HERITABILITY OF PREFERENCES FOR MULTIPLE CUES OF MATE QUALITY IN HUMANS

Brendan P. Zietsch,1,2,3 Karin J. H. Verweij,3,1 and Andrea V. Burri4

1 School of Psychology, University of Queensland, St. Lucia 4067, Brisbane, Queensland, Australia
2 E-mail: Brendan.Zietsch@qimr.edu.au
3 Genetic Epidemiology Laboratory, Queensland Institute of Medical Research, Herston 4006, Brisbane, Queensland, Australia
4 Department of Twin Research and Genetic Epidemiology, St. Thomas’ Hospital, King’s College, London

Received February 16, 2011
Accepted November 27, 2011

Human mate preferences have received a great deal of attention in recent decades because of their centrality to sexual selection, which is thought to play a substantial role in human evolution. Most of this attention has been on universal aspects of mate preferences, but variation between individuals is less understood. In particular, the relative contribution of genetic and environmental influences to variation in mate preferences is key to sexual selection models but has barely been investigated in humans, and results have been mixed in other species. Here, we used data from over 4000 mostly female twins who ranked the importance of 13 key traits in a potential partner. We used the classical twin design to partition variation in these preferences into that due to genes, family environment, and residual factors. In women, there was significant variability in the broad-sense heritability of individual trait preferences, with physical attractiveness the most heritable (29%) and housekeeping ability the least (5%). Over all the trait preferences combined, broad-sense heritabilities were highly significant in women and marginally significant in men, accounting for 20% and 19% of the variation, respectively; family environmental influences were much smaller. Heritability was a little higher in reproductive aged than in nonreproductive aged women, but the difference was not significant.

KEY WORDS: Heritability, indirect benefits, mate choice, multiple ornaments, sexual selection, twin study.

Sexual selection has helped shape the human mind and body, and will continue to influence the nature of our species into the future (Darwin 1859; Miller 2000). It is therefore crucial to understand how sexual selection operates in humans, and investigating mate preferences is central to this goal. Although there has been much research on species- and sex-typical aspects of human mate preferences (Buss 1989; Gangestad and Scheyd 2005; Li and Kenrick 2006), there has been less focus on the substantial variation between individuals. In particular, the extent to which genetic and environmental factors underlie variation in mate preferences is of central importance to the operation of sexual selection (Jennions and Petrie 1997; Widemo and Saether 1999; Chenoweth and Blows 2006; Chenoweth and McGuigan 2010), but this has rarely been investigated in humans.

In a number of nonhuman species, there is evidence for genetic variation in mate preferences (for reviews, see Bakker and Pomiankowski 1995; Jennions and Petrie 1997), and a handful of studies (in insects, fish, and birds) have attempted to formally quantify this genetic variation (Collins and Carde 1989; Gray and Cade 1999; Jang and Greenfield 2000; Brooks and Endler 2001; Iyengar et al. 2002; Hall et al. 2004; Simmons 2004; Delcourt et al. 2010; see Schielzeth et al. 2010 for a review). These studies have mostly yielded quite low heritability estimates, but results are inconsistent—many did not detect statistically significant genetic effects, and given the large range of the heritability estimates (0–51%) and often small sample sizes, it is unclear to what extent the inconsistency in results is due to sampling error, different methodologies, different species, or the different types of preferences that were measured.
Only one study has attempted to quantify genetic influences on human mate preferences, and this looked at preference for only one trait (altruism) in a relatively small sample of identical and nonidentical female twins ($N = 177$ pairs; Phillips et al. 2010), yielding a heritability estimate of 57%. However, a wide variety of traits contribute to sexual attractiveness, each of which may indicate different aspects of mate quality (Candolin 2003) and may vary in their relative importance depending on individual differences (DeBruine et al. 2010b) and ecological conditions (Lee and Zietsch 2011); heritability may differ considerably between traits. Individual differences in the relative importance placed on different cues of mate quality have hardly been investigated in any species—it is not known if there is a genetic basis to any such variation.

Also, it is difficult to know what heritability to expect in human mate preferences because humans are a pair-bonding species, unlike the species in most previous studies. In pair-bonding species, individuals’ mate preferences will not necessarily correspond to their realized mate “choices,” because of supply and demand constraints in the mating market (Postma et al. 2006; Courtiol et al. 2010). Independent investigations of mate choice for ornament size in a pair-bonding bird species (collared flycatchers) yielded very low heritability estimates of less than 5% (Qvarnstrom et al. 2006; Hegyi et al. 2010). Consistent with this, a recent study (Zietsch et al. 2011) looking at the partners of a large sample of identical and nonidentical twins indicated similarly low (approximately 5%) heritability of mate choice across a range of key traits (age, height, BMI, education, income, social attitudes, religiosity, various personality traits). Genetic variation in unconstrained preferences in pair-bonding zebra finches was also low (approximately 10%) and nonsignificant (Schielzeth et al. 2010). If unconstrained mate preferences are as low in humans, it would contrast with other human psychological and behavioral traits, the vast majority of which have been shown to have moderate-to-high heritability (Turkermeer 2000; Bouchard and McGue 2003).

Genetic and environmental effects on mate preferences are difficult to quantify (Chenoweth and Blows 2006), but such research in humans has some practical advantages over corresponding research in other species. First, we can simply ask men and women what they prefer in a partner, greatly simplifying the acquisition of preference data. Studies have shown correspondence between self-reported mate preferences and those revealed by implicit testing (Wood and Brumbaugh 2009). Second, the availability of large samples of identical (monozygotic; MZ) and nonidentical (dizygotic; DZ) twins allows natural genetic experiments using the classical twin design (Posthuma et al. 2003). This design partitions variance in a trait into that due to genetic, family environmental, and residual factors.

