

Research Report

Major Histocompatibility Complex Alleles, Sexual Responsivity, and Unfaithfulness in Romantic Couples

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ABSTRACT—*Preferences for mates that possess genes dissimilar to one's own at the major histocompatibility complex (MHC), a polymorphic group of loci associated with the immune system, have been found in mice, birds, fish, and humans. These preferences may help individuals choose genetically compatible mates and may adaptively function to prevent inbreeding or to increase heterozygosity and thereby immunocompetence of offspring. MHC-dissimilar mate preferences may influence the psychology of sexual attraction. We investigated whether MHC similarity among romantically involved couples (N = 48) predicted aspects of their sexual relationship. All women in our sample normally ovulated, and alleles at three MHC loci were typed for each person. As the proportion of MHC alleles couples shared increased, women's sexual responsivity to their partners decreased, their number of extra-pair sexual partners increased, and their attraction to men other than their primary partners increased, particularly during the fertile phase of their cycles.*

The major histocompatibility complex (MHC), found in vertebrates, is a set of genes coding for cell-surface markers the immune system uses to discriminate self from pathogens. MHC loci are highly polymorphic; there are many different variants individuals could possess at each gene site. Two unrelated individuals, then, are unlikely to possess identical MHC genotypes. Mice can detect MHC identities in scents of other mice (Yamazaki, Beauchamp, Curran, Baird, & Boyse, 2000) and

prefer mates who possess dissimilar MHC genotypes, based on scent (Penn & Potts, 1999). Such preferences also exist in species of birds (Freeman-Gallant, Meguerdichian, Wheelwright, & Sollecito, 2003), fish (Milinski et al., 2005), and lizards (Olsson et al., 2003), though not all vertebrate species possess them (e.g., Sommer, 2005).

Studies examining this preference in humans have yielded generally supportive but mixed evidence. Preferences for the scent of opposite-sex individuals with dissimilar MHC genotypes have been detected in three of four studies of normally ovulating women (Santos, Schinemann, Gabardo, & Bicalho, 2005; Wedekind & Furi, 1997; Wedekind, Seebeck, Bettens, & Paepke, 1995; cf. Thornhill et al., 2003)¹ and two of three studies of men (Thornhill et al., 2003; Wedekind & Furi, 1997; cf. Santos et al., 2005). A study of Hutterites found married couples to be more MHC-dissimilar than expected by chance (Ober et al., 1997); studies of South American Indian and Japanese couples did not (Hedrick & Black, 1997a; Ihara, Aoki, Tokumaga, Takahashi, & Juji, 2000).

Two non-mutually exclusive, adaptive hypotheses may explain MHC-dissimilar mate preferences (Penn & Potts, 1999). First, they may suppress inbreeding. Second, MHC-dissimilar mates produce offspring who are heterozygous at MHC loci. MHC alleles are expressed codominantly, with each coding for different cell-surface receptors. Relative to two redundant copies of a single allele, then, two distinct MHC alleles at a locus permit the immune system to recognize a greater range of foreign peptides (Brown, 1997). Indeed, heterozygous mice are more fit than homozygous mice when multiple strains of pathogens are

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¹In another study, women preferred the scent of MHC-similar men, but the preference measure used may not tap sexual attraction (Jacob, McClintock, Zelano, & Ober, 2002).

present (Penn, Damjanovich, & Potts, 2002). Among offspring of human couples who share MHC alleles, homozygotes are underrepresented, possibly because of in utero selection against homozygotes (Hedrick & Black, 1997b).

Given a sex difference in minimum parental investment (Trivers, 1972), past selection favoring genetically compatible mate choices may have been stronger on women than men. Accumulating evidence suggests that women possess adaptive design to seek genetic benefits for offspring at midcycle, when they are fertile (see Gangestad, Thornhill, & Garver-Apgar, 2005a, 2005b; also Havlicek, Roberts, & Flegr, 2005; Puts, 2005). Hence, preferences for MHC compatibility may be sensitive to women's fertility status (cf. Thornhill et al., 2003).

