Variation in Human Mate Choice: Simultaneously Investigating Heritability, Parental Influence, Sexual Imprinting, and Assortative Mating

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ABSTRACT: Human mate choice is central to individuals' lives and to the evolution of the species, but the basis of variation in mate choice is not well understood. Here we looked at a large community-based sample of twins and their partners and parents ($N > 20{,}000$ individuals) to test for genetic and family environmental influences on mate choice, while controlling for and not controlling for the effects of assortative mating. Key traits were analyzed, including height, body mass index, age, education, income, personality, social attitudes, and religiosity. This revealed near-zero genetic influences on male and female mate choice over all traits and no significant genetic influences on mate choice for any specific trait. A significant family environmental influence was found for the age and income of females' mate choices, possibly reflecting parental influence over mating decisions. We also tested for evidence of sexual imprinting, where individuals acquire mate-choice criteria during development by using their opposite-sex parent as the template of a desirable mate; there was no such effect for any trait. The main discernible pattern of mate choice was assortative mating; we found that partner similarity was due to initial choice rather than convergence and also at least in part to phenotypic matching.

Keywords: mate choice, mate preferences, behavior genetics, evolutionary psychology, sexual imprinting, assortative mating.

Introduction

The choice of a relationship partner (mate choice) often determines who will contribute half of the genome and care of our offspring, the vessels that may carry our genes into future generations. The sexual choices of our ancestors over hundreds of thousands of years have helped to shape our evolution (Miller 2000), yet the factors governing human mate choice are poorly understood.

One pervasive finding is that romantic partners are sim-ilar to each other in many respects. Romantic partners correlate positively and strongly on age, social attitudes, and religiosity; correlate moderately on general intelligence, education, and physical attractiveness; and correlate weakly on height, weight, and personality traits (Price and Vandenberg 1980; Martin et al. 1986; Feingold 1988; Watson et al. 2004; Koenig et al. 2009; Hatemi et al. 2010). Several lines of evidence indicate that similarity between partners is due to initial choice (assortative mating) rather than convergence during the relationship (Mascie-Taylor 1989; Caspi et al. 1992; Watson et al. 2004). Family studies suggest that assortative mating is at least partly due to similarity in social background (i.e., social homogamy), and it is probably also due to individuals preferring or being more likely to encounter one another because they have similar phenotypes (i.e., phenotypic matching; Nagoshi et al. 1987; Reynolds et al. 1996, 2000).

Beyond matching on similarity, little is known about why we choose whom we choose. It seems intuitively obvious that individuals choose partners on the basis of more than just their level of self-resemblance, and many studies have established the general tendency of men and women to prefer certain physical and behavioral characteristics over others (Buss and Barnes 1986; Buss 1989; Gangestad and Simpson 2000). There has been much research into mate preferences (e.g., self-reported preferences, factors influencing attractiveness), but it is less understood how these preferences relate to the formation of long-term pair bonds. Some studies show that women find appealing the smell of men who have dissimilar immune-related (MHC) genes (Havlicek and Roberts 2009), but actual couples have no more similar or dissimilar MHC genes than is expected by chance (A. Abdellaoui, B. P. McEvoy, B. P. Zietsch, D. I. Boomsma, and P. M. Visscher, unpublished manuscript). Similarly, speed-dating studies show surprisingly low concordance between self-reported mate preferences and actual choices (Todd et al. 2007; Eastwick

and Finkel 2008). Other research shows that self-reported preferences do predict whom an individual finds attractive (Wood and Brumbaugh 2009), but the constraints of the mating market must considerably decrease the concordance between mate preferences and actual choices, especially for exclusive long-term relationships. For example, most women might prefer a husband with an above-average income (Buss and Barnes 1986), but not all women can actually have a husband with an above-average income. Although population-wide mate preferences are very important in that they reveal what is evolutionarily valued in a partner (e.g., indicators of genetic quality, parental investment), it is equally important to understand the basis of variation in actual mate choices because most human offspring are born to pair-bonded couples (Anderson 2006). These pair-bond mate choices necessarily vary greatly between individuals (since individuals themselves vary greatly), but the sources of this variation are not well understood.

Broadly, the factors underlying variation in mate choice could be genetic or nongenetic. One possible nongenetic factor is the influence of parents on their children's mate decisions. Anthropological evidence shows that in many cultures throughout history, mate choice has been heavily influenced by an individual's parents (see Buunk et al. 2008 for a review). It has been proposed that this is because parents have an evolutionary interest in ensuring that their daughters mate with higher-investing (e.g., older and higher-income) men (Buunk et al. 2008), and this may take subtle forms even in Western populations today. To the extent that parental influence over a child's mate decisions varies between families, it should be revealed in a twin study as a family environmental effect on females for mate choice regarding investment-related traits. On the other hand, Bereczkei et al. (2004) argue for sexual imprinting, a nongenetic mechanism whereby individuals acquire mate-choice criteria during development by using their opposite-sex parent as the template of a desirable mate. This has been observed in animals (Oetting et al. 1995; Kendrick et al. 1998; though not for continuous traits; Schielzeth et al. 2008), but its role in human mating is controversial.