Here, we quantify the relative influence of genes and environment on variation in self-reported mate preferences using a community sample of over 4000 mostly female twin individuals. We use the same methodology for assessing mate preferences as in Buss’ seminal cross-cultural work (Buss 1989), in which 13 traits are ranked as to their importance in a potential partner. We account for age effects, analyze male and female preferences separately, and estimate the genetic and environmental influences on preferences for the 13 traits individually as well as for data combined over all the traits. This is the first study to quantify genetic influences on a range of human mate preferences, and the first in any species to test for genetic variation in the relative importance placed on different cues of mate quality.

**Methods**

**PARTICIPANTS**

We use data from 4625 twin individuals from the U.K. Adult Twin Registry (TwinsUK). The TwinsUK is a cohort of unselected volunteer Caucasian twins that started in 1993 (Spector and Williams 2006). Note that the cohort consists of predominantly females (90%) and same-sex pairs, because initial research focused on diseases with higher prevalence in women than in men (e.g., osteoporosis and osteoarthritis). All volunteers in the registry were recruited through successive national media campaigns in the United Kingdom and Ireland and from other twin registers, including the Aberdeen Twin Registry and the Institute of Psychiatry Adult Registry. The TwinsUK population has been compared for a number of diseases, traits, socio-demographic and environmental factors to an age-matched U.K. population, and a singleton population cohort from Northeast London and was found to be no different in terms of social class, lifestyle characteristics, and disease prevalence (Andrew et al. 2001). The only significant difference found was for weight, where MZ twins were slightly lighter and showed smaller variance compared with DZ twins and singletons. Numerous epidemiologic studies using the TwinsUK cohort have further demonstrated the comparability of MZ and DZ twins for a variety of traits (e.g., sexual orientation, sexual dysfunction, number of partners, emotional intelligence, anxiety) (Cherkas et al. 2004; Burri et al. in press; Burri and Spector in press) therefore making a systematic bias unlikely.

Of these 4625 twins, 39 were excluded from further analysis because they were adopted ($N = 17$), of unknown zygosity ($N = 12$), part of a triplet or quadruplet ($N = 2$), or regular siblings of a twin pair ($N = 8$). The remaining 4586 twin individuals ranging in age from 19 to 83 included 4045 females (mean age ± standard deviation [SD] = 51.1 ± 12.7) and 541 males (mean age ± SD = 49.2 ± 14.0). Approximately half (49.1%) of these twins were identical (MZ) and half (50.9%) nonidentical (DZ). The sample consisted of 1763 full pairs and 1060 single twins, the latter group retained
to increase precision of the means. There were only 16 opposite sex pairs, too few for stable correlation estimates, so these were treated as single twins. Sixty-four percent of participants were married, but mate preferences differed little depending on marital status after controlling for age. Homosexual participants were not identified, but as self-identified homosexuals only account for approximately 1% and 3% of the female and male populations, respectively (Kirk et al. 2000), any differences in the variance components of their preferences would not substantively affect the results. Zygosity of the twins was determined based on standardized questions about physical similarity that have over 95% accuracy when judged against genotyping, and when uncertain zygosity was checked by genotyping (Peeters et al. 1998). Further details about the sample, data collection, and zygosity determination can be found elsewhere (Spector and Williams 2006). The data used in this project are available through http://www.twinsuk.ac.uk/collaborations.html.

MEASURES
In 2002, participants completed a Lifestyle questionnaire including a measure of long-term mate preferences: “Below are listed a set of characteristics that might be present in a potential mate or marriage partner. Please rank them on their desirability when you are/were considering a long-term relationship.” There were 13 traits (see Table 1), so participants were to assign each characteristic a different score ranging from 1 (most important characteristic for potential mate) to 13 (least important characteristic for potential mate). This measure was developed and validated by Buss and Barnes (1986) and later administered across 37 cultures by Buss (1989) to test evolutionary hypotheses. Because the omission of one or more trait rankings can affect the other trait rankings, we excluded individuals from further analysis when their summed rank scores deviated 10 or more points from the “correct” score (i.e., 91; 1 + 2 + · · · + 13)—this allowed for minor departures from the standard ordering scheme (e.g., ranking traits as equally important) but eliminated more serious departures that would compromise the integrity of the scale. Along with the exclusion of those who did not complete the item at all, this resulted in a reduction of sample size of 18.6% (N = 855).

The rankings of each trait were analyzed as continuous variables. To attenuate the effects of outliers and skewed distribution, outliers were winsorized (three SDs from the mean) and variables were transformed (log, square root, or inverse, depending on the degree of skewness) where necessary.

STATISTICAL ANALYSES
Data preparation was performed in PASW-Statistics 17.0. Statistical analyses employed full information maximum-likelihood modeling procedures using the statistical package Mx (Neale et al. 2006), which accounts for the nonindependence of twins within a pair. In maximum-likelihood modeling, the goodness-of-fit of a model to the observed data is distributed as chi-square ($\chi^2$). By testing the change in chi-square ($\Delta \chi^2$) against the change in degrees of freedom ($\Delta \text{df}$), we can test whether dropping or equating specific model parameters (for example, the MZ and DZ twin pair correlations) significantly worsens the model fit. In this way, we can test hypotheses regarding those parameters.

We determined twin pair correlations per zygosity group (MZ females, MZ males, DZ females, DZ males) for each trait, and also equated (i.e., effectively averaged) twin pair correlations over all traits in a multivariate model. We tested whether MZ twin pairs were correlated significantly more strongly than DZ twin pairs, which would demonstrate a genetic influence on individual differences in mate preferences.