The current study is the first to test the hypothesis that MHC similarity predicts aspects of actual human sexual relationships. Specifically, we asked whether women paired with men with whom they share a relatively high proportion of MHC alleles, compared with women paired with men with whom they share a relatively low proportion of MHC alleles, are (a) less sexually responsive to their partners, (b) more likely to have had extrapair sex (sex with someone other than their partner) while involved with their partners, and (c) more attracted to extrapair men, particularly during the fertile phase of their cycles. We also examined the first two questions with respect to men and explored other aspects of couples' sex across the cycle.

METHOD

Participants were 48 romantically involved heterosexual couples recruited at the University of New Mexico. All women (ages 18–35) were normally ovulating. Participants were compensated with \$20 plus research credit for a psychology course or with either \$50 (if male) or \$70 (if female). Mean ages were 20.5 and 21.3 for the women and men, respectively ($SD = 3.1$ and 3.2). All couples were dating exclusively ($n = 36$), cohabiting ($n = 5$), or married ($n = 7$). No participant was divorced. Five women and 6 men had children; 4 couples had children together. Median relationship duration was 17 months (range = 1 month to 12 years). For analyses, relationship duration was truncated to 99 months and log-transformed to reduce positive skew; untransformed values yielded identical results. For 1 couple, data on age and relationship duration were missing; mean values were imputed.

The couples reported for three questionnaire sessions: one at the start of the study, one scheduled during the fertile period of the woman's cycle, and one scheduled during the nonfertile, luteal phase. Women reported to the lab for luteinizing hormone (LH) tests (using the over-the-counter Ovusign[®] tester) for up to 5 days, self-testing on weekends (verified by lab inspection) if necessary. All women included in the analyses surged within 5 days after or 2 days prior to their high-fertility session. Low-fertility sessions were conducted more than 5 days after an LH surge; we tried not to schedule these sessions during the last 3 days of the cycle.

Individuals completed questionnaires in separate private rooms. During the initial session, we obtained the following measures:

- *Relationship satisfaction on 29 attributes*: Two of these attributes were central to our hypotheses: “the extent to which [the relationship partner turns] me on sexually” and “how sexually adventurous [the relationship partner is] (with me).” Others included “financial resources,” “physical attractiveness,” “faithfulness and loyalty,” “intelligence,” and “ambition.”² Participants responded on 9-point scales ranging from 1 (*my partner does not satisfy me at all on this condition*) to 9 (*my partner completely satisfies me on this condition*).
- *Partner's perceived satisfaction*: Individuals rated their perception of their partners' satisfaction with them on the same 29 attributes, using 9-point scales ranging from 1 (*I do not satisfy my partner at all on this condition*) to 9 (*I completely satisfy my partner on this condition*).
- *Ellis's (1998) Partner-Specific Investment Inventory (both self- and partner-reports)*: For the analyses reported here, we used responses to five self-reported items (two reverse-coded) in this inventory that concern sexual responsivity: “I want to have sex with my partner,” “I try to please my partner sexually,” “I refuse to have sex with my partner,” “With my partner, I am a willing and enthusiastic sexual partner,” and “I am not sexually responsive to my partner.” Participants responded to the first three items on a 5-point scale from 0 (*never*) to 4 (*very often*) and to the last two items on a 5-point scale from 1 (*strongly disagree*) to 5 (*strongly agree*). Partner-reported items had identical content, with appropriately altered pronouns (e.g., “My partner wants to have sex with me.”). Responses were aggregated to form separate self- and partner-reports.³
- *Number of sex partners*: Participants reported the number of individuals other than their primary partner with whom they had sex while being romantically involved with their current primary partner, as well as with previous primary partners.
- *Sociosexual Orientation Inventory (SOI; Simpson & Gangestad, 1991)*: This instrument measures willingness to have sex in the absence of emotional closeness and commitment.

During sessions on low- and high-fertility days, we asked participants to report on their experiences, thoughts, and feelings in the past 2 days. Two questions assessed individuals' sexual attraction to their own partners during this period: “I felt strong sexual attraction toward my primary current partner” and “I fantasized about sex with a current partner.” Five questions assessed women's sexual attraction to men other than their

²A full list of the attributes is available from the authors upon request.

³Ellis's (1998) inventory also contains the item “I have sexual intercourse with my partner.” We did not include it in the reported analyses because it does not concern sexual responsivity per se. Its inclusion, however, made no substantive difference to the results. The full inventory, which participants completed, also includes a number of additional subscales concerning other facets of relationship investment that we did not examine for this report.

