



Comparing the biological and cultural inheritance of personality and social attitudes in the Virginia 30 000 study of twins and their relatives

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Measures of four dimensions of personality (Psychoticism, Extraversion, Neuroticism, and Lie scores) and six aspects of social attitudes (to sex, taxation, militarism, politics, religion and a general conservatism scale) were obtained by mailed questionnaire from 29 691 US subjects including adult twins ($n = 14\,761$) their parents ($n = 2360$), their spouses ($n = 4391$), siblings ($n = 3184$) and adult children ($n = 4800$). After correction for the average effects of age, sex and source of sample, familial correlations were computed for 80 distinct biological and social relationships. The data allow for the estimation of the additive and non-additive effects of genes, assortative mating, vertical cultural inheritance and other non-parental effects of the shared environment on differences in personality and social attitudes. The interaction of genetic and environmental effects with sex may also be analyzed. Model-fitting analyses show that personality and social attitude measures differ markedly in major features of family resemblance. Additive and dominant genetic effects contribute to differences in both personality and attitudes, but the effects of the family environment, including vertical cultural transmission from parent to child, are much more marked for social attitudes than for personality. There is substantial assortative mating for social attitudes and almost none for personality. The causes of family resemblance depend significantly on sex for almost every variable studied. These findings clarify and extend the more tentative findings derived from previous twin, family and adoption studies.

Keywords: personality, attitudes, cultural transmission, assortative mating, twins, behavior genetics, heritability, sex differences

Introduction

Four primary sources of data have been exploited in separate studies of the inheritance of personality: twins reared together,^{1–5} twins reared apart,^{6–9} nuclear families^{10,11} and adoption studies.^{12–15} These studies concur in showing a small to moderate contribution of genetic factors to variation in the major dimensions of personality. They also appear to show virtually no effect of the shared family environment on the correlations between relatives. Indeed, even when attempts have been made to measure particular environmental factors^{1,4,16} their contribution to personality differences has been pitifully small.

Such studies, however, have left unanswered a number of important questions. It has been claimed that the different kinds of data yield different estimates of heritability – those from twin studies being greater than those from adoption and nuclear

family studies.^{12,13} Whether such differences could be attributed to genetic non-additivity, the interaction of genetic effects with age, or to methods of ascertainment or choice of measures cannot be decided with certainty given the available data. Furthermore, although twin studies have been large enough to suggest sex differences in the expression of genes and environment on personality, the studies of other types of relationship have typically been too small to confirm or refute this basic finding. Also, it is not clear whether the results for personality can be generalized to other non-cognitive behavioral domains, notably social attitudes. Several large studies of twins reared together⁵ have suggested that family resemblance is greater for social attitudes than personality and that there are indications from twin data of a large effect of the shared family environment and assortative mating. However, the weight of this claim is based on twin studies and these leave open the issue of whether the claim that attitudes are transmitted different from personality can be borne out by studies of other kinds of relationships.

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Experience with computer simulation studies,^{17,18} and with the outcome of actual data analyses suggested that a large study of an extremely broad range of different relationships was necessary if we were to have a reasonable hope of analyzing the inheritance of complex traits with any degree of subtlety. A study was needed which could not just detect the effects of genes or the shared environment, but allow us to resolve different kinds of gene action such as additive and non-additive gene action. Such a study must also provide for the resolution of the different sources of non-genetic family resemblance including the environmental impact of mothers and fathers on their children and those environmental effects originating independently of the parental phenotype which are, nevertheless, shared by siblings and twins. Within this basic requirement it is also necessary that the study permits analysis of the contribution of assortative mating to variation and family resemblance and allows for the interaction of all the major sources of variation with sex differences. For example, the design should permit separation of the effects of sex-limited gene expression from the differential social interactions which may occur between mothers and fathers and their male and female offspring.

The Virginia 30 000

The series of simulation studies¹⁸ had indicated that, although the full adoption study involving adoptees with both their adopting and biological parents were more powerful for the purpose of detecting the effects of the parental environment, the difficulty of securing large enough samples vitiated the theoretical advantage, especially when the sexes were likely to differ in the contribution and type of genetic and environmental effects. Furthermore, given we cannot know in advance that the parental environment is not the only salient determinant of individual differences, and given the need for large samples in order to resolve subtle genetic and environmental effects, the study of the extended kinships of adult identical and non-identical twins, with their parents, siblings, spouses and adult children, had many advantages. Indeed, it provides a powerful basis for the resolution of additive and non-additive genetic effects, alternative models of assortative mating¹⁹ and a wide variety of components of the shared family environment including the environmental effects of the maternal and paternal phenotype and the additional environmental correlation induced between siblings ('sibling environment') and members of a twin pair ('twin environment').

The Virginia 30 000 study was designed to exploit this strategy in a comprehensive examination of the

causes of individual differences in attitudes, personality, habits, life styles, life events, physical characteristics, social support and psychosocial variables known to affect risk to physical and mental health.

Figure 1 gives an idealized pedigree sought for the Virginia 30 000. In practice, very few three-generation pedigrees were ascertained. Most families comprised either twins with their collateral relatives and parents, or twins and their collateral relatives and children. Ascertainment was in two stages. Names and addresses of Virginia-born twins were supplied by the Virginia Twin Registry under the supervision of Dr Linda Corey. In addition, a nationwide sample of volunteer twins aged 50+ was recruited through publicity provided by the American Association of Retired Persons ('AARP'). Truett *et al*²⁰ describe some of the properties of the sample. Twins were mailed a 16-page 'Health and Life-styles Questionnaire for Twins' (HLQ-T) developed for the study. At the end of the questionnaire twins were asked to supply names, addresses and telephone numbers of their parents, spouses, siblings and children who were then asked to complete versions of the HLQ identical to the twin versions as far as the measures of personality and attitudes were concerned. These questionnaires were designed for the parents of twins (HLQ-P) and other relatives of twins, including their spouses (HLQ-R).

Zygosity of the twins was established on the basis of two questions dealing with perceived similarity (Table 1). Any pair of twins who agree that they were frequently mistaken for each other and describe themselves as identical may be classified as monozygotic with a high degree of confidence. The validity of this approach to zygosity diagnosis has been generally accepted for large-scale studies as providing correct zygosity diagnoses in about 95% of cases. In cases where the zygosity algorithm identified inconsistent or uncertain responses, the twins were classified as unknown and used only for those

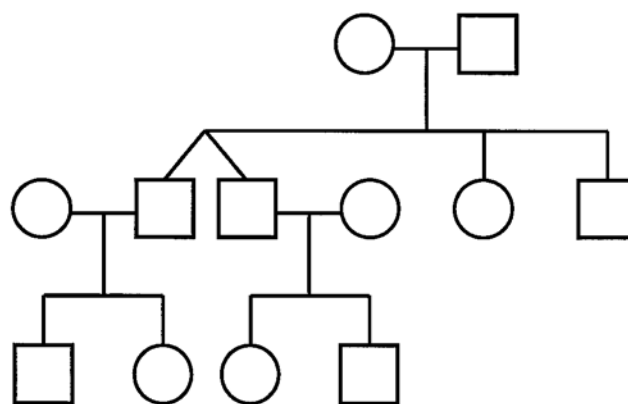


Figure 1 Idealised pedigree for Virginia 30 000 study: a three-generational pedigree including twins and their parents, children, siblings and spouses

Table 1 Items used in questionnaire zygosity diagnosis

1. As children, were you and your twin mistaken by people who knew you?
 (1) ___ Frequently
 (2) ___ Sometimes
 (3) ___ Rarely

2. Non-identical twins are no more alike than ordinary brothers and sisters. Identical twins, on the other hand, have such a strong resemblance to each other in stature, coloring, facial features, etc., that people often mistake one for the other, or say they are 'as alike as two peas in a pod'.

Having read the above statement, do you think you are:
 (1) ___ An identical twin
 (2) ___ A non-identical twin?

correlations in which the zygosity of twins was expected to make no difference (eg spousal correlations, parent-offspring and sibling correlations).

The final sample comprised 29 691 individuals. Table 2 summarizes the composition of the sample by sex and relationship to the twins. A few other relationships (eg half-siblings, adoptees) are also represented in the sample but their numbers are generally too small to have a significant impact on the analysis and these individuals are not included in these numbers.

