



Published in final edited form as:

Behav Genet. 2014 May ; 44(3): 282–294. doi:10.1007/s10519-014-9648-8.

Genetic Influences on Political Ideologies: Twin Analyses of 19 Measures of Political Ideologies from Five Democracies and Genome-Wide Findings from Three Populations

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Abstract

Almost forty years ago, evidence from large studies of adult twins and their relatives suggested that between 30-60% of the variance in social and political attitudes could be explained by genetic influences. However, these findings have not been widely accepted or incorporated into the dominant paradigms that explain the etiology of political ideology. This has been attributed in part to measurement and sample limitations, as well the relative absence of molecular genetic studies. Here we present results from original analyses of a combined sample of over 12,000 twins pairs, ascertained from nine different studies conducted in five democracies, sampled over the course of four decades. We provide evidence that genetic factors play a role in the formation of political ideology, regardless of how ideology is measured, the era, or the population sampled. The only exception is a question that explicitly uses the phrase “Left-Right”. We then present results from

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one of the first genome-wide association studies on political ideology using data from three samples: a 1990 Australian sample involving 6,894 individuals from 3,516 families; a 2008 Australian sample of 1,160 related individuals from 635 families and a 2010 Swedish sample involving 3,334 individuals from 2,607 families. No polymorphisms reached genome-wide significance in the meta-analysis. The combined evidence suggests that political ideology constitutes a fundamental aspect of one's genetically informed psychological disposition, but as Fisher proposed long ago, genetic influences on complex traits will be composed of thousands of markers of very small effects and it will require extremely large samples to have enough power in order to identify specific polymorphisms related to complex social traits.

Keywords

Ideology; Politics; GWAS; Attitudes; Authoritarianism

More than half a century of research in genetics, neuroscience and psychology has demonstrated that human behaviors, including social and political attitudes, are influenced by genetic and neurobiological factors (for a review see Hatemi and McDermott 2012a). Lindon Eaves, Hans Eysenck and Nicholas Martin pioneered this radical departure, finding that genetic variance accounted for a substantial portion of individual differences in conservatism, sub-dimensions of social, economic and defense ideologies, as well as individual social and political attitudes (Eaves and Eysenck 1974; Martin et al. 1986; Eaves et al. 1989). Additional twin and extended kinship studies which included parents, non-twin siblings, spouses, and twins reared apart confirmed these earlier results and found that most individual political attitudes were influenced by a combination of genetic effects (which explain between 30 and 60% of variance) and environmental influence (Truett et al. 1994; Eaves et al. 1999; Bouchard and McGue 2003; Hatemi et al. 2010). In this way, children resemble their parents because of their genetic relatedness as much as parental upbringing and social environments.

The notion of a genetically informed model of attitudes and ideology, understood as a psychological disposition that guides behavior, independent of, and interacting with, social forces presented a fundamental challenge to the dominant rational choice and behaviorist social science paradigms (for a review see Hatemi and McDermott 2011a). Yet, despite the growing body of evidence that genetic factors play an important role in the development and maintenance of political attitudes (Loehlin 1993; Posner et al. 1996; Hatemi et al. 2007; Hatemi, Funk, et al. 2009; Hatemi, Medland, et al. 2009; Eaves et al. 2011; Hatemi, Dawes, et al. 2011; Cranmer and Dawes 2012; Hatemi 2012; Hatemi, Eaves, et al. 2012; Hatemi and McDermott 2012a; Orey and Park 2012; Smith et al. 2012), the role of genetic influences on individual differences remains largely absent in the greater discourse on political ideology. Rather, the literature in the social sciences regarding the development and transmission of political values, remains largely focused on social and cultural mechanisms and the belief that human beings long ago transcended any genetic history that guides social behavior. In this model, elite discourse is believed to create the frames of reference through which social forces and personal experience influence parents, who in turn socialize their offspring into predictable ideological patterns.

This lack of integration of the social and genetic paradigms of ideology could be attributed to five primary sources. First, the evidence for the majority of findings that genes have some role in ideological formation or transmission has relied on three samples, two in the U.S. from Virginia and Minnesota based registries and one from the Australian Twin Registry. Most of the subjects were ascertained in the 1980's and early 1990's (Martin et al. 1986; Eaves et al. 1989). In fact, with the exception of the Minnesota twins reared apart studies (Bouchard et al. 1990), most of the papers that explored the genetic influences on political attitudes relied on the Eaves and Martin samples, thereby limiting generalizability and independent replication of results.

Second, almost all of the published genetic studies of attitudes and ideology have relied on a single type of measure, the Wilson and Patterson (1968) Attitude Inventory (for an exception see Smith et al. 2012). While the operational definition of ideology is understood to refer to the grouping of attitudes to form some type of coherent political framework or worldview, which can then be used to guide behavior, and is not unlike the Wilson-Patterson (WP) inventory, the WP is not one of the standard measures commonly used to assess ideology in political science, the field which has been the most preoccupied with understanding the formation and function of political ideology. Specifically, there are a series of measures that have provided the ability to categorize human behavior in meaningful ways that have remained somewhat consistent across time and location, and are considered valid measures of ideology by both political scientists and psychologists. Indeed, most empirical explorations of ideological beliefs rely on self-identification measures of liberalism and conservatism, measures of authoritarianism, and more global measures of ideology that focus on collectivism, individualism, egalitarianism, freedom and equality, rather than the more psychometrically designed attitude inventory such as a WP scale (for a review see Treier and Hillygus 2009). So far, these measures have remained absent from behavioral genetic analyses. Thus, the heterogeneity between the measures used to test more standard social science hypotheses regarding ideology versus the WP measure used in most twin studies has drawn criticism (e.g., Charney 2008a), limiting the integration of biological factors into mainstream conceptualizations of political ideology.

