Review

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The genetics of politics: discovery, challenges, and progress

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For the greater part of human history, political behaviors, values, preferences, and institutions have been viewed as socially determined. Discoveries during the 1970s that identified genetic influences on political orientations remained unaddressed. However, over the past decade, an unprecedented amount of scholarship utilizing genetic models to expand the understanding of political traits has emerged. Here, we review the 'genetics of politics', focusing on the topics that have received the most attention: attitudes, ideologies, and pro-social political traits, including voting behavior and participation. The emergence of this research has sparked a broad paradigm shift in the study of political behaviors toward the inclusion of biological influences and recognition of the mutual co-dependence between genes and environment in forming political behaviors.

Why use genetics to explore politics?

> Hence it is evident that the state is a creation of nature, and that man is by nature a political animal. And he, who by nature and not by mere accident is without a state, is either a bad man or above humanity; he is like the 'Tribeless, lawless, hearthless one' whom Homer denounces-the natural outcast is forthwith a lover of war; he may be compared to an isolated piece at draughts. Aristotle (Politics, Bk. I) [1].

Aristotle's claim is widely cited to emphasize the importance of politics to human nature, yet the fuller argument implies something deeper about the intrinsic interconnection between being human and being political. The natural inclination to be political constitutes a core component of existing in society; it is ingrained in humanity.

Historically, the life sciences have overlooked this connection and ignored politics, focusing instead on improving human health. Diseases and psychopathologies are critically important and potentially devastating to those afflicted, yet affect only a fraction of the population. Politics affects everyone. Every person has attitudes and values; in aggregate, these shape the structures, institutions, and cultures that guide the rules of society, including how resources are allocated among various groups (e.g., education and health care), laws controlling discrimination, sex, marriage, and reproduction, and decisions about war and peace. The inevitable inequalities that derive from these choices contribute to an untold number of health-related disparities.

At the same time, the idea that genes could influence behavior was considered impossible by those in the social sciences [2]. The increasingly impersonal social interactions typical of society were considered too recent a phenomenon and too context dependent to be shaped by evolutionary forces or influenced by biological differences. Indeed, one of the most enduring and contentious debates in western intellectual history revolves around the relative importance of genetic and environmental influences on human traits (nature vs nurture). Until recently, the study of social traits remained embedded in a paradigm that assumed that social differences were socially determined, and that humans remained unique from other species because not only could we transcend our evolution, but we had already done so [3]. Because of such transcendence, social learning approaches stipulated that the intergenerational transmission of political preferences could only occur through social mechanisms. Culture and nature were viewed as separate and opposing forces [2], despite the number of studies and observations that found otherwise [4].

However, there has been a recent shift in perspective by both life and social scientists that emphasizes the interplay between genes and the environment, and gene–culture coevolution, which has proven more accurate than any position favoring either nature or nurture. It is against this background that a growing movement has begun to address the substantial, but not exclusive, role of genetic influences in the manifestation of political differences [5,6]. Today, some 40 years after Eaves, Eysenck, and Martin [7–9] established that differences in attitudes are genetically influenced, an unprecedented amount of literature exploring genetic, neurological, physiological, and hormonal influences on political attitudes [10,11], ideologies [12,13], vote choice [14,15], political participation [16,17], political trust [18,19], sophistication [20], party identification [21], out-groups [22,23], and political violence [24,25] has emerged [6,26–32]. Numerous journals and highly ranked academic presses have recently published books and special issues devoted to the topic [31,33–37]. These findings are summarized in Figure 1, which shows that genetic influences account for a substantial proportion of individual differences in political traits.

Here, we review this nascent but burgeoning integration of genetics and politics, with a specific focus on original