The contribution of genetic influences on variation in mate choice is also unclear. The handful of animal studies quantifying genetic influences on female mate choice (Schielzeth et al. 2008) have mostly found low or zero heritability (the proportion of variation due to genetic variation). Only two human studies have investigated the heritability of mate choice, and those have conflicting conclusions. The first measured various personality-style traits of 269 pairs of identical (monozygotic [MZ]) and nonidentical (dizygotic [DZ]) twins and their spouses and found mostly weak correlations between the twins'

spouses, regardless of whether the twins were MZ or DZ (Lykken and Tellegen 1993). The authors concluded that mate choice in humans is determined by romantic infatuation, and that this phenomenon is inherently random. The second study (Rushton and Bons 2005) also investigated twins ($N = 123$ pairs) and their spouses on traits including height, weight, income, education, social attitudes, and Eysenck's personality scales. In this study, there were higher correlations between the spouses of MZ twins than between the spouses of DZ twins, and the authors reported that "both correlational and model fitting analyses showed that at least 10 to 30% of the variance in partner choice is due to genetic factors, at least 10% is due to shared environmental factors, and the remaining 60% is due to unique or chance environmental events" (Rushton and Bons 2005, p. 558). Thus, the results and interpretation of the two existing quantitative genetic studies of human mate choice are strongly at odds.

Although not acknowledged in these two studies, there must necessarily be some familiarity (i.e., genetic and/or shared environmental components) to mate choice whenever there is assortative mating on familial traits (e.g., height, intelligence; Heath and Eaves 1985). That is, because twins are of similar intelligence, for example, and because there is assortative mating on intelligence, the intelligence of twins' spouses will automatically be correlated. Of interest is whether there are any familial influences on mate choice beyond that created by assortative mating, but no studies have assessed this (in any species, to our knowledge).

In this article, we use genetic modeling to quantify genetic and environmental influences on mate choice, using data from a large community-based sample of identical and nonidentical twins ($N = 11,357$ individuals), their partners ($N = 7,266$ individuals), and their parents ($N = 4,238$ individuals). Key traits are analyzed, including height, body mass index (BMI), age, education, income, Eysenck's and Cloninger's personality traits, social attitudes, and religiosity (some of these measures were available for only a subset of the full sample). The larger sample size compared with that of previous studies affords greater power and more detailed analyses, including the separate estimation of effects in males and in females (cross-culturally, men and women differ in the traits they value in a potential partner; Buss 1989). In contrast to previous studies, we also control for the twins' own traits, to eliminate the effects of assortative mating on the genetic and family environmental components of mate choice. With the availability of twin and parental data for the same traits, we can also test the sexual-imprinting hypothesis of human mate choice (Bereczkei et al. 2004). On average, each nonidentical twin is equally genetically similar to each of his or her parents and his or her co-twin; if sexual imprinting

plays a role in mate choice, then a twin's partner should be more similar to the twin's opposite-sex parent than to a co-twin or a same-sex parent, controlling for age and sex. Further, we check that partner similarity is not due to convergence over time, and we test whether assortative mating can be explained by social homogamy or whether phenotypic matching plays a role. This is one of the largest and most comprehensive studies on the genetic and environmental influences on mate choice in any species.

Methods

Participants

Health and lifestyle questionnaires were sent to two cohorts of adult Australian twins and their families (parents, children, partners, and siblings), first in 1988 and for a second time in 1990. The total number of participants was >27,000. For this study, we use data from the twins and from their parents and partners, including 22,861 individuals from 6,105 independent families (see table 1 for sample details). The number of available data varied widely per measured variable. Data collection was approved by the Queensland Institute of Medical Research Ethics Committee, and informed consent was obtained from all participants. Further details about the sample, data collection, and zygosity determination can be found elsewhere (Heath et al. 1994).

Measures

Education was analyzed as the highest level of education completed, using the following categories: (1) primary school/high school (8–10 years of education), (2) high school (11–12 years of education), (3) apprentice/diploma, etc., (4) technical/college, (5) university degree, and (6) university postgraduate. Data were available for 1,794 complete sets of twins and both twins' partners (hereafter referred to as complete sets), but all available data contributed to estimation of means, variances, and covariances using full information maximum likelihood.

Individuals' yearly income was assessed by the response options: (1) none, (2) <$5,000, (3) $5,000–$10,000, (4) $10,000–$15,000, (5) $15,000–$25,000, (6) $25,000–$35,000, (7) $35,000–$50,000, and (8) >$50,000. The average full-time annual income at the time of the questionnaire was ~$25,000. Income of twins' parents was not assessed. Data for this category were available for a total of 1,197 complete sets.

Religiosity was measured as frequency of church attendance (or other observances), with the following response options: (1) rarely, (2) once or twice a year, (3) every month or so, (4) once a week, and (5) more than once a week. Data for this category were available for 1,765 complete sets.

Social attitudes were scored from responses to a list of topics (e.g., birth control, private schooling, casual sex, Asian immigration). Participants were asked to indicate whether they agreed with each topic (with a score of 0 or 2, depending on direction) or whether they were uncertain (with a score of 1). On the basis of an exploratory factor analysis, we combined 23 items (those with absolute factor loadings >0.3) into a scale ranging from 0 (most conservative) to 46 (most liberal); see table A1 for details. Missing scores were set to the sample mean unless there were more than three, in which case the scale score was treated as missing. Data for this category were available for 441 complete sets.

Personality was measured using the short versions of Eysenck's Personality Questionnaire (EPQ-R; Eysenck et al. 1985) and the revised Tridimensional Personality Questionnaire (TPQ). The EPQ includes the personality scales psychoticism (12 items), neuroticism (12 items), and extraversion (12 items), and the revised TPQ (see Cloninger 1994) includes harm avoidance (18 items), novelty seeking (19 items), reward dependence (12 items), and persistence (5 items). Items in the questionnaire were in a true/false format, and responses were summed. Missing responses were replaced with the sample mean, unless >25% of items on a particular scale were missing, in which case the scale score was treated as missing. In order to minimize departures from normality, scores were converted to a proportional scale before transformation into arcsine values (Freeman and Tukey 1950). Data for this category were available for 439–451 complete sets.