Third, the epistemological divide that exists between the life and social sciences has contributed to the lack of acceptance of behavior genetic theory and methods (e.g., see Beckwith and Morris 2008; Charney 2008a; Charney 2008b; Charney 2012; Shultziner 2013). This is particularly true regarding the majority of genetically informed studies of ideology, which have relied on quantitative models of twins, adoptees and kinships. The theoretical premise and statistical methods behind these approaches are foreign to most social scientists making it difficult for many to effectively evaluate and integrate this research into their own work. Indeed, a recent publication in *Political Analysis*, the journal considered to be the leading methods journal in political science, claimed that twin models do not account for gene-environment interaction and twin researchers are unaware of the possibility of gene-environment interplay (see Shultziner 2013), despite the thousands of publications that show otherwise (for a response and review see Verhulst and Hatemi 2013). Behavior genetic approaches have also inspired philosophical objections due to the firm belief that behavioral differences are entirely socialized. Several publications in the political

science literature have begun to erode this view and explicate the theoretical and empirical justification for inclusion of genetic influences and biological mechanisms in general, including gene-environment interplay (Alford et al. 2005; Hatemi et al. 2007; Fowler et al. 2008; Fowler and Schreiber 2008; Hatemi, Funk, et al. 2009; Hatemi, Medland, et al. 2009; Medland and Hatemi 2009; Hatemi et al. 2010; Boardman 2011; Boardman et al. 2011; Hatemi, Dawes, et al. 2011; Hatemi, Gillespie, et al. 2011; Hatemi and McDermott 2011b; Boardman et al. 2012; Hatemi, Byrne, et al. 2012; Hatemi, Eaves, et al. 2012; Hatemi and McDermott 2012b; Hatemi and McDermott 2012c; Fowler and Dawes 2013). Nevertheless, normative criticisms of twin models, often couched in the equal environments assumption emerged, recapitulating the debates of decades ago (Charney 2008a).

On the surface, equal environments violations for politics would appear to be a functional impossibility. Parents would have to decide to raise their twins more similarly if they were monozygotic than if they were dizygotic twins, and to operationalize the differential rearing by liberal versus conservative children in the same household. That is, they would have to be systematically raising one child more liberal or conservative than the other, during the same time-period. This is not to say parents do not treat children differently in other domains. This occurs, for example, when parents react differently to different children depending on the children's personality (e.g., Scarr and McCartney 1983). However, this would be a type of reactive heritability and not a violation of the equal environment assumption (Rose et al. 1990). Nevertheless, a series of studies have empirically addressed this criticism regarding political orientations. Hatemi et al.'s (2010) extended kinship analyses found no special twin environments existed for political attitudes; Littvay (2012) partitioned common variance into that which is shared and that specific to each twin, and found explicit differences in rearing had little influence on the heritability of attitudes or ideology; Smith et al. (2012) relied on a gene-environment interaction design and found sharing a room, attending the same class and other similarity-in-rearing measures had almost no influence on the heritability of ideology. One of the most powerful tests for unequal environments on attitudes was conducted by Eaves et al. (1997) and later by Hatemi, Funk, et al. (2009), in which MZ and DZ twins were assessed for attitudes from ages 9-18 every 2 years. They found no differences in co-twin similarity on attitudes by zygosity type throughout childhood, but once children left home DZ correlations dropped. That is, the home environment kept DZ twins more similar, not more different.

The fourth criticism focused on assigning the genetic influences on ideology to other related psychological traits. The most prominent hypothesis in this vein is the belief that political ideologies and attitudes are merely manifestations of personality, and it is the genetic influence on personality that is being measured through univariate studies on attitudes and ideology (e.g., Mondak et al. 2010; Smith et al. 2011). However a series of papers by Verhulst and colleagues challenged this view by decomposing the variance between personality traits and ideologies, finding that while the majority of the relationship between the two resided at the genetic level, the majority of genetic variance remained unique to attitudes and ideologies (Verhulst et al. 2010; Verhulst, Hatemi, et al. 2012). Furthermore, employing a direction of causation model and relying on longitudinal analyses, Verhulst, Eaves, et al. (2012) found that if there was a causal flow it would operate through attitudes and not personality, and that changes in personality over time did not result in changes in

attitudes over time (also see Verhulst and Hatemi 2011; Verhulst and Estabrook 2012). In essence, whatever genetic influences account for individual differences on attitudes and ideologies they are not subsumed by other covariates, but they remain quite specific to ideological differences.

Finally, findings of genetic transmission of political attitudes from parents to their children have largely relied on estimates of genetic variance at a latent level, and have remained agnostic as to the identity of the specific genetic variants involved. Thus, the results appear like a black box to many social scientists; something is happening at the genetic level, but the specific genetic variants and mechanisms underlying the neurobiological pathways by which attitudes are formed and maintained, remained out of reach. Moreover, some have argued that without specific genetic and neurobiological systems to focus on, integrating genetic research into testable hypotheses and modifying extant conceptions of ideology remains abstract. Therefore, critics have claimed that heritability studies offer little value (Charney 2008b; Charney 2012; Charney and English 2012).