To quantify any genetic effect, the classical twin design was used to partition variance in mate preferences into that due to additive genetic (A), nonadditive genetic (D), shared (or family) environmental (C), and residual (E) sources (Neale and Cardon 1992). Additive genetic variance is due to summed allelic effects across multiple genes; because MZ twins share all of their alleles, whereas DZ twins share on average only half of their segregating alleles, A influences are correlated at 1.0 for MZ pairs, and 0.5 for DZ pairs. Nonadditive genetic variance includes dominance (allelic interactions within genes) and epistasis (interaction between multiple genes); D influences are modeled as correlating at 1.0 for MZ pairs, and 0.25 for DZ pairs (see Posthuma et al. 2003 for more details). Shared environmental factors may include shared home environment, parental style, and uterine environment; C influences are assumed to correlate at 1 for both MZ and DZ pairs. Residual variance includes environmental factors not shared by twin pairs (e.g., idiosyncratic experiences), stochastic biological effects, and measurement error; E influences are correlated at zero for both MZ and DZ twin pairs. In reality, observed MZ and DZ twin correlations generally reflect a combination of A, C, D, and E influences, and structural equation modeling determines the combination that best matches the observed data (Posthuma et al. 2003).

Although the classical twin design above is a very standard technique that has been used in countless behavioral genetic studies, it is important to note that when using only twins reared together, certain parameter estimates can be subject to severe biases and imprecision depending on the true nature of influences on the trait (see Keller and Coventry 2005; Keller et al. 2010 for detailed treatments of this). First, it is not possible to estimate C and D simultaneously, because C and D are negatively confounded: C influences increase and D influences decrease the DZ correlation relative to the MZ correlation, and so if both effects are
Table 1. Descriptive statistics for the 13 trait preferences.

<table>
<thead>
<tr>
<th>Trait preferences</th>
<th>Males (N = 446)</th>
<th></th>
<th>Transformed scale</th>
<th>Females (N = 3285)</th>
<th></th>
<th>Transformed scale</th>
<th>Sex diff</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rank</td>
<td>Mean</td>
<td>SD</td>
<td>Vp</td>
<td>r (age)</td>
<td>N wins'ed</td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Kind and understanding</td>
<td>1</td>
<td>12.27</td>
<td>1.46</td>
<td>2.12</td>
<td>-0.06</td>
<td>7</td>
<td>7.98</td>
<td>3.00</td>
</tr>
<tr>
<td>Easy going</td>
<td>2</td>
<td>9.53</td>
<td>2.53</td>
<td>6.28</td>
<td>0.15</td>
<td>0</td>
<td>5.79</td>
<td>2.57</td>
</tr>
<tr>
<td>Intelligent</td>
<td>3</td>
<td>9.38</td>
<td>2.38</td>
<td>5.65</td>
<td>-0.04</td>
<td>2</td>
<td>20.75</td>
<td>5.65</td>
</tr>
<tr>
<td>Healthy</td>
<td>4</td>
<td>9.37</td>
<td>2.08</td>
<td>4.24</td>
<td>-0.15</td>
<td>0</td>
<td>20.96</td>
<td>4.85</td>
</tr>
<tr>
<td>Physically attractive</td>
<td>5</td>
<td>9.28</td>
<td>2.74</td>
<td>7.32</td>
<td>0.16</td>
<td>1</td>
<td>20.75</td>
<td>6.46</td>
</tr>
<tr>
<td>Exciting personality</td>
<td>6</td>
<td>8.21</td>
<td>3.00</td>
<td>8.15</td>
<td>0.31</td>
<td>0</td>
<td>23.14</td>
<td>6.56</td>
</tr>
<tr>
<td>Wants children</td>
<td>7</td>
<td>6.42</td>
<td>3.38</td>
<td>11.45</td>
<td>0.01</td>
<td>0</td>
<td>6.42</td>
<td>3.38</td>
</tr>
<tr>
<td>Good earning capacity</td>
<td>8</td>
<td>6.08</td>
<td>2.43</td>
<td>5.81</td>
<td>-0.12</td>
<td>4</td>
<td>6.08</td>
<td>2.43</td>
</tr>
<tr>
<td>Creative and artistic</td>
<td>9</td>
<td>5.38</td>
<td>2.57</td>
<td>6.59</td>
<td>0.00</td>
<td>0</td>
<td>22.51</td>
<td>5.63</td>
</tr>
<tr>
<td>Good housekeeper</td>
<td>10</td>
<td>5.19</td>
<td>2.36</td>
<td>5.57</td>
<td>-0.01</td>
<td>0</td>
<td>22.13</td>
<td>5.38</td>
</tr>
<tr>
<td>Good heredity</td>
<td>11</td>
<td>3.95</td>
<td>2.27</td>
<td>4.95</td>
<td>-0.19</td>
<td>7</td>
<td>19.07</td>
<td>5.55</td>
</tr>
<tr>
<td>University graduate</td>
<td>12</td>
<td>3.14</td>
<td>2.22</td>
<td>4.92</td>
<td>0.02</td>
<td>10</td>
<td>4.02</td>
<td>2.83</td>
</tr>
<tr>
<td>Religious</td>
<td>13</td>
<td>2.96</td>
<td>2.88</td>
<td>8.01</td>
<td>-0.18</td>
<td>10</td>
<td>6.25</td>
<td>3.64</td>
</tr>
</tbody>
</table>