In subsequent computations of the correlations between relatives, three-generational relationships (eg grandparent/grandchild), were omitted because sample sizes were small. However, all the unique combinations of relatives with respect to the sex of both parents and children were kept separate for the purposes of computing the correlations between relatives since, under a full model for the effects of sex on familial transmission, subtle differences may be introduced as a function of the sex of both the parents and children contributing genetic and environmental effects to a particular relationship. For example, if the impact of maternal effects depends on the sex of the offspring, then unlike-sex cousins related through unlike-sex dizygotic twin parents produce two distinct correlations, one involving the male offspring of the female twin as parent and one

Table 2 Sample sizes of twins and the principal adult relatives of twins in the Virginia 30 000 study

	Males	Females	Total
Twins	5 325	9 436	14 761
Parents of twins	913	1 447	2 360
Spouses of twins	2 515	1 876	4 391
Children of twins	1 890	2 910	4 800
Siblings of twins	1 260	1 924	3 184
Other	67	128	195
Total	11 970	17 721	29 691

with the male twin as the parent of the male offspring. When such distinctions are made, we have so far identified 80 distinct biological and social relationships, excluding those across three generations, in the extended kinships derived from monozygotic male, monozygotic female, dizygotic male, dizygotic female and unlike-sex dizygotic twin pairs.

Table 3 lists all the relationships distinguished in this analysis, together with an acronym for each correlation which is used to identify the correlations in subsequent tables. It is important to note that within each of the major categories of relationship tabulated, apart from nuclear families, there are two main sub-categories. Although the graphical structure of kinships based on MZ and DZ twins is the same, relationships within MZ kinships are biologically different from relationships within DZ kinships. Thus, the table distinguish relationships involving MZ twins from those involving DZs and siblings. For example, the spouses of MZ twins ('SPMZ') are expected to correlate differently from the spouses of DZ twins ('SPDZ') if genetic factors influence the choice of mate.^{19,21,22} Similarly, avuncular relationships between a nephew or niece and the MZ co-twin of a father or mother ('PatMav' and 'MatMav') are expected to involve a higher genetic correlation (equal to that between parents and offspring) than the conventional avuncular relationships involving a DZ co-twin or a sibling of a parent (eg 'PatSav' and 'MatDav').

Measurement of personality and attitudes

The HLQ included, with the authors' permission, the short form (54 items) of the Eysenck Personality Questionnaire.²³ The short EPQ is scored for the three principal dimensions of Eysenck's personality theory: Psychoticism, Extraversion and Neuroticism (P, E and N). A fourth scale may also be scored, measuring the tendency of the subjects to 'fake good' – the 'Lie-scale' (L). The authors' scales were used to obtain scores for P, E, N and L. The E, N and L scales are represented by 12 items each and the P scale by 13 items. The items comprising the scales are reproduced in Table 4. In order to minimize the impact of occasional missing values scores were imputed for those subjects who had ten or more valid responses to a given scale.

Social attitudes were assessed by a 28-item inventory modeled on the Wilson-Patterson Conservatism scale. The items were chosen after review of the loadings on the first principal component of the

Table 3 Key to relationships in Virginia 30 000

Group and Acronym	Description	Group and Acronym	Description
Nuclear families		MZInIMF	Wife with husband's MZ male cotwin
Spouses	Spouses	MZInIFM	Husband with wife's MZ female cotwin
Sibs: MM	Male–male sibling pairs	Parent-in-Law	
Sibs: FF	Female–female siblings	Fa–DIL	Father with daughter-in-law
Sibs: MF	Male–female siblings	Fa–SIL	Father with son-in-law
Fath–Son	Father–son	Mo–DIL	Mother with daughter-in-law
Fath–Dau	Father–daughter	Mo–SIL	Mother with son-in-law
Moth–Son	Mother–son	Spouses of uncles and aunts	
Moth–Dau	Mother–daughter	SPaDavFM	Male with wife of father's DZ twin
Twins		SPaDavFF	Female with wife of father's DZ twin
DZ: MM	Dizygotic male–male	SMADavMM	Male with husband of mother's DZ
DZ: FF	Dizygotic female–female	SMADavMF	Female with husband of mother's DZ
DZ: MF	Dizygotic male–female	SPaDavMM	Male with husband of father's DZ
MZ: MM	Monozygotic male	SPaDavMF	Female with husband of father's DZ
MZ: FF	Monozygotic female	SMADavFM	Male with wife of mother's DZ
Avuncular		SMADavFF	Female with wife of mother's DZ
PatSavMM	Nephew with father's brother	SPaMavFM	Male with wife of father's MZ twin
PatSavMF	Niece with father's brother	SPaMavFF	Female with wife of father's MZ
MatSavFM	Nephew with mother's sister	SMAmavMM	Male with husband of mother's MZ
MatSavFF	Niece with mother's sister	SMAmavMF	Female with husband of mother's MZ
PatSavFM	Nephew with father's sister	Spouses of twins	
PatSavFF	Niece with father's sister	SPDZM	Wives of DZ male twins
MatSavMM	Nephew with mother's brother	SPDZF	Husbands of DZ female twins
MatSavMF	Niece with mother's brother	SPDZMF	Spouses of DZ male–female twins
PatDavMM	Nephew with father's DZ brother	SPMZM	Wives of male MZ twins
PatDavMF	Niece with father's DZ brother	SPMZM	Husbands of female MZ twins
MatDavFM	Nephew with mother's DZ sister	Cousins	
MatDavFF	Niece with mother's DZ sister	MZMCsMM	Male–male
PatDavFM	Nephew with father's DZ sister	MZMCsFF	Female–female
PatDavFF	Niece with father's DZ sister	MZMCsMF	Male–female
MatDavMM	Nephew with mother's DZ brother	MZFCsMM	Male–male
MatDavMF	Niece with mother's DZ brother	MZFCsFF	Female–female
PatMavMM	Nephew with father's MZ twin	MZFCsMF	Male–female
PatMavMF	Niece with father's MZ twin	DZMCsMM	Male–male
MatMavFM	Nephew with mother's MZ twin	DZMCsFF	Female–female
MatMavFF	Niece with mother's MZ twin	DZMCsMF	Male–female
Siblings-in-law		DZMCsMM	Male–male
SibInIMF	Wife with husband's brother	DZMCsFF	Female–female
SibInIFM	Husband with wife's sister	DZMCsMF	Male–female
SibInIMM	Husband with wife's brother	DZFCsMM	Male–male
SibInIFF	Wife with husband's sister	DZFCsFF	Female–female
DZInIMF	Wife with husband's DZ male cotwin	DZFCsMF	Male–female
DZInIFM	Husband with wife's DZ female cotwin	DZMFCsMM	Male–male
DZInIMM	Husband with wife's DZ male cotwin	DZMFCsFF	Female–female
DZInIFF	Wife with husband's DZ female cotwin	DZMFCsMF	Male–female
		DZMFCsFM	Female–male

items of the full scale used in an earlier study of Australian twins.⁵ Some supplementary items were added to reflect issues (eg segregation, busing, moral majority) deemed newsworthy in the US at the time the survey was constructed. The items are listed in Table 5. Each may be answered 'Yes', 'Uncertain', 'No' (scored 1,2,3) to indicate agreement or otherwise with the topic.

The eigenvalues of the inter-item correlations for the attitude items suggested that a general 'conservative–liberalism' factor is a substantial, but not

exhaustive, component of the social attitudes sampled in our brief inventory. A conservatism scale (Con) was thus constructed using all of the items keyed according to whether they had a positive or negative loading on the first general factor (Table 5). More detailed preliminary factor analysis of the attitude items confirmed that five (oblique) factors were clearly defined. On the basis of the factor pattern, we constructed scales (see Table 5) to reflect these main dimensions of the attitude responses: sexual permissiveness (Sex); economic liberalism

