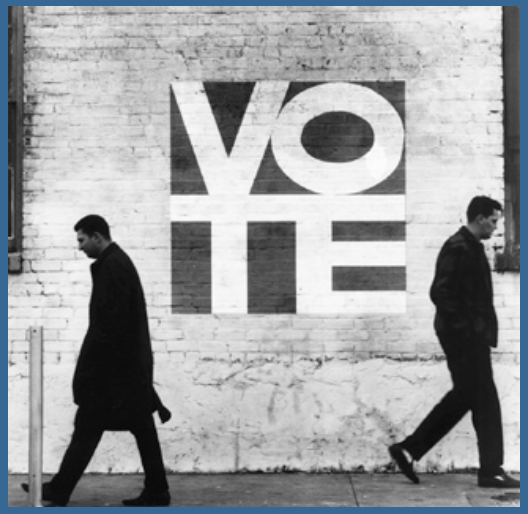
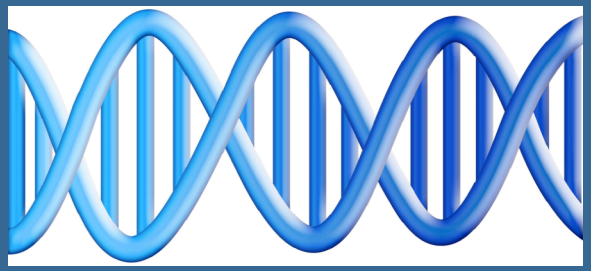


Two Genes Predict Voter Turnout

James H. Fowler
UCSD
Christopher T. Dawes
UCSD



Big Picture: Cooperation

The most important unanswered question in evolutionary biology, and more generally in the social sciences, is how cooperative behavior evolved and can be maintained in human or other animal groups and societies.

--Robert May 2006, *Nature*

Big Picture: Collective Action

[T]he theory of collective action is the *central subject of political science.... If political scientists do not have an empirically grounded theory of collective action, then we are hand-waving at our central questions.*

I am afraid that we do a lot of hand-waving!

Elinor Ostrom 1997, *APSR*

Cooperation and Participation

- Evolutionary Game Theory
  - Fowler 2005, *PNAS*
  - Fowler 2005, *Nature*
- Behavioral economics experiments
  - Fowler, Johnson, Smirnov 2005, *Nature*
  - Dawes, Fowler, Johnson, McElreath, Smirnov 2007, *Nature*
  - Fowler 2006, *JOP*
  - Fowler, Kam 2007, *JOP*
- Genetic Studies
  - Fowler, Baker, Dawes 2008 (*R&R APSR*)
  - Fowler, Dawes 2008, *JOP*
  - Dawes, Fowler 2008
  - Cesarini, Dawes, Fowler, Johannesson, Lichtenstein, Wallace 2008, *PNAS*

Overview for the Talk

- Review Twin Study Results
- Establish hypotheses for two genes that might influence turnout
- Discuss methods and results of a gene association study for turnout
- Preview results of a gene association study for partisanship

Game Theoretic Models of Turnout

- Typically assume individuals are
  - self-interested
  - fully optimizing $PB - C$
- Equilibrium turnout approaches 0 as population becomes large
  Palfrey and Rosenthal 1985
- Yet millions vote!
  - self-interest or optimizing assumptions are wrong
    Bendor, Diermeier, Ting 2003; Fowler 2006
- And millions abstain
  - inherent variation in cooperation

An Empirical Model of Turnout

TABLE 5. The Effects of Life Events After the First Election on Turnout Growth

	Predicting β_0		Predicting β_1	
	γ	SE	γ	SE
Variables in previous model				
Intercept	−0.316	0.272	0.972	0.135**
Sex (female = 1)	0.010	0.162		
Race (black = 1)	0.343	0.287		
Parental average education	0.246	0.097**		
Family income	−0.083	0.086		
Head-of-household occ. prestige	0.087	0.094		
Parental political interest	0.000	0.078		
Parental political knowledge	0.145	0.087*		
Parental political trust	−0.149	0.082		
Parental strength of partisanship	−0.061	0.083	0.143	0.063*
Parent voted in 1964 (voted = 1)	0.840	0.247**		
High school GPA	0.063	0.078		
High school activities	0.033	0.100		
Church attendance 1965	0.042	0.074		
Engagement in politics	0.260	0.077**		
Political knowledge	0.395	0.090**		
Trust in government	0.054	0.069		
Strength of partisanship	−0.009	0.073		
Attended college (yes = 1)	0.420	0.180**		
Married in 1968 (yes = 1)	0.100	0.173		
Toddler in home in 1968 (yes = 1)	0.047	0.237		
Interstate move 1965–1968 (yes = 1)	−0.352	0.152*		
Resources/disruptipons after election				
Educational achievement (−1 to +1)	—	—	0.163	0.088*
Professional in 1973 (yes = 1)	—	—	−0.108	0.120
Family income 1973	—	—	0.038	0.057
Home ownership in 1973 (yes = 1)	—	—	−0.036	0.137
Church attendence 1973	—	—	0.177	0.055**
Number of moves 1965–1973	—	—	0.000	0.055
Marriage/family events				
Married in 1973 (yes = 1)	—	—	0.442	0.156**
Divorced/separated in 1973 (yes = 1)	—	—	−0.266	0.264
Has toddler in home in 1973 (yes = 1)	—	—	−0.230	0.150
School-age child in home 1973 (yes = 1)	—	—	−0.312	0.197

$N_1 = 1061$, $N_2 = 3773$, likelihood ratio = −1749.8

Note: N_1 refers to number of respondents; N_2 refers to number of observations in the level 1 analysis. *$p < 0.05$; **$p < 0.01$ (one tailed).

