https://doi.org/10.1038/s41562-020-0850-9



The dual evolutionary foundations of political ideology

Scott Claessens ¹, Kyle Fischer ¹, Ananish Chaudhuri ^{2,3}, Chris G. Sibley ¹ and Quentin D. Atkinson ^{1,4} □

Research over the last fifty years has suggested that political attitudes and values around the globe are shaped by two ideological dimensions, often referred to as economic and social conservatism. However, it remains unclear why this ideological structure exists. Here we highlight the striking concordance between these dual dimensions of ideology and independent convergent evidence for two key shifts in the evolution of human group living. First, humans began to cooperate more and across wider interdependent networks. Second, humans became more group-minded, conforming to social norms in culturally marked groups and punishing norm-violators. We propose that fitness trade-offs and behavioural plasticity have maintained functional variation in willingness to cooperate and conform within modern human groups, naturally giving rise to the two dimensions of political ideology. Supported by evidence from across the behavioural sciences, this evolutionary framework provides insight into the biological and cultural basis of political ideology.

n recent decades, the concept of political ideology has enjoyed a resurgence in the social sciences1. Political ideology is defined as a set of stable, interrelated beliefs and attitudes that organise views on political and social issues. While scholars had previously attributed only a minor role to ideology in shaping political behaviour^{2,3}, it has since become clear that political ideology both motivates voting and coherently structures views on a wide range of social issues, from taxation and welfare to crime and religion⁴. Traditionally, ideology has been conceptualised as varying along a unidimensional spectrum, with liberalism on the left and conservatism on the right⁵. Broadly, liberalism emphasises equality, social change and system reform, while conservatism emphasises hierarchy, conventionalism and tradition. This left-right distinction dates back more than 200 years to the 1791 French legislative assembly (monarchists sat on the right) but remains the primary means of describing political opinion in social science and public discourse (Fig. 1).

Despite the popularity of this unidimensional model, political views cannot be neatly summarised by a single liberal–conservative spectrum⁶. Recent events in US politics highlight how divergent political views can be within left or right discourse, such as the disagreements of Hillary Clinton and Bernie Sanders within the Democratic Party or the opposition to Donald Trump from within the Republican Party. In the electorate itself, many people express conflicting political beliefs that cross party lines⁷. Libertarians are a classic case of this misalignment, harbouring 'liberal' views on social issues but 'conservative' views regarding economic policy. It is perhaps not a surprise, then, that unidimensional self-report scales of political ideology often have low internal consistency⁸ and low external validity⁶, and they frequently produce more than one latent variable in factor analyses⁹. In short, a single left–right dimension misses important features of the political landscape.

By contrast, scholars from many disciplines have converged upon two dimensions of political ideology. These dual dimensions have repeatedly emerged in the literature over the last 50 years (Table 1), despite researchers using different methodologies and, indeed, different labels to capture ideology. Some researchers have focused on the attitudes that people hold about political and social issues, clustering these into correlated categories using data-driven, atheoretical factor-analytic methods^{10,11}. Others have defined core universal human values (for example, benevolence, tradition, security) and then determined how they influence ideology¹². Lexical approaches have abstracted even further, allowing the underlying structure of political attitudes to emerge from ratings of dictionarybased 'isms' (for example, Machiavellianism or traditionalism)¹³. Moral psychology has inductively derived clusters of moral values and noted how they strongly predict political ideology¹⁴, and crosscultural approaches have validated scale items across many different societies, finding that the same dimensions recur¹⁵. Across this myriad of methodologies, both exploratory and confirmatory, researchers have found very similar two-dimensional ideological structures, strongly suggesting that the scales in Table 1 are all capturing the same underlying psychological phenomena.

How should we understand these two dimensions of political ideology? The first dimension, often referred to as economic conservatism or social dominance, predicts stances on issues like taxation, government-funded healthcare, welfare programs and free education¹¹. Economic conservatives view the world as a 'competitive jungle', in which dominance, inequality and power imbalances are commonplace⁹. The second dimension, often referred to as social conservatism or authoritarianism, predicts stances on issues like traditional social values, criminal justice, patriotism, national security, same-sex marriage and religion^{8,11}. These social conservatives view the world as more threatening, dangerous and unpredictable⁹.

It remains unclear why political attitudes tend to be structured along these two particular ideological dimensions and why the dual dimensions are linked with distinct worldviews. Here we argue that an evolutionary approach to political ideology can shed light on both questions. Recent research challenges the common assumption that ideological variation is best understood as the result of historically contingent social, cultural and environmental factors^{2,5,8,16} with little basis in biology. Variation in political ideology is

PERSPECTIVE

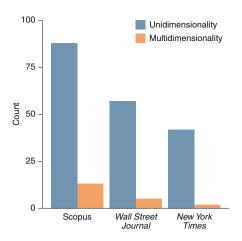


Fig. 1 | The number of scholarly and newspaper articles mentioning unidimensional and multidimensional approaches to political ideology.

We collected data from three sources: the peer-reviewed literature database Scopus and two US newspapers, the *Wall Street Journal* and the *New York Times*. For our review of Scopus, we selected the top 100 most-cited articles from the last 20 years under the search term 'political ideology'. For our review of the US newspapers, we selected the top five most relevant articles in every year from 1999–2018 under the search term 'political ideology'. If the articles contained explicit references to unidimensionality or any of the terms liberal, conservative, Democrat, Republican, or variations thereupon, we coded them as mentioning unidimensionality. If the articles contained explicit references to multidimensionality or any of the terms social dominance, authoritarianism, economic conservatism, social conservatism, or variations thereupon, we coded them as mentioning multidimensionality. Full dataset for this review and code to reproduce this plot at https://osf.io/gckw7/.

heritable¹⁷⁻²⁴, remains stable over long periods of time²⁵ and covaries with basic physiological²⁶⁻³² differences (but see refs. ³³⁻³⁵). The two dimensions of ideology are also repeatedly observed across a wide range of cultures^{15,36,37}, suggesting that they may be universal. This recurrent pattern of ideological variation across cultures, together with heritable stable individual differences, points to the possibility that the two dimensions are at least partly grounded in biology.

A number of promising evolutionary approaches have already derived important insights about the dimensions in Table 1. This includes work linking social conservatism to negativity bias³², disgust sensitivity³⁸ and adherence to social norms³⁹, as well as work linking economic conservatism to upper-body strength⁴⁰. These findings have improved our understanding of each dimension separately, but have not yet explained why political ideology is structured along these two dimensions specifically. To organise, integrate and expand on this work, we need an evolutionary framework that explains the two-dimensional structure of ideology from first principles.

In this Perspective, we begin with the premise that politics is fundamentally the process of dealing with the conflicts of interest that arise from human group living^{41–43}. To understand the foundations of political ideology, one must therefore understand how human group living has evolved. Here we review independent convergent evidence from anthropology, primatology and developmental psychology suggesting that, following the divergence from great apes, human group living evolved via two key shifts. First, humans began to cooperate more across wider interdependent networks and share the spoils of cooperation more evenly. Second, humans became more committed to group viability, conforming to social norms in culturally marked groups and punishing norm-violators. We highlight the striking concordance between these two social drives and the two dimensions of political ideology captured in Table 1. We then outline how

Table 1 Various definitions for the two dimensions of political ideology				
Cooperation dimension	Group conformity dimension	Reference		
Economic conservatism	Social conservatism	157		
Social dominance orientation	Right-wing authoritarianism	9		
Tough vs tender	Conservatism vs liberalism	158		
Humanism	Normativism (conservatism)	159		
Equality	Freedom	160		
Power distance	Collectivism vs individualism	161		
Liberalism (i.e., humanism- egalitarianism)	Conservatism	162		
Idealism (altruism-social concern)	Relativism (i.e., group orientation)	163		
Humanitarianism- egalitarianism	Protestant ethic	164		
Economic conservatism vs equality	Cultural conservatism vs openness	165		
Hierarchy vs egalitarianism	Group loyalty vs individualism	166		
International harmony	National strength and order	167		
Self-enhancement vs transcendence	Conservation vs openness	168		
Vertical vs horizontal values	Collectivism vs individualism	169		
Unmitigated self-interest ('beta-isms')	Tradition-oriented religiousness ('alpha-isms')	13		
Competition vs compassion	Moral regulation vs individual freedom	15		
Egalitarianism	Conservatism	170		
Humanitarianism	Religiosity	171		
Capitalist vs socialist	Religious vs secular	172		
Tolerance of inequality	Opposition to change	10		
Individualising (care-harm, fairness-reciprocity)	Binding (authority—respect, in-group-loyalty, purity-sanctity)	14		
Table data adapted and extended from ref. $^{\circ}$.				

fitness trade-offs and behavioural plasticity are expected to maintain functional variation in cooperation and group conformity, naturally giving rise to the two dimensions of variation in political ideology. We show how this dual evolutionary framework integrates previous approaches and illuminates prior work in political science, and we conclude with a set of predictions for future research.