Table 4 Items from Eysenck Personality Questionnaire

	Scale	Scoring	Scale	Scoring
1. Does your mood often go up and down?	N	+	E	+
2. Do you take much notice of what people think?	P	-	N	+
3. Are you a talkative person?	E	+	P	-
4. If you say you will do something, do you always keep your promise?	L	+	E	-
5. Do you ever feel 'just miserable' for no reason?	N	+	P	-
6. Would being in debt worry you?	P	+	L	-
7. Are you rather lively?	E	+	N	+
8. Were you every greedy by helping yourself to more than your share?	L	-	P	+
9. Do you stop to think things over before doing anything?	P	-	E	+
10. Are you an irritable person?	N	+	E	+
11. Would you take drugs which may have strange or dangerous effects?	P	+	L	-
12. Do you enjoy meeting new people?	E	+	N	+
13. Have you ever blamed someone for what was really your fault?	L	-	P	-
14. Are your feelings easily hurt?	N	+	E	+
15. Do you prefer to go your own way rather than act by the rules?	P	+	L	-
16. Can you usually let yourself go and enjoy yourself at a lively party?	E	+	N	+
17. Are all your habits good and desirable ones?	L	+	P	+
18. Have people said that you sometimes act too rashly?	E	+	L	-
19. Do you often feel 'fed-up'?	N	+	E	+
20. Do good manners and cleanliness matter much to you?	P	-	N	+
21. Do you usually take the initiative in making new friends?	E	+	P	-
22. Have you ever taken anything that belonged to someone else?	L	-	E	+
23. Would you call yourself a nervous person?	N	+	L	-
24. Do you think marriage is old-fashioned and should be done away with?	P	+	N	+
25. Can you easily put some life into a rather dull party?	E	+	L	-
26. Have you ever broken or lost something belonging to someone else?	L	-	E	+
27. Do you often make decisions on the spur of the moment?	E	+	E	+
28. Are you a worrier?	N	+	N	+
29. Do you enjoy co-operating with others?	P	-	P	-
30. Do you tend to keep in the background on social occasions?	E	-	E	-
31. Does it worry you if you know there are mistakes in your work?	P	-	P	-
32. Have you ever said anything bad or nasty about anyone?	L	-	L	-
33. Would you call yourself tense or 'high-strung'?	N	+	N	+
34. Do you think people spend too much time safeguarding their future with savings and insurances?	P	+	P	+
35. Do you like mixing with people?	E	+	E	+
36. Do you often take on more activities than you have time for?	E	+	E	+
37. As a child, were you ever 'fresh' towards your parents?	L	-	L	-
38. Do you worry too long after an embarrassing experience?	N	+	N	+
39. Do you try not to be rude to people?	P	-	P	-
40. Do you like plenty of bustle and excitement around you?	E	+	E	+
41. Have you ever cheated at a game?	L	-	L	-
42. Do you suffer from 'nerves'?	N	+	N	+
43. Would you like other people to be afraid of you?	P	+	P	+
44. Have you ever taken advantage of someone?	L	-	L	-
45. Do you like doing things in which you have to act quickly?	E	+	E	+
46. Are you mostly quiet when you are with other people?	N	+	N	+
47. Do you often feel lonely?	E	-	E	-
48. Is it better to follow society's rules than go your own way?	P	-	P	-
49. Do other people think of you as being very lively?	E	+	E	+
50. Do you always practice what you preach?	L	-	L	-
51. Are you often troubled about feelings of guilt?	N	+	N	+
52. Do you sometimes put off until tomorrow what you ought to do today?	L	-	L	-
53. Can you get a party going?	E	+	E	+
54. Would you call yourself happy-go-lucky?	E	+	E	+

Table 5 Key to social attitude items

Item	Conservatism	Primary
1. Death penalty	+	Mil
2. Astrology	-	Sex
3. X-rated movies	-	Sex
4. Modern art	-	Sex
5. Women's liberation	-	Sex
6. Foreign aid	-	Tax
7. Federal housing	-	Tax
8. Democrats	-	Pol
9. Military drill	+	Mil
10. The draft	+	Mil
11. Abortion	-	Sex
12. Property tax	-	Tax
13. Gay rights	-	Sex
14. Liberals	-	Sex
15. Immigration	-	Tax
16. Capitalism	+	Tax
17. Segregation	+	Rel
18. Moral majority	+	Rel
19. Pacificism	-	Mil(-) Rel(-)
20. Censorship	+	Rel
21. Nuclear power	+	Mil
22. Living together	-	Sex
23. Republicans	+	Pol(-)
24. Divorce	-	
25. School prayer	+	Rel
26. Unions	-	
27. Socialism	-	
28. Busing	+	

Note: Subjects are asked to indicate agreement or otherwise by circling 'Yes' or 'No' as appropriate, or to indicate uncertainty by circling '?'. In the above key a '+' indicates 'Yes' is the keyed direction of response.

(Tax); militarism (Mil); political preference for democrats or republicans (Pol); religious fundamentalism (Rel).

Data summary

In order to remove specific extraneous causes of variation and correlation between relatives that might interfere with the analysis of other genetic and environmental effects, the subjects' scores for each scale were examined for their regression on dummy variables coded for sex, whether or not the subject was a twin, and the source of ascertainment (the Virginia Twin Registry vs the AARP registry). Interactions between these effects were specified as the regressions on products of the dummy variables. The linear and quadratic effects of age, and the interactions of these components with the dummy variables and their interactions were also included in the regression model. The SAS regression procedure was used for this part of the analysis and the residuals from the regression model were then normalized using the 'BLOM' method incorporated in the SAS 'RANK' procedure.

In an ideal world, the correlations between relatives for the extended pedigrees should be computed by the method of maximum likelihood.^{5,24} With 80 distinct relationships, however, securing ML estimates of the correlations is prohibitive with current algorithms since, in addition to the 80 correlations of primary concern, it would be necessary also to estimate a large number of others (eg three-generational correlations) which are based on numbers too small to provide estimates of any practical value. We chose an acceptable but not ideal alternative. All possible pairs of individuals contributing to a given relationship were identified and a pooled correlation for that group of individuals was computed. Although simulation studies have shown such estimates to be unbiased, the repeated use of the same individual in computing a correlation leads to estimates that are less precise than might be assumed as they have been based on samples of independent pairs.²⁵ One consequence of the false assumption of independence among the estimated correlations is that tests of goodness of fit tend to be more likely to be rejected than should be the case.

We present the correlations between relatives for the normalized residuals for personality in Table 6 and for social attitudes in Table 7.

In order to simplify preliminary perusal of the patterns of family resemblance, the correlations were pooled across sexes. Also, correlations which involved the DZ twin relationship were pooled with those involving the sibling relationship. Note that these correlations are frequently heterogeneous, given the very large sample sizes, and they are pooled for the purposes of preliminary inspection only. Subsequent model-fitting analyses are based on the entire set of 80 correlations and allow for the various possible sources of heterogeneity. The pooled correlations for personality are summarized in Table 8. Those for attitudes are given in Table 9.

The summary correlations for personality (Table 8) are all quite small, the only exception being those for MZ twins. Even here, however, that for the 'P' scale is only 0.29. Thus, over 50% of the variation in personality as measured by the short EPQ is due to non-familial factors such as errors of measurement and within-family environmental factors. In no case does the DZ correlation exceed half of the MZ correlation, suggesting that shared environmental effects are likely to be small. Generally, the sibling and parent offspring correlations are about equal. The avuncular correlations involving MZ co-twins of parents ('MZ avuncular') are close to the parent-offspring correlation for E,N and L and higher than the conventional avuncular correlations involving siblings and DZ co-twins of parents ('avuncular'). These correlations point to a small additive genetic contribution to family resemblance accounting for

Table 6 Correlations between relatives for Eysenck Personality Questionnaire scales