Height and age were self-reported. Data for these cat-

Table 1: Sample description

	Twins				Partner	
	Male	Female	Father	Mother	Male	Female
No. individuals	4,388	6,969	2,037	2,201	4,835	2,431
Age (SD)	32.0 (12.4)	34.4 (13.6)	62.4 (9.9)	59.6 (9.7)	40.9 (13.9)	35.8 (12.6)

Note: All values for number of individuals include partner-reported data where self-report data were missing. The average age of twins is lower than that of partners because many younger twins do not have partners but are included in the study. For actual couples, men are, on average, 2.7 years older than their partners.

egories were available for 439 and 2,195 complete sets, respectively.

Body mass index (BMI) was calculated from self-reported height and weight values and log transformed to normalize the distribution. Data for this category were available for 426 complete sets.

Length of relationship with current partner was self-reported. For twins' parents, this variable was used only if the current partners were the twins' parents. This information was available for 7,723 couples.

For religiosity, education, income, and age, participants were also asked to give information about their partners. We used this information when partners did not participate or when there were missing data on any of these variables. Over the whole sample, this increased the available data for these measures by 23%–33%, but it increased data specifically for twins' partners by 110%–180% for these variables. For the participants with both sets of information, correlations between self-reported data and partner-reported data were 0.87 (religiosity), 0.84 (education), 0.74 (income), and 0.99 (age).

Statistical Analyses

Data preparation was performed in PASW-Statistics, version 17.0. Statistical analyses employed full-information maximum-likelihood modeling procedures using the statistical package Mx (Neale et al. 2006). Mx accounts for the nonindependence of family members by producing maximum-likelihood estimates that are corrected for kinship by explicitly modeling the family relationships within the covariance structure. In a maximum-likelihood model, the goodness of fit of a model to the observed data is distributed as χ^2. By testing the change in χ^2 against the change in degrees of freedom, we can test whether dropping or equating specific model parameters (e.g., the MZ and DZ twin pair correlations) significantly worsens the model fit. In this way, we can test hypotheses regarding those parameters. For all analyses, mean effects of sex, age, and sex × age were controlled for (separately for males and females) by regressing age and standardizing each trait.

Correlations between different family members (twin pairs, partner pairs, parent-offspring, etc.) on each trait were determined in Mx. For each trait, we investigated whether social homogamy (i.e., partner similarity in social backgrounds) could account for all of the similarity between partners. Heath and Eaves (1985) mathematically show that the social homogamy model makes a number of predictions regarding the correlations between various family members and partners, but power simulations showed that the most statistically powerful prediction is that the correlation between a twin and the co-twin's partner is equal for MZ and DZ twin pairs and is equal to the correlation between a twin and that twin's own partner (these correlations are indicated in table 2). If these correlations are significantly different (i.e., the prediction from social homogamy is violated), then phenotypic matching must play a role (as it is the only alternative). See the study by Heath and Eaves (1985) for further details.

We tested whether sexual imprinting plays a role in mate choice by testing whether twins' partners were more similar to their opposite-sex parent than to others who are equally genetically similar to the twin (i.e., same-sex parent, DZ co-twin). This "genetic control" is necessary because of the tendency for assortative mating in humans: twins' partners might be similar to their opposite-sex parent simply because they tend to partner with someone similar to themselves (and therefore similar to their genetic relatives). Note that this analysis does not account for the possibility of imprinting on a same-sex parent or siblings.

To test for a genetic effect on mate choice for each trait, we tested whether MZ twin pairs' partners (i.e., mate choices) resemble each other more than do DZ twin pairs' partners. For each trait, we also performed the same test after regressing the twins' own trait values to control for the effects of assortative mating (which increases resemblance between partners of twin pairs, as twins themselves are similar). To test for an "overall" genetic effect on mate choice, combining data from all traits, we included all traits in a single model and constrained the twin pair correlations to be equal across traits, effectively creating a weighted average of twin correlations across traits.

Estimating Genetic and Environmental Influences on Traits and Mate Choice for Those Traits. We used the classical twin design, in which variation in traits and mate choice is partitioned into that due to genetic sources (additive and nonadditive), that due to family environmental sources (environmental factors shared by twin pairs), and that due to residual sources (Neale and Cardon 1992). Additive genetic variation results from the sum of allelic effects within and across genes. Nonadditive genetic effects include dominance and epistasis, which are allelic interactions within and across genes, respectively. Family environmental factors may include shared home environment, parental style, and uterine environment. Residual variation includes that due to environmental factors not shared by twin pairs (e.g., idiosyncratic experiences), that due to stochastic biological effects, and that due to measurement error. Trait variances are standardized to equal 1, so the genetic, family environmental, and residual parameters equal the proportion of variance accounted for by each source. Note that the proportion of trait variance accounted for by additive genetic factors is the narrow-sense heritability (h^2) of the trait and the proportion of

Table 2: Correlations between family members for each trait after controlling for age and sex effects