Two key shifts in the evolution of human group living

The socio-political lives of great apes are complex⁴⁴. Chimpanzee social groups, for example, are organised by dominance hierarchies. Owing to the fitness benefits of higher status within these hierarchies, rank positions are hotly contested and change dynamically over time⁴⁵, with individuals frequently engaging in Machiavellian social strategies to contest the status quo⁴⁴. Chimpanzees also patrol territorial borders to defend their group against outsiders⁴⁶. Much like humans, then, the political lives of great apes are spent dealing with the challenges of group living.

Human group living shares much of this complexity. However, the ancestral human hunter-gatherer communities that emerged over the course of the Pleistocene were vastly different from those of other great apes. They were characterised by contact and trade

between extended networks^{47–49}, relatively egalitarian socio-political structures⁵⁰ and deeply embedded cultural norms, conventions and institutions⁵¹. To explain the emergence of this unique social organisation, researchers have posited two key shifts in the evolution of human group living^{52–57} that are thought to have paved the way for more complex human societies.

In the first shift, humans began to cooperate more across wider interdependent networks and share the spoils of cooperation more evenly. Resource scarcity in the Pleistocene required early humans to forage collaboratively for rarer but higher-value calorie-dense foods⁵². As fitness interdependence⁵⁸ with group members increased, selection favoured those who could readily work together with and provide benefits for others. Shifting to a riskier mode of subsistence also selected for egalitarian meat-sharing as a form of risk pooling⁵⁹, replacing the great ape system of resource distribution based on dominance and hierarchy. These changes resulted in a human psychology uniquely sensitive to cooperative interactions with others. Building upon psychological mechanisms for kin altruism, reciprocity and reputation-management, humans developed otherregarding preferences and empathic concern⁵⁴ that allowed them to extend cooperation beyond kith and kin to a wider network of interdependent individuals. In line with this, evidence suggests that, unlike other great apes⁶⁰⁻⁶², humans spontaneously help others⁶³, effectively communicate to solve coordination problems^{64,65}, prefer egalitarian divisions of resources^{59,66} and favour cooperative over exploitative individuals⁶⁷.

In the second key shift, humans became more group-minded, conforming to social norms in culturally marked groups and punishing norm-violators. Throughout the Pleistocene, human groups began to expand in size and compete with rival groups, further increasing fitness interdependence within groups⁵². To deal with the coordination problems inherent to larger groups, social norms created the conventions, common knowledge of conventions and shared meta-knowledge necessary for group-wide joint action⁶⁸. In response to inter-group competition, individual-level selection favoured a sense of group identity, conformity to group norms and punishment of norm-violators to promote group cohesion in the face of external threats⁶⁹. These changes resulted in a 'groupminded' human psychology underlain by self-conscious normative emotions, such as shame, group pride and moral disgust^{42,70}, as well as psychological mechanisms for cultural learning within groups⁵¹. In line with this, evidence suggests that, unlike other great apes^{52,71,72}, humans conform to group-wide social norms⁷³, punish third-parties who violate social norms⁷⁴ and discern group membership by attending to cultural markers like religion⁷⁵, language⁷⁶ and accent⁷⁷.

These two foundations of human group living are thought to have allowed us to transition from small kin bands of great apes to the larger, more socially complex communities of Pleistocene huntergatherers⁵². But these communities were still small relative to modern human societies. Over the course of the Holocene, a process of cultural evolution following the advent of agriculture transitioned the default mode of group living from hunter-gatherer communities to ethnically and economically diverse mega-cities and nation states⁵⁷. Yet beneath these recent cultural innovations, the cognitive mechanisms underlying human cooperation and group conformity have remained largely unchanged.

We argue that these two fundamental human responses to the challenges of group living—cooperation and group conformity—explain why scholars have repeatedly identified a two-dimensional structure of political ideology and provide a principled foundation for the domain of each dimension. The first domain (left column of Table 1) is concerned with cooperating more across wider interdependent networks and sharing the spoils of cooperation more evenly. In our ancestral past, individuals had to constantly navigate cooperative dilemmas, such as collaborative foraging and meat sharing, as well as determine how to share the spoils of cooperation.

Today, analogous dilemmas underlie policy issues like taxation, welfare programs and free education. The second domain (right column of Table 1) is concerned with group conformity. For early humans living in highly interdependent social groups, it was vital to abide by group-wide social norms, sanction norm-violators and defend the group against outsiders. Today, we expect that analogous concerns about group viability will manifest themselves in attitudes regarding traditional social values, criminal justice, patriotism and national security. Hence cooperation and group conformity provide the dual evolutionary foundations of modern political ideology.

Variation in cooperative and group conformist behaviour

As well as explaining how cooperation and group conformity came to be species-typical human social drives, an evolutionary approach provides a natural framework and set of mechanisms for understanding observed variation in such traits⁷⁸. Here we consider two mechanisms—fitness trade-offs and behavioural plasticity—to show how both genes and environment together predict strategic variation in cooperation and group conformity in human populations.

Fitness trade-offs exist when extreme levels of a trait confer both benefits and costs to individuals. Such trade-offs can lead to the evolution of functional, heritable individual differences via fluctuating selection⁷⁹. In other words, variation in a trait is preserved if different levels of the trait provide different benefits at different times. For example, researchers have attributed personality variation in both humans⁷⁹ and non-human animals⁸⁰ to fitness trade-offs. In humans, high levels of extraversion are associated with a greater number of sexual partners, but also with greater risk of accident or illness⁸¹. This trade-off results in an extraversion spectrum along which individuals can vary.

In a similar vein, we expect fitness trade-offs to have shaped individual differences in the basic social drives for cooperation and group conformity in human populations. Model-based simulations of evolution show that uncertain social environments can select for general drives ('heuristics') for cooperation and group conformity⁸²⁻⁸⁷. Researchers argue that these general drives apply across different situational contexts and are proximately motivated by other-regarding preferences and empathic concern (cooperation) or shame, group pride and moral disgust (group conformity)^{42,53,54}. As with extraversion, the general drives for cooperation and group conformity come with both costs and benefits. Individuals with a general cooperative drive benefit from good reputations and subsequent partner choice, but leave themselves open to exploitation from free-riders. Individuals with a general conformist drive benefit from adaptability to the group's local conditions and increased group viability, but sacrifice possibilities for individual learning and innovation88. These fitness trade-offs are expected to maintain heritable individual differences in general drives for both cooperation and group conformity within human populations. In line with this, individual differences in cooperation are heritable⁸⁹, and cooperative behaviour is positively correlated across a variety of anonymous one-shot economic games90-93 and predicts self-reported trust and altruism91,94, as well as a range of real-world cooperative behaviours^{95,96}. Similarly, individual differences in norm-enforcing punishment are heritable⁹⁷, and conformist behaviour is positively correlated across various measures of norm-enforcement and norm-adherence92,98.

In addition to heritable individual differences, phenotypic variation in willingness to cooperate and conform is also expected as an adaptive response to the social environment, either on-the-fly or canalized in early development, a phenomenon usually referred to as behavioural plasticity⁹⁹. There is reason to believe that both humans and non-human animals calibrate their cooperative and conformist behaviour based on feedback from their social environment. With regards to cooperation, psychological mechanisms integrate cues about both the situation (for example, the presence

PERSPECTIVE

Table 2 Item exemplars from a subset of scales measuring the two dimensions of political ideology				
Cooperation dimension	Group conformity dimension			
Economic conservatism (core issues) ¹¹	Social conservatism (core issues)			
Do you think there should be a government insurance plan that would cover all medical and hospital expenses for everyone?	Do you think gay or lesbian couples (in other words, homosexual couples) should be legally permitted to adopt children?			
the government should provide fewer services, even in areas such as health and education, to reduce spending?	a woman's place is in the home?			
\dots the government in Washington should see to it that every person has a job and a good standard of living?	abortion should never be permitted?			
Social dominance orientation ¹⁴²	Right-wing authoritarianism ⁸			
Some groups of people are simply inferior to other groups.	What our country really needs is a strong, determined leader who will crush evil and take us back to our true path.			
It's OK if some groups have more of a chance in life than others.	The 'old-fashioned ways' and the 'old-fashioned values' still show the best way to live.			
It's probably a good thing that certain groups are at the top and other groups are at the bottom.	God's laws about abortion, pornography and marriage must be strictly followed before it is too late, and those who break them must be strongly punished.			
Unmitigated self-interest (beta-isms) ¹³	Tradition-oriented religiousness (alpha-isms) ¹³			
Machiavellianism: craft and deceit are justified in pursuing and maintaining power in the political world.	Legalism: I adhere strictly and literally to a code of religion and morality.			
Materialism: physical well-being and worldly possessions are the greatest good and highest value in life.	Ecclesiasticism: I am devoted to the principles and interests of the church.			
Solipsism: the self is the only reality.	Traditionalism: I adhere to tradition, especially in cultural and religious practice.			
Self-enhancement vs self-transcendence ¹⁶⁸	Conservation vs openness ¹⁶⁸			
Equality (equal opportunity for all)	Obedient (dutiful, meeting obligations)			
Unity with nature (fitting into nature)	National security (protection of my nation from enemies)			
Helpful (working for the welfare of others)	Respect for tradition (preservation of time-honoured customs)			
Individualising (care-harm, fairness-reciprocity) ¹⁴	Binding (in-group-loyalty, authority-respect, sanctity-purity) ¹⁴			
Compassion for those who are suffering is the most crucial virtue.	People should be loyal to their family members even when they have done something wrong.			
When the government makes laws, the number one principle should be ensuring that everyone is treated fairly.	Respect for authority is something all children need to learn.			
I think it's morally wrong that rich children inherit a lot of money while poor children inherit nothing.	What matters is whether or not someone's action showed love for his or her country.			