There have been a handful of “candidate gene” studies proposing a link between specific genetic variants and specific political traits, including monoamine oxidase (MAO) with behavioral aggression (McDermott et al. 2009), serotonin and MAO with voting participation (Fowler and Dawes 2008) and dopamine with partisanship (Dawes and Fowler 2009). However, similar to the study of other complex human traits, these candidate gene studies have found only nominally significant results and have not withstood long-term replication. Single SNP studies also raise concerns about reliability and false positives (Duncan and Keller 2011). In general, genome-wide approaches have begun to provide more clarity, and have yielded more reproducible genetic associations than any other approach (Nicolae et al. 2010). However, a recent series of works have found that it will take extremely large sample sizes to have enough power to identify individual genetic variants related to complex social traits (e.g., Rietveld et al. 2013). This is a particularly daunting scenario for researchers who focus on political attitudes and ideologies; unlike health related conditions, there are no funding mechanisms to support large genotyping efforts on social traits. Thus, so far only two genome wide studies published have attempted to identify quantitative trait loci (QTLs) responsible for variation in measures of political attitudes using small samples. Hatemi, Gillespie, et al. (2011), relying on genome wide linkage of 13,000 individuals assessed for political attitudes, found 3 genomic regions putatively containing quantitative trait loci accounting for some 8-13 percent of the variation in Liberalism-Conservatism. The significant and suggestive regions included genes thought to be part of the dopaminergic, serotonergic, NMDA and olfactory pathways. However, the resolution of linkage mapping is typically very low and is better suited to identify genes of large effects, and not individual variants that are typically very small for complex traits. Benjamin et al. (2012) then conducted genome wide association analyses of certain attitudes on 3,233 individuals in Sweden, and found no markers that approached significance.

Here we address the previously unanswered criticisms surrounding the sample and measurement limitations and the relative absence of genome wide explorations, through two sets of original empirical analyses. First, we conduct variance decomposition on a diverse set of ideological measures that represent those most commonly used throughout the

political ideology literature. These include political attitudes, left-right self-placement, right wing authoritarianism, life values, economic egalitarianism, individualism vs. collectivism, and freedom vs. equality, from nine studies drawn from five countries, Australia, Denmark, Sweden, Hungary and the US, conducted over the course of four decades (1980-2011). We find that genetic factors account for a significant amount of the variance in individual differences in ideology across time, location, measures and populations, with one exception, which we discuss below.

We then conduct genome wide association (GWA) analyses based on single nucleotide polymorphisms (SNPs) on two Australian samples and one Swedish sample. Due to the limited sample sizes, we consider these analyses a preliminary step to facilitate future research. For example, prior to the consortium that formed to conduct GWA on educational attainment of over 125,000 individuals (Rietveld et al. 2013), numerous genome-wide analyses were conducted on smaller samples allowing independent researchers the ability to identify one another, pool resources and work together in the future. We are only at the beginning of integrating genetics into the study of complex social traits, and the findings here may help begin to provide the theoretical and methodological foundation for a more comprehensive exploration of ideology that can serve to integrate both biological and social fields of inquiry.

Sample

Data collection and analysis was approved or conducted within the guidelines set forth by the Queensland Institute of Medical Research human research ethics committee, The Danish Data Protection Agency, Uppsala University, University of Minnesota, Central European University and the Virginia Commonwealth University institutional review boards or equivalent.

Australia 1980

Twin participants, aged 19-87 years ($\mu=33.5$, $\sigma=14.2$) were first ascertained in 1980 to complete a Health and Lifestyle Questionnaire (HLQ). Liberalism-Conservatism was assessed by a 50-item scale of contemporary socially and politically relevant Australian attitudes in a Wilson and Patterson (1968) format. The inventory presented participants with a short stimulus word or phrase and asked them to respond positively, negatively, or neutrally to each. Attitudes scores are summed to generate a Liberalism-Conservatism measure. Complete phenotypic data were available for 7,612 individuals, or 3,806 twin pairs (36% males). Parts of these data were used in the original Martin et al. (1986) study.

Australia 1990

Participants enrolled in the Australian Twin and Family Registry (ATR) aged 19 to 90 years ($\mu=36.9$, $\sigma=16.0$) completed a Health and Lifestyle Questionnaire (HLQ) between 1988 and 1990 and gave blood samples for DNA extraction and genotyping. Liberalism-Conservatism was assessed by a 50-item scale of contemporary socially and politically relevant Australian attitudes in a Wilson-Patterson (1968) inventory, similar in format to the 1980 sample, but with updated attitude measures. Complete phenotypic data were available for 16,140

individuals from 7,619 families (47.4% males), which included parents, siblings, spouses, and offspring. Heritability analyses on the WP scale for the complete sample has not been previously reported. Approximately 5,000 of these individuals were also assessed in the earlier (1980) wave noted above. We conduct separate analyses in the variance components analysis but consider them from the same population for the genotypic analyses. Phenotypic and genotypic data were available for 6,894 individuals from 3,516 families, which included parents, siblings, spouses, and offspring.

