

The Genetic Basis of Political Cooperation

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Although evolutionary models and laboratory experiments explain the existence of cooperation in humans, no research has investigated whether large-scale cooperation in well-mixed populations results from biological or social forces. In this article we study voter behaviour as a form of cooperation that bears close resemblance to theoretical models in which individuals in a large population make anonymous decisions about whether or not to contribute to a public good.

Matching public voter turnout records to a twin registry, we study the political behaviour of monozygotic and dizygotic twins. The results show that the decision to vote—and thus cooperate—is strongly influenced by genetic factors. Our findings suggest that humans exhibit genetic variation in their tendency to cooperate and that biological evolution plays an important role in the development of political cooperation.

Many scholars have argued that the decision to vote is much like the decision to cooperate or contribute to a public good.¹⁻³ When one person votes, everyone with the same preferences benefits from the increased likelihood that their preferred outcome will result. Yet those who do vote must bear the cost of time and effort required to learn about election alternatives and go to the polls. In large populations, the probability that a single vote will change the outcome of an election is miniscule,⁴ meaning that even very small costs to the individual typically outweigh the expected benefits to the individual. As a result, classic game theoretic models that assume individuals are self-

interested and fully optimizing in their behaviour show that the equilibrium amount of voter turnout (cooperation) approaches 0 as the population becomes large.⁵ Yet in spite of these predictions millions of people do vote, suggesting that something other than self-interest and optimizing behaviour drives their decision to cooperate.^{3,6,7} And the fact that millions of people abstain suggests that there may be inherent variation in the human tendency to cooperate.

Empirical models of turnout⁸⁻¹⁰ typically contain numerous covariates including demographic factors (age, gender, race, marital status, education, income, occupational prestige, home ownership), attitudinal and behavioural factors (interest in the campaign, access to political information, strength of partisanship, feelings of civic duty, internal and external efficacy, political trust, church attendance, personal skill acquisition, humanitarianism, altruism, and patience), and institutional factors (closeness of the election, contact from political organizations, barriers to registration). Yet in spite of this everything-but-the-kitchen-sink approach, these models usually fit poorly to the data. For example, one prominent model includes 32 variables but explains only 31% of the variance in turnout.⁸ Moreover, the theories underlying these empirical models typically ignore genetic or biological sources of variation. The implication is that the decision to vote is determined exclusively by environmental factors.¹¹

Recent work in neuroeconomics suggests we should look beyond the environment to explain political cooperation. In fMRI studies of behaviour in trust and social dilemma games, cooperation activates areas of the brain that have been linked with reward processing^{12,13}, suggesting that the brain has developed a mechanism to override self-interest in cooperation dilemmas. Cooperation in trust games also appears to increase in the presence of oxytocin¹⁴ which reduces activation of the amygdala's fear response.¹⁵ Thus, variation in biophysical attributes like hormone levels and brain function may help to explain variation in cooperative behaviour. However, the

neuroeconomics literature leaves open the question of whether biophysical differences in cooperation result from environmental or genetic factors.

In order to estimate the degree to which cooperation is heritable, we study the turnout behaviour of (identical) monozygotic (MZ) and (non-identical) dizygotic (DZ) twins. MZ twins share 100% of their genes, while DZ twins share only 50% on average. Thus, if political cooperation is based in part on genetic characteristics, then MZ twins should exhibit more concordance (both twins vote or both twins abstain) than DZ twins. Moreover, if we assume that MZ twins and DZ twins share comparable environments, then we can use these concordances to estimate explicitly the relative influence of genetic, shared environmental, and unshared environmental factors (see Methods). Although this method will not reveal specific causal mechanisms, it will help to establish whether our genes play a role in voting and thus whether they should be studied further in the attempt to explain political cooperation.