	BMI	Height	Education	Income	Religiosity	Attitudes	Neuroticism	Extraversion	Psychoticism	Harm avoidance	Novelty seeking	Reward dependence	Persistence
MZF twins	.69 (.01)	.84 (.01)	.64 (.01)	.32 (.03)	.62 (.01)	.64 (.01)	.42 (.02)	.45 (.02)	.35 (.02)	.42 (.02)	.40 (.02)	.37 (.02)	.35 (.02)
MZM twins	.71 (.02)	.87 (.01)	.69 (.02)	.47 (.04)	.62 (.02)	.59 (.02)	.36 (.03)	.51 (.03)	.37 (.03)	.44 (.03)	.40 (.03)	.37 (.03)	.35 (.03)
DZF twins	.37 (.03)	.48 (.02)	.47 (.02)	.32 (.05)	.50 (.02)	.51 (.02)	.17 (.03)	.17 (.03)	.23 (.03)	.14 (.03)	.12 (.03)	.16 (.03)	.14 (.03)
DZM twins	.41 (.04)	.41 (.04)	.48 (.03)	.28 (.06)	.50 (.04)	.48 (.04)	.10 (.05)	.17 (.05)	.19 (.05)	.15 (.05)	.12 (.05)	.13 (.05)	.11 (.05)
DZOS twins	.25 (.03)	.47 (.02)	.41 (.02)	.10 (.04)	.39 (.03)	.40 (.03)	.12 (.03)	.14 (.03)	.09 (.03)	.11 (.03)	.14 (.03)	.08 (.03)	.10 (.03)
Parents[a]	.18 (.03)	.22 (.03)	.44 (.02)	...	.70 (.01)	.62 (.02)	.10 (.03)	.09 (.03)	.14 (.03)	.06 (.03)	.09 (.03)	.08 (.03)	.08 (.03)
Partners[a]	.12 (.02)	.20 (.02)	.45 (.01)	.08 (.02)	.73 (.01)	.62 (.01)	.06 (.02)	.04 (.02)	.16 (.02)	.03 (.02)	.04 (.02)	.02 (.02)	.03 (.02)
Father–daughter	.20 (.03)	.39 (.02)	.26 (.02)	...	.46 (.02)	.39 (.02)	.14 (.03)	.19 (.02)	.04 (.03)	.15 (.03)	.21 (.03)	.14 (.03)	.09 (.03)
Mother–daughter	.20 (.02)	.46 (.02)	.25 (.02)	...	.46 (.02)	.43 (.02)	.16 (.02)	.18 (.02)	.11 (.02)	.14 (.02)	.13 (.02)	.16 (.02)	.08 (.02)
Father–son	.15 (.04)	.42 (.03)	.26 (.03)	...	.47 (.02)	.41 (.02)	.15 (.03)	.17 (.03)	.13 (.03)	.11 (.03)	.16 (.03)	.12 (.03)	.11 (.03)
Mother–son	.17 (.03)	.44 (.02)	.19 (.03)	...	.43 (.02)	.39 (.02)	.10 (.03)	.16 (.03)	.07 (.03)	.08 (.03)	.14 (.03)	.10 (.03)	.09 (.03)
Father–son's partner	−.02 (.07)	.15 (.04)	.15 (.03)	...	.34 (.03)	.24 (.04)	.07 (.06)	.07 (.05)	.09 (.05)	.03 (.06)	−.01 (.05)	−.01 (.05)	.10 (.06)
Mother–son's partner	.05 (.05)	.10 (.05)	.15 (.03)	...	.32 (.03)	.24 (.04)	.06 (.06)	−.06 (.05)	.11 (.05)	.01 (.05)	.00 (.05)	.06 (.05)	.03 (.05)
Father–daughter's partner	.06 (.04)	.13 (.04)	.22 (.03)	...	.40 (.02)	.21 (.03)	−.03 (.05)	.00 (.04)	.01 (.04)	.02 (.05)	−.01 (.04)	.01 (.05)	−.03 (.04)
Mother–daughter's partner	.06 (.03)	.11 (.03)	.19 (.03)	...	.35 (.02)	.23 (.03)	.01 (.04)	.03 (.04)	.07 (.04)	−.02 (.04)	.01 (.04)	.04 (.04)	.02 (.04)
MZF twin–co-twin's M partner[a]	.09 (.03)	.18 (.03)	.38 (.02)	.05 (.03)	.45 (.02)	.37 (.02)	.01 (.03)	.04 (.03)	.07 (.03)	.04 (.03)	.07 (.03)	.01 (.03)	.03 (.03)
MZM twin–co-twin's F partner[a]	.10 (.04)	.18 (.03)	.33 (.02)	.06 (.04)	.43 (.03)	.42 (.03)	.03 (.05)	.03 (.05)	.09 (.05)	.02 (.05)	.09 (.05)	.01 (.05)	.03 (.05)
DZF twin–co-twin's M partner[a]	.04 (.05)	.11 (.04)	.27 (.03)	.06 (.04)	.39 (.02)	.32 (.03)	−.01 (.05)	−.03 (.05)	.02 (.05)	−.01 (.05)	−.03 (.05)	−.10 (.05)	−.04 (.05)
DZM twin–co-twin's F partner[a]	−.03 (.06)	.23 (.07)	.31 (.03)	.08 (.05)	.40 (.04)	.32 (.05)	.15 (.07)	−.03 (.06)	.02 (.07)	.00 (.07)	−.12 (.06)	.00 (.07)	.08 (.06)
DZ twin–OS co-twin's M partner	.02 (.08)	.21 (.06)	.31 (.04)	.06 (.05)	.34 (.04)	.34 (.05)	−.03 (.07)	−.06 (.06)	.04 (.07)	.02 (.07)	−.09 (.07)	−.05 (.07)	.06 (.07)
DZ twin–OS co-twin's F partner	.11 (.06)	.10 (.05)	.32 (.03)	.02 (.06)	.26 (.03)	.34 (.05)	.06 (.07)	−.09 (.06)	.18 (.06)	.10 (.06)	.01 (.06)	−.04 (.06)	.03 (.06)

Note: Values in parentheses are standard errors. Correlations between partner of twin 1 and partner of twin 2 are presented in table 4. M = male, F = female, OS = opposite-sex, MZ = monozygotic, DZ = dizygotic.

[a] Correlations used in the test of social homogamy.