Australia 2008

Participants enrolled in the Queensland Twin and Family Registry (QTR) took part in a first wave of data collection as part of an ongoing study of cognition and melanoma in 1999 (Wright and Martin 2004). In 2007, respondents aged 19 to 30 years ($\mu=27.1$, $\sigma=3.3$) were assessed with a 28 item social attitudes inventory in a Wilson-Patterson format. This sample also included a 10 item authoritarian attitudes index and an economic egalitarianism measure. The question format is detailed in the supplementary information (SI 1). This is the first time heritability analyses have been conducted on any of these measures. Phenotypic and genotypic data were available on 1,160 individuals from 635 families (43% males), which included parents, twins and their siblings.

United States Mid Atlantic Twin Registry (MATR) 1988

The sample, previously dubbed the Virginia 30K, consists of 29,682 individuals (8,636 families), including twins (14,753), non-twin siblings (3,184), parents (2,362), offspring spouses (4,390) and other relatives (4,993) aged 18-96 years ($\mu=49.5$, $\sigma=17.6$; 43% males). The sample was derived from a population registry that originated in the late 1970s. A large questionnaire on "Health and Life Styles" (HLQ) was first administered in the late 1980s. Political attitudes were measured by a 28-item Wilson-Patterson (1968) attitude index, and a Life Values index that shares certain elements with published measures of Right Wing Authoritarianism (SI 1). Only the twins are used in this study. The individual attitudes, but not authoritarian values, from these data have been used extensively in the extant literature (Eaves et al. 1999; Eaves and Hatemi 2008; Eaves et al. 2008; Hatemi, Medland, et al. 2009; Hatemi et al. 2010; Eaves and Hatemi 2011; Eaves et al. 2011; Smith et al. 2012).

United States Health Habits and Opinions study (HHO) 1990

The sample is a follow up of the 1988 MATR study above. Approximately 4,200 twins aged 40-93 ($\mu=64$, $\sigma=7.9$; 27.2% males), took part in a 2 years follow up the HLQ. Political attitudes were measured by a 50-item Wilson-Patterson (1968) attitude index. Heritability analyses on the WP scale for this survey have not been previously reported.

United States Minnesota (MTR) 2008

The Minnesota Twin Family Registry, a birth-record based registry containing approximately 8,000 twin pairs born in Minnesota from 1936 to 1955 (Lykken et al. 1990), completed a detailed survey on social and political issues, values, and behaviors. The sample of middle-aged twins ranged from about 53 to 61 years ($\mu=56$, $\sigma=2.4$; 37.4% males). Data collection was conducted between July 24, 2008 and October 30, 2009. A total of 1,349

individuals completed the survey. Of these, 1,192 were members of twin pairs and 157 had a twin that did not complete the survey. The study provided responses to a Wilson-Patterson Political Attitudes index, Self-Placed ideology measured in an American National Election Studies format, Right Wing Authoritarianism, and Economic Egalitarianism measures. Heritability analyses have been reported on the WP and self-placed ideology measure (Smith et al. 2012; Smith and Hatemi 2013) and several combinations of political attitudes (Cranmer and Dawes 2012; Orey and Park 2012; Stam et al. 2012).

Denmark 2009

Participants were drawn from the Danish Twin Registry aged between 19 and 39 years ($\mu=29.27$, $\sigma=6.13$; 41% males) (Skytthe et al. 2006). The survey was conducted between October 1 2009 and February 16 2010. The overall response rate was 54 percent ($N=3,616$). Measures of ideology include a Wilson-Patterson Political Attitude Index, an Individualism-Collectivism index, and a Freedom-Equality index (SI 1). This is the first time heritability analyses have been conducted on these measures and on this sample.

Sweden 2010

Participants were drawn from the Swedish Twin Registry between 2008 and 2010. The sample of twins for this study ranged from 52 to 67 years ($\mu=60$, $\sigma=4.6$; 45.7% males). The response rate from contacted individuals was 47.1%. The sample is comprised of 1,143 complete MZ pairs (464 of them male); 1,237 complete, same-sex DZ pairs (502 of them female); 1,114 complete, opposite-sex DZ pairs; and 4,394 singletons. Only the same sex MZ and DZ pairs were available for this study. Two measures of political ideology are included: an additive index based on a battery on attitudes toward 34 different policy issues and a single-item measure of left-right attitudes. Heritability analyses on the ideology index for this sample have not been previously reported.

Hungary 2012

Participants in the Hungarian sample were drawn from a very small volunteer survey conducted during January of 2012 at Central European University (Littvay et al. 2013). The sample is comprised of 46 families with 29 complete MZ twin pairs and 14 complete DZ twin pairs aged between 19 and 79 years ($\mu=43$, $\sigma=14.8$; 20% males) surveyed on two measures of ideology, a self-report Liberalism-Conservatism measure and a Left-Right measure (SI 1). Heritability analyses on this sample have not been previously reported.

In sum, in order to capture the myriad measures that reflect the most common definitions of political ideology, we include measures extensively employed in the American, Danish and Swedish National Elections Studies, the European Social Survey, and the World Values survey. These measures include ideological self-placement, which is perhaps the most commonly used measure of ideology employed in the social science literature (e.g., Extremely Liberal, Liberal, Slightly Liberal, Middle of the Road, Slightly Conservative, Conservative, and Extremely Conservative); life values; measures of authoritarianism; egalitarianism, individualism, collectivism, equality and freedom, as well as several Wilson-Patterson composite measures of Liberalism-Conservatism (Table 1).

Item coding and pooled co-twin correlations are presented in SI 1. All scales are normally distributed or slightly skewed. For the sake of simplicity and replication, raw sum scores are used for the individual univariate analyses and transformed Z-scores are used for the combined model fitting analyses. Different measurements, such as factor scores, may result in different estimates.