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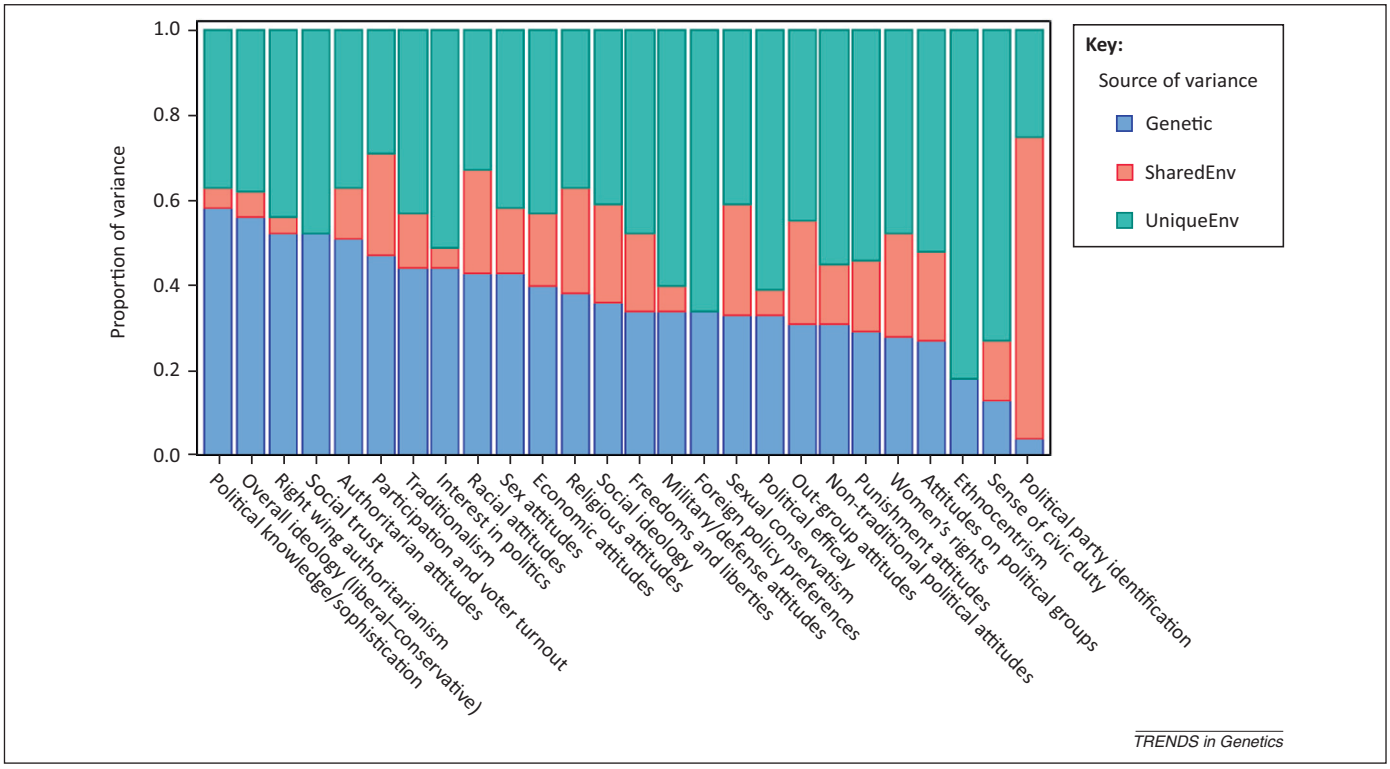

Figure 1. Summary of relative genetic and environmental influences on political traits. Findings from all reported twin and kinship studies that provided estimates of genetic and environmental influences on political traits from 1974 to 2012 were aggregated into 26 domains. The chart displays the relative proportion of variance on each trait explained by additive genetic factors, the aggregate effect of all genetic influences; shared or common environmental influences, those influences shared among family members; and unique environmental influences, which includes idiosyncratic experiences.

contributions that explicate the role that genes have on attitudes, ideologies, and voting behavior. In so doing, we describe how the study of political traits is moving from one that assumes that preferences are socially derived to one that recognizes that beliefs are in part genetically informed, interacting with the environment in countless and reciprocal ways [36], leading to a new understanding of the etiology of political outcomes.

Genetic influences on political attitudes and ideologies

Lindon Eaves and Hans Eysenck [7] conducted perhaps the first study exploring genetic influences on individual differences in political values using a classical twin design (CTD) that estimated genetic and environmental sources of variance. Monozygotic (MZ) co-twins correlated more highly than did dizygotic (DZ) co-twins on measures of ideology constructed from a scale of attitudes, including the death penalty, ethnocentrism, morality, unions, unemployment, and abortion, among others. The relative amount of variance due to additive genetic influences was between 0.54 and 0.65 (on a scale of 0–1). In essence, parent and adult child concordance appeared to be a function of genetic transmission and personal experience rather than of social learning in the home. Nicholas Martin and others, in what is considered the foundational study in this area, [8] extended these findings using a more comprehensive battery of political and social attitudes and a larger sample of twin pairs reared together (approximately 4600). Ideology and attitudes were heritable on par with personality, averaging approximately 0.50 [38]. Similar findings were reported in subsequent studies that extended these populations to include over 11,000 twin pairs from the USA and Australia, [9,27,39] as well as other studies that explored different constructions of ideological values and relied on alternative methods, including identical twins reared apart and adoption studies [11,40–46].

One of the most recent studies combined the data from previous research with new data collected from the 1970s to 2010 on populations from Australia, Denmark, Sweden, and the USA, and assessed a wide variety of ideological measures, including individual attitudes, measures of left–right orientations, social, economic and defense ideologies, and authoritarianism. Significant mean differences existed across measures, populations, and time periods; however, variances were comparable and heritabilities consistently manifested in the 0.30–0.64 range [47]. Genetic influences could be statistically equated across populations and measures, but environmental components could not. This suggests that the relative importance of genetic influences remains common across cultures, but the relative influence of family and personal environments varies greatly across societies, time, and measures in explaining the variance in attitudes.