Table 3: Mean values (±SD), partner correlations (including parents), and broad-sense heritability estimates (uncorrected and corrected for assortative mating) for each trait

Trait	Mean ± SD		Partner correlation		Heritability	
	Males	Females	r (95% CI)	No. pairs forming basis	% (95% CI)	Corrected for AM
Body mass index	24.4 ± 3.3	23.2 ± 4.1	.14 (.11, .17)	3,479	68 (64, 70)	68
Height (cm)	178 ± 7.0	164 ± 6.8	.20 (.17, .24)	3,544	75 (69, 82)	85
Education	4.1 ± 1.3	3.8 ± 1.4	.45 (.42, .147)	7,320	43 (36, 49)	58
Income	2.9 ± 1.6	2.5 ± 1.5	.08 (.04, .11)	4,150	34 (19, 40)	34
Religiosity	6.1 ± 1.5	4.1 ± 1.9	.72 (.69, .75)	7,389	30 (22, 38)	39
Attitudes	25.0 ± 9.1	23.3 ± 8.8	.61 (.58, .64)	3,469	32 (25, 40)	38
Neuroticism	2.5 ± 1.7	1.8 ± 1.5	.07 (.04, .11)	3,586	39 (35, 42)	39
Extraversion	6.7 ± 3.6	7.0 ± 3.5	.05 (.02, .08)	3,545	46 (42, 49)	46
Psychoticism	4.0 ± 3.1	5.1 ± 3.1	.16 (.12, .19)	3,595	36 (28, 39)	36
Harm avoidance	6.2 ± 4.2	8.0 ± 4.3	.04 (.01, .07)	3,480	40 (37, 44)	40
Novelty seeking	7.8 ± 3.9	7.8 ± 3.7	.06 (.02, .09)	3,474	38 (34, 42)	38
Reward dependence	6.5 ± 2.7	8.2 ± 2.5	.04 (.01, .07)	3,477	35 (30, 38)	35
Persistence	3.0 ± 1.5	2.9 ± 1.5	.05 (.02, .08)	3,516	33 (29, 37)	33
Age	41.7 ± 17.0	39.8 ± 16.2	.97 (.95, .99)	8,315	...	...

Note: AM = assortative mating, CI = confidence interval.

trait variance accounted for by all genetic factors is the broad-sense heritability (H^2) of the trait.

Partitioning of phenotypic variance into genetic, shared environmental, and residual components can be achieved because MZ twins share all of their genes, while DZ twins share on average only one-half of their segregating genes. Thus, if additive genetic influences were the sole source of variance in a trait, we would expect twin correlations of 1.0 for MZ pairs and 0.5 for DZ pairs. If nonadditive genetic influences were the sole source of variance in a trait, we would expect twin correlations of 1.0 for MZ pairs and, at most, 0.25 for DZ pairs (see Posthuma et al. 2003 for an explanation). By definition, if family environment were the sole source of variance in a trait, we would expect a twin correlation of 1 for both MZ and DZ pairs; conversely, if residual factors were the sole source of variance in a trait, we would expect a twin correlation of 0 for both MZ and DZ pairs.

For most traits, observed MZ and DZ twin correlations reflect a combination of these genetic and environmental influences, and (using the expected correlations above) structural equation modeling allows us to determine the combination that best matches the observed data. A limitation of the classical twin design is that there is little statistical power to resolve nonadditive from additive genetic effects and, further, nonadditive genetic effects are confounded with family environmental effects. Preliminary analyses showed little evidence for nonadditivity (in no cases were DZ correlations significantly less than one-half of the MZ correlations), so we estimated only additive genetic variation with the caveat that this estimate includes any nonadditive effects. (When nonadditive effects are not

modeled, all nonadditive genetic variance is absorbed into the estimate of additive genetic variance. This is because the expected pattern of twin correlations for nonadditive genetic variation is similar to that for additive genetic variation but very different from that of family environmental and residual variation [Neale and Cardon 1992].)

Results

Partner Similarity

Table 3 shows that partners correlated very weakly on some traits (e.g., income and personality) but strongly on others (e.g., religiosity and attitudes). As a first step, we examined whether partner similarity could be accounted for by convergence during the relationship. We did this (cross-sectionally) by testing each trait for a correlation between relationship duration (<1 year to 60 years) and absolute difference scores of couples (see table A2). With the large sample, there were significant correlations in both directions (i.e., convergence and divergence), but all were of negligible magnitude ($R^2 < 0.01$), even when limiting to relationships that were <2 years in length. These results suggest that, in general, partner similarity is due to initial choice and not convergence over time.

Social homogamy could not completely account for assortative mating on education, attitudes, religiosity, and age ($P < .001$), indicating that phenotypic matching must play a role in partner similarity. The relevant correlations can be found in table 2. The other traits exhibited much weaker assortative mating, so in those cases there was likely

too little statistical power to distinguish phenotypic matching from social homogamy (Heath and Eaves 1985).

Trait Heritability

MZ and DZ twin pair correlations for each trait can be found in table 2, and table 3 shows heritability estimates for each trait. For each trait, twin pair correlations were significantly greater for MZ pairs than for DZ pairs ($P <$ .001), and heritability estimates as obtained from univariate twin models ranged between 28% for religiosity and 68% for BMI.

Parental assortative mating (assuming it is due to phenotypic matching) on heritable traits increases the genetic correlation between DZ twins but not MZ twins (who are genetically identical). Therefore, the difference between MZ and DZ correlations is lower and heritability is underestimated. It is possible to correct heritability estimates for this potential underestimation by using formulas detailed by Martin et al. (1978); doing so increased the heritability estimates for several of the traits in this study (see the last column in table 3). Note that the above issue is unrelated to that described below, where we control for the effect of assortative mating inflating familial resemblance in mate choice.