Variance Components Modeling of Political Ideologies

The first stage of the analyses rely on the Classical Twin Design (CTD) variance components approach, which compares a population of genetically “identical” (MZ) twin pairs to a population of non-identical (DZ) twin pairs, where both types of twins are reared together and share the same family environment. Shared variance is partitioned into that which is due to genetic effects (A) and that which is due to a common environment (C). Additive genetic effects are the sum of the individual effects of all genes involved. Common or shared environmental (C) influences are those shared by co-twins. Finally, nonshared, or unique, environmental influences (E) represent differences in trait values due to differences in individual experiences. Nonshared environmental influences also include the effects of differences in the perception of an event.

Analyses of twin data were conducted using maximum likelihood estimation in a structural equation model fit to the raw data, corrected for age and sex effects, operationalized in the statistical package Mx (Neale et al. 2003). We report only saturated models that equate estimates for males and females when appropriate (univariate fit statistics are presented in SI 2).

Variance Decomposition Results

The results, presented in Figure 1, provide evidence of a significant and substantial genetic influence on ideological formation across every measure, population and period with one exception: a measure that explicitly used the phrase “Left or Right”. In Hungary, individual differences on this measure are almost entirely due to shared environmental influences, and in Sweden, genetic influences are only marginally significant and minimal. The difference between this measure and all other ideology measures is important. In comparison to a question in the same survey, worded slightly differently in Hungary, one’s Liberal-Conservative orientation, genetic influence is about 0.39; and in Sweden genetic influences for a similar Liberal-Conservative measure account for between 0.37-0.45 of the variance. The term “Left-Right” appears to have a unique meaning in these countries and instigates an entirely different set of psychological processes. We discuss this further below.

We standardized all measures (Z-scores) across samples and conducted a meta-analysis that grouped twins into two groups (MZ and DZ) in order to allow for a combined analysis. The combined weighted mean of relative influences across measures and samples is approximately 0.40 for genetic influences, 0.18 for shared environmental influences, and 0.42 for idiosyncratic environmental influences (final row in Figure 1). A formal test of the data revealed that the genetic component across measures, periods and countries could be statistically equated, and did not significantly decrease the fit of the model (Table 2). The exception being the two measures which explicitly asked about one’s “Left or Right”

position; this question was asked only in Hungary and Sweden. The environmental components, however, could not be equated across most measures and countries. This suggests that the relative import of genetic influences on the variance of political ideology is similar across measures and countries; however, the specific details of the ideological content are dependent on the specific environmental contexts that reside in each measure, including time, culture and measuring instrument (including length of scale).

In these analyses, genetic influences were modeled as additive. While broad sense heritability is unlikely to be very biased, estimates of the common environment may be under-estimated if there are non-additive genetic effects and are over-estimated in the presence of primary phenotypic assortment, as is the case with ideology (e.g., Martin et al. 1986; Eaves et al. 1990; Eaves et al. 1999; Eaves and Hatemi 2008; Hatemi et al. 2010; Eaves et al. 2011).

Genome Wide Association Study of Political Ideologies

The second stage of our study conducts genome wide association analyses (GWAS) based on single nucleotide polymorphisms (SNPs) typed at a high density throughout the genome on two Australian samples and one Swedish sample detailed above. To account for differences in phenotype collection and age across the samples, each sample was analyzed independently, and meta-analysis techniques were used to combine the results.

In the two Australian cohorts, DNA was extracted in accordance with standard protocols; participants were genotyped on the Illumina 317K, 370K, or 610K SNP platforms, and genotypes were called with the Illumina BeadStudio software. After integration of the data sets, the data were screened for missingness within individuals (>5%, taking into account the number of SNPs that were genotyped for each individual), pedigree and sex errors, and Mendelian errors (genotypes for all family members for a given SNP were removed upon detection of errors). Standard quality control filters were applied to the genotyping, restricting the imputation to samples and SNPs with high data quality. A set of SNPs common to the nine subsamples was used for imputation in order to remove bias from the imputed data (for more details see Medland et al. 2010).

As imputation is sensitive to both missingness and SNP distribution, to avoid introducing bias, a set of SNPs common to the nine Illumina subsamples available was used (N=269,840). These data were screened for ancestry outliers. Full siblings and offspring of individuals who had been identified as ancestry outliers were excluded from the reference set used in Mach stage 1. The imputation was run in two stages using Mach. In the first stage, the data from a set of 450 reference individuals was compared to the phased haplotype data from the HapMap CEU I+II data (release 22, build 36). The 450 reference individuals were made up of fifty unrelated individuals (with the lowest missingness) from each of the nine subsamples. In the second stage, data were imputed for all individuals using the HapMap data (release 22, build 36) as the reference panel and the recombination and error files generated in stage 1 were used to customize the imputation.

Swedish Twins who passed initial, lab-based quality controls were genotyped by the SNP&SEQ Technology Platform, Uppsala, using the Illumina HumanOmniExpress

BeadChip genotyping platform. A total of 79,893 SNPs were omitted because their minor allele frequency was lower than 0.01; 3,071 markers were excluded because they failed a test of Hardy-Weinberg equilibrium at $p < 10^{-7}$; and 3,922 SNPs were dropped because of a missingness greater than 3%. IMPUTE Version 2 was used to impute all autosomal SNPs on HapMap, using the publicly-available phased haplotypes from HapMap2 (release 22, build 36, CEU population) as a reference panel (Howie et al. 2009).