TABLE 1
Partial Correlations (η) Between Sexual Behaviors and Sharing of Major Histocompatibility Complex (MHC) Alleles

Sexual behavior	MHC sharing	MHC Sharing \times Fertility Status	MHC sharing	
			High-fertility session	Low-fertility session
Frequency of sex	-.24	-.11	-.20	-.15
Female-initiated sex	.08	.00	.05	.04
Male-initiated sex	.00	.11	.05	-.08
Women's report of orgasm	-.27	-.36*	-.39*	-.09
Women's rejection of male	.40*	.42*	.34 [†]	.14
Men's rejection of female	.16	.21	.19	-.19
Women's compliant sex	.40*	.03	.35*	.22

Note. Relationship duration (log-transformed), female's age, and order of sessions (high fertility first vs. low fertility first) were controlled in these analyses using repeated measures general linear modeling on SPSS. Positive MHC Sharing \times Fertility Status values reflect more positive associations between MHC sharing and the variable during the high-fertility phase than during the low-fertility phase; negative values reflect the converse. All analyses were based on participants' frequency estimates of events in the past 2 days. *Frequency of sex* was based on both partners' responses to "Had sex with a primary current partner." *Initiated sex* was based on self-reports on "Initiated sex." *Women's orgasm* was based on self-reports on "Experienced orgasm with a primary current partner." *Rejection* was based on self-reports on three items ("Was rejected after I initiated sex with my partner," "Got angry at my partner for rejecting sex with me," "Had my feelings hurt when my partner rejected sex with me") and partner's reports on three items ("Rejected my partner's attempts to initiate sex," "Made my partner angry for rejecting sex with [him/her]," "Caused my partner to have [his/her] feelings hurt when I rejected sex with [him/her]"). (Hence, these analyses partly reflect partners' reactions to rejection.) *Women's compliant sex* was based on women's responses to "Had sexual intercourse with my partner even though I didn't want to because he threatened to end our relationship otherwise" and "Had sexual intercourse with my partner when I didn't want to because I felt pressured by his continual arguments." All men reported zero frequency of their own or their partners' compliant sex.

[†] $p < .10$ (two-tailed), $p_{\text{rep}} > .878$. * $p < .05$ (two-tailed), $p_{\text{rep}} > .917$.

partner: "I felt strong sexual attraction toward someone other than a current partner," "I fantasized about sex with a stranger or acquaintance," "I fantasized about sex with a past partner," "I felt sexually aroused by the sight of a very physically attractive person (other than a primary current partner)," and "I felt sexually aroused by the scent of someone (other than a primary current partner)." Participants responded to these seven questions on 5-point scales ranging from 0 (*not at all*) to 4 (*a great deal*). Values were summed across items to create composite measures of attraction to partner and attraction to extrapair individuals. During these sessions, both male and female participants recorded the number of times in the past 2 days that they had engaged in a variety of sexual behaviors. See Table 1 for a list of these behaviors.

During one session, cells were scraped away from mucosal membranes on the inside of each participant's mouth and preserved. DNA was later typed for MHC alleles at the A, B, and DR β loci (see Thornhill et al., 2003). We successfully typed at least two loci for each individual; all three loci were typed for 37 couples (77%), and 92% of all possible loci were typed. Because complete typing was not available for all couples, we used the proportion of shared alleles at typed loci (range = 0 to .67) as our measure of MHC sharing.

RESULTS AND DISCUSSION

Relationship duration and participant's age were statistically controlled in all analyses. Following Killeen (2005), we report

p_{rep} rather than conventional p values. Unless otherwise noted, predicted effects were significant by directed conventional tests at $p < .05$ (Rice & Gaines, 1994).

Women's Sexual Responsivity and Satisfaction

As predicted, as the proportion of shared MHC alleles increased, women reported that they were less sexually responsive to their partners, $r(41) = -.35$, $p_{\text{rep}} = .945$, and men reported that their partners were less sexually responsive to them, $r(39) = -.33$, $p_{\text{rep}} = .932$ (see Fig. 1).