Plutzer 2004

Empirical Models of Political Participation

- Theories ignore genes and biology
- Imply voter turnout is driven purely by environmental factors
- Recent *twin studies* suggest genes might be important too

  Alford, Funk, Hibbing 2005; Hatemi, et al. 2007

Twin Studies

- Compare the behavior of
  - monozygotic (MZ) twins (identical)
    - share 100% of their genes
  - dizygotic (DZ) twins (fraternal)
    - share 50% of their genes on average
- Decompose variance
  - A - genetic
  - C - common environment
  - E - unshared environment

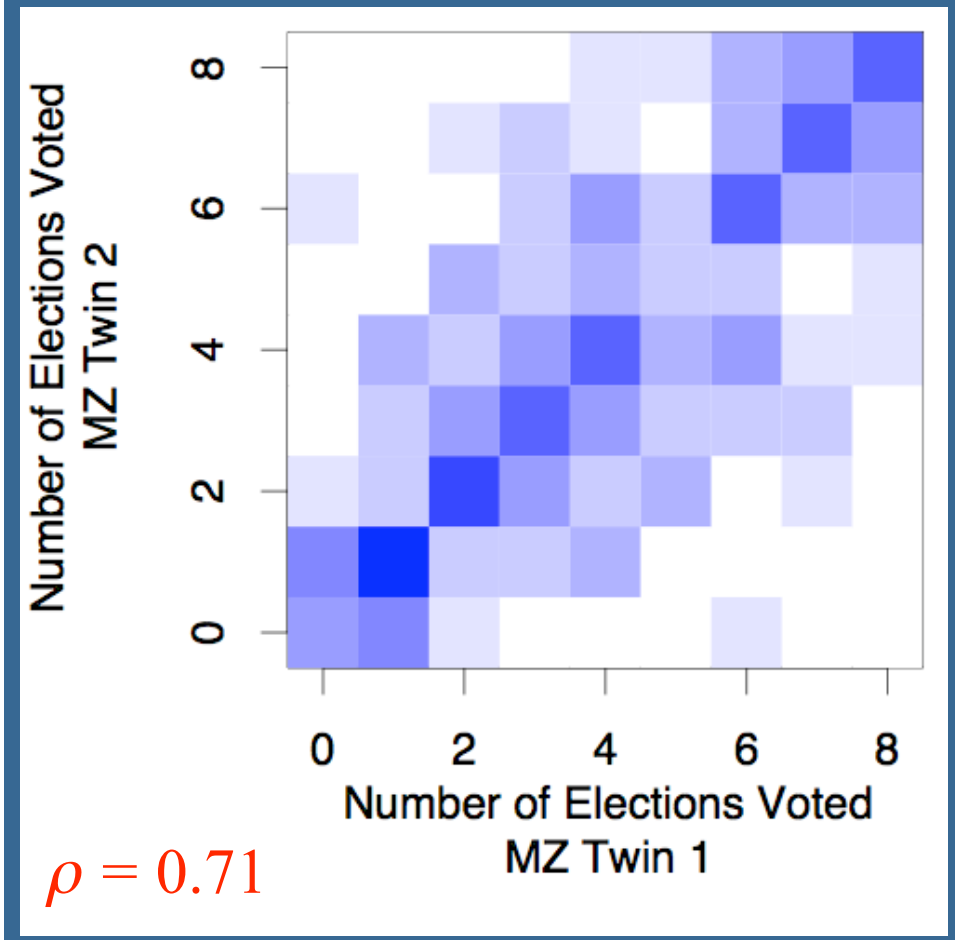
Criticism of Twin Studies

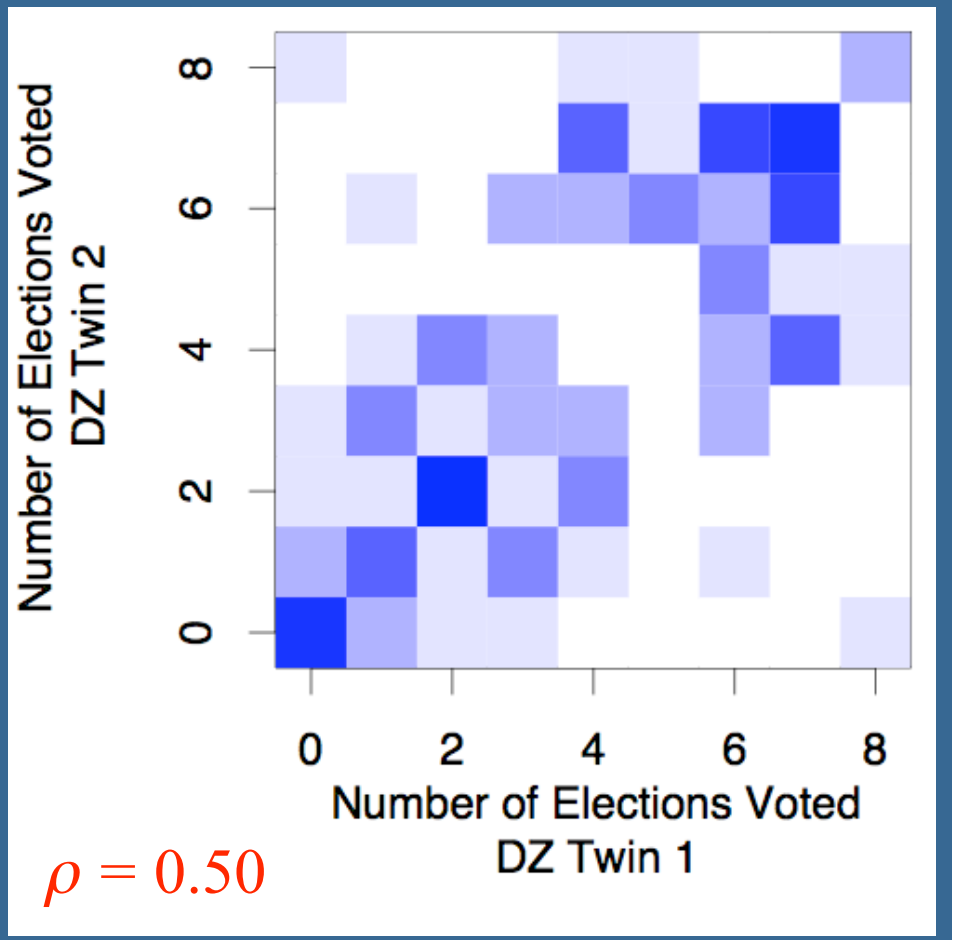
- MZ and DZ environments may not be comparable
  - MZ twins may be more strongly affiliated than DZ twins
- However
  - Studies of twins reared apart validate studies of twins reared together
    Bouchard 1998
  - Differences between MZ and DZ twins persist even among twins whose zygosity has been miscategorized by their parents
    Bouchard and McGue 2003
  - MZ twins are sometimes in more frequent contact, but evidence suggests that this *results from* rather than causes greater similarty
    Posner et al 1996
  - MZ twins living apart become more similar with age
    Bouchard and McGue 2003

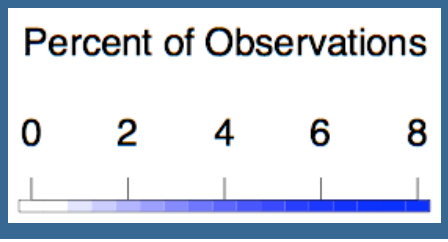
A Twin Study of Turnout

- Electronic voter registration records from Los Angeles County
  - 3.8 million voters
  - complete vote histories
  - 8 elections from 2000-2005 (3 primary, 2 statewide, 3 general)
- Southern California Twin Project (Baker et al. 2007)
  - registry of ~1000 twins living in the Los Angeles area