Models that evaluated ideological positions of the entire family moved beyond estimates of additive genetic, shared familial, and unique experiences, and included estimates of parent–child teaching and learning, sibling and twin environments, passive gene–environment covariance, and assortative mating [27,39,46,48]. Genetic influences accounted for an even greater proportion of individual differences in these analyses, whereas direct learning from parents accounted for a minimal portion of the variance on political attitudes.

One important finding that emerged from extended pedigree studies is that long-term mates correlate more highly on political ideologies (0.65–0.71) than on almost any other clinical, behavioral, or psychological trait [27,39,46,48–51]. Spousal similarity was not due to convergence or social homogamy [49]. Once assortative mating was accounted for, the genetic similarity for political traits between DZ twins increased; the effect being that less genetic variation between twin types accounted for more of the overall phenotypic difference. This recognition led to the conclusion that possibly the most important social influence on a child's ideologies is the parent's choice of mate, which affects a whole repertoire of downstream effects, including genetic transmission, familial environment, and the range of person-specific environments that offspring experience.

Traditionally, political orientations were assumed to result from processes of social learning during adolescence and early adulthood. Yet, most studies of attitudes that included genetic approaches assessed familial upbringing and social background only retrospectively in adulthood. To remedy this, longitudinal and panel studies of twins that explored the developmental trajectories of political attitudes in children integrated theories of social learning with those emanating from genetic transmission [10,52]. In contrast to the adult studies, these studies found no evidence of genetic influences on attitudes until children left home. Rather, the role of the shared environment in the development of ideological orientations increased more than tenfold over adolescence. However, once children left home, DZ co-twin correlations markedly dropped, whereas MZ co-twin correlations stayed the same (Figure 2). This suggests that the home environment keeps DZ co-twins more similar. Once children leave home, they develop their own individual attitudes based on unique experiences, the ability to choose their own environments freely, and individual genetic dispositions [10].

Despite this and other evidence, the conclusion that genetic influences account for variation in attitudes has met with resistance. One critic suggested that if genetic influences account for some portion of the variation in political attitudes it 'would require nothing less than a revision of our understanding of all of human history, much – if not most – of political science, sociology, anthropology, and psychology, as well as, perhaps, our understanding of what it means to be human.' [2]. Differences in training and a lack of proper understanding of genetic methods and assumptions have resulted in several specious criticisms, often framed in debates juxtaposing nature and nurture (Box 1).

Such a simplistic view differs markedly from the scientific understanding that heritable traits are polygenetic and multifactorial and, despite the transparency of research that identifies and clarifies limitations in twin studies, genome-wide approaches, and candidate gene studies, great confusion on genetic methods and findings persists (Box 2). Most researchers consider political traits to be influenced by thousands of genetic markers both indirectly and through interactions with numerous environmental stimuli and other genes in complex genomic, epigenetic, and neural pathways [36]. By contrast, many criticisms are developed as if responding to the view that political traits are simple Mendelian traits, governed by a single gene or a small set of genes [53,54].

Certainly, there is not a gene for liberalism or any political trait. Rather, whatever genetic influences exist