The principal components of the genotypic data were computed using EIGENSTRAT (Price et al. 2006). The program smartpca of the EIGENSTRAT software was used to calculate the principal components of the genotypic data from a subsample of 6,813 unrelated individuals and to project the other individuals in the sample onto those principal components, thus obtaining the loadings of each individual on each of the top 10 principal components. We dropped individuals whose score was at least six standard deviations from the mean on one of the top ten principal components.

All GWAS analyses were screened for non-European ancestry and we used principal component analysis (PCA) of similarly genotyped data from 16 global populations sourced from Hapmap Phase 3, as well as sex, year of study, and age for covariates.

In the 1990 Australian cohort and in the Swedish sample no variant reached genome wide significance. In the 2008 Australia cohort, a group of SNPs in high LD located in a gene involved in the olfactory pathway on chromosome 6, and two additional SNPs located on one olfactory receptor gene, reached genome wide significance. Inverse standard error meta-analyses conducted using METAL, however, confirmed that no variant reached genome wide significance across samples. Figure 2 displays the QQ and Manhattan plots of the meta-analysis. The list of SNPs with p-values better than 5×10^{-06} for all samples and the meta-analysis is provided in SI 3.

Discussion

The results from our first stage of analyses provide strong support of Eaves, Eysenck, and Martin's original studies, and supports the call for a revision of the status quo understanding of the etiology of political ideology in the social sciences, and a broadening of our appreciation for the many effects it exerts on a wide variety of processes, including emotive, cognitive, physiological and perceptual. Using nine samples taken from five countries, over four decades, and employing a wide variety of measures to assess ideology, we found a common genetic influence across all samples and measures, with one exception. The phrase "Left-Right" in European countries takes on a different context than the terms liberal or conservative, or those ideologies formed from political attitude positions. Indeed, the phrase "Left-Right" appears highly subject to local and cultural definitions and may indicate group identification more than ideological position. For example, in Sweden the term "Left-Right" is strongly-related to party identification and voting behavior. The finding that the environment accounts for nearly all the variation on measures which use the phrase "Left-Right" is similar to explorations of party identification in the US during the 1980's and 1990's, which find that ideology is heritable, but party identification is not (Hatemi, Alford, et al. 2009). This might change however, if the measures are taken on a population or during

a time period where the correlation between ideology and group identification is high (e.g., see Fazekas and Littvay forthcoming). Outside of the phrase “Left-Right”, the influence of genetic factors on the development of political ideology appears to be reasonably uniform across time, measure and country, while the influence of common and unique environmental factors differs with the shifting political and social factors in various circumstances. We thus demonstrate systematic, cross-temporal, cross-cultural genetic influence on the emergence of political ideology.

Australia, the US, Denmark and Sweden, and to only a slightly lesser degree Hungary, share a great deal of genetic ancestry, and it would make sense in many regards that many genetic influences would exist uniformly for similar behavioral traits. However, these countries differ politically and culturally. Denmark and Sweden are among the most economically egalitarian democratic states. Hungary has only just begun to reestablish its democratic identity, and the freedoms to consider a wider range of political values. These differences are reflected in our analyses by the large and significant difference in environmental influences. Such a finding is precisely what one should expect if the genetic pathways undergirding political ideology remain similar in people of relatively similar genetic ancestry, but emerge in different manifestations within different cultures and variegated political environments.

Genetic influences on political ideology are not boundless and social influences are far from irrelevant to the transmission of ideology. Political ideologies are complex, interactive, and environmentally contingent and phenotypic heterogeneity is undoubtedly present. The formulation of an integrated theory of political ideology, including the acquisition and application of social values and behavior, requires the integration of genes and environment, embedded within a developmental framework, that allows for the incorporation of parental investment, social groups, cognition, perception, education, and a wide array of neurobiological mechanisms at the very least. In such a framework, there is scope for the roles of gene-environment interplay, including genetic expression, operating in social environments that change with the changing roles of an individual’s life and disposition (e.g., Eaves et al. 1997; Eaves and Hatemi 2008; Hatemi, Funk, et al. 2009; Hatemi 2013). In this way, models of genetic and environmental variation may be useful to provide a critical bridge that merges the research in the social and life sciences into a more comprehensive theory of ideology.

The second analyses conducted GWAS on measures of political ideology. Neither this study, nor those mentioned above, provide any definitive evidence of a specific genetic marker being related to ideology. The failure to identify significant SNPs should not be surprising. Our findings are consistent with genome-wide explorations on almost any complex trait; a single gene or small group of genes does not directly influence ideological preferences. Rather, thousands of genetic variants of very small effects and constellations of genes interact with each other and the environment to influence behavior, indirectly. For social and behavioral traits, such as political attitudes and ideologies, in which measures and definitions change as a function of time, location and climate, sample size and measurement limitations present a challenge. Even if we could ensure the perfect measure, the plethora of relevant individual genes and their complex interactions with other genes, as well as the

environment counsel against expecting that any individual genetic markers could explain a sizable amount of the genetic variance in political temperament and without a very large sample, identifying genes of small effects is unlikely. Our findings are consistent with this polygenic expectation, and spur us to gather larger samples.