Raw scale: untransformed, unwinsorized. Transformed scale: transformed and winsorized, where applicable. Transformations—\(^1\) reflect and inverse: 10 × (1/((14-score))); \(^2\) reflect and log: 10 × (LG10(14-score)); \(^3\) reflected and square root: 10 × ((14-score)\(^0.5\)); \(^4\) no transformation required; \(^5\) square root: 10 × (score\(^0.5\)); \(^6\) log: 10 × (LG10(score)); \(^7\) inverse: 10 × (1/score). \(V_p\), phenotypic variance after controlling for age, raw scale; \(r\) (age), correlation of the trait ranking (raw scale) with age, as obtained from SPSS; \(N\) wins’ed, Number of datapoints winsorized; Sex diff \(P\)-value, the significance of mean differences (transformed scale) between males and females.
present they cancel each other out. The choice of modeling C or D depends on the pattern of MZ and DZ correlations; C is estimated if the DZ twin correlation is more than half the MZ twin correlation, and D is estimated if the DZ twin correlation is less than half the MZ correlation—if C is modeled, its magnitude is underestimated to the extent that D is present, and vice versa if D is modeled. Second, A and D are partially confounded because they predict similar (but not identical) patterns of twin correlations. As such, simultaneous A and D estimates are imprecise and their relative magnitude can be biased down and up, respectively, to the extent that there are multiloci epistatic effects. As such, separate A, C, and D estimates should be treated with caution. However, broad-sense heritability (i.e., A + D; the proportion of variance in a trait accounted for by genetic factors) is quite robustly estimated with classical twin design using only twins reared together (see Keller et al. 2010 for simulations demonstrating this), and we therefore focus our interpretation mainly on this more reliable estimate.

An assumption of the twin design is that trait-relevant environments are equally similar for MZ and DZ twins. Tests of this assumption suggest it is valid for personality and sexual orientation (Loehlin 1992; Kendler et al. 2000), so it seems a reasonable assumption for these mate preferences. Further details of the twin design, including assumptions, can be found elsewhere (Neale and Cardon 1992; Posthuma et al. 2003).

Age was modeled as a covariate, allowing us to determine the direction and significance of age effects but partial them out of genetic models. Because there is no reason to expect that the sources of variation in mate preferences would be the same in men and women, male and female variance components were modeled separately.

**Results**

As a preliminary step, we tested the assumption that MZ and DZ twins are comparable except for their level of genetic similarity—inequality of means and variances of MZ and DZ twins could suggest nonrandom sampling or sibling interaction effects that could bias estimation of variance components (Carey 1992). There were no substantive mean differences between MZ and DZ twins for any trait preferences, with \( \eta^2 < 0.003 \) for each trait (i.e., zygosity accounted for less than 0.3% of the variance in each trait preference). Further, formal testing in Mx revealed no significant mean or variance differences between MZ and DZ twins for trait preferences after correcting for the number of tests performed. As such, all preference means and variance were equated between MZ and DZ twins in subsequent analyses.

Table 1 shows the descriptive statistics for the importance of the 13 traits in a long-term partner. On average, both men and women valued “kind and understanding” the most; “easy going,” “intelligent,” “healthy,” and “physically attractive” were also highly valued traits, but “good heredity,” “university graduate,” and “religious” were relatively unimportant. Some trait preferences showed significant mean sex differences, largely in line with previous cross-cultural work (Buss 1989): compared with men, women more strongly valued “kind and understanding,” “wants children,” “good earning capacity,” whereas men more strongly valued “physically attractive,” “good housekeeper,” “exciting personality,” and “creative and artistic.” Most trait preferences exhibited significant mean effects of age; increasing in importance with age were “kind and understanding,” “religious,” “good housekeeper,” “good heredity,” “good earning capacity,” “intelligent,” and “healthy,” and decreasing in importance were “exciting personality” and “easy going.” Other trait preferences showed age effects that were significantly different in males and females: “physical attractiveness” (decreased with age in women, no effect in men); “earning capacity” and “good heredity” (increased with age in women, decreased in men); and “wants children” and “good housekeeper” (increased with age in men, no effect in women). We could not distinguish cohort effects from true age effects due to the cross-sectional sample.

There were a few modest correlations between the different trait preferences, ranging from –0.19 (“physically attractive” and “kind and understanding”) to 0.32 (“intelligent” and “university graduate”), but the average \( R^2 \) was only 0.014 so we treated them as independent traits in subsequent analyses.

Table 2 shows the twin pair correlations for mate preferences—for each trait separately and averaged over all traits. Of the 13 traits for both men and women, all but one (“kind and understanding” in males) showed higher MZ than DZ twin pair correlations, suggesting widespread genetic influences. In women, twin pair correlations could not be equated across traits, indicating significant variability in the relative effect of genes and environment between different trait preferences \((P < 0.001)\). The highest broad-sense heritability estimates (see Table 3) in women were for “physically attractive” “exciting personality” “kind and understanding” “good earning capacity” and “healthy” \((P < 0.001)\), while “good housekeeper” was the least heritable. Shared environmental influences were significant for “intelligent” \((P = 0.02)\) and “good housekeeper” \((P = 0.02)\).

Male twin pair correlations could be equated across traits without significant loss of model fit, indicating that the wide variability across traits in twin pair correlation and heritability estimates could be explained by error (due to the much smaller male sample). Nevertheless, male preferences showed significant genetic influences for “religious” \((P = 0.002)\) and “good housekeeper” \((P = 0.007)\). No shared environmental influences were significant in males.
Table 2. Twin pair correlations (and standard errors) for mate preferences for 13 traits. “Overall” correlations (and 95% confidence intervals [CIs]) are estimated by equating correlations across all traits in a multivariate model.

