense, may often be defined as heterozygosity at certain loci. He proposed that heterozygosity should be correlated with the expression of condition-dependent male traits and that females should value heterozygosity in their offspring and, in some cases, their mates. Many studies investigating influences of heterozygosity on mating patterns have focussed on genes in the major histocompatibility complex (MHC, known in humans as human leukocyte antigen loci, HLA). MHC genes encode proteins involved in immunological self/nonself recognition and are among the most polymorphic in the genome (Mungall et al., 2003).

It is now well-established that MHC disassortative mating preferences exist in several species, with beneficial effects in terms of offspring heterozygosity (Bernatchez & Landry, 2003; Jordan & Bruford, 1998; Penn & Potts, 1998), but the extent to which heterozygosity in mates plays a role in female mate preferences is less clear. Preferences for heterozygosity in mates could result in direct benefits to females, for example, through reduced risk of disease transmission or provision of high-quality paternal care (Kirkpatrick & Ryan, 1991) because heterozygous males are often less susceptible to infectious diseases (Carrington et al., 1999; McClelland, Granger, & Potts, 2003; McClelland, Penn, & Potts, 2003; Penn, Damjanovich, & Potts, 2002; Thursz, Thomas, Greenwood, & Hill, 1997). Although heterozygote mating advantages have been demonstrated less often than predicted by theory (Brown, 1997, 1999), higher reproductive success has been found in male rhesus macaques, *Macaca mulatta*, which were heterozygous at a Class II locus (Sauermann et al., 2001), and in male spotless starlings, *Sturnus unicolor*, of intermediate heterozygosity

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