Similarly, as MHC sharing increased, women's satisfaction with the extent to which their partner aroused them sexually decreased, as assessed by their own reports, $r(43) = -.30$, $p_{\text{rep}} = .919$, and by their partners' reports, $r(43) = -.27$, $p_{\text{rep}} = .893$. MHC sharing negatively predicted men's satisfaction with how sexually adventurous their partner was with them, $r(42) = -.31$, $p_{\text{rep}} = .922$; the association with women's reports of men's satisfaction with women's sexual adventurousness fell short of statistical significance, $r(43) = -.25$, $p = .062$, $p_{\text{rep}} = .878$.

Of 27 other components of relationship satisfaction rated by men and women (none directly pertaining to sexual satisfaction) for both self and partner—108 ratings altogether—MHC sharing significantly predicted 8 (7.4%), a result close to chance levels. For none of these other components of relationship satisfaction did it significantly predict both self- and partner-reports. Though it is predictive of women's sexual satisfaction, MHC sharing does not broadly predict relationship satisfaction.

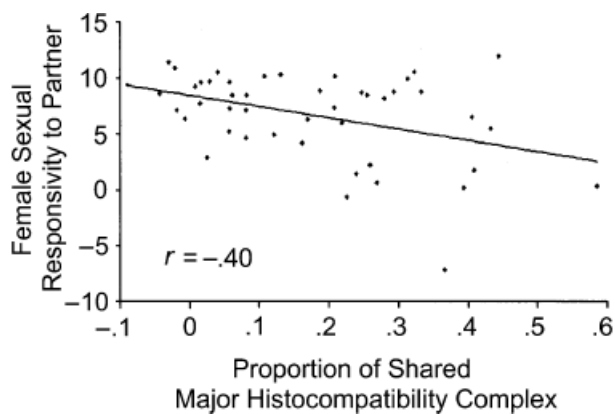


Fig. 1. Association between sharing of major histocompatibility complex (MHC) alleles and females' sexual responsiveness to their partners. The values for sexual responsiveness were obtained by averaging men's and women's reports, which had a correlation of .57. Age and relationship duration were controlled. Hence, both MHC sharing and women's sexual responsiveness are scaled as residuals partialing out age and relationship duration and centered around the sample mean.

Women's Extrapair Sex

As MHC sharing increased, women reported more extrapair sexual partners during the current relationship, $r(43) = .28$, $p_{\text{rep}} = .908$. This association held when women's general willingness to have casual sex (SOI score) was controlled, $r(42) = .33$, $p_{\text{rep}} = .939$. As expected, MHC sharing did not predict the number of extrapair partners women reported from previous relationships, $r(42) = -.10$, $p_{\text{rep}} = .676$, n.s., or the SOI score, $r(43) = -.02$, $p_{\text{rep}} = .530$, n.s. A repeated measures analysis showed that MHC sharing predicted the number of extrapair partners in the current relationship significantly more positively than it predicted the number of extrapair partners in past relationships, $F(1, 42) = 9.12$, $p_{\text{rep}} > .978$, $\eta = .42$.

Changes in Women's Sexual Attraction and Fantasy Across the Cycle

We conducted a 2 (fertility status: high vs. low fertility) \times 2 (target: partner vs. extrapair men) repeated measures analysis of variance on women's reports of attraction and fantasy, with MHC sharing treated as a quantitative predictor and order of session (high fertility first vs. low fertility first) controlled as a between-subjects factor. (One couple was excluded because they were no longer involved during the last two sessions.) A significant Target \times MHC Sharing interaction emerged, $F(1, 36) = 5.11$, $p_{\text{rep}} = .938$, $\eta = .35$; MHC sharing predicted attraction to extrapair men more positively than it predicted attraction to partners. Also as predicted, fertility status moderated this interaction, $F(1, 36) = 6.76$, $p_{\text{rep}} = .960$, $\eta = .40$. Follow-up analyses on fertile women revealed a sizable Target \times MHC Sharing interaction, $F(1, 36) = 11.35$, $p_{\text{rep}} = .986$; MHC sharing predicted fertile women's attraction to extrapair men, $r(36) = .41$, $p_{\text{rep}} = .964$, but not their attraction to primary partners,