of an audience) and the target of the interaction (for example, whether the target previously defected) when determining whether or not to cooperate¹⁰⁰. For example, both chimpanzees¹⁰¹ and humans¹⁰² are less cooperative in hierarchical or competitive social environments, likely because they perceive potential targets as less trustworthy partners for long-term cooperative relationships. With regards to group conformity, psychological mechanisms integrate cues about environmental unpredictability and threat when determining whether or not to conform to the group. Nine-spined sticklebacks¹⁰³, rats¹⁰⁴ and humans¹⁰⁵ all engage in conformist social learning when environments are perceived to be unpredictable with a high cost of individual learning. Furthermore, in humans, several classes of threat have been shown to increase group conformity. Cues of disease-causing pathogens motivate conformity^{106,107} to reduce the risk of infection⁵¹. Cues of dangerous situations motivate group conformity as self-protection¹⁰⁸. Cues of threats to group viability (for example, intergroup conflict, rapid immigration) motivate conformity in the form of adherence to religious norms¹⁰⁹, punishment of in-group norm violators¹¹⁰ and out-group prejudice111, maintaining group solidarity and increasing in-group coordination efficiency. Thus, behavioural plasticity is expected to adaptively calibrate individuals' willingness to cooperate and conform.

We propose that both heritable individual differences and functional behavioural plasticity have maintained strategic variation in cooperation and group conformity in human populations, naturally giving rise to variation along the two dimensions of political ideology. Heritable individual differences in a general cooperative drive, combined with the presence of relevant situational cues (for example, perceptions of targets' need or ability to reciprocate¹¹²), produce variation in willingness to cooperate with others, giving rise to variation along the first dimension of political ideology (left column of Table 1). Heritable individual differences in a general group conformist drive, combined with the presence of relevant situational cues (for example, perceived unpredictability or threats to group norms), produce variation in willingness to conform to and enforce group-wide social norms and defend the group, giving rise to variation along the second dimension of political ideology (right column of Table 1). Hence, in addition to explaining the essential nature of the two dimensions of political ideology, an evolutionary approach outlines how predictable interactions between genes and environment produce variation along the two dimensions.

Cooperation, group conformity and political ideology

Our dual evolutionary framework illuminates existing work in political psychology, explaining why scholars have repeatedly converged

on two dimensions of ideology, one referring to cooperation and the other referring to group conformity (Table 1). A close look at some exemplar items from the self-report scales in Table 1 reveals this pattern more clearly (Table 2). The scale items in the left column of Table 2 measure willingness to cooperate with others. Some items refer to helping, empathy and prosocial concern, qualities that would have been crucial prerequisites for collaboration in early human groups. Other items emphasise egalitarianism, equality and fairness, reminiscent of the kinds of anti-hierarchical levelling mechanisms early humans would have employed when sharing the spoils of cooperation⁵². Solipsism and unity with nature represent constrained versus extended cooperative networks, respectively. The reverse-coded scales (social dominance orientation and the beta-isms) describe competitive tendencies, such as self-interested and dominating behaviour, that aim to distribute resources according to hierarchy. The scale items in the right column of Table 2, by contrast, measure adherence to group-wide social norms, punishment of in-group norm-violators and parochialism. Many items focus on traditionalism, obedience and deference to authority, which can be understood as outcomes of psychological predispositions for majority-biased and prestige-biased conformist learning within groups¹¹³. Several items emphasise strict laws, justice and penalties for offenders, which clearly relate to norm-enforcement. Other items refer to patriotism and the need for national security, reflecting parochial in-group favouritism and concern for group viability.

Our framework also makes sense of the policy stances that these ideological scales predict. Economic conservatism predicts stances on issues like government-funded healthcare, welfare programs and free education¹¹. Though far removed from the cooperation problems faced by early human groups, these issues can all be framed as cooperative dilemmas, in which an individual's short-term selfinterest is at odds with the group's long-term collective interest¹¹⁴. For such issues, people's willingness to cooperate versus compete with others influences their political views. For example, individuals with a greater willingness to cooperate are more likely to support extra taxes to fund a healthcare system that is accessible to everyone in the group (a cooperative dilemma). Social conservatism, by contrast, predicts stances on issues like traditional social values, criminal justice, national security and religion^{8,11}. Group conformity underlies all these political stances. Social conservatives are more likely to conform to their group's traditional social norms (for example, family structures, gender roles and marriage norms), support policies that increase the influence of these norms in the public sphere8 and endorse punitive rather than rehabilitative action towards criminals and other in-group norm-violators 115,116. They often support tougher borders and military intervention abroad, as they are keenly aware of cultural group boundaries and are motivated to maintain a viable in-group in the presence of perceived out-group threats. Normadherence and norm-enforcement in social conservatives is also often tied up with religion⁸. Anthropologists have long recognised religion as partly functioning to enforce sacred group norms and thus create moral communities¹¹⁷. Similarly, evolutionary theorists have argued that religions are culturally group-selected packages of norms outlining which behaviours are permissible and how normviolators should be punished¹¹⁸.

Even for more complex issues that do not relate straightforwardly to one dimension or the other, the dual evolutionary foundations of political ideology can help us unravel the psychological motivations behind the patterns we observe. Anti-immigration views, for example, can be associated with economic and/or social conservatism⁹. Our framework predicts that these associations reflect different motives, with economic conservatives more sensitive to the possibility that successful immigrants will compete with them for resources and threaten the existing hierarchy, and social conservatives more concerned with the potential for cultural deviance and incompatibility of social norms, threatening group viability.

Consistent with these predictions, social (but not economic) conservatives from the US and Switzerland were found to have less favourable attitudes towards immigrants who they thought were unlikely to assimilate to their group's norms, whilst economic (but not social) conservatives had less favourable attitudes towards immigrants who they thought were more likely to assimilate and thereby compete for resources and status¹¹⁹. When immigrants are seen as a threat to egalitarian safety nets like the welfare system, we would also expect economic progressives to oppose immigration; in fact, precisely this justification was offered when Denmark's Social Democratic party announced policies seen as anti-immigration¹²⁰.

With its emphasis on social norms, our framework acknowledges that the attitudes of social conservatives should differ depending on the particular norms present in their society. However, this account does not reduce to cultural constructivism. Social norms are not entirely arbitrary; they often govern fitness-relevant behaviours (for example, pathogen avoidance, mate choice and reproduction) and group viability. For example, Fijian food norms that forbid pregnant women from ingesting toxic marine species are cultural adaptations that avoid deadly foetal poisoning⁵¹. Likewise, religious norms surrounding infidelity, abortion and sexual orientation can be seen as culturally evolved mechanisms that promote larger families and increase group size¹¹⁸. Thus, this framework explains why social conservatives in the United States can become focused on behaviours such as marriage, contraception, prayer in school and alcohol and drug use^{8,11}: they are adhering to and enforcing social norms that govern fitness-relevant behaviours and group viability.

Cooperation is itself a fitness-relevant behaviour that social norms can govern. As a result, our framework predicts that economic conservatism (cooperation) and social conservatism (group conformity) may be correlated within populations, but the strength and direction of this relationship will vary across populations (i.e., the two dimensions are distinct). Consistent with these predictions, in developed Western democracies, economic and social conservatism are often weakly-to-moderately positively correlated with one another among political elites. For example, the Republican Party in the United States supports both economically conservative policies (for example, free-market capitalism and less taxation) and socially conservative policies (for example, national defence and opposition to gay marriage). However, in many cultures around the world, economic and social conservatism are weakly negatively correlated¹²¹. For example, the Fidesz party in Hungary supports economically progressive policies (for example, minimum wage increases and equitable pension systems) but socially conservative policies (for example, strong border control)122. This negative correlation is stronger in post-communist countries, like Hungary, where traditional social norms promote national equality, egalitarianism and fairness¹²¹. Intriguingly, at the individual level, the negative correlation is stronger among politically unengaged people across countries^{121,123}, suggesting this may be the default organisation of the two dimensions in the absence of clear norms or cues from political elites. This is expected under our account if people readily interpret more egalitarian norms as in the interests of the group.