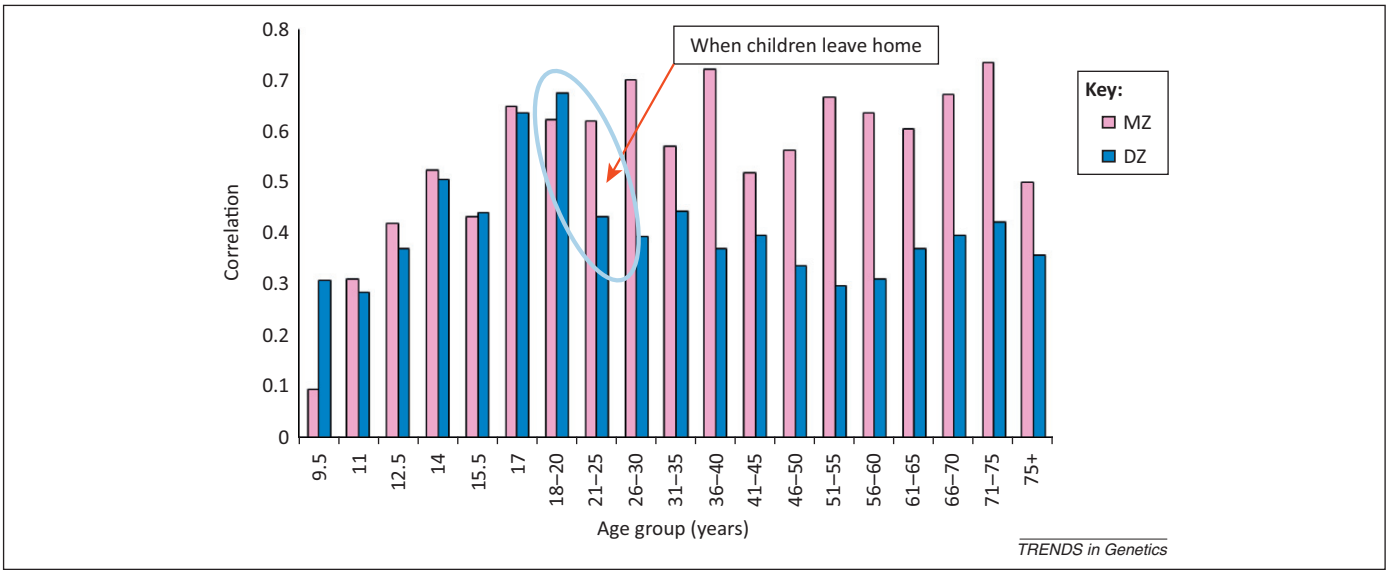

Figure 2. Co-twin correlations for political ideology by zygosity over the life course. The figure displays evidence that genetic influences on attitudes are expressed only when powerful social pressures, such as the parental environment, are no longer present. The chart combines the co-twin correlations on a 28-item attitude index of political ideology from two samples; a longitudinal sample of adolescents assessed every 1.5 years from ages 9 to 17, and a larger cross-sectional sample of adult twins aged 18 and older [10,52]. The most important features of the chart are that the correlations for attitudes of monozygotic (MZ) and dizygotic (DZ) co-twins remains nearly identical through adolescence before the age of 20, signifying that ideology is not genetically influenced in these age groups. However, once children leave home, the pattern changes significantly. Starting at age 21, there is a substantial drop in the DZ co-twin correlations, whereas MZ correlations remain largely the same. At this age, ideology emerges as being genetically influenced. The family environment is keeping siblings more similar, but once removed, MZ twins, who share 100% of their chromosomal sequence, remain more similar to one another. Additional analyses compared the MZ and DZ correlations between twin pairs in the age group where twins begin to leave home (age 21–25) [10]. Co-twins concordant for living at home had statistically similar attitudes regardless of zygosity (MZ = 0.575; DZ = 0.571). However, for twins not living at home in this age group, the co-twin correlations were 0.577 for MZ pairs and 0.229 for DZ pairs. The significant drop in DZ co-twin correlation from childhood to adulthood stems almost wholly from leaving the parental home environment [10,52].

Box 1. Challenges to kinship studies and the twin design

The CTD derives its explanatory power from the difference in the genetic similarity of MZ twin pairs, who share almost identical chromosomal DNA sequences, and DZ twins, who share on average 50% of their DNA sequence. Comparison of phenotypic concordance between populations of MZ and DZ twin pairs reared together controls for the effects of familial socialization, allowing for differences in co-twin correlations to be partitioned into broad estimates of heritability and environment [26].

The approach relies on several assumptions. The most contested, yet dependable, is that the familial environment influences the examined trait to the same degree for MZ and DZ twins. If MZ twins were specifically socialized to be more similar for the trait of interest, then genetic influences would be overestimated in the CTD. A series of studies on political traits using extended kinships [48], longitudinal designs [10], and models that included specific measures of familial environments [28,79] found no significant differences in social influences by zygosity.

A more difficult challenge, which has yet to be fully addressed, is the interpretation of broad-sense heritability estimates. The CTD provides standardized estimates of individual differences, which partitions variance into latent factors, additive genetic influences, common environmental influences shared among family members, and unique environmental influences, which includes idiosyncratic experiences. Interpretation of these models initially relied on a model focused on chromosomal DNA and an additive model of influence. However, genetic influence as well as heritability extends beyond differences in the DNA sequence. It is now known that genetic influence is not simply additive, but occurs through epigenetic, genomic, and numerous other genetic pathways. For example, epigenetic modifications of DNA have a role in phenotypic outcomes, and these are also heritable, thus complicating interpretation [80].

This suggests that all the variation that is attributed to the latent additive genetic factor in twin and kinships studies is confounded by some unknown portion of gene–environment interaction, gene–gene interaction, and epigenetic influences. Thus, interpretation of twin models has developed as the field of molecular genetics has progressed. This interpretation is common knowledge in genetics research, but often not explicitly stated. For example, the label 'additive genetic' remains the same in twin models and can cause confusion. Even when stated explicitly, the nuances of such terms are often not understood by those unfamiliar with genetics terminology.