Voting in Los Angeles

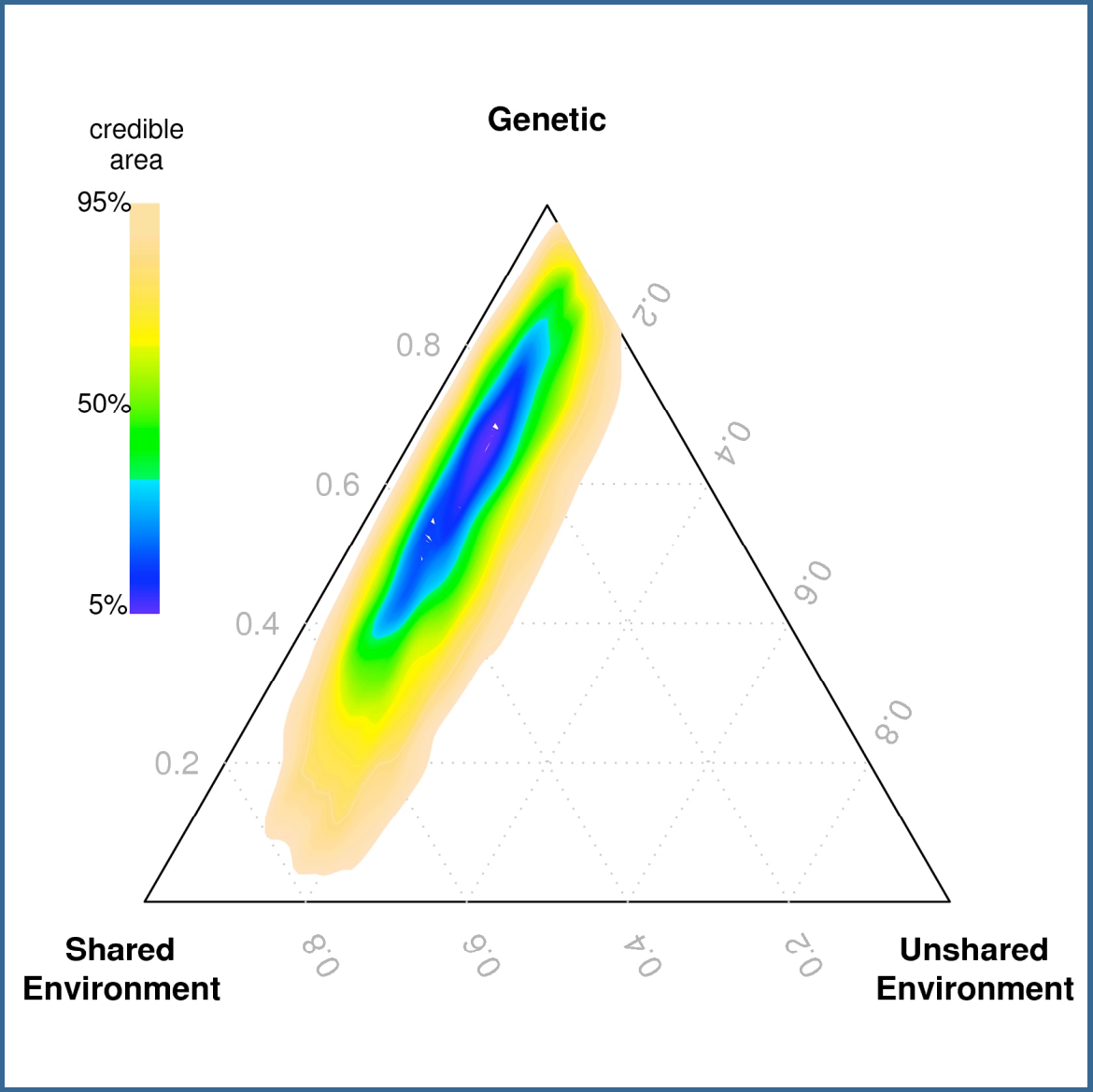






Los Angeles Voter Turnout

- Posterior mean
  - A 53% (10%,89%)
  - C 35% (2%,73%)
  - E 12% (3%, 26%)
- Better model fit when we drop C