An understanding of the fitness trade-offs associated with the evolution of cooperation and group conformity makes sense of individual differences in economic decision-making, personality traits and neurophysiology, and it explains why this variation reliably correlates with political ideology. Stable individual differences in both cooperation and norm-enforcing punishment in experimental economic games have been linked to political ideology (for example, social dominance orientation^{124–126}) and real-world social values regarding taxation and revenge⁹². Economic conservatism covaries with personality traits like agreeableness¹²⁷, social value orientation¹²⁸ and Machiavellianism¹²⁹, while social conservatism covaries with openness to experience¹³⁰ and need for closure¹⁰. Individual differences in basic neural and physiological processes

PERSPECTIVE NATURE HUMAN BEHAVIOUR

also covary with ideology. When viewing images of others in distress, people higher in economic conservatism show less activation in brain regions associated with empathic concern¹³¹. People higher in social conservatism are also more likely to attend to and respond to threatening stimuli^{26,30,32}. Our framework explains these individual differences and correlations with political ideology as resulting from fitness trade-offs in general drives for cooperation and group conformity.

Similarly, our framework provides insight into the influence of socio-environmental context on political ideology⁹. We expect that psychological mechanisms designed to integrate cues of potential long-term cooperative partnerships¹⁰⁰ will cause people to adapt their levels of cooperation based on the amount of competition they perceive in their environment. Consistent with this prediction, individuals who view the world as a 'competitive jungle' score higher on measures of economic (but not social) conservatism⁹. Similarly, we expect that people will adapt their levels of conformity based on perceived environmental unpredictability and cues of infectious diseases, dangerous situations and threats to group viability. Consistent with this prediction, those who view the world as threatening, dangerous and unpredictable score higher on measures of social (but not economic) conservatism⁹.

Finally, our framework provides a theoretical scaffold for prior evolutionary approaches to the two dimensions of political ideology. Economic conservatism correlates with upper-body strength and resource-holding power⁴⁰ because these are important cues for the psychological mechanisms underlying cooperation. If an individual correctly perceives their own resource-holding power as high, this will motivate the accumulation of resources via dominance and power rather than egalitarian sharing¹³², thus predicting economic (but not social) conservatism. By contrast, social conservatism correlates with disgust sensitivity and threat sensitivity^{32,38} because disease-causing pathogens and threats to individual safety and group viability are important cues for the psychological mechanisms underlying group conformity.

Discussion and future directions

We propose that two key human adaptations to group living—cooperation and group conformity—are the evolutionary foundations underlying the two repeatedly identified dimensions of political ideology in humans. It is possible that these two dimensions alone are not sufficient to capture the full breadth of political views. Several evolutionary approaches have posited three 133,134, five 42 or even six135 underlying dimensions. However, more complex factor models are not supported by the data¹³⁶ and are readily reduced down to two dimensions when using principal components analyses and other factor-analytic statistical methods 133,137,138. Other promising approaches in political psychology have attempted to carve the two dimensions into distinct sub-dimensions^{139,140}. For example, right-wing authoritarianism has been split into authoritarian submission, conventionalism and authoritarian aggression¹⁴⁰. Consistent with our framework, these can be understood as an evolved commitment to group viability via conformity to existing group norms, conformity to traditional group norms and punishment of norm-violators, respectively³⁹. While such approaches add nuance, the strong and reliable positive correlations between these sub-dimensions 139,140 suggest that they represent two coherent packages of social motives that act together to organise cooperative and conformist behaviour.

Some scholars have suggested that, since most people in the electorate are unable to articulate why they harbour particular attitudes, the public is largely non-ideological^{2,3}. We acknowledge that not everyone is politically knowledgeable, aware and engaged. However, a lack of political sophistication in the population should not be used as evidence against individual variation showing an underlying structure⁴. Much like the use of language without the

metacognitive awareness of its grammatical rules, people can hold ideologically consistent political attitudes without any explicit awareness of their structure.

Other scholars have argued that the structure of political attitudes emerges not from an underlying ideology but from the interplay between (inclusive) fitness interests and coalitions constructed by political elites^{41,141}. Under this account, people simply align with political parties that best advance their fitness interests and then form political coalitions around clusters of interests. We acknowledge that self-interest undoubtedly plays a role in policy preferences (for example, support for lower tuition fees among students versus support for retirement benefits among the elderly). Political elites also clearly drive some aspects of policy organisation (for example, the Republican and Democratic parties aligning economic and social policies). However, this account is, at best, incomplete. As we highlight, the two dimensions of political ideology are heritable and emerge across cultures^{15,22,23}, suggesting an underlying structure that is not arbitrarily packaged by political elites. Furthermore, policy views frequently contradict people's fitness interests. For example, social dominance orientation is only marginally related to socioeconomic status142, and wealthy individuals often support economic redistribution while disadvantaged individuals often oppose welfare policies10.

Nevertheless, we acknowledge that people do naturally group together with others who share their political views and show intense disliking for groups with inconsistent views¹⁴³. Although there is some evidence that social conservatives are more sensitive to the 'value violations' motivating this ideological conflict144, even economic and social progressives reveal their intolerance if asked their opinions on wealthy business people, pro-lifers and religious fundamentalists. Our framework suggests that this dislike stems from the fundamental conflicts between cooperation versus competition and individualism versus conformity as opposing strategies for navigating human group living. In line with this, recent work has shown that political intolerance is "dimension-specific" 145. Economic progressives and economic conservatives are intolerant of one another's views on cooperative dilemma issues. Separately, social progressives and social conservatives are intolerant of one another's views on normative issues.

Future research should empirically test predictions of our evolutionary framework. First, variation in cooperative and conformist behaviour in abstract experimental settings should predict the two dimensions of political ideology. There is already suggestive evidence that cooperation and norm-enforcing punishment in economic games can predict social values⁹². More work is needed to systematically examine how other behavioural measures, especially measures that capture some of the complexity of real-world politics, relate to variation across both ideological dimensions. Second, variation in cooperative and conformist behaviour at a young age should predict the two dimensions of political ideology decades later. Building on prior work showing that personality in young children predicts later placement along a liberal-conservative dimension²⁵, we make the more specific predictions that sharing and helping behaviour will negatively predict economic (but not social) conservatism, while feelings of guilt, focus on social norms and enforcement of rules will positively predict social (but not economic) conservatism. Third, neurological and physiological correlates of cooperative 146,147 and group conformist 148,149 behaviour should show corresponding relationships to the two dimensions of political ideology. Fourth, competitive and threatening socio-environmental conditions should differentially predict the two dimensions of ideology. Previous work has shown that high-profile events like terrorism can increase conservatism¹⁵⁰, but this work has largely considered only a single dimension of ideology. Our framework makes more nuanced predictions. For example, acute events invoking threat (for example, disease outbreaks), particularly

group threats (for example, terrorism and warfare), should induce short-term increases in social (but not economic) conservatism. Chronic conditions, either actual or perceived, invoking competitive hierarchy (for example, income resulting from effort rather than luck¹⁵¹) or threats to group viability (for example, political unrest and criminality) should predict economic and social conservatism, respectively. Our behavioural plasticity account also opens up the possibility for, but does not require, the existence of critical periods early in development during which environmental conditions are most likely to shape cooperative or conformist phenotypes (for example, ref. 152). Fifth, more research is needed into why, compared to other cultures, Western countries such as Great Britain and the United States are outliers in showing a positive correlation between scores on the two dimensions¹²¹. Do modern capitalist social norms and party politics in these countries encourage social conservatives to adopt more competitive views? Or can the cultural origins of these differences be traced back much further to the effects of religion¹⁵³, agriculture¹⁵⁴ or deep linguistic ancestry¹⁵⁵? Finally, we should be able to identify the two dimensions of cooperation and group conformity even in non-WEIRD (Western, educated, industrialized, rich and democratic) societies156 and small-scale societies. As in other societies, social conservatives in these societies should adhere to and enforce local norms and taboos, the content of which will differ from culture to culture, and should be sensitive to local threats to group viability. Testing these predictions will require newly devised self-report scales targeting cooperative and conformist preferences without culturespecific political content (for example, avoiding items like those measuring right-wing authoritarianism in Table 2). Such scales hold the promise of a sturdier theoretical foundation for political science and more robust measures of the two dimensions of political ideology across cultures.