Some scholars have objected to the assumption that MZ and DZ environments are comparable, arguing that MZ twins tend to be more strongly affiliated and more influenced by one another than DZ twins. If so, then greater concordance in MZ twins might merely reflect the fact that their shared environments cause them to become more similar than DZ twins. However, studies of twins raised together have been validated by studies of twins reared apart,¹⁶ suggesting that the shared environment does not exert enhanced influence on MZ twins. Moreover, personality and cognitive differences between MZ and DZ twins persist even among twins whose zygosity has been miscategorized by their parents,¹⁷ indicating that being mistakenly treated as an identical twin by one's parents is not sufficient to generate the difference in concordance. And, although MZ twins are sometimes in more frequent contact with each other than DZ twins, it appears that twin similarity (e.g., in attitudes and personality) may cause greater contact rather than vice versa.¹⁸ Finally, contrary to the

expectation that the influence of the unshared environment would tend to decrease concordance over time once twins reach adulthood, MZ twins living apart tend to become more similar with age.¹⁷

To assess the impact of genetics on turnout, we obtained electronic voter registration records for 3.8 million voters from Los Angeles County with complete vote histories for 8 elections (three primary, two statewide, and three general) from 2000-2005 and matched them to the Southern California Twin Registry,¹⁹ a list of MZ and DZ twins who live in the Los Angeles area. A principal advantage of this approach is the use of field evidence based on third-party observations of actual voter behaviour rather than self-reports. This kind of data is rarely used in twin studies and is an especially important source for evaluating political cooperation since a significant number of individuals who did not vote typically report that they did.²⁰

About 30% of the adult population in Los Angeles County is not registered to vote, so we cannot include them in our sample. We cannot merely assume that all unregistered twins chose not to vote—for example, it is possible that they died or moved out of the county and registered elsewhere. However, focusing on registered individuals allows us to exclude those who might generate false concordance because they are *ineligible* to vote due to foreign citizenship status—this is a particular concern in Los Angeles County where 22% of the total population are foreign citizens (2000 U.S. Census). It also allows us to avoid false concordance generated by individuals with cognitive or literacy deficits who are not *capable* of voting since these individuals probably do not register.

To test the comparable environments assumption for our sample, we performed a series of tests on the mean difference between MZ and DZ twins for a number of variables (see supplementary material). High *p*-values suggest that differences between types of twins are not significant for rates of turnout ($p=0.79$), Democratic Party

membership ($p=0.84$), Republican Party membership ($p=0.83$), third party membership ($p=0.88$), age ($p=0.25$), house value ($p=0.49$), house square footage ($p=0.86$), and lot square footage ($p=0.15$). Furthermore, t -tests of data obtained from previous studies of subsets of these twins revealed no differences in their education level ($p=0.72$) or personality, including extraversion ($p=0.38$) and neuroticism ($p=0.92$). Thus, the similarity of the MZ and DZ twin samples suggests that differences in concordance cannot be explained by mean differences in political cooperation, political affiliation, personality, education or other socioeconomic factors. We also note that in our sample MZ twins are not more likely than DZ twins to live at the same address ($p=0.69$) or in the same postal code ($p=0.84$). Thus, greater concordance in MZ twins is probably not due to higher frequency of contact.

Results

Polychoric correlation (a method to measure associations for ordered-category data) is frequently used as a first test of the rate of twin concordance in behaviour. In our pooled observations, the correlation in turnout was significantly higher ($p=0.006$) between the MZ twins (0.71) than the DZ twins (0.50). However, naïve correlation measures are only a crude guide since they make no provision for multiple observations of each twin's behaviour across elections. Instead, we conduct a more detailed mixed-effects Bayesian ACE analysis which uses observed turnout decisions for each of the eight elections to estimate a latent tendency to cooperate for each twin and the degree to which this tendency is influenced by genetic factors (A), and environmental factors which are shared or common to co-twins (C), and unshared environmental (E) factors which are specific to each twin (see Methods). The analysis provides estimates of proportions of observed variance in turnout due to the respective effects of A, C, and E.

The left panel in Fig.1 shows the posterior distribution of the estimated factors in an ACE model. These results suggest that heritability (h^2) generates about 61% of the variance in turnout behaviour. The 95% credible interval (C.I.) for the estimate is (28%,77%), indicating that we can reject the hypothesis that genes play no role in political cooperation. The ACE model also shows that the environment plays a role, but the unshared environment accounts for much more variance ($e^2=31\%$, C.I. 22%,41%) than the shared environment ($c^2=8\%$, C.I. 0%, 30%).