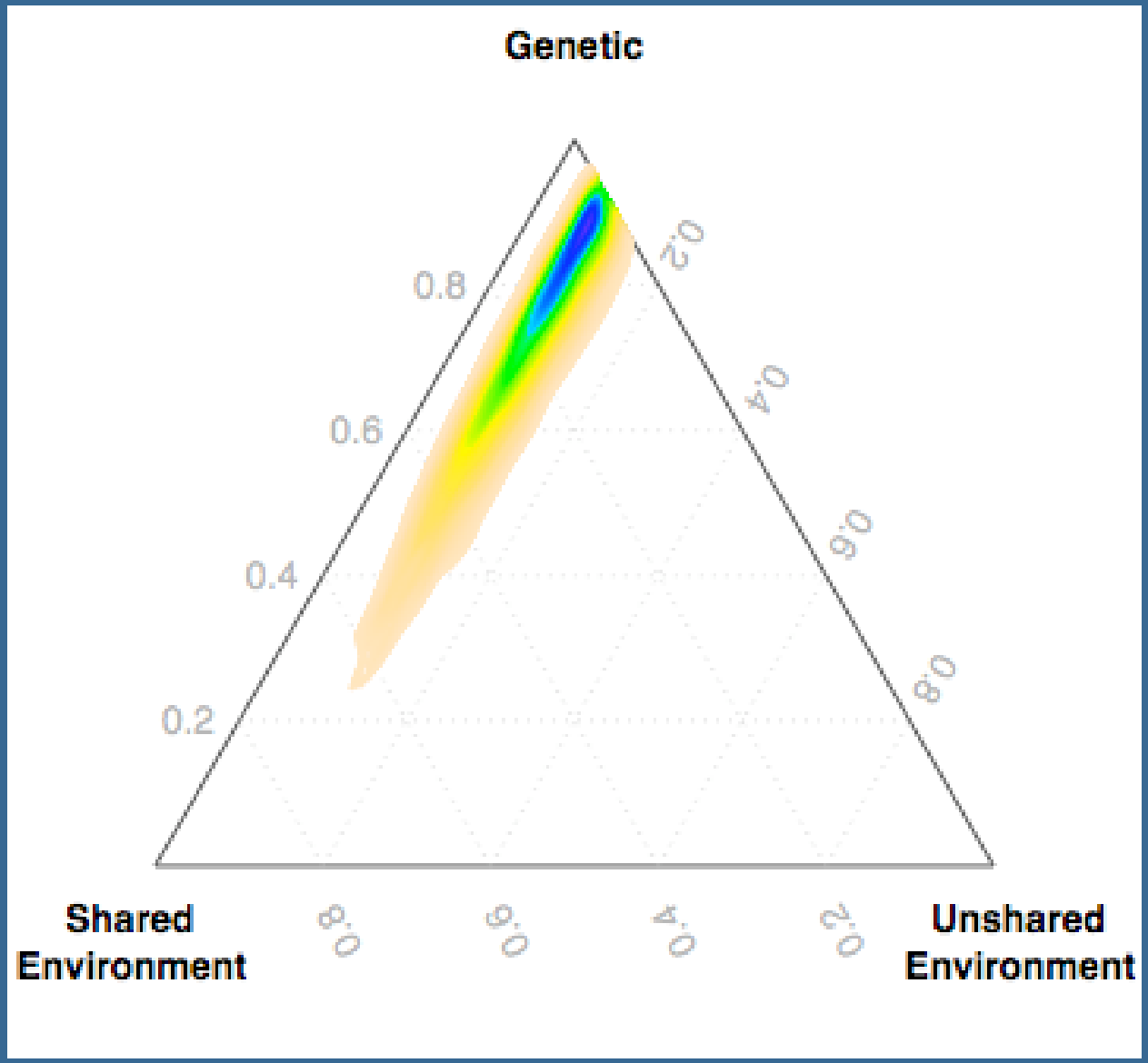
Independent Sample Replication

- National Longitudinal Study of Adolescent Health

  - 3 waves of health, social network, and genetic data
  - Oversampled twins (MZ=442, DZ=364)
  - Asked about political, civic behavior in Wave 3 when subjects were in early adulthood

Add Health Voter Turnout

- Posterior mean
  - A 72% (32%,93%)
  - C 20% (1%,57%)
  - E 9% (5%, 15%)
- Better model fit when we drop C