Box 2. Epistemological challenges

Differences in knowledge and training between genetics and social scientists contribute to difficulties in integrating these fields of research. Most political science degree programs do not require any coursework in the life sciences, much less genetics. Unfortunately, much of the social scientific community's understanding of genetics comes from the media and often rests on the belief that particular genes 'cause' particular behaviors. Media claims that 'Researchers find the Liberal Gene' (http://www.foxnews.com/scitech/2010/10/28/researchers-liberal-gene-genetics-politics/), or that 'Some Politics May Be Etched in the Genes' (http://www.nytimes.com/2005/06/21/science/21gene.html) serve to both exacerbate and reflect the epistemological divide between the social and life sciences.

Divergent approaches to scientific method also contribute to this divide. The social sciences rarely, if ever, experience rapid technological advances or undergo periods of fundamental discovery. Genetics research relies on the aggregation of knowledge and incremental discovery. No one study or method reigns supreme or remains indefinitely. This approach is contrary to social science debates that advocate a single approach or method to address all social research. Thus, criticisms of genetic approaches by social scientists remain unaware or unconvinced that publication of preliminary or novel results or models that acknowledge limitations and develop incrementally are the norm and necessary for discovery and improvement [54,77]. As a result, any flaw or limitation acknowledged in a specific approach is then used to indict the entire research program [2,53].

A disconnect has developed between criticisms that focus on improving existing models and those that seek to abolish or eliminate the entire research agenda, oftentimes for ideological reasons, such as wholesale objections to biological work because of fear of past abuse, or threats to current dominant models [81]. As a result of such largely unspoken existential divides, it has proven difficult for life and social scientists to enter an honest discussion about the limitations inherent in genetic work and still employ the methods in a progressive and useful manner. This divide presents a real challenge for creating a common language, evaluating research, understanding methods and limitations, and discussing current issues in genetics, such as redefining heritability, epistasis, gene–environment interactions, epigenetics (including parent-of-origin effects), rare variants, low power to detect small effects, trait heterogeneity (lots of different traits with the same phenotype), poor tagging (i.e., rare mutations of large effect, problematic genomic regions, and lack of systematic coverage of small copy number variants), undefined genetic pathways, unresolved functionality of genetic markers, and tissue-specific expression, among other concerns.

probably operate through those emotional, cognitive, or rational processes that are instigated when individuals are asked particular questions about their attitudes. Political attitudes in modern human society encompass fundamentally the same issues of reproduction and survival that confronted group life in ancient humans because they involve the same interpersonal traits [5,9,35,36,55,56]. For example, modern questions about immigration are similar to the primal need to recognize and deal with out-groups. Likewise, welfare is essentially a question of the best way to share resources; foreign policy and punishment are matters of protecting one's in-group and defending against the out-group; and issues of sexual freedom are related to finding a mate and raising children. Some combination of mutation, genetic drift, assortative mating, recombination, culture, institutions, social learning, experience, and ecological adaptation drives variance on these traits [56]. The manifestation of genetic influence on these preferences appears more complicated because of large-scale societies, institutions, and modern social structures, such as states and governments. The labels and meanings of issues, groups, and policies might change across time and cultures [36], but the underlying connection between the core issues that are important to humans, including survival, reproduction, and defense, will remain. Indeed, genetic influences on attitude differences may be a remnant of ancient behavioral adaptation pre-dating modern human society [46].

Therefore, studies of genetic influence on attitudes have begun to focus on identifying specific genetic, environmental, and neurobiological mechanisms underlying political beliefs [31]. The first published genome-wide study examining political attitudes and ideology [56] advocated for explicating the emotional, cognitive, or rational mechanisms elicited when measuring specific attitudes and overall left–right orientations. The aim was to establish whether political temperaments shared the same genetic mechanisms that operate on cognition, threat sensitivity, morality, disgust, risk taking, fitness, fear, aggression, pursuit of power, mate choice, and self-interest [27,39,46,48–51,57,58]. In this linkage study, the most

significant associations resulted in logarithm of odds scores ranging from 3.4 to 2.5, providing suggestive evidence that *N*-methyl-D-aspartate, serotonin, glutamate, dopamine, olfactory, and G protein-coupled related receptors were implicated in liberalism–conservatism [56]. These receptors have been associated with cognitive-behavioral performance, aggression, anxiety, cooperation, fear conditioning, impulsivity, pro-social behaviors, and social learning.

This study led to a second, larger wave of research that transitioned from identifying latent genetic influences to more complex integrations of social and genetic theories. This phase explored how genetic influences on attitudes operate through the complex emotive and psychological architectures by which humans process information, emotionally connect with others, and perceive and react to political stimuli. Below, we highlight several studies that represent the general findings and approaches in this area.