$r(36) = -.20$, $p = .146$, $p_{\text{rep}} = .800$. Analyses on nonfertile women's attraction yielded no comparable interaction, $F(1, 36) = 0.42$, n.s., $p_{\text{rep}} = .675$; for these women, sharing did not predict attraction to extrapair men or to partners during the luteal phase, $r(36) = .08$, $p_{\text{rep}} = .633$, and $r(36) = -.08$, $p_{\text{rep}} = .629$, n.s.⁴

Men's Sexual Responsivity and Extrapair Sex

We found no evidence that MHC sharing predicts men's sexual responsiveness to partners, whether self- or partner-reported, $r(37) = -.12$, $p_{\text{rep}} = .691$, and $r(39) = -.09$, $p_{\text{rep}} = .645$, n.s., or men's satisfaction with their partners' ability to arouse them sexually, $r(42) = -.13$, $p_{\text{rep}} = .719$, and $r(42) = -.02$, $p_{\text{rep}} = .527$, n.s. Men reported no increase in extrapair sex as the proportion of shared MHC alleles increased, $r(40) = -.11$, $p_{\text{rep}} = .683$, n.s. As MHC sharing increased, men perceived partners to be less satisfied with their sexual adventurousness, $r(42) = -.29$, $p_{\text{rep}} = .915$, but women's self-reports for this item revealed no effect of MHC sharing, $r(42) = .11$, $p_{\text{rep}} = .696$, n.s. Future research should further evaluate the null results reported here for the relation between men's sexual responsiveness and MHC sharing.

Additional Measures

Table 1 presents partial correlations between reported frequencies of sexual behaviors and MHC sharing, both overall and on high- and low-fertility days. MHC sharing did not predict frequency of sex. As sharing increased, however, women more often rejected partners' attempts to initiate sex (particularly when they were fertile) or consented to sex only after threats or arguments by partners. When fertile, women experienced fewer orgasms with partners as MHC sharing increased, an interesting finding in light of conjectures that women's orgasm functions to retain sperm in the female reproductive tract (Baker & Bellis, 1995).

MHC Sharing

On average, couples shared 0.98 alleles—17.2% of those typed. By chance under random mating, they would have shared 20.3%. This difference fell short of statistical significance, $t(47) = 1.26$, $p = .137$, $p_{\text{rep}} = .808$. We analyzed Class I (A and B) and Class II (DR β) loci separately. For Class I loci, there was

⁴On the basis of data obtained from a larger sample of which the current sample is a subset, we recently reported that fluctuating asymmetry (FA) of male primary partners also predicts women's attraction to extrapair men, particularly when women are fertile (Gangestad et al., 2005b). When both MHC sharing and partner's FA were included as predictors of female sexual attraction, both significantly moderated the Target (extrapair men vs. partner) \times Fertility Status interaction, $F(1, 35) = 6.48$, $p_{\text{rep}} = .958$, $\eta = .39$, and $F(1, 35) = 3.75$, $p_{\text{rep}} = .908$, $\eta = .25$, respectively. Hence, these putative markers of (ancestral) intrinsic and compatible genetic benefits from male partners independently affect patterns of women's sexual interests (see Jennions & Petrie, 2000).

significant disassortative pairing: 14.6% shared vs. 20.5% by chance, $t(47) = -2.21$, $p_{\text{rep}} = .928$. On DR β , we found no disassortative pairing: 22.3% shared vs. 20.3% by chance, $t(46) = 0.51$, $p_{\text{rep}} = .640$, n.s. Because only Class I receptors present self-peptides, perhaps they alone produce certain information about their nature (e.g., through self-peptides shed from skin) that can be detected in scent (e.g., Leinders-Zufall et al., 2004). Associations presented in this report, however, were not driven by sharing at Class I loci alone.⁵

CONCLUSION

This study provides the first evidence that MHC sharing negatively predicts women's sexual responsivity to and sexual satisfaction with partners. Associations emerged with both self- and partner-reports, which strongly suggests that these effects are real. Furthermore, as MHC sharing increases, women report more extrapair partners (but only in the current relationship) and experience greater attraction to extrapair men relative to their partners, particularly on fertile days of their cycles. These effects may be mediated by scent, though explicit investigation of that possibility awaits future research.

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⁵Analyses of the effects of MHC sharing at the two classes of loci are available from the authors upon request.

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