We are only in the infancy of understanding the genome and epigenome. The mechanisms by which genes influence ideology will most likely emerge as a consequence of developmental and epigenetic processes. Capturing these mechanisms remains an imperfect science. Yet, it appears once ideological orientations become instantiated by some function of genetic disposition, environmental stimulus or epigenetic process, the psychological mechanisms that guide behavior in predictable ways appear somewhat stable and this stability appears to be related to genetic disposition. Thus, future studies that identify genetic and environmental pathways by which genes influence the regulation of hormonal, cognitive and emotive states, which in turn influences the selection into, interpretation of, and reaction to, environmental stimuli relevant to political values, may eventually provide the necessary glue to combine the multitude of neurobiological influences on ideology captured across the sciences.

In summary, the findings suggest that while genes undoubtedly matter in the aggregate for the development of political attitudes, individual common variants will have small effects on ideology. Hunting for a single “political gene” is a fruitless endeavor. Rather, we suggest that until large enough samples and improved techniques allow for the identification of specific genetic variants of small effects related to ideology, measures of latent influence provide important and meaningful estimates to understand variance in ideology. Future studies, which focus on detecting and understanding the full range of rare and common variants influencing ideology, including examinations of copy number variation, genetic expression and epigenetic pathways, will only serve to further elucidate the genetic influence on ideology and explicate the pathways that account for a substantial portion of how ideologies are formed and maintained in a world where both genes and environment interact and remain in continuous dialogue to guide human behavior.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We thank the families for their participation. Funding was provided by the Australian National Health and Medical Research Council (241944, 339462, 389927, 389875, 389891, 389892, 389938, 442915, 442981, 496739, 552485, 552498), the Australian Research Council (A7960034, A79906588, A79801419, DP0770096, DP0212016, DP0343921), the FP-5 GenomEUtwin Project (QLG2-CT-2002-01254), the U.S. National Institutes of Health (AA07535, AA10248, AA13320, AA13321, AA13326, AA14041, MH-20030 MH66206), the U.S. National Science Foundation (SES-1047687, 09210080, 729493, 0721707, 0721378), the Jan Wallander and Tom Hedelius Foundation (P2008-0072:1), the Ragnar Söderberg Foundation (E9/11), the Swedish Council for Working Life and Social Research (2006-1623), the Swedish Research Council (2009-1713), and the Velux foundation, Denmark. Statistical analyses were carried out on the Genetic Cluster Computer, which is financially supported by the Netherlands Scientific Organization (NWO 480-05-003). S.E.M., is supported by the National Health and Medical Research Council Fellowship Scheme. B.V is supported by National Institute on Drug Abuse (5R25DA026119).

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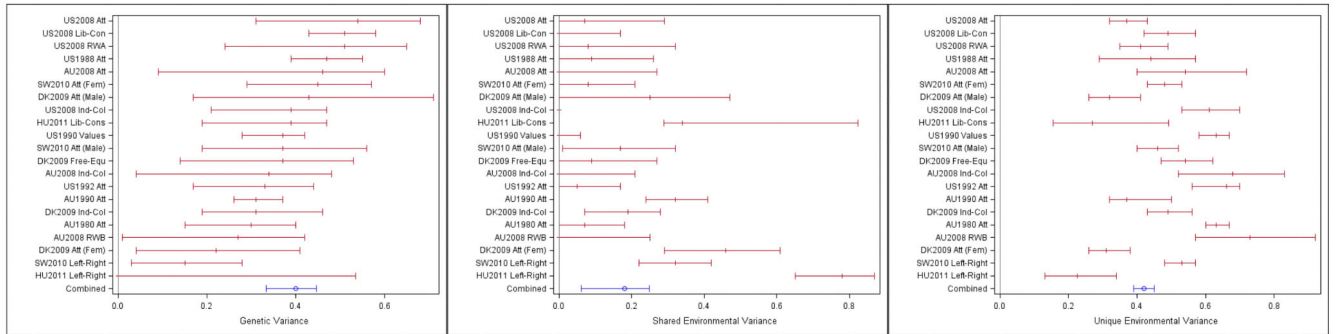


Figure 1. Genetic and Environmental Influences on Political Ideologies in Australia, Denmark, Hungary, Sweden and the US, 1980-2011

Notes: Error bars reflect 95% CI. The combined estimate is obtained from the meta-analysis where groups are equated. Please note the scales for genetic influence range from 0.0-0.6, and for the environmental influences 0.0-0.8.