Relation	n(Pr)	Correlation			
		Psychoticism (P)	Extraversion (E)	Neuroticism (N)	Lie (L)
Nuclear family					
Spouses	4815	0.094	0.017	0.092	0.187
Sibs: MM	1514	0.128	0.139	0.109	0.122
Sibs: FF	3551	0.087	0.196	0.172	0.184
Sibs: MF	4304	0.078	0.131	0.137	0.129
Fath-Son	2218	0.047	0.154	0.134	0.105
Fath-Dau	3033	0.055	0.123	0.127	0.154
Moth-Son	3034	0.078	0.155	0.148	0.150
Moth-Dau	4542	0.087	0.162	0.157	0.173
Twins					
DZ: MM	556	0.170	0.153	0.178	0.271
DZ: FF	1141	0.098	0.120	0.224	0.255
DZ: MF	1295	0.104	0.108	0.097	0.158
MZ: MM	766	0.218	0.480	0.353	0.445
MZ: FF	1799	0.321	0.520	0.410	0.473
Avuncular					
PatSavMM	94	-0.055	0.003	0.062	0.094
PatSavMF	156	-0.052	0.069	-0.028	0.060
MatSavFM	388	0.016	0.163	0.145	0.058
MatSavFF	537	0.009	0.167	0.032	0.107
PatSavFM	130	-0.030	-0.058	0.081	0.245
PatSavFF	192	-0.017	-0.067	0.188	0.024
MatSavMM	234	-0.034	0.025	0.098	-0.005
MatSavMF	291	0.025	0.091	-0.005	0.066
PatDavMM	104	-0.014	0.134	0.118	0.067
PatDavMF	140	0.010	0.087	0.094	0.074
MatDavFM	331	0.127	0.106	0.107	0.103
MatDavFF	511	-0.040	0.174	0.183	0.151
PatDavFM	114	-0.069	0.121	-0.012	0.106
PatDavFF	180	0.028	-0.023	0.089	0.019
MatDavMM	152	-0.006	0.063	0.141	-0.021
MatDavMF	199	0.024	0.082	0.042	0.037
PatMavMM	216	-0.013	0.073	-0.016	0.059
PatMavMF	327	-0.018	0.172	0.034	0.158
MatMavFM	645	0.033	0.121	0.190	0.119
MatMavFF	1006	0.070	0.144	0.118	0.200
Cousins					
MZMCsMM	41	0.366	-0.198	-0.027	0.236
MZMCsFF	93	-0.051	0.205	0.102	-0.073
MZMCsMF	103	0.040	0.164	0.114	0.080
MZFCsMM	153	0.018	0.028	0.097	-0.033
MZFCsFF	341	0.000	0.102	0.096	0.100
MZFCsMF	453	0.005	0.091	0.044	0.121
DZMCsMM	17	-0.066	-0.231	-0.197	0.364
DZMCsFF	40	0.415	-0.228	-0.046	0.220
DZMCsMF	49	-0.134	-0.032	0.042	-0.165
DZFCsMM	52	0.160	0.145	-0.068	-0.105
DZFCsFF	139	0.122	0.201	0.243	0.177
DZFCsMF	158	0.038	0.156	0.189	0.090
DZMFCsMM	38	0.090	0.023	0.250	0.010
DZMFCsFF	72	-0.004	0.179	0.238	-0.095
DZMFCsMF	50	-0.124	-0.182	0.330	0.057
DZMFCsFM	70	-0.249	-0.027	0.154	-0.131
Siblings-in-law					
SibInIMF	350	-0.049	-0.032	0.070	0.057
SibInIFM	732	0.039	0.078	0.056	0.055
SibInIMM	431	0.097	0.066	0.092	0.104
SibInIFF	463	0.094	0.101	0.047	0.064
DZInIMF	405	0.003	-0.048	-0.039	0.156
DZInIFM	594	-0.013	0.049	-0.002	0.043
DZInIMM	361	0.074	0.055	-0.062	0.032
DZInIFF	450	0.008	-0.032	-0.017	0.056
MZInIMF	602	0.038	0.117	0.064	0.066
MZInIFM	1132	0.075	-0.018	0.066	0.074
Parent-in-Law					
Fa-DIL	215	-0.008	0.028	0.085	0.109
Fa-SIL	210	0.067	-0.006	0.002	0.181
Mo-DIL	302	0.045	0.115	0.053	0.068
Mo-SIL	348	0.023	-0.050	-0.047	0.014
Affine avuncular					
SPaDavFM	55	-0.172	0.054	-0.076	0.003
SPaDavFF	77	0.117	-0.147	-0.075	0.133
SMaDavMM	124	-0.050	0.092	0.084	0.079
SMaDavMF	172	-0.003	0.016	0.213	-0.073
SPaDavMM	35	-0.407	-0.036	-0.417	-0.288
SPaDavMF	67	-0.190	0.063	0.033	-0.010
SMaDavFM	69	-0.006	0.101	0.304	0.047
SMaDavFF	95	-0.010	0.013	-0.128	-0.082
SPaMavFM	129	-0.061	0.076	-0.146	0.080
SPaMavFF	212	0.012	0.042	0.105	0.082
SMaMavMM	340	-0.022	0.064	0.051	0.015
SMaMavMF	501	0.053	0.069	0.009	0.124
Twins' spouses					
SPDZM	101	0.200	0.057	0.005	0.048
SPDZF	124	0.059	-0.032	0.098	-0.043
SPDZMF	169	0.050	-0.072	-0.022	0.140
SPMZM	180	0.065	0.040	-0.045	0.089
SPMZF	296	0.030	-0.014	0.018	0.116

Table 7 Correlations between relatives for Social Attitude Scales

Relation	Social Attitudes						Conservatism	
	n(pr)	Sex	Tax	Mil	Pol	Rel	n(pr)	Con
Nuclear family								
Spouses	4692	0.567	0.360	0.413	0.522	0.452	4915	0.619
Sibs: MM	1523	0.328	0.257	0.206	0.234	0.312	1551	0.341
Sibs: FF	3497	0.355	0.256	0.197	0.233	0.330	3643	0.405
Sibs: MF	4262	0.305	0.229	0.193	0.231	0.248	4395	0.328
Fath–Son	2164	0.359	0.284	0.261	0.303	0.318	2247	0.410
Fath–Dau	2988	0.338	0.236	0.212	0.278	0.312	3095	0.396
Moth–Son	3020	0.311	0.238	0.237	0.275	0.300	3138	0.369
Moth–Dau	4466	0.401	0.273	0.254	0.290	0.306	4667	0.456
Twins								
DZ: MM	556	0.377	0.299	0.245	0.308	0.224	579	0.379
DZ: FF	1080	0.435	0.317	0.247	0.341	0.310	1142	0.432
DZ: MF	1239	0.290	0.201	0.218	0.299	0.236	1312	0.319
MZ: MM	765	0.531	0.473	0.478	0.442	0.472	790	0.593
MZ: FF	1739	0.602	0.484	0.384	0.455	0.499	1839	0.637
Avuncular								
PatSavMM	100	0.314	0.298	0.275	0.115	0.263	100	0.334
PatSavMF	153	0.229	0.188	–0.042	0.014	0.261	156	0.324
MatSavFM	388	0.238	0.203	–0.058	0.049	0.219	405	0.200
MatSavFF	520	0.189	0.131	0.063	0.027	0.241	547	0.226
PatSavFM	128	0.324	0.078	0.182	–0.226	0.133	133	0.264
PatSavFF	189	0.211	–0.039	–0.026	0.064	0.034	200	0.112
MatSavMM	226	0.101	0.071	0.121	0.142	0.254	235	0.175
MatSavMF	281	0.047	0.142	0.075	0.071	0.189	297	0.166
PatDavFM	109	0.034	0.124	0.143	0.091	0.164	110	0.107
PatDavMF	143	0.103	0.039	–0.012	–0.047	0.035	144	0.108
MatDavMM	323	0.190	0.032	0.012	0.143	0.206	332	0.200
MatDavFF	489	0.190	0.106	0.081	0.076	0.302	516	0.250
PatDavFM	109	0.186	0.125	0.142	0.395	0.094	114	0.282
PatDavMF	171	0.210	0.235	0.212	0.217	0.122	180	0.314
MatDavFM	151	0.015	0.055	0.241	0.146	0.209	154	0.185
MatDavMF	201	0.115	0.147	0.002	0.036	0.217	206	0.225
PatMavMM	219	0.393	0.234	0.259	0.059	0.294	221	0.428
PatMavMF	333	0.329	0.096	0.085	0.135	0.283	341	0.315
MatMavFM	637	0.323	0.161	0.166	0.054	0.249	661	0.367
MatMavFF	994	0.337	0.229	0.146	0.179	0.251	1035	0.318
Cousins								
MZM CsMM	39	0.273	–0.046	0.175	0.383	0.063	40	0.564
MZM CsFF	95	0.243	0.170	0.226	0.206	0.093	95	0.265
MZM CsMF	107	0.281	–0.068	0.037	0.092	0.042	107	0.264
MZFCsMM	156	0.247	0.033	0.068	0.035	0.212	158	0.239
MZFCsFF	335	0.272	0.178	0.037	0.095	0.205	339	0.287
MZFCsMF	454	0.247	0.131	0.081	0.094	0.381	459	0.309
DZM CsMM	19	0.216	0.532	0.020	0.187	0.203	19	0.091
DZM CsFF	42	0.146	–0.131	0.158	–0.011	0.058	42	0.339
DZM CsMF	52	0.032	–0.030	0.335	–0.019	0.009	52	0.173
DZFCsMM	52	–0.274	–0.018	0.150	0.136	–0.073	53	–0.117
DZFCsFF	137	0.173	0.259	0.134	0.128	0.330	141	0.275
DZFCsMF	153	0.191	0.155	0.050	0.067	0.156	163	0.240
DZMFCsMM	39	–0.043	0.007	0.520	0.427	0.186	39	0.242
DZMFCsFF	69	0.123	0.114	0.267	0.253	0.242	70	0.227
DZMFCsMF	50	0.190	0.014	0.062	0.046	–0.047	52	0.066
DZMFCsFM	69	0.102	0.056	0.141	0.440	–0.017	70	0.112
Siblings-in-law								
SibInIMF	364	0.380	0.322	0.128	0.160	0.265	371	0.386
SibInIFM	710	0.268	0.175	0.103	0.100	0.176	745	0.219
SibInIMM	428	0.229	0.144	0.154	0.145	0.163	443	0.222
SibInIFF	472	0.169	0.131	0.172	0.187	0.127	486	0.175
DZInIMF	402	0.211	0.131	0.096	0.182	0.211	417	0.263
DZInIFM	586	0.328	0.160	0.116	0.190	0.238	618	0.310
DZInIMM	350	0.167	0.173	0.238	0.153	0.201	363	0.202
DZInIFF	434	0.203	0.196	0.205	0.223	0.207	455	0.290
MZInIMF	594	0.405	0.235	0.255	0.303	0.432	625	0.490
MZInIFM	1098	0.343	0.166	0.164	0.241	0.303	1153	0.409
Parent-in-Law								
Fa–DIL	198	0.287	0.152	0.117	0.217	0.226	208	0.312
Fa–SIL	206	0.289	0.215	0.180	0.173	0.172	211	0.219
Mo–DIL	293	0.227	0.213	0.113	0.049	0.262	311	0.250
Mo–SIL	345	0.196	0.122	0.159	0.104	0.292	360	0.308
Affine avuncular								
SPaDavFM	57	–0.063	0.065	–0.083	–0.215	–0.116	57	–0.048
SPaDavFF	80	0.102	–0.019	–0.028	–0.097	–0.009	82	0.159
SMADavMM	120	0.062	0.113	0.100	0.235	0.267	128	0.158
SMADavMF	164	0.152	0.090	0.175	0.017	0.172	179	0.166
SPaDavMM	38	–0.110	–0.052	0.258	0.241	0.115	38	0.015
SPaDavMF	67	0.066	0.092	0.156	0.121	0.052	70	0.055
SMADavFM	69	0.200	0.213	0.270	0.149	0.167	71	0.230
SMADavFF	96	–0.071	0.107	0.159	0.018	0.295	99	0.195
SPaMavFM	129	0.305	0.086	0.199	0.088	0.198	134	0.366
SPaMavFF	213	0.348	0.095	0.083	0.184	0.223	224	0.276
SMAvMM	341	0.166	0.138	0.072	0.028	0.167	353	0.239
SMAvMF	494	0.238	0.169	0.052	0.139	0.182	511	0.222
Twins' spouses								
SPDZM	103	0.154	0.082	0.057	0.163	0.109	104	0.212
SPDZF	120	0.373	0.201	0.241	0.271	0.251	129	0.325
SPDZMF	169	0.106	–0.069	0.204	0.161	0.288	172	0.185
SPMZM	175	0.426	0.128	0.270	0.374	0.355	188	0.378
SPMZMF	289	0.214	0.181	0.065	0.214	0.213	304	0.267

