



Original Article

Genetic analysis of human extrapair mating: heritability, between-sex correlation, and receptor genes for vasopressin and oxytocin

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ABSTRACT

As in other socially monogamous species, pair-bonded humans commonly engage in sex with a partner other than their primary mate. For men, extrapair mating is straightforwardly explained from an adaptive perspective in terms of the reproductive benefits of multiple mates. For women, whose reproductive output is limited by their reproductive biology rather than by their number of mates, the adaptive benefits of extrapair mating are less obvious. Dominant adaptive explanations focus on women obtaining genetic benefits for their offspring by mating with high-quality extrapair partners. Non-adaptive explanations have rarely been considered in humans, but recent findings in birds suggest that females' predisposition to extrapair mating may result from indirect selection, via direct selection on males and a between-sex genetic correlation. To examine the plausibility of this non-adaptive explanation of extrapair mating in women, we used data on recent extrapair mating in 7,378 Finnish twins and their siblings. Genetic modelling showed within-sex broad-sense heritability—i.e. the percentage of variation in extrapair mating due to genetic variation—of 62% in men and 40% in women. There was no between-sex correlation in extrapair mating, making indirect selection unlikely. Based on previous animal and human findings, we also tested for association of the arginine vasopressin receptor 1A gene (*AVPR1A*) and oxytocin receptor gene (*OXTR*) with extrapair mating. We found gene-based association for *AVPR1A* in women but not in men, and *OXTR* showed no significant association in either sex. Overall, these findings confirm genetic underpinnings of extrapair mating in humans, but do not suggest that women's predisposition to extrapair mating is due to selection on men.

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1. Introduction

In most socially monogamous species (e.g. many birds and some mammals), both male and female members of a pair commonly seek copulations with other individuals (Barash & Lipton, 2001; Griffith, Owens, & Thuman, 2002; Reichard, 1995). Males have a low minimal investment to reproduce (i.e. one copulation), so males mating outside the pair can increase their reproductive output; any genes predisposing males to seek extrapair mates would be adaptive (in the absence of strong countervailing selective pressures). However, females' reproductive potential is constrained by their biological capacity to reproduce, so females do not necessarily increase their reproductive potential by extrapair mating—in addition, females may also incur direct costs from extrapair copulations, such as disease transmission and withdrawal of paternal investment into offspring of uncertain paternity (Albrecht, Kreisinger, & Pialek, 2006; Arnqvist & Kirkpatrick, 2005). As such, it is

not clear why females in socially monogamous species have evolved such that they mate outside the pair (Forstmeier, Nakagawa, Griffith, & Kempenaers, 2014).

There have been proposed a number of adaptive explanations for female extrapair mating, along with challenges to the traditional theoretical and empirical basis for the expectation of sex-differentiation in adaptation for extrapair mating (Gowaty, 2013; Gowaty, Kim, & Anderson, 2012). The dominant explanation of female extrapair mating has been that it can be adaptive if females are able to obtain extrapair mates of higher genetic quality than their social mates, thereby increasing the genetic quality of their offspring and increasing their number of grandoffspring (Jennions & Petrie, 2000; Neff & Pitcher, 2005). However, reviews of the empirical evidence in socially monogamous birds suggest that the genetic benefits to offspring of extrapair matings are generally very weak or nonexistent, and are likely to be outweighed by direct costs (Akçay & Roughgarden, 2007; Arnqvist & Kirkpatrick, 2005). While there was debate as to the correct interpretation of these results (Eliassen & Kokko, 2008; Griffith, 2007), several more recent studies directly testing for such indirect benefits in birds suggest that offspring of extrapair matings actually have lower lifetime fitness and

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genetic value than offspring of within-pair matings (Hsu, Schroeder, Winney, Burke, & Nakagawa, 2014; Reid & Sardell, 2012; Sardell, Arcese, Keller, & Reid, 2012; though see Gerlach, McGlothlin, Parker, & Ketterson, 2012), which poses a major challenge to this as a general adaptive explanation of female extrapair mating. As such, alternative explanations need to be considered.

One such alternative (nonadaptive) explanation is the between-sex genetic correlation hypothesis, which is that genetic variants predisposing males to male extrapair mating (and hence putatively selected for) might also predispose females to extrapair mating (Arnqvist & Kirkpatrick, 2005; Forstmeier, Martin, Bolund, Schielzeth, & Kempenaers, 2011; Forstmeier et al., 2014). That is, female extrapair mating behaviour is maintained as a byproduct of selection for this behaviour in males. A recent finding of genetic correlations between measures of male and female extrapair mating behaviour in zebra finches (Forstmeier et al., 2011) is consistent with this hypothesis. While this finding does not in itself invalidate adaptive hypotheses in this or other species, it does warrant the consideration of between-sex genetic correlation as a plausible alternative to adaptive explanations of female extrapair mating.

These findings have important implications for evolutionary research into human mating; socially monogamous partnerships are the most common form of marriage even among forager societies in which other arrangements (e.g. polygyny, polyandry, promiscuity) are also common (Marlowe, 2003). As in other species, extrapair copulation is common in humans across cultures (Greiling & Buss, 2000; Marlowe, 2000), and nonpaternity rates are non-zero in all societies that have been studied (Anderson, 2006) and are quite high (9% and 17%) in the two small-scale natural-fertility (i.e. similar to ancestral) populations in which this has been carefully investigated (Neel & Weiss, 1975; Scelza, 2011)—this rate is comparable to an estimated average rate of extrapair paternity among bird species (11%; Griffith et al., 2002).