To conclude, we hope to encourage a fruitful dialogue between evolutionary scholars and political scientists to further our understanding of the foundations of political ideology. Political scientists have made great complementary strides in studying the two-dimensional structure of ideology, but questions have remained about why this particular structure exists. Evolutionary theory provides the meta-theoretical tools to answer such questions. The framework presented here shines light on existing work in political psychology and offers insight into the volatility in our current political climate. To return to a previous example, many of the within-party disagreements in the 2016 US presidential election can be understood as outcomes of the two dimensions of ideology. Hillary Clinton and Bernie Sanders diverged on egalitarian issues like taxation, healthcare and free higher education. Before running for office, Donald Trump differed from other Republicans in his less-than-stringent approach to traditional social norms regarding abortion and samesex marriage. We are optimistic that, in both political science and everyday public discourse, the multidimensional evolutionary framework we have presented will provide a more nuanced understanding of the politics that both unites and divides us.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Dataset for the literature review in Fig. 1 is available at https://osf.io/gckw7/.

Code availability

R code to reproduce Fig. 1 is available at https://osf.io/gckw7/.

Received: 17 June 2019; Accepted: 3 March 2020;

Published online: 30 March 2020

References

- Jost, J. T., Federico, C. M. & Napier, J. L. Political ideology: its structure, functions, and elective affinities. *Annu. Rev. Psychol.* 60, 307–337 (2009).
- Converse, P.E. The nature of belief systems in mass publics. in *Ideology and Discontent* (ed. Apter, D. E.) 206–261 (Free Press of Glencoe, 1964).
- Zaller, J.R. The Nature and Origins of Mass Opinion. (Cambridge University Press, 1992).
- 4. Jost, J. T. The end of the end of ideology. Am. Psychol. 61, 651-670 (2006).
- Adorno, T., Frenkel-Brunswick, E., Levinson, D. & Sanford, R. The Authoritarian Personality. (Harper, 1950).
- Treier, S. & Hillygus, D. S. The nature of political ideology in the contemporary electorate. *Public Opin. Q.* 73, 679–703 (2009).
- Claassen, C., Tucker, P. & Smith, S. S. Ideological labels in America. Polit. Behav. 37, 253–278 (2015).
- Altemeyer, B. Right-Wing Authoritarianism. (University of Manitoba Press, 1981).
- Duckitt, J. & Sibley, C. G. A dual-process motivational model of ideology, politics, and prejudice. *Psychol. Inq.* 20, 98–109 (2009).
- Jost, J. T., Glaser, J., Kruglanski, A. W. & Sulloway, F. J. Political conservatism as motivated social cognition. *Psychol. Bull.* 129, 339–375 (2003).
- Feldman, S. & Johnston, C. Understanding the determinants of political ideology: implications of structural complexity. *Polit. Psychol.* 35, 337–358 (2014).
- Schwartz, S.H. Universals in the content and structure of values: theoretical advances and empirical tests in 20 countries. in *Advances in Experimental* Social Psychology 25, 1–65 (Elsevier, 1992).
- Saucier, G. Isms and the structure of social attitudes. J. Pers. Soc. Psychol. 78, 366–385 (2000).
- Graham, J., Haidt, J. & Nosek, B. A. Liberals and conservatives rely on different sets of moral foundations. J. Pers. Soc. Psychol. 96, 1029–1046 (2009).
- Ashton, M.C. et al. Two dimensions of political attitudes and their individual difference correlates: a cross-cultural perspective. In *Culture and Social Behavior: The Ontario Symposium* vol. 10 (eds Sorrentino, R. M. Cohen, D., Olson, J. M. & Zanna, M. P.) 1–29 (Lawrence Erlbaum Associates, 2005).
- 16. Campbell, A., Converse, P.E., Miller, W.E. & Stokes, D.E. *The American Voter.* (Wiley, 1960).
- Hatemi, P. K. et al. A genome-wide analysis of liberal and conservative political attitudes. J. Polit. 73, 271–285 (2011).
- Hatemi, P. K., Medland, S. E., Morley, K. I., Heath, A. C. & Martin, N. G. The genetics of voting: an Australian twin study. *Behav. Genet.* 37, 435–448 (2007).
- Kandler, C., Bell, E. & Riemann, R. The structure and sources of right-wing authoritarianism and social dominance orientation. Eur. J. Pers. 30, 406–420 (2016).
- Verhulst, B., Hatemi, P. K. & Eaves, L. J. Disentangling the importance of psychological predispositions and social constructions in the organization of American political ideology. *Polit. Psychol.* 3, 375–393 (2012).
- Alford, J. R., Funk, C. L. & Hibbing, J. R. Are political orientations genetically transmitted? Am. Polit. Sci. Rev. 99, 153–167 (2005).
- Lewis, G. J. & Bates, T. C. Common heritable effects underpin concerns over norm maintenance and in-group favoritism: evidence from genetic analyses of right-wing authoritarianism and traditionalism. *J. Pers.* 82, 297–309 (2014).
- Batrićević, N. & Littvay, L. A genetic basis of economic egalitarianism. Soc. Justice Res. 30, 408–437 (2017).
- Alford, J. R. & Hibbing, J. R. The origin of politics: an evolutionary theory of political behavior. *Perspect. Polit.* 2, 707–723 (2004).
- Block, J. & Block, J. H. Nursery school personality and political orientation two decades later. J. Res. Pers. 40, 734–749 (2006).
- Dodd, M. D. et al. The political left rolls with the good and the political right confronts the bad: connecting physiology and cognition to preferences. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 640–649 (2012).
- Smith, K. B., Oxley, D., Hibbing, M. V., Alford, J. R. & Hibbing, J. R. Disgust sensitivity and the neurophysiology of left-right political orientations. *PLoS ONE* 6, e25552 (2011).
- Shook, N. J. & Fazio, R. H. Political ideology, exploration of novel stimuli, and attitude formation. J. Exp. Soc. Psychol. 45, 995–998 (2009).
- Oosterhoff, B., Shook, N. J. & Ford, C. Is that disgust I see? Political ideology and biased visual attention. *Behav. Brain Res.* 336, 227–235 (2018).
- Oxley, D. R. et al. Political attitudes vary with physiological traits. Science 321, 1667–1670 (2008).
- Fodor, E. M., Wick, D. P., Hartsen, K. M. & Preve, R. M. Right-wing authoritarianism in relation to proposed judicial action, electromyographic response, and affective attitudes toward a schizophrenic mother. *J. Appl. Soc. Psychol.* 38, 215–233 (2008).
- Hibbing, J. R., Smith, K. B. & Alford, J. R. Differences in negativity bias underlie variations in political ideology. *Behav. Brain Sci.* 37, 297–307 (2014).