Note: Sex: sexual permissiveness; Tax: economic liberalism; Mil: militarism; Pol: political preference; Rel: religious fundamentalism; Con: general conservatism factor

Table 8 Summary correlations between relatives (pooled across sexes) for EPQ measures

Relation	n(Pr)	Correlation			
		Psychoticism (P)	Extraversion (E)	Neuroticism (N)	Lie (L)
Spouses	4815	0.094	0.017	0.092	0.187
Sibs	9369	0.089	0.157	0.146	0.149
DZ twins	2992	0.114	0.121	0.161	0.216
MZ twins	2565	0.291	0.508	0.394	0.465
Parents	12827	0.070	0.150	0.144	0.151
Avuncular	3753	0.003	0.097	0.092	0.080
MZ avuncular	2194	0.038	0.135	0.114	0.157
MZ cousins	1184	0.016	0.092	0.074	0.081
DZ cousins	685	0.030	0.074	0.166	0.041
Sib-in-law	3786	0.032	0.036	0.021	0.069
MZ-in-law	1734	0.062	0.029	0.065	0.071
Parent-in-law	1075	0.032	0.021	0.017	0.081
Affine avuncular	694	-0.051	0.025	0.065	-0.011
MZ affine avuncular	1182	0.012	0.064	0.022	0.080
Spouses of DZ	394	0.091	-0.026	0.023	0.059
Spouses of MZ	476	0.043	0.006	-0.006	0.106

Table 9 Summary correlations between relatives (pooled across sexes) for social attitude measures

Relation	Social Attitudes						Conservatism	
	n(pr)	Sex	Tax	Mil	Pol	Rel	n(pr)	Con
Spouses	4692	0.567	0.360	0.413	0.522	0.452	4915	0.619
Sibs	9282	0.328	0.244	0.197	0.232	0.290	9589	0.360
DZ twins	2875	0.363	0.264	0.234	0.317	0.262	3033	0.374
MZ twins	2504	0.581	0.481	0.414	0.451	0.491	2692	0.624
Parents	12638	0.358	0.258	0.241	0.286	0.308	13147	0.414
Avuncular	3681	0.172	0.119	0.067	0.076	0.206	3829	0.216
MZ avuncular	2183	0.337	0.190	0.154	0.124	0.260	2258	0.343
MZ cousins	1186	0.258	0.112	0.077	0.105	0.250	1198	0.296
DZ cousins	682	0.110	0.112	0.164	0.156	0.140	701	0.193
Sib-in-law	3746	0.250	0.176	0.146	0.164	0.197	3898	0.257
MZ-in-law	1692	0.365	0.190	0.196	0.263	0.350	1778	0.439
Parent-in-law	1042	0.241	0.172	0.142	0.124	0.248	1090	0.276
Affine avuncular	691	0.065	0.087	0.128	0.059	0.148	724	0.140
MZ affine avuncular	1177	0.245	0.138	0.080	0.110	0.187	1222	0.253
Spouses of DZ	392	0.203	0.054	0.178	0.196	0.231	405	0.238
Spouses of MZ	464	0.297	0.161	0.144	0.276	0.268	492	0.310

no more than 25–30% of the total variance. The fact that the MZ correlations for E and N somewhat exceed these values may be due to non-additive genetic effects or a special MZ twin environment. The fact that other relationships involving MZ twins, especially those for social attitudes (see below) are also inflated seems to point to a very pervasive effect of monozygosity on other biological and non-biological relationship. Obviously a genetic model has a built-in capability to predict and explain these findings. It is less clear that the often-touted 'special MZ twin environment' has these capabilities.

The spousal correlations, and all correlations by marriage are uniformly small, although with these sample sizes very small correlations are statistically significant. The spousal correlation for the 'Lie' scale is twice that of any of the other EPQ scales and even that is too small to have biologically or socially significant impact of genetic and environmental

correlations between relatives. Thus, in general, the effects of assortment on personality are fairly trivial.

All these findings are consistent with other studies of personality, including adoption studies and studies of separated twins^{5,13–15,26} and the larger studies of twins (see Eaves *et al*⁵ for a summary of these studies).

The correlations for social attitudes (Table 9) extend to other relationships those characteristics of the transmission of social attitudes, as distinct from personality, that we have come to recognize on the basis of earlier studies of twins especially.⁵ The correlations for conservatism ('C') are typical and represent the general trend found in the primary attitude scales. Family resemblance is generally greater. Correlations for first degree relatives are twice those for personality and there is a very striking correlation between spouses which has a

pervasive impact on all the other relationships by marriage ('In-laws', avuncular correlations by marriage, spouses of twins). The potential impact of mate selection on the transmission of, and variation in, attitudes clearly cannot be ignored. The other striking feature of the attitude data is that all the correlations involving monozygotic twins exceed the corresponding correlations involving DZ twins or siblings. This is true for biological relationships and for relationships by marriage. Thus, the avuncular correlations involving an MZ co-twin as uncle/aunt (genetically a parent–offspring relationship) are generally greater than the corresponding conventional avuncular correlations involving aunts and uncles who are siblings or DZ twins of the parents. Similarly, the correlations between cousins related through MZ twin parents (genetically half-siblings²⁷) exceed those for conventional cousins related through DZ twin parents. Thus the data are consistent with previous studies in lending support to the counter-intuitive notion that genetic factors account for some of the variation in social attitudes in western, Caucasian culture.

A model for family resemblance in extended twin kinships

The preliminary examination of the pooled correlations suggests the main features that might emerge from a more rigorous analysis but does not capture the subtleties that are apparent in the full tables of correlations, not does it yield a more thorough quantitative resolution of the effects of biological and cultural transmission which, a priori, are expected to be correlated in kinships based on nuclear families alone. Furthermore, many of the correlations pooled to generate the summary tables are significantly heterogeneous, suggesting that sex differences may interact with the causes of family resemblance.

Figure 2 presents a tractable path model for family resemblance which can be extended to include all the relationships in the kinships of twins listed above in Table 3. It is not the only possible model and others may be developed which feature other nuances of the mate selection process or non-genetic inheritance.¹⁹

Basic parameters of the model

The model is discussed in detail by Truett *et al*²⁰ who illustrate its application to the analysis of biological and cultural inheritance to twin-kinship data on frequency of church attendance. Ignoring, for

the moment, the provision for sex differences in genetic and environmental effects, the model allows for a series of basic genetic and social influences on variation. These are denoted in the path diagram (Figure 2) by lower case letters as follows:

1. additive genetic effects, h ;
2. genetic dominance, d ;
3. path from environment to phenotype, e ;
4. path from parental phenotype to offspring environment, w ;
5. phenotypic correlation between mates, μ ;
6. path from residual sibling shared environment to phenotype, s ;
7. path from additional twin shared environment to phenotype, t ;
8. the correlation between genotype and environment, ρ .