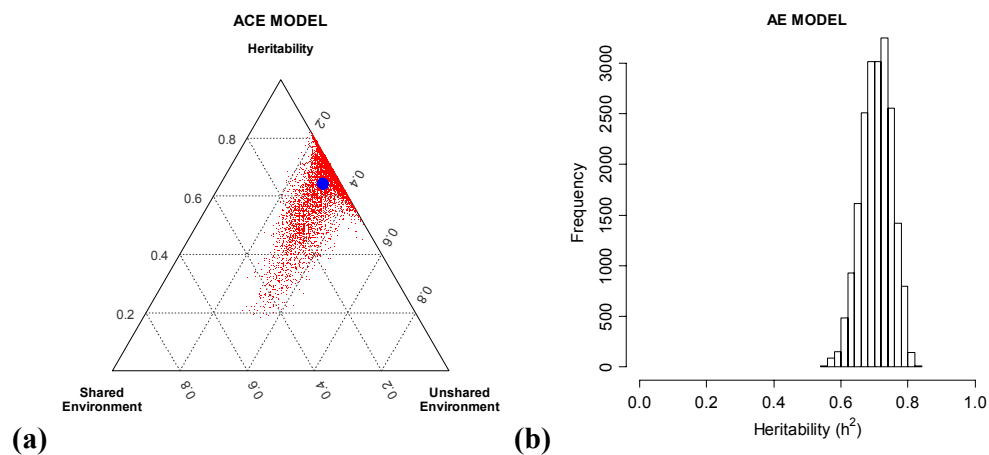


Figure 1. Heritable traits generate more than half of the variation in political cooperation (turnout). **(a)** Ternary diagram of 10,000 draws from posterior Bayesian distribution of estimated components of total variance in an ACE model of voter turnout. The mean of the distribution is noted by the blue solid circle, indicating heritability=0.61, common environment=0.08, unshared environment=0.31. These draws show that we cannot reject the hypothesis that the environment shared by cotwins plays no role in the turnout decision. **(b)** Histogram of 10,000 draws from posterior distribution of estimated heritability from a better-fitting AE model of voter turnout which assumes no common environmental influence. The probability that the true coefficients lie outside the region of the draws shown in both panels is $p=0.0001$.

Notice that in the ACE model we cannot reject the hypothesis that the common environment plays no role in explaining voting behaviour since the credible interval includes 0. This suggests that an AE model (one where we assume $c^2=0$) may be more appropriate. Indeed, measures of model fit indicate that an AE model is superior (see supplementary material). The right panel in Fig.1 shows that the posterior distribution of the estimated heritability in the AE model is somewhat higher than that in the ACE model at 70% (C.I. 62%, 77%).

It is important to note that these results are based on data that pool same-sex male and female pairs. If genes affecting turnout or reactions to the electoral environment were gender-specific, then pooling would be inappropriate. However, when we conduct the same analyses on each gender separately we find that the AE model fits best and significant differences in the estimates do not exist. Heritability of turnout behaviour for males is 74% (C.I. 62%,84%) and for females is 73% (C.I. 60%,84%).

Discussion

To a certain degree, these results should not be surprising. Twin studies have already shown a genetic basis for altruism and prosocial behavior^{21,22} and laboratory experiments have in turn linked these behaviours to voter turnout²³ and political participation.²⁴ However, social scientists (outside of the field of psychology) have been extremely reluctant to admit a role for genetic and biological factors in political phenomena, which has biased scholarly interpretations of several important phenomena.¹¹

For example, if turnout is determined in part by genetics, it would help to explain why models based primarily on environmental variables fit poorly to observed turnout. It would also conform to two well-known features of voting behaviour. First, parental turnout behaviour has been shown to be one of the strongest predictors of turnout

behaviour in young adults.⁸ Although this has previously been interpreted as the result of social influence, the findings here suggest it may be mostly due to heritability since the shared environment appears to play only a small (if any) role. Second, turnout behaviour has been shown to be *habitual*—the majority of people either always vote or always abstain.^{7,8,25-28} Scholars previously interpreted this as the result of reinforcement learning, but given the small effect of environmental variation it might also be largely due to inherent genetic variability.

Social scientists have debated whether or not voting actually constitutes an act of cooperation. Alternative theories suggest we vote as a means to fulfill our desire for self-expression, to adhere to a social norm (e.g. a civic “duty” to vote), or because we are more docile or compliant with authority.² However, note that each of these alternative theories suggest *mechanisms* that would also affect other kinds of cooperative outcomes in small groups with direct implications for fitness. Self-expression may help groups overcome informational barriers to cooperation;²⁹ social norms may help to establish institutions like punishment to reinforce cooperation;³⁰ and compliance may help individuals to coordinate on cooperative outcomes proposed by group leaders.³¹ If natural selection originally favored these mechanisms because they helped individuals to overcome social dilemmas in small groups, they might continue to yield cooperative behaviour like voting on the much larger scale observed in recent human history.