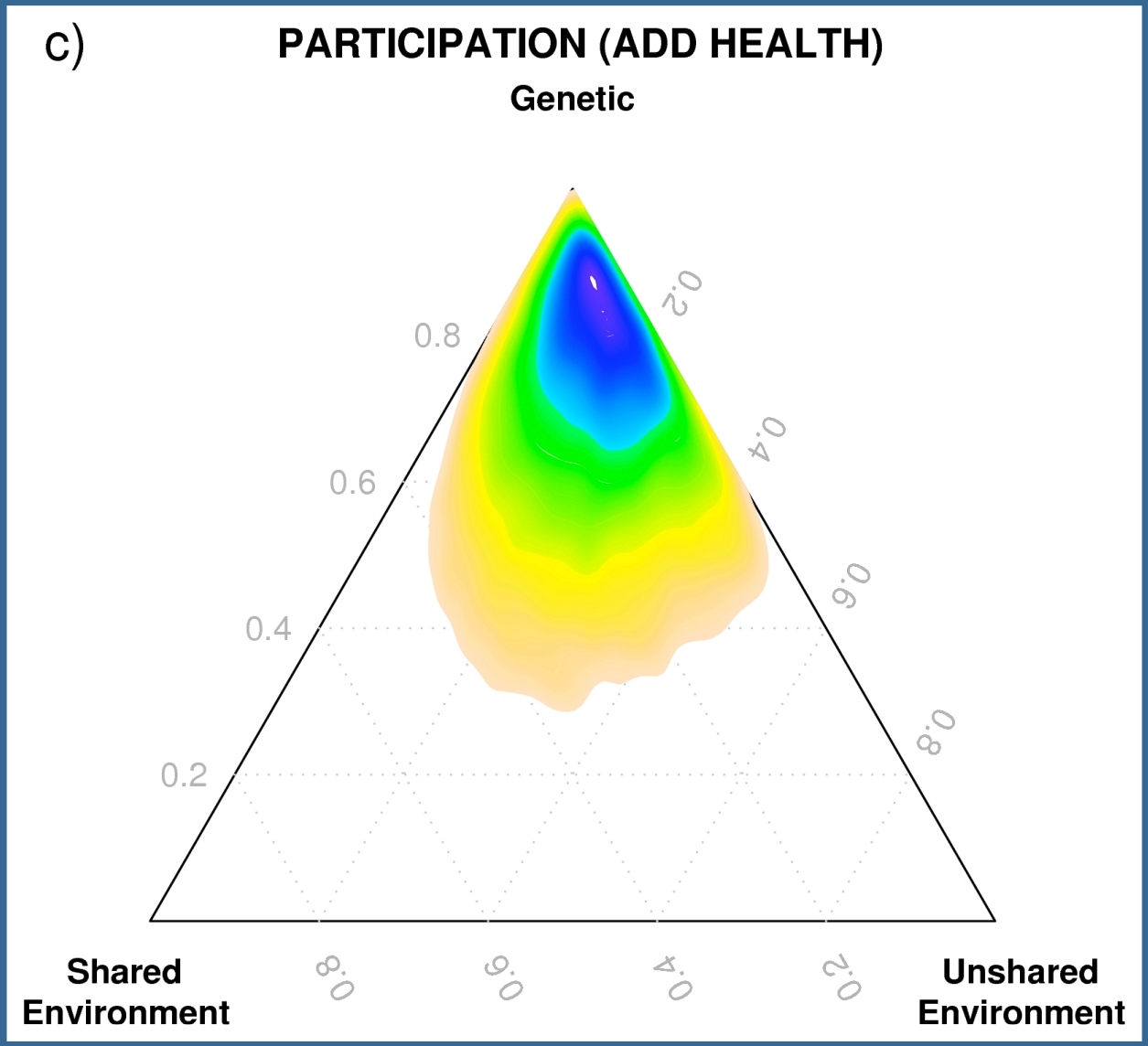


Construct Replication

- Add Health asked several political participation questions
  - Donate to party or candidate
  - Run for office
  - Contact official
  - Join political organization
  - Attend rally

Add Health Political Participation

- Posterior mean
  - A 60% (11%,91%)
  - C 18% (0%,54%)
  - E 23% (4%, 59%)
- Better model fit when we drop C



Two More Replications

- Minnesota Twin Family Study
  - 2764 young voters
  - Validated turnout
  - A = 47% (13%, 60%)
- Twins Days Festival
  - 800 representative adults
  - Self-reported turnout
  - A ~ 40%

MCTFR
MINNESOTA CENTER FOR TWIN & FAMILY RESEARCH
University of Minnesota

TWINSBURG
Twins Days

Some Gene Concepts

- ~25,000 genes in 46 chromosomes in human DNA
- Virtually fixed from moment of conception
  - No endogeneity!
- Some genes have different versions (alleles)
- "Phenotypes" are observable traits and behaviors