<table>
<thead>
<tr>
<th>Kind and Good</th>
<th>Creative and Easy</th>
<th>Physical Attractive</th>
<th>Exciting Personality</th>
<th>Good Intelling</th>
<th>Good Housekeeper</th>
<th>University graduate</th>
<th>Religious</th>
<th>Heredity</th>
<th>Graduate</th>
<th>Religious</th>
</tr>
</thead>
<tbody>
<tr>
<td>MZF (552 pairs)</td>
<td>0.24 (0.04)</td>
<td>0.20 (0.04)</td>
<td>0.28 (0.04)</td>
<td>0.36 (0.04)</td>
<td>0.25 (0.04)</td>
<td>0.22 (0.04)</td>
<td>0.25 (0.04)</td>
<td>0.22 (0.04)</td>
<td>0.20 (0.04)</td>
<td>0.25 (0.04)</td>
</tr>
<tr>
<td>DZF (537 pairs)</td>
<td>0.13 (0.04)</td>
<td>0.10 (0.04)</td>
<td>0.17 (0.04)</td>
<td>0.21 (0.04)</td>
<td>0.16 (0.04)</td>
<td>0.14 (0.04)</td>
<td>0.16 (0.04)</td>
<td>0.15 (0.04)</td>
<td>0.13 (0.04)</td>
<td>0.16 (0.04)</td>
</tr>
<tr>
<td>MZM (71 pairs)</td>
<td>0.11 (0.06)</td>
<td>0.21 (0.10)</td>
<td>0.12 (0.06)</td>
<td>0.13 (0.06)</td>
<td>0.03 (0.06)</td>
<td>0.00 (0.06)</td>
<td>0.19 (0.10)</td>
<td>0.17 (0.10)</td>
<td>0.17 (0.10)</td>
<td>0.26 (0.10)</td>
</tr>
<tr>
<td>DZM (51 pairs)</td>
<td>0.12 (0.11)</td>
<td>0.22 (0.12)</td>
<td>0.15 (0.12)</td>
<td>0.25 (0.12)</td>
<td>0.02 (0.12)</td>
<td>0.01 (0.12)</td>
<td>0.22 (0.12)</td>
<td>0.01 (0.12)</td>
<td>0.00 (0.12)</td>
<td>0.09 (0.12)</td>
</tr>
</tbody>
</table>

MZF, monozygotic female pairs; MZM, monozygotic male pairs; DZF, dizygotic female pairs; DZM, dizygotic male pairs.

To estimate the overall genetic influence on mate preferences, we fitted a multivariate genetic model in which we constrained A, C, and E estimates to be equal across all 13 traits, separately for males and females. This yielded overall heritabilities of 20% (95% confidence interval [CI]: 14–26%) for women ($P < 0.001$) and 19% (0–28%) for men ($P = 0.05$), and shared environmental estimates of 5% in females and 3% in males, but it should be recalled that shared environmental influences are underestimated to the extent that nonadditive genetic effects are present. The overall estimate of the familial effect (i.e., genetic plus family environmental effects) was 25% (23–27%) and 22% (16–28%) in women and men, respectively. In all traits, most of the variation was residual (i.e., unexplained by genes or family environment).

Because of the very large age range of the sample, we also tested whether there was any marked difference between the overall heritability of mate preferences in women of normal reproductive age (40 and under, when mate preferences are most consequential), and those over 40. Broad-sense heritability of the reproductive age group was 25%, and a little lower for the over 40 group at 19%—this difference was not significant ($P = 0.41$). The male sample was too small for a similar age comparison.

**Discussion**

The results from this large twin study provide the first evidence that a range of human mate preferences are heritable, and the first evidence from any species that there is genetic variation in the relative importance placed on different cues of mate quality. Participants ranked 13 traits according to their importance in a potential partner—in both men and women, these trait rankings were consistently more similar in identical than nonidentical twin pairs, indicating genetic influences. Within-sex genetic modeling revealed significant variability in the heritability of the 13 trait preferences in women, with key traits (physical attractiveness, exciting personality, kindness, earning capacity, and health) having the highest (and significant) heritabilities—these traits include purported indicators of genetic quality (physical attractiveness, health) and parental investment (kindness, earning capacity). When data were combined over all trait preferences, the broad-sense heritability of mate preferences was estimated at 20% (highly significant) and 19% (marginally significant) in women and men, respectively. Shared environment significantly influenced women’s preferences for “intelligent” and “good housekeeper,” but overall shared (family) environment was estimated to account for a nonsignificant 5% and 3% of variation in overall mate preferences in women and men, respectively—however, these will be underestimated to the extent that nonadditive genetic variation is present. The remainder of the within-sex variation was residual, likely comprising unshared environmental influences and measurement error.
Table 3. Estimates (and 95% CIs) of the proportion of variance in mate preferences accounted for by additive genetic (A), nonadditive genetic (D), shared environmental (C), and residual (E) influences. A + D represents broad-sense heritability (in bold).