There is by now a large literature on general cooperation in the laboratory,³² but none of this literature addresses the heritability of the behaviours that have been observed. Two previous laboratory studies examined cooperation *between* twins,^{33,34} but none has focused on the question of how twins cooperate with unrelated members of the general population. Thus our results are the first to suggest that humans are endowed with genetic variation in their tendency to cooperate in large, well-mixed

populations. The implication that—by nature—some people are strongly oriented towards political cooperation while others are not lends support to theories of human behaviour in which cooperators and noncooperators coexist. This would tend to favour evolutionary models that yield polymorphic equilibria³⁵ or heteroclinic cycles³⁶ over those that predict monomorphic populations that always cooperate or always defect.

Our results also support models that suggest the evolution of cooperative behaviour is not merely the result of social evolution—instead, cooperation may result from the co-evolution of genetic and cultural characteristics.³⁷ Although here we assume genetic and environmental factors are additively separable, the strong influence of genetic factors suggests that more detailed models of the interaction of genes and culture (G x E models) are likely to identify a significant role for genes in the evolution of cooperation. For example, some people may carry genes that make them more receptive to persuasive appeals to cooperate, helping to explain strong variation in the effectiveness in mobilization efforts like get-out-the-vote campaigns.³⁸

Finally, our results have important implications for recent work in neuroeconomics. Scholars have linked several areas of the brain^{12,13} and some hormonal responses^{14,15} to the tendency to cooperate in behavioural economic experiments. However, these studies do not indicate whether variation in cooperation across individuals is due to environmental or genetic influences on the physiological development of the brain and endocrine systems. Our results suggest an important role for genetic evolution in the development of physiological systems that contribute to an individual's willingness to cooperate. Future studies should attempt to better estimate the specific role of genes in cooperative behaviour, how their effects are mediated by experience, and how general these findings are.

Methods

Twin registry and voter registration records were matched by surname, first name, birthdate, place of birth, and zip code. Full matches were automatically included in our data. Partial matches on three or more of these attributes were manually checked and included in the data if the failure to match fully was determined to be the result of a typographical error. Out of 878 same-sex twins (535 MZ, 343 DZ) on the registry who live in Los Angeles County, this procedure yielded vote histories and party of registration for 399 twins—172 MZ twins and 102 DZ twins in matched pairs, and 78 MZ and 47 DZ “singletons” where we found one twin in the pair but not the other (although singletons cannot help us estimate between-twin concordance, including these observations in the data does help us to estimate the mean turnout rate among twins for each election). A Mann Whitney U test suggests that the difference in the success rate for matching between MZ twins (48.6%) and DZ twins (43.4%) was not significant ($p=0.14$). Although we did not have access to information about the twins’ socioeconomic status for the entire sample, we were able to use addresses to look up estimated home values and square feet on the home appraisal web site zillow.com. We also examined data from previous studies in which subsets of the matched twins had participated through the Southern California Twin Project (SCTP). Although not available for the entire sample, these prior data are used to evaluate possible differences between MZ and DZ pairs which might explain their voting behaviour.

To estimate the effect of unobserved genetic variation on observed turnout behaviour, we employ an ACE model. This model assumes that each individual has an unobserved latent tendency to vote τ and that this latent tendency is additively influenced by three factors: genetics (A), common environment shared by co-twins (C), and non-shared environment (E).³⁹ We can specify this model as a generalized linear mixed-effects model where subject j is a member of family i and choosing to vote