  - May be far downstream from "genotypes"
- Genes "transcribe" proteins that regulate structure and function
- Complex social behavior is "polygenic"

  Mackay 2001, Plomin 2008
  - There probably isn't a single "voter gene"

Which Genes?

- Voter turnout linked to prosocial behavior
  - Altruism
    Edlin, Gelman, Kaplan 2007
  - Giving in Dictator Game
    Fowler 2006; Fowler, Kam 2007; Dawes, Fowler 2006
  - Humanitarianism
    Jankowski 2002, 2007
- For social behavior, Damberg, et al 2001 recommend focusing on genes that influence
  - brain development
  - neurotransmitter synthesis and reception
  - hormone regulation
  - transcription factors

Serotonin System in Humans

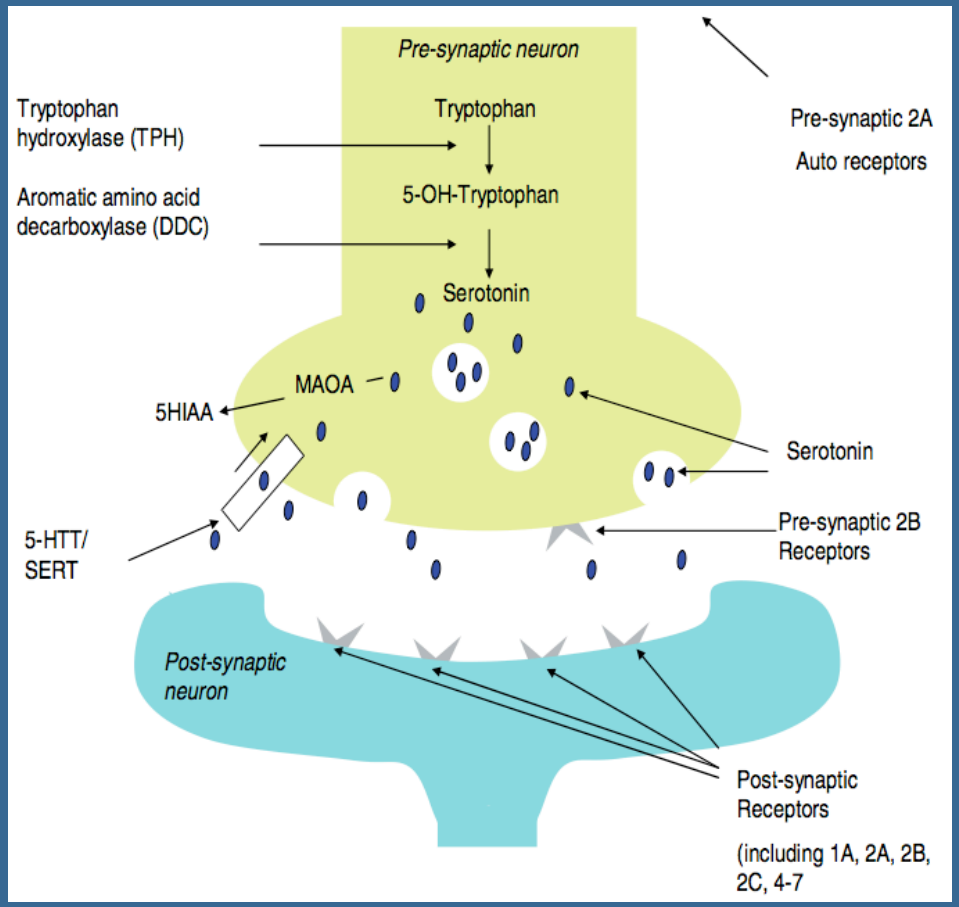
- Affects variety of complex social traits
  Balciuniene et al 2001
- Frequently targeted for antidepressants and illegal recreational drugs
  Craig 2007; Livingston 1996