PERSPECTIVE NATURE HUMAN BEHAVIOUR

- Fiagbenu, M.E., Proch, J. & Kessler, T. Of deadly beans and risky stocks: Political ideology and attitude formation via exploration depend on the nature of the attitude stimuli. *Br. J. Psychol.* https://doi.org/10.1111/ biop.12430 (2019).
- Bakker, B. N., Schumacher, G., Gothreau, C. & Arceneaux, K. Conservatives and liberals have similar physiological responses to threats. *Nat. Hum. Behav.* 4, 823 (2020).
- Osmundsen, M., Hendry, D.J., Lautsen, L., Smith, K.B. & Petersen, M.B. The Psychophysiology of political ideology: replications, reanalysis and recommendations. Preprint at *PsyArXiv* https://doi.org/10.31234/osf. io/49hfg (2019).
- Duriez, B., Van Hiel, A. & Kossowska, M. Authoritarianism and social dominance in Western and Eastern Europe: the importance of the sociopolitical context and of political interest and involvement. *Polit. Psychol.* 26, 299–320 (2005).
- Pratto, F. et al. Social dominance in context and in individuals: contextual moderation of robust effects of social dominance orientation in 15 languages and 20 countries. Soc. Psychol. Personal. Sci. 4, 587–599 (2013).
- Tybur, J. M. et al. Parasite stress and pathogen avoidance relate to distinct dimensions of political ideology across 30 nations. *Proc. Natl Acad. Sci.* USA 113, 12408–12413 (2016).
- Kessler, T. & Cohrs, J. C. The evolution of authoritarian processes: fostering cooperation in large-scale groups. *Group Dyn.* 12, 73–84 (2008).
- Petersen, M. B. & Laustsen, L. Upper-body strength and political egalitarianism: twelve conceptual replications. *Polit. Psychol.* 40, 375–394 (2019).
- Petersen, M.B. Evolutionary political psychology. in *The Handbook of Evolutionary Psychology* (ed. Buss, D. M.) 1–19 (Wiley, 2015).
- Haidt, J. The Righteous Mind: Why Good People are Divided by Politics and Religion. (Pantheon Books, 2012).
- Hibbing, J.R., Smith, K.B. & Alford, J.R. Predisposed: Liberals, Conservatives, and the Biology of Political Differences. (Routledge, 2013).
- 44. de Waal, F.B.M. Chimpanzee Politics: Power and Sex Among Apes. (Johns Hopkins University Press, 1982).
- 45. Foerster, S. et al. Chimpanzee females queue but males compete for social status. *Sci. Rep.* **6**, 35404 (2016).
- Watts, D. P. & Mitani, J. C. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* 138, 299–327 (2001).
- Lee, R. B. Kung spatial organization: an ecological and historical perspective. *Hum. Ecol.* 1, 125–147 (1972).
- Hill, K. R. et al. Co-residence patterns in hunter-gatherer societies show unique human social structure. Science 331, 1286–1289 (2011).
- Bird, D. W., Bird, R. B., Codding, B. F. & Zeanah, D. W. Variability in the organization and size of hunter-gatherer groups: Foragers do not live in small-scale societies. *J. Hum. Evol.* 131, 96–108 (2019).
- Boehm, C. Egalitarian behavior and reverse dominance hierarchy. Curr. Anthropol. 34, 227–254 (1993).
- Henrich, J. The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter. (Princeton University Press, 2015).
- Tomasello, M., Melis, A. P., Tennie, C., Wyman, E. & Herrmann, E. Two key steps in the evolution of human cooperation: the interdependence hypothesis. *Curr. Anthropol.* 53, 673–692 (2012).
- Tomasello, M. & Vaish, A. Origins of human cooperation and morality. Annu. Rev. Psychol. 64, 231–255 (2013).
- Jensen, K., Vaish, A. & Schmidt, M. F. H. The emergence of human prosociality: aligning with others through feelings, concerns, and norms. Front. Psychol. 5, 822 (2014).
- Sterelny, K. Social intelligence, human intelligence and niche construction. Phil. Trans. R. Soc. Lond. B 362, 719–730 (2007).
- Tomasello, M. A Natural History of Human Morality. (Harvard University Press. 2016).
- 57. Sterelny, K. Cooperation, culture, and conflict. Br. J. Philos. Sci. 67,
- Aktipis, A. et al. Understanding cooperation through fitness interdependence. Nat. Hum. Behav. 2, 429–431 (2018).
- 59. Gurven, M. To give and to give not: the behavioral ecology of human food transfers. *Behav. Brain Sci.* 27, 543–559 (2004).
- Warneken, F., Chen, F. & Tomasello, M. Cooperative activities in young children and chimpanzees. *Child Dev.* 77, 640–663 (2006).
- Silk, J. B. et al. Chimpanzees are indifferent to the welfare of unrelated group members. *Nature* 437, 1357–1359 (2005).
- Krupenye, C. & Hare, B. Bonobos prefer individuals that hinder others over those that help. Curr. Biol. 28, 280–286.e5 (2018).
- 63. Warneken, F. & Tomasello, M. Altruistic helping in human infants and young chimpanzees. *Science* 311, 1301–1303 (2006).
- Koomen, R. & Herrmann, E. An investigation of children's strategies for overcoming the tragedy of the commons. *Nat. Hum. Behav.* 2, 348–355 (2018).

- Cooper, R., DeJong, D. V., Forsythe, R. & Ross, T. W. Communication in coordination games. Q. J. Econ. 107, 739–771 (1992).
- Hamann, K., Warneken, F., Greenberg, J. R. & Tomasello, M. Collaboration encourages equal sharing in children but not in chimpanzees. *Nature* 476, 328–331 (2011).
- 67. Hamlin, J. K., Wynn, K. & Bloom, P. Social evaluation by preverbal infants. *Nature* 450, 557–559 (2007).
- Cronk, L. & Leech, B.L. Meeting at Grand Central: Understanding the Social and Evolutionary Roots of Cooperation. (Princeton University Press, 2013).
- Mathew, S. & Boyd, R. Punishment sustains large-scale cooperation in prestate warfare. *Proc. Natl Acad. Sci. USA* 108, 11375–11380 (2011).
- Vaish, A., Carpenter, M. & Tomasello, M. Young children's responses to guilt displays. *Dev. Psychol.* 47, 1248–1262 (2011).
- Burkart, J. M., Brügger, R. K. & van Schaik, C. P. Evolutionary origins of morality: insights from non-human primates. Front. Sociol. 3, 17 (2018).
- Riedl, K., Jensen, K., Call, J. & Tomasello, M. No third-party punishment in chimpanzees. Proc. Natl Acad. Sci. USA 109, 14824–14829 (2012).
- Claidière, N. & Whiten, A. Integrating the study of conformity and culture in humans and nonhuman animals. *Psychol. Bull.* 138, 126–145 (2012).
- 74. Fehr, E. & Fischbacher, U. Third-party punishment and social norms. *Evol. Hum. Behav.* **25**, 63–87 (2004).
- Galen, L. W., Smith, C. M., Knapp, N. & Wyngarden, N. Perceptions of religious and nonreligious targets: exploring the effects of perceivers' religious fundamentalism. J. Appl. Soc. Psychol. 41, 2123–2143 (2011).
- Kinzler, K. D. & Dautel, J. B. Children's essentialist reasoning about language and race. Dev. Sci. 15, 131–138 (2012).
- Kinzler, K. D., Corriveau, K. H. & Harris, P. L. Children's selective trust in native-accented speakers. *Dev. Sci.* 14, 106–111 (2011).
- Buss, D. M. How can evolutionary psychology successfully explain personality and individual differences? *Perspect. Psychol. Sci.* 4, 359–366 (2009).
- Nettle, D. The evolution of personality variation in humans and other animals. Am. Psychol. 61, 622–631 (2006).
- Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J. Life-history trade-offs favour the evolution of animal personalities. *Nature* 447, 581–584 (2007).
- 81. Nettle, D. An evolutionary approach to the extraversion continuum. *Evol. Hum. Behav.* **26**, 363–373 (2005).
- 82. van den Berg, P. & Wenseleers, T. Uncertainty about social interactions leads to the evolution of social heuristics. *Nat. Commun.* **9**, 2151 (2018).
- Delton, A. W., Krasnow, M. M., Cosmides, L. & Tooby, J. Evolution of direct reciprocity under uncertainty can explain human generosity in one-shot encounters. *Proc. Natl Acad. Sci. USA* 108, 13335–13340 (2011).
- Krasnow, M. M., Delton, A. W., Tooby, J. & Cosmides, L. Meeting now suggests we will meet again: implications for debates on the evolution of cooperation. Sci. Rep. 3, 1747 (2013).
- Bear, A. & Rand, D. G. Intuition, deliberation, and the evolution of cooperation. *Proc. Natl Acad. Sci. USA* 113, 936–941 (2016).
- 86. Richerson, P.J. & Boyd, R. Not by Genes Alone: How Culture Transformed Human Evolution. (University of Chicago Press, 2005).
- 87. Gigerenzer, G. Why heuristics work. Perspect. Psychol. Sci. 3, 20-29 (2008).
- Rogers, A. R. Does biology constrain culture? Am. Anthropol. 90, 819–831 (1988).
- Cesarini, D. et al. Heritability of cooperative behavior in the trust game. *Proc. Natl Acad. Sci. USA* 105, 3721–3726 (2008).
- Carlsson, F., Johansson-Stenman, O. & Nam, P. K. Social preferences are stable over long periods of time. J. Public Econ. 117, 104–114 (2014).
- McAuliffe, W. H. B., Forster, D. E., Pedersen, E. J. & McCullough, M. E. Does cooperation in the laboratory reflect the operation of a broad trait? *Eur. J. Pers.* 33, 89–103 (2019).
- Peysakhovich, A., Nowak, M. A. & Rand, D. G. Humans display a 'cooperative phenotype' that is domain general and temporally stable. Nat. Commun. 5, 4939 (2014).
- Yamagishi, T. et al. Is behavioral pro-sociality game-specific? Pro-social preference and expectations of pro-sociality. *Organ. Behav. Hum. Decis. Process.* 120, 260–271 (2013).
- Johansson-Stenman, O., Mahmud, M. & Martinsson, P. Trust, trust games and stated trust: evidence from rural Bangladesh. J. Econ. Behav. Organ. 95, 286–298 (2013).
- Rustagi, D., Engel, S. & Kosfeld, M. Conditional cooperation and costly monitoring explain success in forest commons management. *Science* 330, 961–965 (2010).
- Benz, M. & Meier, S. Do people behave in experiments as in the field?
 evidence from donations. Exp. Econ. 11, 268–281 (2008).
- Wallace, B., Cesarini, D., Lichtenstein, P. & Johannesson, M. Heritability of ultimatum game responder behavior. *Proc. Natl Acad. Sci. USA* 104, 15631–15634 (2007).
- Kimbrough, E. O. & Vostroknutov, A. Norms make preferences social. J. Eur. Econ. Assoc. 14, 608–638 (2016).