<table>
<thead>
<tr>
<th></th>
<th>Kind and understanding</th>
<th>Easy going</th>
<th>Intelligent</th>
<th>Healthy</th>
<th>Physically attractive</th>
<th>Exciting personality</th>
<th>Wants children</th>
<th>Good earning capacity</th>
<th>Creative and artistic</th>
<th>Good housekeeper</th>
<th>Good heredity</th>
<th>University graduate</th>
<th>Religious</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>0.08</td>
<td>0.13</td>
<td>0.16</td>
<td>0.05</td>
<td>0.12</td>
<td>0.00</td>
<td>0.14</td>
<td>0.13</td>
<td>0.12</td>
<td>0.05</td>
<td>0.07</td>
<td>0.17</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>(0.00–0.29)</td>
<td>(0.00–0.28)</td>
<td>(0.00–0.36)</td>
<td>(0.00–0.26)</td>
<td>(0.00–0.28)</td>
<td>(0.00–0.26)</td>
<td>(0.00–0.29)</td>
<td>(0.00–0.30)</td>
<td>(0.00–0.27)</td>
<td>(0.00–0.25)</td>
<td>(0.00–0.37)</td>
<td>(0.00–0.35)</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>0.16</td>
<td>–</td>
<td>0.16</td>
<td>0.18</td>
<td>0.25</td>
<td>–</td>
<td>0.10</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(0.00–0.31)</td>
<td></td>
<td>(0.00–0.37)</td>
<td>(0.00–0.32)</td>
<td>(0.00–0.31)</td>
<td></td>
<td></td>
<td></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>A + D</td>
<td><strong>0.24</strong>***</td>
<td>0.13</td>
<td><strong>0.16</strong></td>
<td><strong>0.20</strong>*****</td>
<td><strong>0.25</strong>***</td>
<td><strong>0.14</strong></td>
<td><strong>0.24</strong>***</td>
<td><strong>0.12</strong></td>
<td><strong>0.05</strong></td>
<td><strong>0.07</strong></td>
<td><strong>0.17</strong></td>
<td><strong>0.14</strong></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.15–0.31)</td>
<td>(0.00–0.36)</td>
<td>(0.22–0.37)</td>
<td>(0.17–0.33)</td>
<td>(0.00–0.28)</td>
<td>(0.16–0.31)</td>
<td>(0.00–0.27)</td>
<td>(0.00–0.25)</td>
<td>(0.00–0.37)</td>
<td>(0.00–0.35)</td>
<td>(0.00–0.35)</td>
<td>(0.00–0.35)</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>–</td>
<td>0.07</td>
<td>0.20*</td>
<td>–</td>
<td>–</td>
<td>0.07</td>
<td>–</td>
<td>0.10</td>
<td>0.21*</td>
<td>0.10</td>
<td>0.14</td>
<td>0.15</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.00–0.21)</td>
<td>(0.04–0.35)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>(0.00–0.09)</td>
<td></td>
<td>(0.00–0.24)</td>
<td>(0.03–0.30)</td>
<td>(0.00–0.21)</td>
<td>(0.00–0.28)</td>
<td>(0.00–0.29)</td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>0.76</td>
<td>0.80</td>
<td>0.64</td>
<td>0.80</td>
<td>0.70</td>
<td>0.75</td>
<td>0.80</td>
<td>0.76</td>
<td>0.75</td>
<td>0.83</td>
<td>0.69</td>
<td>0.71</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.69–0.85)</td>
<td>(0.72–0.88)</td>
<td>(0.57–0.71)</td>
<td>(0.72–0.88)</td>
<td>(0.63–0.78)</td>
<td>(0.68–0.83)</td>
<td>(0.72–0.88)</td>
<td>(0.69–0.83)</td>
<td>(0.70–0.85)</td>
<td>(0.67–0.81)</td>
<td>(0.62–0.72)</td>
<td>(0.65–0.76)</td>
<td></td>
</tr>
<tr>
<td><strong>Males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>0.00</td>
<td>0.17</td>
<td>0.34</td>
<td>0.02</td>
<td>0.11</td>
<td>0.00</td>
<td>0.06</td>
<td>0.06</td>
<td>0.00</td>
<td>0.10</td>
<td>0.00</td>
<td>0.11</td>
<td>0.01</td>
</tr>
<tr>
<td></td>
<td>(0.00–0.41)</td>
<td>(0.00–0.57)</td>
<td>(0.00–0.26)</td>
<td>(0.00–0.35)</td>
<td>(0.00–0.39)</td>
<td>(0.00–0.52)</td>
<td>(0.00–0.37)</td>
<td>(0.00–0.18)</td>
<td>(0.00–0.47)</td>
<td>(0.00–0.32)</td>
<td>(0.00–0.44)</td>
<td>(0.00–0.50)</td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>–</td>
<td>0.04</td>
<td>0.23</td>
<td>–</td>
<td>–</td>
<td>0.21</td>
<td>–</td>
<td>0.17</td>
<td>–</td>
<td>0.35</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.00–0.28)</td>
<td>(0.00–0.44)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>(0.00–0.49)</td>
<td></td>
<td>(0.00–0.34)</td>
<td>–</td>
<td>(0.00–0.53)</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>A + D</td>
<td><strong>0.00</strong></td>
<td><strong>0.17</strong></td>
<td><strong>0.34</strong></td>
<td><strong>0.06</strong></td>
<td><strong>0.11</strong></td>
<td><strong>0.24</strong></td>
<td><strong>0.25</strong></td>
<td><strong>0.06</strong></td>
<td><strong>0.31</strong></td>
<td><strong>0.17</strong></td>
<td><strong>0.11</strong></td>
<td><strong>0.36</strong></td>
<td><strong>0.53</strong></td>
</tr>
<tr>
<td></td>
<td>(0.00–0.41)</td>
<td>(0.00–0.57)</td>
<td>(0.00–0.28)</td>
<td>(0.00–0.35)</td>
<td>(0.00–0.45)</td>
<td>(0.00–0.52)</td>
<td>(0.00–0.37)</td>
<td>(0.00–0.18)</td>
<td>(0.00–0.49)</td>
<td>(0.00–0.35)</td>
<td>(0.00–0.44)</td>
<td>(0.14–0.53)</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>0.23</td>
<td>0.06</td>
<td>0.08</td>
<td>–</td>
<td>0.03</td>
<td>–</td>
<td>0.09</td>
<td>0.10</td>
<td>0.00</td>
<td>–</td>
<td>0.15</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(0.00–0.38)</td>
<td>(0.00–0.48)</td>
<td>–</td>
<td>–</td>
<td>(0.00–0.30)</td>
<td>(0.00–0.42)</td>
<td>(0.00–0.32)</td>
<td>(0.00–0.15)</td>
<td>(0.00–0.40)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>0.77</td>
<td>0.77</td>
<td>0.58</td>
<td>0.94</td>
<td>0.86</td>
<td>0.77</td>
<td>0.66</td>
<td>0.84</td>
<td>1.00</td>
<td>0.69</td>
<td>0.83</td>
<td>0.74</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>(0.61–0.95)</td>
<td>(0.59–0.96)</td>
<td>(0.43–0.79)</td>
<td>(0.72–1.00)</td>
<td>(0.65–1.00)</td>
<td>(0.74–0.83)</td>
<td>(0.50–0.73)</td>
<td>(0.63–1.00)</td>
<td>(0.82–1.00)</td>
<td>(0.51–0.91)</td>
<td>(0.66–1.00)</td>
<td>(0.56–0.93)</td>
<td>(0.47–0.76)</td>
</tr>
</tbody>
</table>