Serotonin System in Animals

- In rhesus macaque monkeys
  - impaired serotonin metabolisms cause impulsive and aggressive behavior in response to social stressors
    Kraemer et al 1989
  - genetic deficiencies in serotonin system reduce their ability to respond to social stress
    Suomi et al 2003; Newman et al 2005
- In rodents
  - Acute emotional stress hinders serotonin function in several areas of the brain
    Popova et al 1989; Virkkunen et al 1995

Social Stress, Serotonin, MAOA, and 5HTT

- Social stress increases serotonin in presynaptic gap
- 5-hydroxytryptamine transporter (5HTT)
  - encodes integral membrane protein that transports serotonin from synaptic spaces into presynaptic neurons
- Monoamine oxidase A (MAOA)
  - encodes enzyme that degrades amine neurotransmitters, particularly serotonin



MAOA and 5HTT Genes

- Regulate transcription, metabolism, and signal transfers between neurons via serotonin system
  - Each stage shown to affect social interactions
    Craig 2007
- Less efficient alleles yield antisocial behaviors
  Vanukov 1995; Hsu 1996; Lawson 2003; Domsche 2005; Saito 2002; Schmidt 2000; Samochowiec 1999; Contini 2006
  - Substance abuse, impulsivity, criminality, precocious sexuality, and antisocial personality disorder
    Rhee & Waldman 2002
  - Corollary brain activations due to *increased* sensitivity to negative social experiences
    Eisenberger 2007

MAOA and 5HTT Genes in Animals

- MAOA knock-out in rats cause enzymatic activity to come to a complete halt
  Cases et al 1995
- In monkeys, 5HTT is densely concentrated in the output regions of the amygdala, which affects fear recognition
  O'Rourke et al 2006
- MAOA alters the structure of the brain in mice
  Cases 1996
- In mice, social stress increases transcription of both MAOA and 5HTT
  Filipenko et al 2002

Hypotheses

- Direct relationship
  - People with more transcriptionally efficient alleles of the MAOA and 5HTT genes are more likely to vote
- Gene-environment (GxE) interaction
  - MAOA and 5HTT genes interact with social activity to influence turnout

Why Focus on Religious Attendance?

- Consistently strong predictor of turnout
  - Probably because of generalized social belonging (Cassel 1999)
  - Might also be development of civic skills (Verba, Schlozman, Brady 1995)
- Best measure of general social group activity
  - Other measures political or low incidence

Add Health Data

- ~ 2900 subjects in both genetic sample and Wave III
- MAOA
  - group 291 and 321 base-pair alleles into a "low" transcription type and 336, 351, and 351 base-pair alleles into a "high" transcription type (Haberstick 2005)
  - Frequency: 41% "low" and 59% "high"
- 5HTT
  - "long" 528 base-pair allele associated with a much higher basal activity than a "short" 484 base-pair allele (Lesch 1996)
  - Frequency: 43% short and 57% long

Add Health Data

- Voter turnout based on self-report for 2000 election
  - Validated vote better
  - But validated and self-reported turnout both have large and similar genetic components
  - Exclude ineligible (non-citizens, underage)
- Religious attendance
  - never
  - at least a few times but no more than once a month
  - more than once a month

Model

- Genetic Association Test
- Mixed-effects logit (Guo & Zhao 2000, Xu & Shete 2006)