A great deal of literature in political science has focused on the importance of fear in the formation of attitudes, largely through social learning. However, several studies have linked fear, ethnocentrism, and out-group attitudes with genetic influences that operate through pathogen avoidance and phobias [59]. These observations were integrated through studies of twins assessed for phobias and political attitudes [22,23,60]. Most of the correlation between social fear and immigration attitudes was due to a common genetic factor. This suggests that genes do not directly affect specific attitudes, but rather genetic propensity influences the disposition and operation of an emotive condition, which then manifests toward many targets, including strangers and out-groups, when elicited. This does not mean that social environments do not matter or that such genetic influence is fixed; individuals learn who the relevant out-group is through social reinforcement, but they can also learn that a perceived out-group is not an out-group at all. Nonetheless, sensitivity to fear of the out-group is in part genetically informed, and this genetic influence manifests as anti-out-group opinions on such topics as immigration.

Another long-standing view has been that personality causes attitudes and that the genetic influence on political attitudes is simply a reflection of personality [61]. However, a series of studies demonstrated that this is not the case [38,45,62]. Longitudinal models from adolescence to adulthood and analyses that estimate the direction of causation from genetic and environmental latent factors revealed that changes in personality did not result in changes in attitudes; instead, genetic influences on attitudes were largely independent of personality [7,38] and whatever relationship exists between them is driven by the genetic variance on attitudes [45]. Although based on self-reported data, this work suggests that attitudes dictate how humans relate to and view the social world. In many respects, this makes sense. Societies of extraverts are not waging war with introverts and spouses do not meaningfully assort on personality; rather, politics and attitudes govern the rules upon which society operates. They also influence who we relate to, not just how we relate to them [63,64].

A series of studies has also begun to focus on gene–environment interplay. For example, among populations where individuals have lost their job, suffered financial loss, or divorced, broad-sense heritability of economic policy attitudes, such as support for unions, immigration, capitalism, socialism, and federal housing, decreased to almost zero [6,65]. Thus, certain environments may trigger entirely different cognitive or emotive processes or be so powerful that they elicit a common response in humans that leaves little room for genetic differences to manifest.

Other studies have focused on specific candidate polymorphisms. For example, individuals with the 7R allele on the dopamine receptor D4, who also have a large number of friends, tend to be more liberal [13]. This ostensibly occurs because a stronger drive for novelty seeking exists among those who have this variant, and this may lead such individuals, when embedded in expansive social networks, to be exposed to more experiences, which in turn leads them to become more liberal. So far, this finding has not yet been replicated. However, emerging work in this area is examining contextual effects, such as the racial composition of neighborhoods, and the importance of educational attainment for genetic influences on a wide array of political traits.

Politics as pro-sociality: participation, cooperation, and voting behavior

Politics is more than attitudes and voting; political engagement, efficaciousness, political sophistication, and participation are of equal significance. Unlike attitudes, genetic influence on these behaviors has only recently been explored. However, the foundational elements of political participatory behavior, such as cooperation, trust, and pro-sociality, have a long history in genetics research. Twin studies indicated the importance of genes in contributing to pro-social behaviors [66], and broad heritability ranging from 0.40 to 0.70 has been observed for self-reported measures of altruism, cooperativeness, trust, and nurturance [67]. Molecular genetic studies of altruism, pro-social behaviors, and cooperation identified several polymorphisms in genes encoding the receptors of the neuropeptides oxytocin and vasopressin, as well as several genes in the dopaminergic system that interact with oxytocin and vasopressin, such as the functional catechol-*O*-methyltransferase (*COMT*) Val158Met polymorphism [68,69].

Working under the theory that political participation is some function of pro-sociality, twin and kinship studies revealed that genetic influences account for approximately 0.53 of the variation in voter turnout [17]. Numerous studies in different countries that measured participation in different ways, such as donating behavior, writing to a member of parliament, attending rallies, or volunteering, reported similar results [70,71]. Molecular genetic studies revealed that variants of dopamine (*DRD2* and *DRD4*), and serotonin (*5HTT*) genes influenced voter turnout and general political participation [16,72]. In a related vein, several twin studies on populations in Sweden, the USA, Australia, and Denmark identified modest to substantial genetic influences on social trust, political efficacy, political sophistication, duty, and political interest, many of which share a common genetic factor with voter turnout and participation [18,19,73,74]. Developing studies are integrating social, genetic, and psychological theories more fully, including contextual factors, genome-wide

approaches, and gene–environment interplay; for example, experiments that introduce varying political stimuli to family members of differing genetic relatedness and to individuals with specific genotypes are beginning to emerge (Box 3).

The future of genetics and political science

In 2008, it was questioned whether 'the recent introduction of genetics as a source for preferences in the political science literature is a rogue wave or a more fundamental challenge to a central theoretical principle of the social sciences, leading to a broader paradigm that encompasses both biological and social influences.' [75]. Four years later, it would be difficult to argue that this area of research is simply a rogue wave. Rather, the number of scholars, hundreds of publications, prominence of conference symposia, media attention, journal issues dedicated to the topic, and interest in the area, both in the larger academic community and public, has only increased [29,30,34,36]. For example, one area of increasing relevance surrounds how genetics might inform public policy (Box 4).