- Snell-Rood, E. C. An overview of the evolutionary causes and consequences of behavioural plasticity. *Anim. Behav.* 85, 1004–1011 (2013).
- 100. Delton, A. W. & Robertson, T. E. How the mind makes welfare tradeoffs: evolution, computation, and emotion. *Curr. Opin. Psychol.* 7, 12–16 (2016).
- Cronin, K. A., van Leeuwen, E. J. C., Vreeman, V. & Haun, D. B. M. Population-level variability in the social climates of four chimpanzee societies. Evol. Hum. Behav. 35, 389–396 (2014).
- Cronin, K. A., Acheson, D. J., Hernández, P. & Sánchez, A. Hierarchy is detrimental for human cooperation. Sci. Rep. 5, 18634 (2015).
- 103. van Bergen, Y., Coolen, I. & Laland, K. N. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proc. Biol. Sci.* 271, 957–962 (2004).
- 104. Galef, B. G. Jr., Dudley, K. E. & Whiskin, E. E. Social learning of food preferences in 'dissatisfied' and 'uncertain' Norway rats. *Anim. Behav.* 75, 631–637 (2008).
- Morgan, T. J. H., Rendell, L. E., Ehn, M., Hoppitt, W. & Laland, K. N. The evolutionary basis of human social learning. *Proc. Biol. Sci.* 279, 653–662 (2012).
- 106. Murray, D. R. & Schaller, M. Threat(s) and conformity deconstructed: perceived threat of infectious disease and its implications for conformist attitudes and behavior. Eur. J. Soc. Psychol. 42, 180–188 (2012).
- Wu, B. P. & Chang, L. The social impact of pathogen threat: how disease salience influences conformity. Pers. Individ. Dif. 53, 50–54 (2012).
- 108. Griskevicius, V., Goldstein, N. J., Mortensen, C. R., Cialdini, R. B. & Kenrick, D. T. Going along versus going alone: when fundamental motives facilitate strategic (non)conformity. J. Pers. Soc. Psychol. 91, 281–294 (2006).
- Henrich, J., Bauer, M., Cassar, A., Chytilová, J. & Purzycki, B. G. War increases religiosity. Nat. Hum. Behav. 3, 129–135 (2019).
- Gneezy, A. & Fessler, D. M. T. Conflict, sticks and carrots: war increases prosocial punishments and rewards. Proc. Biol. Sci. 279, 219–223 (2012).
- 111. Stenner, K. The Authoritarian Dynamic. (Cambridge University Press, 2005).
- Petersen, M. B., Sznycer, D., Cosmides, L. & Tooby, J. Who deserves help?
 Evolutionary psychology, social emotions, and public opinion about welfare.
 Polit. Psychol. 33, 395–418 (2012).
- 113. Henrich, J. Cultural group selection, coevolutionary processes and large-scale cooperation. *J. Econ. Behav. Organ.* **53**, 3–35 (2004).
- 114. Van Lange, P. A. M., Joireman, J., Parks, C. D. & Van Dijk, E. The psychology of social dilemmas: a review. *Organ. Behav. Hum. Decis. Process.* 120, 125–141 (2013).
- Capps, J. S. Explaining punitiveness: right-wing authoritarianism and social dominance. N. Am. J. Psychol. 4, 263–278 (2002).
- Feather, N. T. Reactions to penalties for an offense in relation to authoritarianism, values, perceived responsibility, perceived seriousness, and deservingness. J. Pers. Soc. Psychol. 71, 571–587 (1996).
- 117. Durkheim, É. *The Elementary Forms of the Religious Life.* (George Allen & Unwin Ltd., 1915).
- 118. Norenzayan, A. et al. The cultural evolution of prosocial religions. *Behav. Brain Sci.* **39**, e1 (2016).
- Thomsen, L., Green, E. G. T. & Sidanius, J. We will hunt them down: how social dominance orientation and right-wing authoritarianism fuel ethnic persecution of immigrants in fundamentally different ways. J. Exp. Soc. Psychol. 44, 1455–1464 (2008).
- Henley, J. Denmark's centre-left set to win election with anti-immigration shift. *The Guardian* https://www.theguardian.com/world/2019/jun/04/ denmark-centre-left-predicted-win-election-social-democrats-antiimmigration-policies (4 June, 2019).
- Malka, A., Lelkes, Y. & Soto, C. J. Are cultural and economic conservatism positively correlated? A large-scale cross-national test. Br. J. Polit. Sci. 49, 1045–1069 (2019).
- 122. Bayer, L. The new communists. *Politico* https://www.politico.eu/article/ new-communists-hungary-poland-viktor-orban-jaroslaw-kaczynski/ (2018).
- 123. Johnston, C. D. Authoritarianism, affective polarization, and economic ideology. *Polit. Psychol.* **39**, 219–238 (2018).
- 124. Halali, E., Dorfman, A., Jun, S. & Halevy, N. More for us or more for me? Social dominance as parochial egoism. Soc. Psychol. Personal. Sci. 9, 254–262 (2018).
- Haesevoets, T., Folmer, C. R. & Van Hiel, A. Cooperation in mixed-motive games: the role of individual differences in selfish and social orientation. *Eur. J. Pers.* 29, 445–458 (2015).
- Thielmann, I., Spadaro, G. & Balliet, D. Personality and prosocial behavior: A theoretical framework and meta-analysis. *Psychol. Bull.* 146, 30–90 (2020).
- Heaven, P. C. L. & Bucci, S. Right-wing authoritarianism, social dominance orientation and personality: an analysis using the IPIP measure. *Eur. J. Pers.* 15, 49–56 (2001).
- 128. Balliet, D., Tybur, J. M., Wu, J., Antonellis, C. & Van Lange, P. A. M. Political ideology, trust, and cooperation: in-group favoritism among Republicans and Democrats during a US national election. J. Conflict Resolut. 62, 797–818 (2018).

- Jones, D. N. & Figueredo, A. J. The core of darkness: uncovering the heart of the Dark Triad. Eur. J. Pers. 27, 521–531 (2013).
- Duckitt, J. & Sibley, C. G. Personality, ideology, prejudice, and politics: a dual-process motivational model. J. Pers. 78, 1861–1893 (2010).
- Chiao, J. Y., Mathur, V. A., Harada, T. & Lipke, T. Neural basis of preference for human social hierarchy versus egalitarianism. *Ann. NY Acad. Sci.* 1167, 174–181 (2009)
- 132. Geniole, S. N., MacDonell, E. T. & McCormick, C. M. The threat premium in economic bargaining. *Evol. Hum. Behav.* 38, 572–582 (2017).
- Sinn, J. S. & Hayes, M. W. Replacing the moral foundations: an evolutionary-coalitional theory of liberal-conservative differences. *Polit. Psychol.* 38, 1043–1064 (2017).
- 134. Tuschman, A. Our Political Nature: The Evolutionary Origins of What Divides Us. (Prometheus Books, 2013).
- Iyer, R., Koleva, S., Graham, J., Ditto, P. & Haidt, J. Understanding libertarian morality: the psychological dispositions of self-identified libertarians. PLoS ONE 7, e42366 (2012).
- 136. Curry, O. S., Jones Chesters, M. & Van Lissa, C. J. Mapping morality with a compass: testing the theory of 'morality-as-cooperation' with a new questionnaire. *J. Res. Pers.* **78**, 106–124 (2019).
- 137. Glover, R. J. et al. Moral rationality and intuition: an exploration of relationships between the Defining Issues Test and the Moral Foundations Questionnaire. *J. Moral Educ.* **43**, 395–412 (2014).
- 138. Federico, C. M., Weber, C. R., Ergun, D. & Hunt, C. Mapping the connections between politics and morality: the multiple sociopolitical orientations involved in moral intuition. *Polit. Psychol.* 34, 589–610 (2013).
- 139. Ho, A. K. et al. The nature of social dominance orientation: Theorizing and measuring preferences for intergroup inequality using the new SDO₇ scale. *J. Pers. Soc. Psychol.* 109, 1003–1028 (2015).
- Duckitt, J., Bizumic, B., Krauss, S. W. & Heled, E. A tripartite approach to right-wing authoritarianism: the authoritarianism-conservatismtraditionalism model. *Polit. Psychol.* 31, 685–715 (2010).
- 141. Weeden, J. & Kurzban, R. The Hidden Agenda of the Political Mind: How Self-Interest Shapes Our Opinions and Why We Won't Admit It. (Princeton University Press, 2014).
- Pratto, F., Sidanius, J., Stallworth, L. M. & Malle, B. F. Social dominance orientation: a personality variable predicting social and political attitudes. *J. Pers. Soc. Psychol.* 67, 741–763 (1994).
- 143. Brandt, M. J., Reyna, C., Chambers, J. R., Crawford, J. T. & Wetherell, G. The ideological-conflict hypothesis: intolerance among both liberals and conservatives. Curr. Dir. Psychol. Sci. 23, 27–34 (2014).
- Czarnek, G., Szwed, P. & Kossowska, M. Right- and left-wing prejudice toward dissimilar groups in cultural and economic domains. *Eur. J. Soc. Psychol.* 49, 807–823 (2019).
- 145. Crawford, J. T., Brandt, M. J., Inbar, Y., Chambers, J. R. & Motyl, M. Social and economic ideologies differentially predict prejudice across the political spectrum, but social issues are most divisive. *J. Pers. Soc. Psychol.* 112, 383–412 (2017).
- Decety, J., Jackson, P. L., Sommerville, J. A., Chaminade, T. & Meltzoff, A. N. The neural bases of cooperation and competition: an fMRI investigation. *Neuroimage* 23, 744–751 (2004).
- Dawes, C. T. et al. Neural basis of egalitarian behavior. *Proc. Natl Acad. Sci. USA* 109, 6479–6483 (2012).
- De Dreu, C. K. W. et al. The neuropeptide oxytocin regulates parochial altruism in intergroup conflict among humans. *Science* 328, 1408–1411 (2010).
- Stallen, M., De Dreu, C. K. W., Shalvi, S., Smidts, A. & Sanfey, A. G. The herding hormone: oxytocin stimulates in-group conformity. *Psychol. Sci.* 23, 1288–1292 (2012).
- Nail, P. R. & McGregor, I. Conservative shift among liberals and conservatives following 9/11/01. Soc. Justice Res. 22, 231–240 (2009).
- Alesina, A. & Giuliano, P. Preferences for redistribution. Handbook of Social Economics 1, 93–131 (2011).
- Bauer, M., Cassar, A., Chytilová, J. & Henrich, J. War's enduring effects on the development of egalitarian motivations and in-group biases. *Psychol. Sci.* 25, 47–57 (2014).
- Schulz, J. F., Bahrami-Rad, D., Beauchamp, J. P. & Henrich, J. The Church, intensive kinship, and global psychological variation. *Science* 366, eaau5141 (2019).
- Talhelm, T. et al. Large-scale psychological differences within China explained by rice versus wheat agriculture. Science 344, 603–608 (2014).
- Matthews, L. J., Passmore, S., Richard, P. M., Gray, R. D. & Atkinson, Q. D. Shared cultural history as a predictor of political and economic changes among nation states. *PLoS ONE* 11, e0152979 (2016).
- Henrich, J., Heine, S. J. & Norenzayan, A. The weirdest people in the world?
 Behav. Brain Sci. 33, 61–83 (2010). discussion 83–135.
- Hughes, A. Psychology and the Political Experience. (Cambridge University Press. 1975).
- 158. Eysenck, H. The Psychology of Politics. (Routledge and Keagan Paul, 1954).