The dominant evolutionary theories of human mating strategies (e.g. sexual strategies theory Buss & Schmitt, 1993; strategic pluralism Gangestad & Simpson, 2000, dual mating strategies Fisher, 1992) regard both men and women as having evolved distinct psychological mechanisms adapted for both long-term and short-term (including extrapair) mating strategies. Pillsworth and Haselton (2006) specifically propose that women are endowed with suites of adaptations that function to form a social partnership with a man she judges to be a reliable investing partner while surreptitiously seeking good genes (for her offspring) from another man through extrapair sexual encounters. While there is indirect evidence from a variety of sources consistent with this hypothesis (reviewed in Gangestad, 2006; Pillsworth & Haselton, 2006), there is no direct evidence to this effect (e.g. there is no evidence that offspring of extrapair matings are fitter than offspring of within-pair matings). Given this and the aforementioned recent findings in socially monogamous birds, which suggest that extrapair offspring are less fit than within-pair offspring (Hsu et al., 2014; Reid & Sardell, 2012; Sardell et al., 2012) and that there is substantial cross-sex correlation in extrapair mating behaviours (Forstmeier et al., 2011), it is worthwhile investigating the plausibility of the between-sex genetic correlation as an alternative explanation for female extrapair mating in humans. Previously, this alternative explanation has barely been considered.

There is evidence from studies of identical and nonidentical twins that sociosexuality (i.e. orientation towards short- or long-term mating strategy) is heritable in both men and women. Bailey, Kirk, Zhu, Dunne, and Martin (2000) estimated that genetic factors account for 26% and 43% of the variance in men and women, respectively, although it should be noted that the male genetic variance did not reach statistical significance. Furthermore, there was a significant between-sex correlation, consistent with the between-sex genetic correlation hypothesis. However, the sociosexuality score was made up of a variety of measures, most of which did not pertain to extrapair mating per se (i.e. copulating with others while in a pair-bond relationship). There has been one twin study specifically on extrapair mating, but only in women (Cherkas, Oelsner, Mak, Valdes, & Spector, 2004); in that study, 41% of the

variance in female infidelity was estimated to be accounted for by genetic factors. It remains unknown as to what extent genetic factors influence men's extrapair mating behaviour and whether they are the same genetic factors as influence on women's extrapair mating behaviour. This knowledge is crucial in weighing the relative merits of adaptationist and genetic-constraint explanations of female extrapair mating in humans.

Here we conduct two studies investigating potential genetic influences on male and female extrapair mating, and whether the same genetic factors influence the behaviour in both sexes. Study 1 uses the classical twin design to estimate the proportion of variation in extrapair mating that can be attributed to genetic differences in general, while study 2 tests variation in two specific genes (oxytocin and vasopressin receptor genes) for association with extrapair mating.

2. Study 1

In study 1 we used data from 7,378 twins and siblings who are in long-term relationships to estimate within-sex heritability and test for a between-sex correlation in recent extrapair copulation in order to assess the plausibility of the between-sex genetic correlation explanation of female extrapair mating in humans.

3. Methods

3.1. Participants

The full Finnish community-based twin-sibling sample consisted of 13,092 individuals aged from 18 to 49 ($M = 29.2$, $SD = 7.3$) from 7,737 families (see Johansson et al., 2013); for analysis we used the subset of individuals who had been in a relationship for at least the last year (see Measures for details), which consisted of 7,378 individuals aged from 18 to 49 ($M = 29.8$, $SD = 6.4$). Families with only one participating member who was in a relationship were retained because those data help stabilise the group means, even though they do not contribute to the correlations between family members. Twins of unknown zygosity were excluded from analysis. A maximum of three siblings were retained per family, because models including more siblings were unstable due to the small number of larger sibships. Number of pairs of each type is included in Table 1.

3.2. Measures

3.2.1. Relationship status

In the first wave of data collection, participants were asked their relationship status [divorced; not seeing anybody at the moment; never had a sexual relationship; widowed; engaged, living together; seeing only one person; married, registered partnership; seeing several persons]. In the second wave of data collection participants were instead asked firstly: Do you have a steady sexual partner? [Yes/No] and secondly: For how long have you been in a relationship with this partner? [Less than a month; For a month or more, but less than 6 months; 6–12 months; 1–3 years; 4–10 years; more than 10 years]. Participants who were married (wave 1) or had a steady sexual partner for at least a

Table 1
Intra-class tetrachoric correlations (and 95% confidence intervals) for extrapair mating.

	Tetrachoric correlations(95% CI)
Identical twin females (N pairs = 370)	.43 (.17, .64)
Identical twin males (N pairs = 101)	.67 (.32, .88)
Identical twins all (N pairs = 471)	.50 (.30, .67)
Nonidentical twin/sibling females (N pairs = 973)	.08 (–.16, .32)
Nonidentical twin/sibling males (N pairs = 239)	–.07 (–.33, .30)
Opposite-sex twin/siblings (N pairs = 697)	.03 (–.21, .26)
Nonidentical twins/siblings all (N pairs = 1909)	.04 (–.12, .19)

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