Despite the growth of interest, the integration of politics and genetics is in the earliest of days. Replication of twin and kinships studies has been fruitful, but replication of genome-wide, candidate gene and gene–environment interaction studies is almost nonexistent. Indeed, only three genome-wide analyses for attitudes or ideologies have been published; none use the same measures that would allow for true replication and, so far, no single variant has emerged as significant [47,56,76]. Table 1 provides a list of genetic markers identified that correlate with variation in political traits.

Gene expression studies and the combination of genetic and neural pathway models for political traits are only now emerging. Criticisms, some valid and others not, will continue to inspire caution when exploring genetic influences on political and social preferences, and all other behaviors. Concerns include the fact that heritability estimates from twin studies are confounded by gene–gene and gene–environment interplay and force variation into large latent factors that obscure any specific genetic influences [2,77]. Other concerns note that many candidate gene or polymorphism studies do not replicate, do not account for a substantial portion of the heritability, or do not account for epigenetic and epigenomic processes, and suffer from publication bias [2,77,78]. In addition, limitations in genome-wide association studies (GWAS) include markers of little interest because they map to regions of unknown function,

Box 3. Experimental work

One of the promising new developments in research integrating genetics and politics involves the novel use of experimental methods to traction the influence of environmental factors on identical genotypes at the same moment in time. These involve the use of twins as controls to better understand environmental stimuli. In a traditional experiment, subjects are exposed to a particular manipulation, such as providing them with identical candidates who only differ on party identification and asking them who they would vote for, or they are put in a control condition that does not have the manipulation. Mean effects in response, in this example vote choice, are statistically estimated between the experimental condition and the control condition. Most of this work implicitly relies on the unspoken assumption that dispositional differences between subjects do not exist, are random in nature, or have no role in the importance of the effect of the stimulus. Genetically informed samples, where related individuals participate, or where genotype information is available for participants, allow for the explicit examination of such an assumption; they make it possible to examine the effect of dispositional differences on the perception and effect of stimuli.

This design was used in a study of welfare attitudes [82]. Welfare attitudes are heritable at approximately 0.40 when assessed with a general question on welfare. In an experiment conducted on a national sample in Denmark, subjects rank ordered an injured older woman as the most deserving and a younger healthy man as the least deserving of welfare. By including a group of MZ twins discordant in their exposure to the different vignettes, the exact amount of difference in the stimuli necessary to move the heritability of welfare attitudes from 0.40 to 0.00 was identified. That is, the experiment tested the power of the condition on a person with as close to an identical genotype as possible (MZ co-twin). This approach provides a means to design experiments for the general population that might screen out dispositional influences. In this case, it required two degrees of difference to remove genetic influences on individual differences in welfare attitudes. The novel use of experimental techniques with twins to control for genotype, while exploring the relative role of the environment on behaviors of interest, can offer tremendous traction in understanding how various individuals react to certain stimuli. Such insights can also be leveraged for clinical applications to help create more effectively targeted intervention policies.

Box 4. Genetics for public policy?

Public policy is to political science what clinical studies are to the life sciences: the immediate application of research to improve human conditions. A novel stream of research is now examining how social structures and political institutions affect the environment in ways that trigger or suppress the expression of particular genetic factors, as well as how genetic information might shape and develop policy intervention. For example, understanding how exposure to violence, whether abuse of children or populations suffering from famine or war can cause genetic and neurobiological damage has profound implications for how social structures, legal policies, and political institutions may most effectively alleviate such damage [83]. This field also includes questions of how genetic research might inform school policies to moderate the genetic influence on childhood obesity [84], how smoking cessation strategies might better be implemented in light of genetic research [85], or explicating the importance of parental leave on genetic and developmental pathways for child health [86]. Additional research has begun to explore how genetic approaches might inform foreign policy, including the propensity to engage in political violence [24,25].

Perhaps the most successful application to policy, although indirect, resides on an issue central to current political discourse: discrimination against homosexuals. Although the specific results of the study remain debated, after the team at the National Cancer Institute implicated Xq28 on the X chromosome in male homosexuality [87], the concept of sexual preference began to shift public discourse from morality and choice to inherent disposition. Many factors contributed to change in attitude about homosexuality, but genetic research had an important role in shifting elite and legal discourse, which has filtered down and influenced public opinion and policies on the legality of gay marriage [88,89]. Turning the eugenics movement on its head, the integration of genetics and public policy has been used to help protect individuals in meaningful ways, thereby reducing health risks, promoting healthy lifestyles, and increasing tolerance for differences. There are of course major challenges and limitations associated with applying genetic research to public policy questions, and there is an equal risk of developing harmful policies if such information is used inappropriately, but this risk exists with the misuse of other forms of information as well. Nevertheless, genetic research is beginning to influence, inform, and enlighten the public, including the formulation and evaluation of significant public policies.