PERSPECTIVE NATURE HUMAN BEHAVIOUR

- 159. Tomkins, S. The Polarity Scale. (Springer, 1964).
- 160. Rokeach, M. The Nature of Human Values. (Free Press, 1973).
- 161. Hofstede, G. Culture's Consequences (Sage, 1980).
- Kerlinger, F.N. Liberalism and Conservatism: The Nature and Structure of Social Attitudes. (Erlbaum, 1984).
- Forsyth, D. R. A taxonomy of ethical ideologies. J. Pers. Soc. Psychol. 39, 175–184 (1980).
- Katz, I. & Hass, R. G. Racial ambivalence and American value conflict: correlational and priming studies of dual cognitive structures. *J. Pers. Soc. Psychol.* 55, 893–905 (1988).
- 165. Middendorp, C. Ideology in Dutch Politics. (Van G. Corcum, 1991).
- 166. Trompenaars, F. Riding the Waves of Culture. (Brealey, 1993).
- Braithwaite, V. Beyond Rokeach's equality-freedom model: two-dimensional values in a one-dimensional world. J. Soc. Issues 50, 67–94 (1994).
- 168. Schwartz, S.H. Value priorities and behavior: applying a theory of integrated value systems. in *The Psychology of Values: The Ontario Symposium* (eds. Seligman, C., Olson, J. M. & Zanna, M. P.) 1–24 (Erlbaum, 1996).
- Triandis, H. C. & Gelfand, M. J. Converging measurement of horizontal and vertical individualism and collectivism. J. Pers. Soc. Psychol. 74, 118–128 (1998).
- Stangor, C. & Leary, M. Intergroup beliefs: investigations from the social side. in *Advances in Experimental Social Psychology* (ed. Zanna, M.) 38, 243–281 (Academic, 2006).
- 171. Ferguson, L. W. Primary social attitudes. J. Psychol. 8, 217-223 (1939).
- 172. Boski, P. Socio-political value orientations among Poles in Presidential '90 and Parliamentary '91 elections. *Pol. Psychol. Bull.* **24**, 151–170 (1993).

Acknowledgements

We wish to thank A. Aktipis and members of the Language, Cognition, and Culture Lab at the University of Auckland for helpful comments on preliminary versions of this manuscript. This work was supported by a Royal Society of New Zealand Marsden Fund grant (#17-UOA-074) and a Rutherford Discovery Fellowship (#11-UOA-019) to Q.D.A. The funders had no role in the preparation of the manuscript or the decision to publish.

Author contributions

S.C. and Q.D.A. drafted the manuscript, with significant input from K.F, A.C. and C.G.S.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41562-020-0850-9.

Correspondence should be addressed to Q.D.A.

Peer review information Primary handling editor: Aisha Bradshaw

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© Springer Nature Limited 2020



Corresponding author(s):	Quentin D. Atkinson
Last updated by author(s):	10/02/2020

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see <u>Authors & Referees</u> and the <u>Editorial Policy Checklist</u>.

Chatiatian					
Statistics	Constitution Cities to the Constitution of the				
1	es, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.				
n/a Confirmed					
	ple size (n) for each experimental group/condition, given as a discrete number and unit of measurement				
	n whether measurements were taken from distinct samples or whether the same sample was measured repeatedly				
	The statistical test(s) used AND whether they are one- or two-sided Only common tests should be described solely by name; describe more complex techniques in the Methods section.				
A description of	of all covariates tested				
A description of	of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons				
	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)				
For null hypothesis testing, the test statistic (e.g. <i>F</i> , <i>t</i> , <i>r</i>) with confidence intervals, effect sizes, degrees of freedom and <i>P</i> value noted Give <i>P</i> values as exact values whenever suitable.					
For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings					
For hierarchical	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes				
Estimates of e	ffect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i>), indicating how they were calculated				
ı	Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.				
Software and c	ode				
Policy information abou	ut <u>availability of computer code</u>				
Data collection	No software was used.				
Data analysis	R version 3.4.1 was used to plot the data in Figure 1.				
For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.					
Data					
 Accession codes, uni A list of figures that I 	It <u>availability of data</u> It <u>availability of data</u> Include a <u>data availability statement</u> . This statement should provide the following information, where applicable: que identifiers, or web links for publicly available datasets have associated raw data restrictions on data availability				
Dataset for the literature review in Figure 1 is available at https://osf.io/gckw7/					
Field-speci	fic reporting				
Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.					
Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences					

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Behavioural & social sciences study design

All studies must disclo	se on these points even when the disclosure is negative.		
Study description	Quantitative literature review.		
Research sample	We reviewed articles from the peer-reviewed literature database Scopus and two US newspapers, the Wall Street Journal and the New York Times.		
Sampling strategy	For our review of Scopus, we selected the top 100 highest-cited articles from the last 20 years under the search term "political ideology". For our review of the US newspapers, we selected the top five most relevant articles in every year from 1999-2018, under the search term "political ideology".		
Data collection	If the articles contained explicit references to unidimensionality or any of the terms liberal, conservative, Democrat, Republican, or variations thereupon, we coded them as mentioning unidimensionality. If the articles contained explicit references to multidimensionality or any of the terms social dominance, authoritarianism, economic conservatism, social conservatism, or variations thereupon, we coded them as mentioning multidimensionality. A research assistant at the University of Auckland conducted this data collection, supervised by the lead author.		
Timing	Data collection was conducted between 28th August 2018 and 27th October 2018.		
Data exclusions	No data were excluded from the analyses.		
Non-participation	No participants dropped out/declined participation.		
Randomization	No randomisation occurred.		

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems		Me	Methods	
n/a	Involved in the study	n/a	Involved in the study	
\boxtimes	Antibodies	\boxtimes	ChIP-seq	
\boxtimes	Eukaryotic cell lines	\boxtimes	Flow cytometry	
\boxtimes	Palaeontology	\boxtimes	MRI-based neuroimaging	
\boxtimes	Animals and other organisms			
\boxtimes	Human research participants			
\boxtimes	Clinical data			