*P < 0.05; **P < 0.01; ***P < 0.001. NB: Estimates of E are not significance tested, because measurement error is always present.
Our estimate of about 20% heritability in men and women fits with the generally low heritabilities found for mate preferences in other species (Collins and Carde 1989; Gray and Cade 1999; Jang and Greenfield 2000; Brooks and Endler 2001; Iyengar et al. 2002; Hall et al. 2004; Simmons 2004; Schielzeth et al. 2010), but our study is one of the few in which the estimate is significantly different from zero. We had more statistical power than many animal studies because of our large sample and multiple preference measures. This is important, because significant heritability demonstrates that mate preferences are partly under genetic control, a critical assumption of most theoretical models of mate choice and sexual selection (e.g., runaway, fitness indicators, sensory bias [Fisher 1930; Zahavi 1975; Ryan 1998])—further, the idea that mate preferences genetically vary in populations (and genetically covary with preferred traits themselves) is central to certain models (e.g., runaway [Fisher 1930]). Establishing significant genetic control of mate preferences therefore helps validate models of mate choice and sexual selection, and more precisely quantifying the genetic variation helps improve the models (Widemo and Saether 1999). Importantly, we found for the first time that there is genetic variation in the relative importance placed on different cues of mate quality, which is key to developing models of sexual selection that take into account the use of multiple cues (Candolin 2003).

Quantifying the heritability of unconstrained mate preferences in addition to that of realized mate choices (see Zietsch et al. 2011) is also of considerable importance (Postma et al. 2006), especially in pair-bonding species. Zietsch et al. (2011) showed that realized mate choices display very low heritability (approximately 5% for both sexes averaged over numerous traits)—much lower than for unconstrained preferences as found in the present study (approximately 20% for both sexes averaged over numerous traits). Although mate choices will relate to preferences, the relationship may be multifactorial and indirect, especially under mutual mate choice as is the case in humans. An individual’s realized mate choice depends not only on the individual’s preferences, but also on the ability of the individual to obtain a mate that matches those preferences. This in turn depends on a multitude of factors that influence supply and demand dynamics in the mating market. These may include the number of mates from which the individual could choose; the distribution of preferences and preferred traits among those potential mates; and the number of same-sex competitors and the distribution of their preferences and traits. These and other variables in the mating environment may explain why we find much higher proportion of environmental variation (i.e., lower heritability) in realized pair-bond mate choice (Zietsch et al. 2011) than in unconstrained mate preferences (present results).

This has implications for testing models of sexual selection, which make predictions about genetic (co)variation in mate preferences (Fisher 1930; Zahavi 1975). Although the “process” of sexual selection operates through realized mate choices, the direct “products” of sexual selection are characteristics of the individual (including mate preferences but also signaling traits, etc.), which in turn influence mate choices along with the multitude of external factors described above. As such, it would be most powerful to investigate the direct products of sexual selection (e.g., mate preferences) to test predictions from different models of selection (i.e., to determine which model(s) were most likely to have generated current phenotypes)—this is especially the case given that we show that unconstrained preferences are much more heritable than realized choices, because greater heritability affords more power to detect genetic (co)variation, all else being equal. Of course, an integrated understanding of the operation and outcomes of sexual selection requires the study of both preferences and realized choices, and especially how mate preferences and other traits affect realized choices.

Although mate preferences are considerably more heritable than realized mate choices (see Zietsch et al. 2011), it is interesting that mate preferences seem still to be less heritable than most other human behavioral characteristics. Human personality traits tend to be estimated at 30–60% heritability (Johnson et al. 2008), and intelligence, mental disorders, and drug and alcohol use tend to have heritabilities in this range or higher (Bouchard and McGue 2003; Deary et al. 2006; Levinson 2006; Agrawal and Lynskey 2008; Verweij et al. 2010).