The model assumes initially that assortative mating, if present, is based on the measured phenotype, P ('primary phenotypic assortative mating'¹⁹). Similarly, it is assumed that vertical cultural transmission from parent to offspring is based on the measured phenotype of the parents rather than on some latent or correlated variable (' P to E ' vertical cultural inheritance). The effects of the sibling and twin shared environments are assumed to contribute to variation among individuals regardless of relationship. However, the sibling environment is perfectly correlated in sibling and twin pairs, and the twin environment is perfectly correlated in twin pairs. Thus, the model assumes that twins and siblings will differ in correlation as a result of how they are influenced by their shared environment but not in their variance. That is, twins and siblings are assumed to sample the same marginal distribution of environmental effects as other individuals but they differ in the environmental correlation. The genotype–environment correlation, ρ , occurs when the parental phenotype, which contributes to the offspring's environment through parent–offspring transmission, is partly genetic in origin. This results in a correlation between the offspring's environment and genes. The process of transmission and assortment is assumed to be in equilibrium, and thus, ρ is constant between generations. That is, ρ_{parent} is constrained to be equal to ρ_{child} . Since models are fitted to correlations, the scale of measurement has unit variance; therefore, we impose the further constraint that the sum of all sources of variation is unity.

Allowing for sex differences in model parameters

One of the principal advantages of a study involving large samples of relatives is the provision of an opportunity to test a variety of models of sex-dependent etiology and transmission. For the simple case of randomly mating populations, a model for sex differences in gene action was specified by Eaves³⁰ which allowed for the same genes to have different magnitudes of effect on males and females. This model allows for estimation of separate genetic variances for males and females and a correlation between gene effects in males and females. The genetic correlation between the sexes will be unity if the effects of all autosomal loci on one sex are constant multiples of their effects on the other sex. In this case, we speak of 'scalar sex limitation of the gene effects'. Analogous definitions may be given for the 'sex-limited' effects of the shared environment. If the magnitudes of the loci or, by analogy, 'environmental effects' on one sex are not constant multiples of their effects on the other sex, then we speak of non-scalar sex limitation of genetic (or environmental) effects.

The present model extends the analysis of sex-dependent effects to the more difficult case of combined assortative mating and cultural inheritance. In the path diagram (Figure 2) we employ the following notation for the effects of dominance, sibling environment and special twin environment: d_m , s_m , and t_m in males respectively, and d_f , s_f and t_f for their counterparts in females; and r_d , r_s and r_t for the correlations across sexes of the dominant, sibling environmental and twin environmental effects.

Since vertical cultural transmission is assumed under this model to be based on the parental phenotype for the trait under investigation the question of 'non-scalar' vertical cultural transmission does not apply. However, the cultural impact of mothers may differ from that of fathers, and may further depend on the sex of the offspring. In the model for sex differences, therefore, we require four cultural parameters: w_{mm} ; w_{mf} ; w_{fm} ; w_{ff} . The first subscript denotes the sex ($m = \text{male}$) of the offspring and the second denotes the sex of the parent.

Specification of sex-limited additive genetic effects is more difficult when there is assortative mating which induces correlations between loci that would otherwise be independent, see, for example, Fisher.³¹ We have adopted one of several, formally equivalent, ways of parameterizing the additive sex-limited effects. Recognizing that the additive genetic variances in the two sexes and the genetic covariance between them require three free parameters for their complete specification, we assume that one set of genes explains all the genetic variance in females, and the genetic covariance between the sexes. The

paths from this 'common' set of genes to the male and female phenotypes are denoted by h_{mc} and h_{fc} , respectively. A second set of genes has effects which are specific only to males and the path from these genes to the male phenotype is specified by h_{mm} . Although the 'male-specific' genes are not expressed in females, they are still present in females and correlated, through phenotypic assortment, with the 'common genes'. We denote the induced correlation between the two sets of additive genetic effects by α_{cm} .

The joint effects of assortment and vertical cultural transmission induce four genotype–environment correlations: two between the 'common' additive genetic effects and the environments of males and females, ρ_{cm} and ρ_{cf} , respectively; two between the 'male-specific' additive genetic effects and the environments of males and females, ρ_{mm} and ρ_{mf} , respectively. These genotype–environment correlations are estimated as constrained parameters when fitting the model (ie they are functions of other parameters). Separate parameters are required to specify the path from male environment to phenotype (e_m) and female environment to phenotype (e_f). Under the simple model for 'phenotypic assortment with error', the paths from true score to observed score, rel_m and rel_f , may differ between males and females.

Since the total phenotypic variance is standardized to unity in both sexes, two further constraints are required to enforce these conditions. Thus, seven constraints are imposed on parameter values under the full model. The full model for sex-limited effects is given for pairs of unlike-sex DZ twins in Figure 2.

Fitting the model

The method of iterative constrained diagonal weighted least squares was used to fit the full (non-linear) model to the 80 correlations for each personality and social attitude variable in turn. The model is fitted to the z-transforms of the raw correlations to improve the approximation to normality.³² Truett *et al*²⁰ give further details of the model fitting method. The expected correlations between relatives may be derived algebraically from the path model. These are extremely complex and are not reproduced here. However, copies of the FORTRAN program, which incorporates annotated code for the algebraic expectations for the correlations between relatives and expressions for derived estimates of variance components (see following), are available from the first author by electronic mail. The Numerical Algorithms Group's FORTRAN subroutine E04UEF was used

for constrained numerical minimization of the residual sum of squares.³³

The full model, involving 19 free parameters, was fitted first. The weighted residual sum of squares for $80 - 19 = 61$ d.f. is employed as a guide to the overall goodness of fit of the model. The false assumption of independence in the observed correlations is likely to result in our rejecting the model too often if we treat this statistic uncritically as χ^2 . However, comparisons of alternative models based on examination of changes in χ^2 associated with reductions in the full model are less open to such biases.³⁴

In order to test the significance of combinations of effects having particular theoretical importance, a series of reduced models was fitted in every case and the increase in the residual sum of squares noted as a guide to the deterioration in fit associated with deleting specific effects from the model. Reduced models were fitted to test the following specific hypotheses:

- 1) that all genetic and environmental effects were homogenous over sexes;
- 2) that there were no genetic effects ($h = 0$, $d = 0$ in both sexes);
- 3) that there were no non-additive (dominant) genetic effects ($d = 0$ in both sexes);
- 4) that there were no effects of the shared environment of any kind ($s = t = w = 0$ in both sexes). In the presence of significant shared environmental effects a further test was conducted:
- 5) that there was no vertical cultural inheritance ($w = 0$ in both sexes).

These tests do not exhaust all the possibilities. However, in view of the danger of capitalizing on chance with multiple tests it is more appropriate to restrict testing to a few major effects of a priori importance.

Results

Tables 10 and 11 present the weighted least squares estimates of the parameters of the full model for the correlations for personality and attitudes respectively. The models for personality involve two fewer parameters than those for social attitudes because the virtual absence of assortative mating and vertical cultural inheritance meant there was no need to test whether these effects were based on a latent variable. That is, $r_m = r_f = 1$ for all the models of personality. Two χ^2 statistics are also tabulated testing for approximate goodness of fit of the model and testing for

heterogeneity of the model parameters across sexes.

Tables 12 and 13 summarize, for personality and social attitude measures respectively, the estimated contributions of the various effects included in the 'full' model to variation in males and females. The formulae used to compute these components of variance from the parameters of the path model are given by Truett *et al.*²⁰

Discussion

Before considering the positive findings, it is essential to note what possible causes of variation are not considered in the current model. There are three main exclusions. First, although we correct for population linear and quadratic trends in response with age, we do not consider the implications of the interaction between age, cohort effects or generational differences and individual genetic and environmental differences. Modeling these effects requires different approaches from those used here^{5,35,36} and remains a goal for future data analysis. One consequence of these effects is the decay of family resemblance with increasing age differences between relatives. As a result, analyses of family resemblance which ignore these effects may find increased non-additivity (because parent-offspring correlations are reduced relative to siblings who are more similar in age but share same additive genetic similarity and 'twin environment effects' because MZ and DZ twins are being measured at more comparable stages of gene expression than siblings who have larger age differences within pairs. Second, although we allow for an increased environmental correlation for MZ and DZ twins, we do not specify any extra 'special MZ' shared environment. If such environmental effects are important they will increase the MZ correlation relative to the DZ correlation and inflate the estimate of non-additive genetic effects in our model. Finally, although we model social interactions between parents and children ('vertical cultural inheritance') we assume that any additional environment correlation between siblings and twins is not due to the social interaction between the siblings and twin themselves ('sibling effects';³⁷ or 'imitation and contrast effects'³⁸). The extra environmental correlation of siblings and twins is assumed to arrive from residual shared environmental influences external to the pair and the family. These may include the effects of peers, schooling etc as long as these are not caused by the phenotypes of the parents or the measured behavior of their children. Such 'sibling' effects will produce differences in the dispersions of traits in families of different density and, again, require different models