Genetic and Environmental Influences on Mate Choice

Table 4 shows the correlations between twin pair partners (i.e., twin pair correlations for mate choice) on each trait. Correlation between twin pair partners was not significant for BMI, height, and all personality scales, but there were small but significant correlations between twin pair partners for education, income, religiosity, attitudes, and age. For the traits with significant correlation between twin pair partners, we tested whether the correlation between MZ twin pair partners was significantly higher than that between DZ twin pair partners. This was not the case for any trait or over all of the traits equated, indicating no significant genetic influence on mate choice. Over all of the traits, the nonsignificant heritability estimate for mate choice was 4% and 6% for males and females, respectively. After controlling for assortative mating (i.e., regressing the twins' own trait values), the correlations between twin pair partners decreased, particularly for those variables with stronger assortative mating; again, correlations between twin pair partners did not differ for MZ twins versus DZ twins over all of the traits equated or for any specific trait. Over all of the traits, the nonsignificant heritability estimate for mate choice after controlling for assortative mating was 5% for males and 8% for females. The relative magnitude of familial (including genetic) effects is limited by the MZ twin correlation; given the confidence intervals

in table 4, we can be confident that familial (including genetic) influences account for <13% of the variation in male and female mate choice averaged across all measured traits, after controlling for assortative mating.

However, specifically for income and age, correlations between female MZ and DZ twin pair partners were highly significant and similar in size, indicating a genuine family environmental influence on women's mate choice for these traits even after controlling for assortative mating. Modeling showed significant family environmental influences accounting for 25% and 18% of the variance in mate choice for income and age, respectively.

On the other hand, there was no evidence for the sexual imprinting hypothesis. Twins' partners were not significantly more similar in any trait to the twins' opposite-sex parent than to the twins' same-sex parent or a DZ co-twin of either sex, nor was there even a trend in this direction (see table 2 for the relevant correlations).

Discussion

Using a large sample of twins and their parents and partners, we found that genetic variation accounts for very little individual variation in human mate choice. Over all of the measured traits, twins' partners correlated very weakly (except for age), and MZ twins' partners did not correlate significantly more than DZ twins' partners (mate choice heritability = 4% for males and 6% for females). After correcting for the twins' own trait values (i.e., correcting for assortative mating), the correlation between twins' partners over all traits was even lower, and it was again not significantly different between MZ and DZ twin pairs (mate choice heritability = 5% for males and 8% for females, respectively). Because of the large sample size and tight confidence intervals, we can be confident that familial effects (including genetic effects) accounted for <13% of the variance in male and female mate choice across all of the traits. Furthermore, there were no significant genetic effects on mate choice in either males or females for any individual trait. Nor were there any sexual imprinting effects, whereby the opposite-sex parent is used as the template of a desirable mate. That is, for males and females in every measured trait, twins' partners were not more similar to the twins' opposite-sex parent than to others with the same level of genetic sharing with the twin (i.e., same-sex parent, DZ co-twin). There was, however, a genuine influence of family environment on female mate choice in terms of age and income, supporting previous evolutionary predictions of such an effect (Buunk et al. 2008).

The finding of near-zero heritability of human mate choice accords with the findings of Lykken and Tellegen (1993), and it extends those results with a broader range

Table 4: Correlations between twin pair partners (i.e., twin pair correlations for mate choice), uncorrected and corrected for assortative mating

Mate choice	BMI	Height	Education	Income	Religiosity	Attitudes	Neuroticism	Extraversion	Psychoticism	Harm avoidance	Novelty seeking	Reward dependence	Persistence	Age	Overall (95% CI)
Raw data:															
MZF	.02 (.07)	.15 (.07)	.35 (.03)**	.30 (.04)**	.38 (.02)**	.27 (.05)**	.00 (.08)	−.05 (.07)	.15 (.07)	−.01 (.07)	−.07 (.07)	.05 (.07)	.04 (.07)	.93 (.01)**	.18 (.14, .21)**
MZM	.28 (.11)	.15 (.12)	.26 (.05)**	.12 (.06)	.30 (.04)**	.31 (.06)**	.07 (.11)	.10 (.11)	.05 (.12)	−.08 (.12)	−.02 (.11)	−.16 (.10)	.06 (.11)	.92 (.02)**	.14 (.09, .19)**
DZF	−.24 (.12)	.01 (.11)	.23 (.04)**	.37 (.05)**	.32 (.03)**	.18 (.08)	.04 (.12)	−.13 (.12)	−.15 (.13)	.03 (.11)	.11 (.10)	−.12 (.11)	−.01 (.11)	.90 (.02)**	.15 (.10, .20)**
DZM	.06 (.18)	−.26 (.15)	.18 (.06)*	.24 (.08)*	.36 (.05)**	.30 (.09)*	.32 (.17)	−.29 (.14)	.07 (.17)	−.33 (.14)	−.07 (.14)	.09 (.16)	.09 (.15)	.92 (.03)**	.12 (.05, .19)**
DZOS	−.20 (.12)	−.07 (.10)	.22 (.04)**	.06 (.06)	.26 (.04)**	.40 (.09)**	−.30 (.12)	.06 (.10)	−.24 (.09)	−.02 (.11)	.13 (.10)	−.02 (.10)	.08 (.12)	.90 (.02)**	.09 (.04, .13)**
Controlling for assortative mating:															
MZF	.03 (.07)	.11 (.08)	.20 (.04)**	.24 (.05)**	.12 (.03)**	.07 (.07)	.00 (.07)	−.08 (.07)	.14 (.07)	−.01 (.07)	−.09 (.07)	.03 (.07)	.04 (.07)	.19 (.03)**	.10 (.07, .13)**
MZM	.26 (.11)	.09 (.12)	.12 (.06)	.07 (.06)	−.01 (.05)	.09 (.10)	.05 (.10)	.09 (.11)	.02 (.12)	−.07 (.11)	−.06 (.11)	−.17 (.10)	.04 (.11)	.09 (.06)	.05 (.00, .06)
DZF	−.31 (.13)	−.06 (.12)	.08 (.05)	.30 (.06)**	.03 (.05)	−.03 (.12)	.03 (.11)	−.10 (.12)	−.17 (.13)	.05 (.11)	.11 (.10)	−.12 (.10)	−.01 (.11)	.18 (.05)**	.06 (.02, .11)*
DZM	.08 (.17)	−.29 (.15)	.04 (.08)	.21 (.09)	.09 (.08)	.17 (.14)	.25 (.18)	−.33 (.13)	.00 (.19)	−.36 (.13)	−.09 (.14)	.09 (.17)	.07 (.16)	−.02 (.04)	.01 (−.04, .07)
DZOS	−.21 (.11)	−.09 (.10)	.02 (.05)	−.09 (.07)	.06 (.06)	.22 (.14)	−.23 (.11)	.06 (.10)	−.25 (.10)	−.02 (.10)	.11 (.11)	−.03 (.11)	.09 (.12)	.00 (.07)	−.02 (−.06, .03)