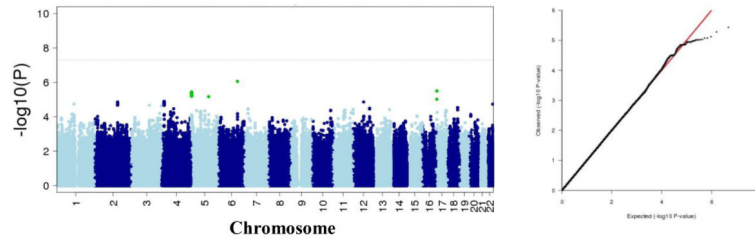


Figure 2.
Manhattan and QQ plot for Meta-Analysis of Liberalism-Conservatism

Table 1

Measures of Ideology

Ideology Type	Measure	Sample Sizes
Liberal-Conservative Attitudinal Ideology		
Attitude Ideology - US 1988 (MATR)	28 item scale (e.g., school prayer, death penalty, gay rights, foreign aid)	9,072
Attitude Ideology - US 1990 (MATR)	50 item scale (e.g., gun control, welfare, immigration, school prayer)	4,040
Attitude Ideology - US 2008 (MINN)	27 item scale (e.g., torture, war in Iraq, immigration, evolution, gun rights)	1,158
Attitude Ideology - Australia 1980 (ATR)	50 item scale (e.g., women's liberation, abortion, unions, bible truth, defence)	7,612
Attitude Ideology - Australia 1990 (ATR)	50 item scale (e.g., immigration, birth control, unions, euthanasia, medicare)	6,698
Attitude Ideology - Australia 2008 (QTR)	29 item scale (e.g., defence spending, foreign doctors, gay marriage, global warming, Iraq war)	502
Attitude Ideology- Denmark 2009 (DK)	15 item scale (e.g., warrantless searches, porn, lower taxes, tougher on crime, immigration)	2,136
Attitude Ideology- Sweden 2009 (SW)	34 item scale (e.g. public spending, defense, welfare, taxes, pornography, abortion, harder punishments, immigration)	4,644
Liberal-Conservative or Left-Right Self-Placement		
Self-Report Liberal/Conservative-- US 2008 (MINN)	Generally speaking, which of these best describes your political views? (7 pt. scale ranging from Strongly Liberal to Strongly Conservative)	1,158
Self-Report Liberal/Conservative-- Hungary 2011 (HU)	Many use the terms liberal and conservative to describe political standing. This figure shows the degrees between being liberal and being conservative. On this figure how would you place your own political standing? (10 pt. radial)	65
Self-Report Left-Right-- Hungary 2011 (HU)	Many use the terms left and right to describe political standing. This figure shows the degrees between being one the left and being on the right. On this figure how would you place your own political standing (10 pt. radial)	65
Self-Report Left-Right--Sweden 2010 (SW)	In politics you sometimes talk about left and right. Where would you place yourself on a 1-10 scale where 1 stands for left and 10 stands for right?	4,644
Individualism-Collectivism and Economic Egalitarianism		
Economic Egalitarianism AU 2008 (QTR)	1 two sided question (Incomes should be made more equal/we need larger income differences as incentives for individual effort)	502
Economic Equality US 2008 (MINN)	3 questions on whether more should be done for economic equality (see SI 1)	1,158
Individualism-Collectivism Denmark 2009 (DK)	5 questions on whether the individuals or the state should take more responsibility for personal welfare and economic equality (see SI 1)	2,136
Authoritarianism and Authoritarian Values		
Life Values -US 1990 (MATR)	11 item scale (e.g., obey law, obey parents, self-control, be ambitious, defend one's self)	3,442
Equality vs. Freedom -Denmark 2009 (DK)	1 two sided question -I would consider [personal freedom/ equality] as more important (see SI 1)	2,136
Right Wing Authoritarianism -US 2008 (MINN)	15 item scale to measure RWA (e.g., Our country needs a powerful leader in order to destroy the radical currents prevailing in society, see SI 1)	1,158
Authoritarian Beliefs- Australia 2008 (QTR)	10 two-sided statements (e.g., Society works better if people adhere to a simple unbending moral code, see SI 1)	502

Notes: MATR is the Mid Atlantic Twin Registry, USA; MINN is the Minnesota Twin Registry, USA; ATR is the Australian Twin Registry; QTR is the Queensland Twin Registry, Australia; DK is the Danish Twin Registry, SW is the Swedish Twin Registry, and HU is a small twin study from Central European University, Budapest.

Table 2

Model Fitting Results of Variance Components Analyses of Ideology

Equating Variance Across Measures, Cohorts and Countries	-2LL	X ²	df	p-value
All Attitude and Egalitarian Ideologies	82945.542			
- Genetic Variance Equated	82956.687	11.145	8	0.19
- Common Environment Equated	82978.413	32.871	8	<.001
- Unique Environment Equated	83084.639	127.952	8	<.001
- All Components Equated	83178.197	199.784	24	<.001
All Authoritarian Ideologies	22855.686			
- Genetic Variance Equated	22859.006	3.32	3	0.34
- Common Environment Equated	22860.716	5.03	3	0.16
- Unique Environment Equated	22906.169	50.483	3	<.001
- All Components Equated	22931.567	72.561	9	<.001
All Self-Report Ideologies	16886.174			
- Genetic Variance Equated	16896.567	10.393	3	0.02
- Common Environment Equated	16901.178	15.004	3	0.01
- Unique Environment Equated	16903.386	17.212	3	<.001
- All Components Equated	16917.274	20.707	9	0.01
All Self-Report Liberal-Conservative Ideologies				
- Genetic Variance Equated	16887.465	1.291	1	0.26
- Common Environment Equated	16888.266	2.092	1	0.15
- Unique Environment Equated	16890.939	4.765	1	0.02
- All Components Equated	16893.359	7.185	3	0.13
All Self-Report Left-Right Ideologies				
- Genetic Variance Equated	16887.384	1.21	1	0.27
- Common Environment Equated	16890.617	4.443	1	0.03
- Unique Environment Equated	16897.558	11.384	1	<.001
- All Components Equated	16900.514	14.34	3	0.01
All Measures and All Samples of Ideology <i>Except "Left-Right"</i>	109727.85			
- Genetic Variance Equated	109748.52	20.661	14	0.11
- Common Environment Equated	109786.09	58.237	14	<.001
- Unique Environment Equated	110053.63	325.772	14	<.001
- All Components Equated	110235.58	507.725	42	<.001

Notes: Bold Font indicates the best fitting models