($T_{ijk} = 1$) or abstain ($T_{ijk} = 0$) in election k . Since the observed phenotypes are dichotomous variables we assume they are distributed according to a probit function:

$$\Pr(T_{ijk} = 1) = \Phi(\mu_k + \tau_{ij})$$

where Φ is the cumulative standard normal distribution, μ_k is an unobserved election-specific fixed effect controlling for different mean rates of turnout in each election, and τ is an unobserved individual-specific tendency to vote. Note especially that μ_k takes into account the fact that there may be different institutional influences on turnout that vary from election to election (primary vs. general, national vs. state). If we were to conduct a similar analysis of cross-national turnout, we would additionally expect μ_k to be influenced by the type of party system, variation in barriers to registration, and so on. For our purposes we use μ_k to control for these election-specific factors in order to explore whether or not there is a persistent general tendency to vote. We assume that this tendency is itself a function of three random effects variables for MZ twins:

$$\tau_{ij}^{MZ} = A_i + C_i + E_{ij}$$

where A_i is the family genetic factor, C_i is the family shared environment factor, and E_{ij} is the individually-experienced unshared environment factor. For DZ twins the tendency to vote is a function of four random effects variables:

$$\tau_{ij}^{DZ} = A_{1i} + A_{2ij} + C_i + E_{ij}$$

where A_{1i} is the family genetic factor shared by both twins, A_{2ij} is the individually-inherited genetic factor that is unique to each twin, and C_i and E_{ij} are the same as for MZ twins. It is important to note that there are no observed covariates in the model—everything on the right hand side is estimated from the observed turnout decisions. If we were to include other covariates, we would need to determine whether they influenced election-specific mean turnout, heritability, shared environment, and/or the unshared environment and model them appropriately. However, the goal of this study is simply to establish whether or not heritability is an important factor.

Models of discrete phenotypes present computational challenges for structural equation modelling (SEM) software packages because the likelihoods contain integrals that cannot be evaluated in closed form and thus must be evaluated numerically. The maximum likelihood estimation of complex models with many random effects requires repeated numerical evaluation of high-dimension integrals.³⁹ As a result, researchers have begun to use Bayesian models implemented using Markov Chain Monte Carlo (MCMC) algorithms.⁴⁰ These algorithms evaluate the high-dimension integrals using random draws rather than analytically. Recent studies have successfully applied Bayesian methods to binary data,^{39,41} survival analysis,⁴² nonlinear developmental change and GxE interaction,⁴³ item response theory,⁴⁴ longitudinal models,⁴⁵ and multivariate models for ordinal data.⁴⁶ In particular, simulation studies suggest that MCMC methods perform better than SEM for models like ours with repeated observations of binary variables.⁴¹

Replicating the methods used in this literature, we assume that our unobserved random effects are normally distributed: $A \sim N(0, \sigma_A^2)$, $A_1 \sim N(0, \sigma_A^2 / 2)$, $A_2 \sim N(0, \sigma_A^2 / 2)$, $C \sim N(0, \sigma_C^2)$, and $E \sim N(0, \sigma_E^2)$. Notice that the variance of A_1 , the family genetic effect for DZ twins, is fixed to be half the variance of A , the family genetic effect for MZ twins, reflecting the fact that MZ twins on average share twice as many genes as DZ twins. Moreover, DZ twins are also influenced by individually-specific genes that are drawn from the same distribution as the shared genes since on average half their genes are shared and half are not. These assumptions about the genetic variance help to distinguish shared genes from the shared environment variable C that is assumed to have the same variance for both MZ and DZ twin families, and the residual unshared environment variable E from which a unique draw is made for each individual. If we tried to estimate all three components of variance simultaneously the model would not be identified, so we fix the variance of the unshared environment $\sigma_E^2 = 1$ and then use the estimates of σ_A^2 and σ_C^2 to derive the proportion of variance

generated by each factor. This procedure generates estimates for the influence of heritability $h^2 = \sigma_A^2 / (\sigma_A^2 + \sigma_C^2 + 1)$, common environment $c^2 = \sigma_C^2 / (\sigma_A^2 + \sigma_C^2 + 1)$, and the unshared environment $e^2 = 1 / (\sigma_A^2 + \sigma_C^2 + 1)$. For the AE model we fixed $\sigma_C^2 = 0$ and for the A model we also fixed $\sigma_E^2 = 0$.

In our MCMC procedure we use vague priors to ensure they do not drive model results (a mean-zero normal distribution with variance 1,000,000 for μ and a gamma distribution with scale parameter 0.001 and shape parameter 0.001 for σ_A and σ_C). To detect convergence in the estimates we ran two MCMC chains and applied a Brooks-Gelman test to the output.⁴⁷ The ‘potential scale reduction factors’ for each variable in our simulations were reduced to 1.1 or less by the 10,000th draw, indicating convergence. To sample the posterior we discarded the first 10,000 draws and kept the next 10,000 draws from each of the two chains. Test results drawn from thinned samples of 2 million draws yielded nearly identical estimates. To compare the fit of ACE, AE, and A models we used the deviance information criterion (DIC – see supplementary material).