The lower heritability of mate preferences could be partly due to our measure of mate preferences, which might contain more measurement error (thus a lower proportion of genetic variation) than the highly developed personality and intelligence tests. On the other hand, mental disorders and drug and alcohol use are often measured crudely and scored dichotomously, yet still yield high heritability estimates. Another possible explanation for low heritability of mate preferences is that mate preferences may be less stable within individuals than other traits; for example, women’s mate preferences are known to vary across their ovulatory cycle (Gangestad et al. 2007). Also, ranked mate preferences change according to environmental cues of pathogen prevalence and resource scarcity (Lee and Zietsch 2011), and could also be influenced by past relationship experiences—further, these environmental influences may interact with genetic predispositions. Intraindividual variation, environmental variance, and gene-by-environment interaction all contribute to variation that is unexplained by genes, hence lowering the heritability. On the other hand, the low or absent family environmental influence on mate preferences is in line with many other adult psychological traits (e.g., personality, intelligence, psychopathology; Bouchard and McGue 2003), although the possible underestimation of shared environment estimates should be kept in mind.
Another possible reason for low heritability is selection, which is expected to deplete genetic variation in traits affecting fitness (Fisher 1930). Considering the centrality of mate preferences to sexual selection and their potential to confer direct (genetic) and/or indirect (investment) benefits to offspring, selection is likely to be a factor. This raises the question of why any genetic variation is maintained; this question applies to practically all fitness-related quantitative traits (Mitchell-Olds et al. 2007), but there are some factors that may specifically apply to mate preferences. For example, the observation that mate preferences vary across geographical regions (DeBruine et al. 2010a) suggests that there may be environmental heterogeneity in selection pressures, which can in some circumstances maintain variation (i.e., balancing selection; Turelli and Barton 2004). On the other hand, if mate choices map only weakly onto mate preferences, selection on the latter may be weak; given that mate preferences are likely to depend on many genes (i.e., a large mutational target area), mutational variance is likely to be substantial (i.e., mutation—selection balance; Zhang and Hill 2005; Whitlock and Agrawal 2009).

It should also be noted that mate preferences might depend on other heritable traits, creating indirect (or “reactive”) heritability in mate preferences. Given the tendency for humans to mate with individuals similar to themselves (Price and Vandenberg 1980; Martin et al. 1986; Feingold 1988; Watson et al. 2004; Koenig et al. 2009; Zietsch et al. 2011) with regard to many traits (e.g., physical attractiveness), reactive heritability in mate preferences seems likely. For example, physically less-attractive individuals tend to place less importance on physical attractiveness in a partner (Todd et al. 2007)—physical attractiveness is heritable (McGovern et al. 1996), and so this would cause heritable variation in preference for physical attractiveness even in the absence of genetic influences acting directly on the preference itself. Mate preferences are also likely to relate to personality characteristics, but as there is little assortative mating on most personality traits (McCrae et al. 2008; Zietsch et al. 2011), it is less clear what pattern of association to expect. More research is needed on how mate preferences depend on other characteristics (e.g., mate value, personality) of the holder.

In addition to the aforementioned shortcomings of our measurement of mate preferences, there are other limitations to this study. First, there are further limitations of the measure. One important limitation is that the ranking system prevents the valid estimation of coefficients of additive and nonadditive genetic variance (Houle 1992), because this requires ratio-scale measures (i.e., measures with a meaningful zero-point) (Hansen et al. 2011). These absolute statistics can be compared across different traits and species and can be more evolutionarily informative than heritability (Hansen et al. 2011)—future studies should aim to use ratio-scale measures of human mate preferences. Another problem with the ranking system is that it does not measure the direction of preferences regarding various traits, only the traits’ relative importance. While it is safe to assume that a partner is always preferred to be healthy, the same cannot be said for the partner being religious or a university graduate. Further, the measure only assessed preferences for 13 traits, leaving out many traits of known importance (e.g., masculinity/femininity, body size). It also gives no indication of how selective (or choosy) an individual is when assessing mates—two individuals who rank traits in the same order of relative importance might differ greatly in the absolute importance of the traits when considering whether to pursue or accept a mate. Further still, we only measured preferences in a long-term partner, whereas humans are known to commonly engage in short-term as well as long-term mating. More broadly, self-report measures are potentially subject to inaccuracies (e.g., limited awareness of own preferences) or biases (e.g., social desirability), so future work should assess revealed or implicit preferences. The fact that the sample was primarily female meant less precision of male heritability estimates and no ability to investigate potentially interesting cross-sex correlations (i.e., between opposite-sex twins). Finally, despite the advantages of the twin design, the lack of additional data from partners and other relatives of twins precludes more complete characterization of the sources of variance (see Keller et al. 2009, 2010).

Given these limitations, there is clearly much more work to be done to fully understand the genetic and environmental variation in human mate preferences and what they reveal about our evolution. Nevertheless, this study represents an important first step—it demonstrates significant heritable within-sex variation in mate preferences for multiple cues, and gives an idea of the relative magnitude of genetic and environmental influences. Further investigation of the sources of variation within-sex will be an important complement to the mass of existing and ongoing research on species- and sex-typical aspects of mate preferences.

ACKNOWLEDGMENTS

We would like to thank the twins for their voluntary contribution to this research project. We would also like to thank the staff of the Twin Research Unit (KCL) for their help and support in undertaking this project. The Welcome Trust provides core support for Department of Twin Research. BPZ is supported by a UQ Postdoctoral Fellowship. KJHV is supported by an ANZ Trustees Ph.D. scholarship in Medical Research.

LITERATURE CITED


Neale, M. C., S. M. Boker, G. Xie, and H. H. Maes. 2006. Mx: statistical modeling. Department of Psychiatry, Virginia Commonwealth University Box 900126, Richmond, VA.


Associate Editor: R. Bonduriansky