Table 10 Results of model-fitting to personality correlations

Parameter		Estimate				
		P	E	N	L	
Genetic	h_{fc}	0.136	0.525	0.566	0.617	
	h_{mc}	0.101	0.413	0.391	0.446	
	h_{mm}	0	0	0	0	
	d_f	0.520	0.477	0.209	0.188	
	d_m	0.268	0.508	0.337	0.295	
	r_d	1.000	0.306	1.000	-0.287	
Assortment	μ	0.099	0.003	0.098	0.194	
	α_{cm}	0	0	0	0	
Cultural transmission	w_{ff}	0.090	0.029	-0.017	-0.045	
	w_{mf}	0.078	0.055	0.043	-0.003	
	w_{fm}	0.046	0.002	-0.005	-0.018	
	w_{mm}	0.036	0.070	0.043	-0.022	
Other shared environment	s_f	0.087	0	0.059	0	
	s_m	0.310	0	0	0.041	
	r_s	1.000	-	-	-	
	t_f	0.123	0.018	0.223	0.262	
	t_m	0.195	0.120	0.251	0.400	
	r_t	1.000	-1.000	-0.790	0.272	
Unique environment	e_f	0.829	0.700	0.767	0.730	
	e_m	0.884	0.734	0.810	0.746	
Genotype-environment correlations	r_{ef}	0.010	0.008	0.023	-0.020	
	r_{cm}	0.008	0.031	0	-0.007	
	r_{mf}	0	0	0	0	
	r_{mm}	0	0	0	0	
Tests of significance						
	Goodness-of-fit	χ^2_{63}	66.85	94.01	88.96	66.46
	Sex heterogeneity	χ^2_{11}	15.58	29.59	24.31	34.35
	Genetic effects	χ^2_6	614.01	1834.83	?	91.71
	Dominance	χ^2_3	239.45	503.77	361.80	?
	Family environment	χ^2_{10}	16.07	3.53	8.46	8.37

Note: '?' denotes instances where numerical difficulties precluded computation of reliable parameter estimates

from those we have presented here, (for instance, Zajonc and Markus³⁹).

Such warnings having been sounded, we note that the data from these large samples of more heterogeneous relationships allow us to test the claims based on other studies of fewer kinds of relationship, including the very large twin studies of personality and attitudes that have been reported.⁵

With the exception of psychoticism and political preference, the results show consistent evidence of heterogeneity in the parameter values across sexes. The fact that the sex-specific additive genetic effect on males is always zero suggests that the cause of heterogeneity in the additive genetic effects over sexes is epigenetic, ie the same genes are having effects of differing magnitudes in males and females. Although the sexes differ in the magnitudes of the expressed additive genetic effects, there is no suggestion that the traits are under the control of different genes in these data. When we turn to epigenetic effects, however, including genetic non-additivity,

we see almost every conceivable variety of sex dependence. The same genes seem to be involved in non-additive interactions for psychoticism and extraversion ($r_d = 1$) whilst distinct genetic effects may interact in males and females to create differences in extraversion and lie scores ($r_d < 1$). We note that the sibling and twin environments generally play a larger role in the development of female attitudes than is the case for males (see estimates of twin and sibling environmental variance components in Table 13).

The results confirm the now commonplace finding of the inheritance of personality and attitudes that by far the most consistent effects on individual differences are those of the unique, within family, environment ('residual' in Tables 12 and 13). In our cross-sectional study, these effects include both long-term environmental influences and short term fluctuations. Previous studies⁵ suggest strongly the short-term influences outweigh long-term effects in creating the within-family environment.

Table 11 Results of model-fitting to correlations in social attitudes

Parameter		Estimate					
		Sex	Tax	Mil	Pol	Rel	Con
Genetic	h_{fc}	0.720	0.557	0.266	0.261	0.649	0.580
	h_{mc}	0.703	0.368	0.441	0.090	1	0.867
	h_{mm}	0	0	0	0	0	0
	d_f	0	0.354	0.424	0.328	0.393	0.360
	d_m	0.382	0.547	0.561	0.512	0.315	0.297
	r_d	–	0.486	1	1	0.456	–0.002
Assortment	μ	0.706	0.546	0.593	0.633	0.750	0.720
	α_{cm}	0	0	0	0	0	0
Cultural transmission	w_{ff}	0.020	0.208	0.258	0.164	0.181	0.172
	w_{mf}	–0.339	0.008	0.119	0.135	–0.271	–0.368
	w_{fm}	–0.028	0.066	0.119	0.267	–0.062	0.026
	w_{mm}	0.375	0.445	0.338	0.426	–0.200	0.208
Other shared environment	s_f	0.223	0.238	0.228	0.251	0.322	0.233
	s_m	0.256	0.328	0.118	0.289	0	0
	r_s	0.406	0.796	1	1	–	–
	t_f	0.315	0.271	0.272	0.355	0.106	0.210
	t_m	0.080	0.038	0.277	0.274	0.015	0.036
	r_t	–1	–0.934	1	1	1	1
Unique environment	e_f	0.521	0.597	0.581	0.746	0.386	0.493
	e_m	0.580	0.595	0.755	0.775	0.506	0.592
Genotype–environment correlations	r_{ef}	–0.005	0.122	0.133	0.086	0.079	0.124
	r_{cm}	0.022	0.228	0.169	0.110	–0.322	–0.094
	r_{mf}	0	0	0	0	0	0
	r_{mm}	0	0	0	0	0	0
Latent variable	r_f	0.948	0.838	0.867	0.958	0.801	0.979
	r_m	0.848	0.790	0.801	0.862	0.749	0.878
Tests of significance							
Goodness-of-fit	χ^2_{61}	84.76	84.53	90.72	110.05	90.03	62.51
Sex heterogeneity	χ^2_{12}	66.43	22.07	96.27	19.22	141.13	65.46
Genetic effects	χ^2_6	107.52	96.23	116.29	102.29	212.83	233.89
Dominance	χ^2_3	?	4.32	12.73	11.42	76.39	195.36
Family environment	χ^2_{10}	28.03	16.47	22.87	63.38	13.01	25.25
Vertical cultural inheritance	χ^2_4	12.38	6.64	16.34	33.99	5.91	16.24

Note: ‘?’ denotes instances where numerical difficulties precluded computation of reliable parameter estimates

Our new data confirm the earlier claims based on a variety of relationships, that the shared environment plays only a small and non-significant role in the creation of personality differences in adults. There are noticeable contributions of the ‘twin’ environment (t) to neuroticism and lie scores but the direct environmental impact (w) of parental personality on children is virtually non-existent.

Previous twin studies of social attitudes have shown that the correlations for DZ twins are significantly greater than one half of the correlations for MZ twins, pointing to the importance of either the shared environment, or the genetic consequences of assortative mating, or both. The new results allow us to be clearer about the confounded role of assortment and the shared environment. It is clear that, for all the social attitude measures, the high degree of marital resemblance can account for some of the

apparent excess DZ correlation in terms of the increased genetic resemblance of family members arising from the fact that like spouses bring together alleles of similar effect (‘assortment’, Table 13). These effects are absent in the personality scales (Table 12). However, for many attitude factors, the total effects of the shared environment equal or exceed those of assortment. We also see that vertical cultural inheritance within the family – the direct impact of parental attitudes on offspring attitudes⁴⁰ – is a significant factor in parent offspring similarity in attitudes. The path coefficients (w) in Table 11 show values ranging from –0.368 for the impact of maternal conservatism on the environment of her sons, to +0.445 for the impact of paternal attitudes to taxation for welfare of others on the environment of their sons. In this respect, the proportions of variance attributed to the cultural impact of parents on

Table 12 Estimated contributions (%) of principal sources of variation to differences in personality among males and females based on parameter estimates from most general path model