To test the sensitivity of our method we tried a variety of alternative methods, including simple analysis of polychoric correlations on the observed turnout rate for each twin, Defries-Fulker methods that regress an interaction of zygosity and co-twin behaviour on a twin’s behaviour, and SEM methods in which we fit a common factor model with ordinal outcomes to the individual elections. We also tried a variety of alternative Bayesian specifications—such as adding parameters to estimate variance in turnout and its ACE components for each election—all of which generated poorer model fit according to DIC. All alternatives (Bayesian and non-Bayesian) suggested that heritability plays a large and significant role in turnout behaviour, with mean h^2 consistently estimated to be greater than 0.5 and significantly different from 0 at $p < 0.01$.

Supplementary material

	<i>Mar</i> 2000 <i>primary</i>	<i>Nov</i> 2000 <i>general</i>	<i>Mar</i> 2002 <i>primary</i>	<i>Nov</i> 2002 <i>general</i>	<i>Oct</i> 2003 <i>statewide</i>	<i>Mar</i> 2004 <i>primary</i>	<i>Nov</i> 2004 <i>general</i>	<i>Nov</i> 2005 <i>statewide</i>
<i>All twins</i> (N=399)	0.54 (0.25)	0.76 (0.18)	0.36 (0.23)	0.57 (0.25)	0.68 (0.22)	0.44 (0.25)	0.84 (0.13)	0.46 (0.25)
<i>MZ twins</i> (N=250)	0.55 (0.25)	0.75 (0.19)	0.36 (0.23)	0.58 (0.24)	0.71 (0.21)	0.42 (0.24)	0.86 (0.12)	0.49 (0.25)
<i>DZ twins</i> (N=149)	0.53 (0.25)	0.79 (0.17)	0.37 (0.23)	0.56 (0.25)	0.62 (0.24)	0.46 (0.25)	0.8 (0.16)	0.42 (0.24)
<i>Population</i>	0.48 (0.25)	0.68 (0.22)	0.26 (0.19)	0.45 (0.25)	0.55 (0.25)	0.38 (0.24)	0.79 (0.17)	0.47 (0.25)

Table 1. Comparison of mean turnout and variance in turnout in twin sample and general population in Los Angeles County, by election. Variances are shown in parentheses. These results show that DZ twins and MZ twins turn out at about the same rate as one another, meaning that zygosity does not affect levels of political cooperation. Turnout rates for all twins were somewhat higher than those for the population, but this should not bias estimates of the magnitude of the difference in concordance between MZ and DZ twins. This is because the variances are not systematically different (the twin variance is higher than the population variance in two elections and lower in three). If the twin variance was much lower than the population variance, this would compress the difference in the MZ and DZ twin concordances, causing us to underestimate heritability (for example, in the extreme case where all twins are perfectly cooperative and the turnout rate = 1.00, the variances shrink to 0, the concordances for both MZ and DZ twins grow to 1, and the difference between the concordances would also shrink to 0, suggesting 0 heritability). Conversely, if the twin sample variance was much higher than the population variance we would overestimate the effect of heritability. The lack of a systematic difference in the sample and population variances suggests that mean differences will not generate bias in the estimates.

	<u>MZ Twins</u>		<u>DZ Twins</u>		<i>Difference of Means Test p-value</i>
	<i>Mean</i>	<i>Standard Error</i>	<i>Mean</i>	<i>Standard Error</i>	
<u><i>Voter file data</i></u>					
<i>Turnout Rate, All Elections</i>	0.57	0.03	0.58	0.03	0.79
<i>Democrat</i>	0.51	0.05	0.52	0.05	0.84
<i>Republican</i>	0.24	0.04	0.25	0.05	0.83
<i>Third Party</i>	0.05	0.02	0.05	0.02	0.88
<i>Age</i>	36.8	2.5	33.6	2.8	0.25
<i>Same Address</i>	0.47	0.07	0.52	0.08	0.69
<i>Same Postal Code</i>	0.54	0.07	0.64	0.07	0.84
<u><i>Zillow.com data</i></u>					
<i>Was House in Zillow?</i>	0.71	0.04	0.71	0.05	0.89
<i>House Value</i>	821,729	40,577	784,421	49,412	0.49
<i>House Square Feet</i>	2148	111	2106	137	0.86
<i>Lot Square Feet</i>	8062	392	9117	1014	0.15
<u><i>SCTP data</i></u>					
<i>Highest Grade</i>	15.48	0.36	15.25	0.55	0.72
<i>Extraversion</i>	.66	0.04	0.71	0.04	0.38
<i>Neuroticism</i>	.43	0.03	0.43	0.05	0.92