Note: Values in parentheses are standard deviations, except where indicated. "Overall" correlations (and 95% CIs) are estimated by constraining twin correlations to be equal across all traits (except for age in the raw data). MZF = monozygotic female pairs, MZM = monozygotic male pairs, DZF = dizygotic female pairs, DZM = monozygotic male pairs, DZOS = dizygotic opposite-sex pairs.

* Significant at $P < .01$.

** Significant at $P < .001$.

of traits, a larger sample, sex-specific analyses, and control of the effects of assortative mating. On the other hand, these results contradict the conclusions of Rushton and Bons (2005), who report a substantial genetic component (∼30%) to mate choice. However, their reported correlations between twins' partners actually suggest a lower genetic estimate (18%), and this genetic component is nonsignificant. Thus, their larger estimate of heritability may reflect greater sampling error due to the much smaller sample size in that study.

Given that variation in practically every behavioral trait studied has been revealed to be under substantial genetic influence (Bouchard and McGue 2003), it is remarkable that a choice behavior so central to individuals' lives (Headey et al. 2010) exhibits a near-zero genetic component. A difference between mate choice and many other choice behaviors (e.g., smoking [Vink et al. 2005], food [Teucher et al. 2007]: ∼50% heritable) is that choice of a mate requires reciprocity: person A cannot "choose" person B in this sense unless person B also chooses person A. Therefore, the choice of partner may only partially reflect underlying mate preferences, and the extent to which choice reflects preferences will differ between individuals according to characteristics such as their mate value and mating strategies (Penke et al. 2007b). Thus, the formation of a couple depends on a complex interaction between the characteristics of both members, characteristics that may themselves be heritable. Components of mate value (e.g., height in men, intelligence, BMI: 50%–90% heritable) and mating strategies (sociosexuality, number of sexual partners: ∼50%–60% heritable) are known to be substantially influenced by genes (Bailey et al. 2000; Zietsch et al. 2008), but the heritability of mate preferences has not been investigated in humans. It is thought that much variation in mate choice behavior (e.g., preferences and strategies) is due to facultative calibration to local reproductive conditions (e.g., pathogen prevalence, resource availability) and availability of mates (e.g., operational sex ratio; Schmitt 2005; DeBruine et al. 2010), which is consistent with the high levels of nongenetic variation we see here. Ideally, we would measure mating preferences, strategies, and behavior; mate value (attractiveness, fitness traits); and relevant environmental factors in a large sample of twins and their partners. Genetic and/or environmental variation, covariation, and interaction between these factors, and their association with mate choice, would be very revealing in terms of how sexual selection operates in humans and perhaps in other pair-bonding species. Knowledge of the relationships between these factors could also allow the development of more sophisticated twin/family models that take into account the reciprocity of human mate choice; for example, knowledge of mate value and mate preferences could be used to estimate the extent to which each individual had free choice of a mate, which could in turn alter expected covariances between partners the of twins.

One positive finding in our results is an influence of family environment on female mate choice in terms of the income and age of a partner, even after controlling for the effect of assortative mating. For both traits, female twins' spouses were correlated modestly but highly significantly, to the same degree, in DZ twins and MZ twins. This family environment effect, which explains 18% and 25% of the variance in mate choice for age and income, respectively, may reflect parental influence over mating decisions. On the basis of evolutionary theory and anthropological evidence, this parental influence is expected to primarily involve pressure on a daughter to mate with a high-investing (e.g., older and higher-income) man (Buunk et al. 2008). There was little evidence for substantial familial effects on other aspects of mate choice. In particular, the sexual imprinting hypothesis was not supported: twins' spouses showed no more similarity to the twin's opposite-sex parent than would be expected given assortative mating and genetic relatedness between a twin and his or her parent. A strong previous demonstration of sexual imprinting was subsequently found to contain serious errors (Bereczkei et al. 2009). The distinct lack of an effect in the current large sample using appropriate genetic controls indicates that sexual imprinting does not play a role in human mate choice, at least in terms of the range of physical and psychological traits investigated here.

Given that assortative mating remains the primary detectable pattern to mate pairings in humans, it is worth briefly describing how our understanding of it has been furthered by this study. First, we extended the previous findings for intelligence, personality, and social attitudes that similarity between partners is not due to becoming more similar over time (Mascie-Taylor 1989; Caspi et al. 1992), since partner similarity was not substantively related to relationship length for any trait. Second, we showed that strong assortative mating (i.e., on age, social attitudes, education, religiosity) was not solely due to social homogamy, so phenotypic matching must play a significant role. (Weak assortative mating [e.g., height, BMI] afforded little statistical power to detect phenotypic matching.) Given its effect of increasing the genetic variance of traits in the population, phenotypic matching is an area worth exploring further with regard to the maintenance of genetic variation in fitness-related traits (Keller and Miller 2006; Penke et al. 2007a). For example, a possible cause of phenotypic matching could be a genetic correlation between preference for a trait and the trait itself, which could reflect runaway (Fisherian) sexual selection (Andersson 1994).