Component	Proportion of variance(%)							
	P		E		N		L	
	Male	Female	Male	Female	Male	Female	Male	Female
Genetic								
Additive	1.0	1.8	16.9	27.4	14.9	31.3	18.8	36.2
Assortment	0	0	0.1	0.2	0.3	0.7	1.0	2.0
Dominance	7.2	27.0	25.8	22.8	11.3	4.4	8.7	3.5
Total	8.2	28.8	42.8	50.4	26.6	36.4	28.6	41.7
Environmental								
Maternal	0.5	0.6	0.2	0	0.1	0	0	0.1
Paternal	0.1	0.2	0.3	0	0.1	0	0	0
Sibling	9.6	0.8	0	0	0	0.4	0	0
Twin	3.8	1.5	1.4	0	6.3	5.0	16.0	6.9
Residual	77.6	67.9	53.4	49.0	65.4	58.8	55.7	53.1
Total parental	0.6	0.8	0.5	0	0.3	0	0	0.1
Total shared	14.0	3.0	1.9	0	6.5	5.4	16.2	7.0
Total	91.7	71.0	55.3	49.0	71.9	64.1	71.9	60.2
G-E covariance	0.1	0.2	1.9	0.6	1.5	-0.5	-0.5	-1.9

Table 13 Estimated contributions (%) of principal sources of variation to differences in social attitudes among males and females based on parameter estimates from most general path model

Component	Proportion of variance(%)											
	Sexual		Taxes		Military		Political		Religious		Conservatism	
	M	F	M	F	M	F	M	F	M	F	M	F
Genetic												
Additive	35.5	46.6	7.0	18.0	11.0	4.7	0.6	6.2	30.7	14.8	35.5	19.8
Assortment	12.9	16.9	1.5	3.8	1.5	0.6	0	0.2	25.4	12.3	22.2	12.4
Dominance	10.5	0	18.7	8.8	20.2	13.5	19.5	9.9	5.6	9.9	6.7	12.5
Total	46.0	46.6	27.2	30.6	32.7	18.8	20.1	16.1	61.6	37.0	64.5	44.7
Environmental												
Maternal	0.5	0	0.6	1.3	0.8	3.6	2.3	3.0	1.0	0.4	1.5	0.1
Paternal	1.0	0	4.9	0.3	3.0	1.4	9.0	5.5	0.7	0	0	0
Sibling	4.7	4.5	6.7	4.0	0.9	3.9	6.2	5.8	0	6.7	0	5.2
Twin	0.5	8.9	0.1	5.1	3.3	5.6	5.6	11.6	0	0.7	0.1	4.2
Residual	45.5	40.4	58.2	53.2	53.7	62.7	55.7	54.9	50.6	40.3	40.1	36.6
Total parental	1.5	0	5.5	1.6	3.8	5.0	11.3	8.5	1.7	0.4	1.5	0.1
Total shared	6.7	13.4	12.3	10.6	8.0	14.5	23.1	25.8	1.7	7.8	1.6	10.6
Total	52.2	53.8	66.5	63.8	61.7	77.2	78.8	80.7	52.3	59.7	41.7	47.2
G-E covariance	1.2	-0.4	6.3	5.7	5.6	4.0	1.1	3.2	-13.9	3.3	-6.2	8.1

their children are misleadingly small because quite large parent-offspring paths are squared when computing the contributions to variation in the next generation. Furthermore, negative paternal effects may tend to cancel out positive maternal effects and vice versa when there is substantial assortative mating. Although the specific parameters of vertical cultural inheritance should probably be treated with some sensitivity to the possible role of sampling error, we note that the coefficients for like-sex relationships are usually somewhat higher than those for unlike-sex parent-offspring pairs. This finding is consistent with the view that children

model on their like-sex parent. In data on ordinary nuclear families alone, such effects are confounded with those of sex-limited gene expression. An extreme example of this tendency in our data is provided by the marked opposition between the roles of mothers and fathers in creating the attitudes of sons on sexual issues (Table 11). The path from mothers' attitudes to sons' environments is estimated as -0.339. That from fathers' attitudes to sons' environments is +0.375. The opposite signs of these effects result in an apparent contribution of the paternal environment (Table 13) of only 1.5% although, if the finding is replicated, the process

would seem to be very important for understanding the process of socialization in the development of sexual values.

The total contribution of genetic factors to differences in personality and attitudes is significant and pervasive. We note that the total estimated contribution of genetic variability to social attitudes is not much different from their effects on personality. We confirm the findings of previous twin studies that the effect of genetic factors in creating variation for social attitudes, as distinct from personality, may be exaggerated by the genetic consequences of assortative mating. The estimated contributions of 'assortment' to genetic variation are larger for attitudes (Table 13) than personality (Table 12).

Non-additive genetic effects also appear to play a significant role in the creation of the personality and attitude variables measured in our study. Although these are parameterized as 'dominance' in the model, other epistatic interactions between loci will tend to be confounded with the additive and dominance effects. Epistasis of the duplicate type, in which the phenotype is buffered against change by the evolution of multiple loci having parallel functions, is especially likely to inflate the estimate of dominant genetic effects.⁴¹

Taken as a whole, the data from the Virginia 30 000 show remarkable consistency with the earlier twin, family and adoption studies as far as personality as concerned and allow a far more detailed analysis of the transmission of social attitudes than has been possible in the past.^{42,43} We note the same apparent inconsistencies between the findings for personality that had been noted before between studies using different instruments and separate populations. It is clear from our data that this result is not a matter of the population sampled or the choice of measurement but that it resides in a large effect of genetic non-additivity. In our model these effects contribute to the large estimate of the dominance parameter because the correlations between parents and siblings are much lower than those between MZ twins. Another possibility is that some of the genetic non-additivity is due to the interaction of genetic differences with age. Such effects would produce a lot of apparent dominance in our model, because parents are measured at different ages from children and twins. They would also tend to inflate the twin correlation relative to the sibling correlation. The overall effect of additive genetic effects, and thus the narrow heritability, is small for most of the personality dimensions.

One of the truly remarkable findings to emerge from behavior genetics over the past 20 years in the replication and consistency of findings about the transmission of personality and social attitudes in different studies using different approaches and

methods of analysis. Even if investigators may differ in the models they use to interpret their data, it is still little short of astonishing that the actual correlations between relatives show such consistency between studies, not merely in their relative magnitudes for a given variable but also for the differential patterns of family resemblance seen between measures in different domains. This does not mean that the last word has been said on the subject. Understanding the origin of the apparently large non-additive genetic component will require more detailed analysis of the effects of age on family resemblance. We still do not understand the adaptive significance of assortment for social attitudes in contrast to the essentially random mating we see persistently for personality. We have little idea about the developmental role of genetic differences in shaping the environment to which individuals are subjected. Such effects all serve to enhance the expression of genetic differences which might be small at the outset and may still provide a foundation for behavioral rather than medicinal intervention in certain kinds of behavioral disorder. Finally, we do not yet know certainly whether the absence of shared environmental effects on adult personality is simply a feature of adult adaptation or whether it characterizes personality measures throughout development. Such findings will be crucial for how personality is viewed biologically.

Our results underscore the striking differences between the inheritance of personality and social attitudes. What appeared as an excess correlation among DZ twins reared together in previous twin studies of social attitudes has now been resolved into a number of different possible factors. Some of the additional variation between DZ twin pairs may indeed be the genetic consequences of assortative mating as implied by the model of Martin *et al*,⁴³ but our data show that this is not the whole story because the vertical cultural inheritance of attitudes from parents to children cannot be discounted, neither can the extra-familial environmental effects shared by siblings and twins. The Virginia 30 000 data confirm the repeated findings of other twin studies that genetic factors cannot be ignored in the creation of social attitude differences. The consistent difference between attitudes and personality may point to different roles in human adaptation. The absence of any assortment and vertical cultural inheritance for personality may indicate that personality is the manifestation of phylogenetically early properties of the nervous system that predate the evolution of the human brain. The fact that researchers have proposed animal models for personality⁴⁴ is consistent with this view. On the other hand, it is impossible to conceive of attitudes without a culture depending on learning and social interaction for its

maintenance and requiring, therefore, those aspects of the brain which are most fully differentiated in humans. In evolving systems to deal with life in society humans have not left behind their genetic diversity. Individual differences at the genetic level, as well as differences in personal history and family environment, still bias for good or ill the choices and prejudices of individuals in society.

The significant contribution of genetic factors to social attitudes means that virtually no measurable aspect of human behavioral variation is so far removed from the impact of events at the genetic level as to be considered in complete isolation from the emerging theory and knowledge in genetics and sociobiology. It is as naive to suppose that there is a simple link between events at the DNA level and complex behavioral outcomes such as social attitudes, as it is to suppose that culture has completely immunized humans from the effects of their genes. We conceive of an ontogenetic process in which small initial genetic differences in behavior and preference are augmented over time by the incorporation into the phenotype of environmental information, correlated with the genotype, in a continual process of sifting and evaluation. Much of the apparent genetic variation in normal human behavior may ultimately turn out to be of this type. It will require far greater ingenuity to understand the processes of developmental feedback and gene-environment correlation which create such 'extended phenotypes'⁴⁵ than it has taken so far to quantify the complex contributions of genes and environment to adult behavioral outcomes.

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