Table 2. Summary statistics, by zygosity. These data show that we could find no significant differences in the MZ and DZ twin samples, suggesting that they are drawn from comparable environments. Data is derived from three sources: 1) the Los Angeles County voter registration and vote history files for matched twins, 2) housing characteristics for 71% of the matched twins found on zillow.com on October 25, 2006, and 3) education and personality information for 15% of the matched twins (this subsample is limited to those who participated in previous studies in which education and personality questions were asked). We utilized Mann Whitney U tests to analyze differences in means in the voter registration and zillow data and *t* tests for the SCTP data.

	Heritability h^2	Common Environment c^2	Unshared Environment e^2	Deviance Information Criterion (DIC)	D_{bar}	pD
Pooled						
ACE	0.61 (0.28, 0.77)	0.08 (0.00, 0.37)	0.31 (0.22, 0.41)	2849.550	1926.630	922.922
AE	0.70 (0.62, 0.77)		0.30 (0.23, 0.38)	2834.210	1902.450	931.761
A	1.00 (N/A)			2839.480	1908.560	930.920
Males						
ACE	0.58 (0.09, 0.80)	0.12 (0.00, 0.53)	0.30 (0.18, 0.45)	1236.750	832.834	403.915
AE	0.74 (0.62, 0.84)		0.26 (0.16, 0.38)	1205.390	790.976	414.418
A	1.00 (N/A)			1226.050	817.726	408.322
Females						
ACE	0.64 (0.15, 0.84)	0.08 (0.00, 0.45)	0.27 (0.16, 0.40)	1570.310	1019.940	550.371
AE	0.73 (0.60, 0.84)		0.27 (0.16, 0.40)	1564.040	1011.540	552.499
A	1.00 (N/A)			1566.850	1015.750	551.099

Table 3. Summary of model results. These results show that we consistently found that a large proportion of variance in turnout behaviour is due to heritability and that the best fitting models are those that assume a role for heritability and the unshared environment (but not the common environment). The first column describes each model—pooled results combine data from all same-sex twin pairs whereas male and female models include data only from a specific gender. ACE models estimate a parameter for genetic (A), common environment (C), and unshared environment (E); AE models assume the common environment has no effect and A models assume that neither the common nor shared environment have an effect. Columns 2, 3, and 4 show the mean estimated proportion of total variance attributable to heritability (h^2), common environment (c^2), and unshared environment (e^2), with 95% credible intervals indicated in parentheses below each estimate.

Model fit is assessed using the deviance information criterion (DIC), a Bayesian method for model comparison analogous to the Akaike Information Criterion (AIC) in

maximum likelihood estimation. Models with smaller DIC are considered to have the best out of sample predictive power.⁴⁸ The DIC penalizes models for deviance (\bar{D}), which captures model fit, and the effective number of parameters (pD), which captures model complexity. The results show that the AE model generates the best fit for the pooled sample and also for the male-only and female-only samples.

To ensure that the key parameters in these models converged to what we believe to be their target posterior distribution, we began sampling from the joint posterior distribution after convergence was established using the Brooks-Gelman statistic (values of less than 1.1 on each parameter indicate convergence).⁴⁷ For the pooled models the “burn-in” period was 10,000 iterations, for the male AE and A models and female ACE, AE, and A models it was 20,000 iterations, and for the male ACE it was 40,000 iterations. The empirical means, 95% credible intervals, and DICs reported for the pooled models are based on 10,000 iterations after burn-in, for the male AE and A models and female ACE, AE, and A models are based on 20,000 iterations, and for the male ACE model 40,000 iterations.

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