Table 1. Summary of candidate genes implicated for political traits based on six published studies that sought to identify specific genetic markers that correlate with attitudes, ideologies, or voting behavior

Phenotype	Gene	Marker	Description	Interaction	Method[a]	*P* value and/or Lod score	Replication	Refs
Ideology (liberal–conservative)	*NAA15/NARG-1*	–	Glutamate	–	GW linkage	Lod = 3.38	None attempted	[56]
	GRIN1	–	Glutamate	–	GW linkage	Lod = 2.78	None attempted	[56]
	DBH	–	Dopaminergic	–	GW linkage	Lod = 2.28	None attempted	[56]
	LCNL1	–	Lipocalins and/or olfaction	–	GW linkage	Lod = 2.78	None attempted	[56]
	OLFM1	–	Olfactomedin	–	GW linkage	Lod = 2.55	None attempted	[56]
	LCN6,8-12,1	–	Lipocalins and/or olfaction	–	GW linkage	Lod = 2.78	None attempted	[56]
	OBP2A	–	Odorant binding protein	–	GW linkage	Lod = 2.55	None attempted	[56]
	KYNU	–	Kynurenine	–	GW linkage	Lod = 3.01	None attempted	[56]
	HTR1E	–	Serotonin	–	GW linkage	Lod = 2.36	None attempted	[56]
	MANEA	–	Mannosidase, endo-alpha	–	GW linkage	Lod = 2.43	None attempted	[56]
	GPR63, GPR6	–	G protein-coupled receptors	–	GW linkage	Lod = 2.43	None attempted	[56]
	OR2N1P	rs9295794; rs4713201	Olfactory	–	GWAS	*P* = 3.519e-08	Failed to replicate	[47]
	OR21J	rs9295794; rs929579; rs9393945; rs7766902	Olfactory	–	GWAS	*P* = 4.526e-08	Failed to replicate	[47]
	DRD4	7R	Dopaminergic	Number of friends	Candidate VNTR	*P* = 0.049	Failed to replicate	[13]
Partisan attachment	*DRD2*	A2	Dopaminergic	–	Case-control and/or family-based candidate SNP	*P* = 0.02–0.04	None attempted	[16]
Voter turnout	*MAOA*	5-repeat –291 and 321 allele vs 336, 351, and 381 base-pair alleles	Monoamine oxidase A	–	Case-control candidate VNTR	*P* = 0.03	None attempted	[17]
	5-HTT	Long 528 allele vs. shorter 484 base-pair allele	Serotonin	Religious attendance	Case-control candidate VNTR	*P* = 0.04	None attempted	[17]
Violence (political)	*MAOA*	2-, 3- and 5-repeat allele vs 5- and 4-repeat alleles	Monoamine oxidase A	Exposed to violence in youth	Family-based candidate VNTR	*P* = 0.02	Replicated within study	[25]

[a]Abbreviations: GW, genome-wide; SNP, single nucleotide polymorphism; VNTR, variable number tandem repeat.

require large samples, and suffer from small effect sizes and gene–gene interactions. GWAS have considerably surpassed early expectations, reproducibly identifying hundreds of variants in scores of traits. However, for most traits, GWAS have explained only a small proportion of estimated heritability and the frequency of the assayed markers does not correlate with the frequency of the trait. That is, the common disease and/or common variant assumption may not be accurate.

The study of genetic influences on political traits will move forward as the greater field of genetics moves forward. To model accurately the behavior of a living human organism that creates and maintains his or her own environments, institutions, and cultures, and interacts with others in untold complex ways over the life course, the exploration of the overall biological, social, and psychological pathways, and the genetic and epigenetic mechanisms that inform these processes is necessary. Studies are only now beginning to combine the entire suite of tools, which include twin and kinship studies, genome-wide studies, candidate gene approaches, genetic pathway analysis, copy number variants, neural pathways, gene expression, next-generation sequencing, rare variants, hormonal levels, and gene–behavior experiments, such as those using identical twins to serve as genetic controls, to examine the influence of environments on outcomes. While the methods and approaches for the integration of genetics and complex behaviors will continue to evolve, the enduring interest in political topics will continue to motivate and expand scholarship in this area.

What is immigration if not an issue revolving around out-groups? Laws on marriage, gay rights, sodomy, contraception, and women's reproductive rights are about sex, just as arguments over social welfare policies and health care reflect contentious disagreements over the allocation of resources. In addition, the ultimate failure of politics, war, is among the greatest of human concerns. The fundamental topics of interest in the life, clinical, and social sciences are intertwined, and the conversation between political science and genetics is starting to unravel these strands.

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