Despite the large, genetically informative sample and

broad range of traits, there are some important limitations to this study. One is that we may not have measured the "right" traits; that is, unmeasured traits such as pheromones or facial characteristics could potentially inform mating decisions more than the traits we investigate here. However, countless human mating studies support the importance of preferences for intelligence (correlated with education), age, earning capacity (men's), height (men's), BMI (especially women's), and personality traits (Buss 1989; Kurzban and Weeden 2005; Fink et al. 2007; Todd et al. 2007; Lukaszewski and Roney 2010). Therefore, although we have not measured all of the traits that are important to human mate selection, we are confident we have measured some of them. Another limitation is that the mate pairings we sampled are biased toward established couples. Although most children today are born to pair-bonded couples, a substantial portion result from short-term sexual liaisons; this was probably even more common before the recent availability of contraception. Evolutionary psychology shows that humans have psychological adaptations to short-term as well as long-term mating (Gangestad and Simpson 2000; Gangestad and Thornhill 2008), indicating the importance of short-term sexual liaisons in the evolutionary past. Although the relationships sampled in this study range in length from 1 month to 60 years, the bias toward established couples limits evolutionary interpretations of the findings. Another issue is that the potential for nonrandom missingness of data cannot be discounted, particularly as fewer partners than twins participated. However, there were no large differences in the mean values of the twins and those of their partners, suggesting that the partners' lower rate of participation was not substantively related to any traits of interest. Finally, although our sample is large compared with that of most previous genetic studies of mating, our power is still limited and there may be extremely low heritability in mate choice that we are not detecting. A recent large study of mate choice in birds ($N = 8{,}500$) found a significant heritability of <3% (Qvarnström et al. 2006). Our study could not detect genetic contributions to mate choice of this magnitude, and these could still be important over evolutionary time.

In summary, we found near-zero genetic effects and no sexual imprinting effects on human mate choice on a range of physical, psychological, and demographic traits. Despite being one of the most important choices in human life, variation in partner choice followed no apparent order aside from a small family environmental influence on the age and income of females' mate choices and the similarity of partners in some traits. Partner similarity was due at least in part to matching on phenotype, and the causes of phenotypic matching should be further investigated. Our results are consistent with theory and data suggesting that much variation in mate choice behavior arises from facultative calibration to local reproductive conditions and mating markets; however, an integrated evolutionary genetic understanding of human mating and pair bonding calls for examining mating preferences, strategies, and behavior; fitness traits; and relevant environmental factors in a large sample of twins and their families and partners.

APPENDIX

Supplemental Tables

Table A1: Items regarding social attitudes, to which participants recorded their agreement or otherwise, along with factor loadings

Item	Factor loading
1. Death penalty	−.14
2. Casual sex	**.45**
3. Privatization	−.07
4. Medicare	.20
5. Stiffer jail terms	−.27
6. Trade unions	.24
7. Patriotism	−.21
8. Voluntary euthanasia	**.50**
9. Nuclear power	−.05
10. Working mothers	**.44**
11. Bible truth	**−.63**
12. Gay rights	**.60**
13. Inborn conscience	−.15
14. Government welfare	.15
15. Divine law	**−.57**
16. Socialism	**.34**
17. White superiority	−.14
18. Herbal remedies	.06
19. Charity work	−.08
20. Suicide	**.37**
21. Conservationists	.26
22. Licensing laws	−.03
23. Birth control	**.31**
24. Evolution theory	**.50**

Table A1 (*Continued*)

Item	Factor Loading
25. Sabbath observance	**−.57**
26. Multiculturalism	.20
27. Chastity	**−.52**
28. Fluoridation	.01
29. Royalty	**−.34**
30. Women judges	.21
31. Strict rules	**−.40**
32. Test-tube babies	**.39**
33. Apartheid	−.10
34. Asian immigration	.21
35. Church authority	**−.58**
36. Disarmament	.28
37. Censorship	**−.36**
38. White lies	.29
39. Caning	−.25
40. Teenage dole	.24
41. Private schools	−.15
42. Chiropractors	.01
43. Defense spending	−.26
44. Divorce	**.52**
45. Foreign ownership	.17
46. Surrogate mothers	**.44**
47. Legalized abortion	**.62**
48. Modern art	**.36**
49. Condom machines	**.63**
50. Legalized prostitution	**.57**

Note: Bold items (absolute factor loading >0.30) are summed to form the Attitudes scale.

Table A2: Correlations between relationship duration and partner difference scores (i.e., dissimilarity) on 12 traits

Trait	Correlation with relationship duration	
	Whole sample[a]	Couples in a relationship up to 2 years[b]
BMI	−.06**	.07
Education	−.01	.07*
Income	.02	.02
Religiosity	.07**	−.03
Attitudes	−.02	.02
Neuroticism	−.03*	.08
Extraversion	−.04*	.04
Psychoticism	−.02	.08
Harm avoidance	−.02	.00
Novelty seeking	−.04*	.08
Reward dependence	−.09**	−.04
Persistence	.00	.03

Note: We did not perform these analyses for height, because no effect can be expected. Negative and positive correlations indicate convergence and divergence over time, respectively. BMI = body mass index.

[a] N = up to 6,382 couples.
[b] N = up to 802 couples.
* Significant at P < .05.
** Significant at P < .01.

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