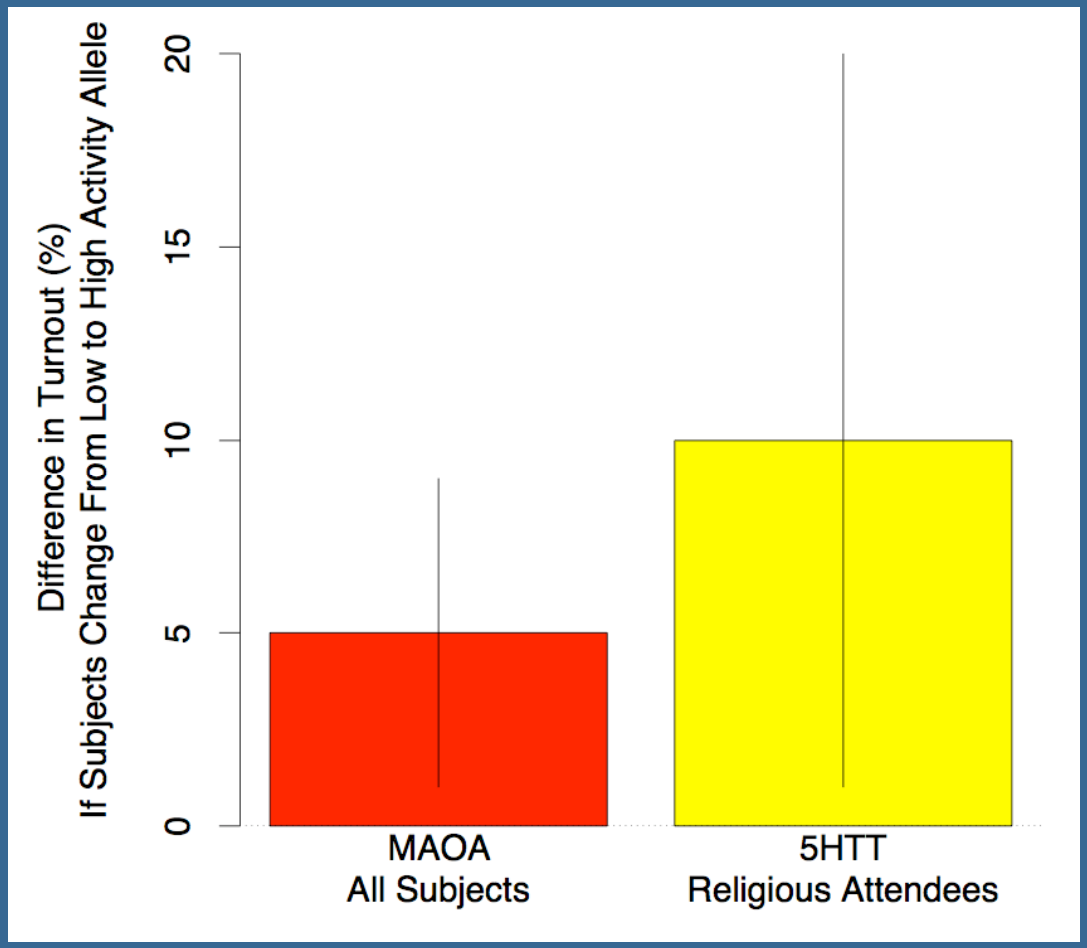
$$P[Y_{ij} = 1|Z_{kij}, U_j] = logit\,(\beta_0 + \beta_G G_{ij} + \beta_E E_{ij} + \beta_{GxE}(G_{ij} * E_{ij}) + \beta_k Z_{kij} + U_j)$$

- Association means
  - allele influences voting behavior
  - "linkage disequilibrium" with allele at another locus
  - false positive due to population stratification (Z_{kij})

	Model 1		*Model 2*		*Model 3*		*Model 4*		*Model 5*		*Model 6*	
	OR	*p*	OR	*p*	OR	*p*	OR	*p*	OR	*p*	OR	*p*
High MAOA	**1.26**	**0.03**			**1.29**	**0.02**			**1.28**	**0.02**	**1.28**	**0.04**
High*Attend					0.99	0.93						
Long 5HTT			1.00	0.99			0.97	0.83	0.96	0.77	1.04	0.81
Long*Attend							**1.58**	**0.01**	**1.46**	**0.03**	**1.51**	**0.04**
Attend					2.17	0.00	1.46	0.01	1.59	0.00	1.28	0.17
Black	1.59	0.00	1.45	0.01	1.33	0.04	1.19	0.19	1.28	0.08	1.54	0.02
Hispanic	0.76	0.11	0.76	0.11	0.75	0.10	0.73	0.07	0.73	0.07	0.93	0.72
Asian	0.83	0.39	0.79	0.30	0.75	0.19	0.72	0.13	0.74	0.18	0.91	0.72
Nat Am	0.81	0.56	0.82	0.58	0.81	0.56	0.82	0.58	0.80	0.55	0.96	0.92
Age	1.13	0.00	1.12	0.00	1.13	0.00	1.12	0.00	1.13	0.00	1.06	0.08
Male	0.96	0.68	1.04	0.72	1.06	0.56	1.15	0.17	1.07	0.54	1.09	0.47
Partisan											3.66	0.00
Income											1.02	0.36
Cognitive											1.01	0.02
College											2.34	0.00
Intercept	0.05	0.00	0.07	0.00	0.05	0.00	0.06	0.00	0.05	0.00	0.02	0.00
N	2273		2290		2283		2265		2254		1800	
Deviance	3059		3092		2966		2936		2918		2125	
NullDeviance	3091		3117		3109		3081		3067		2458	

Results

- MAOA “high” increases turnout ~5%
- 5HTT “long” increases turnout among attendees ~10%



Other Results

- Gene-turnout relationship not mediated by
  - partisanship
  - income
  - cognitive ability
  - education
- Main effect of religious attendance disappears when GxE and controls are in the model
  - Reappears when 5HTT removed ($p<0.0001$)
  - Analogous to Caspi et al. (2002)

Reinterpreting Turnout Empirics

- Parental turnout strong predictor for turnout in young adults Plutzer 2004
  - Previously interpreted as social influence
  - More likely genetic, since shared environment component is small
  - Could be due in part to MAOA and 5HTT

Reinterpreting Turnout Empirics

- Turnout is *habitual* -- people typically either always vote or always abstain
  Fowler 2006b; Gerber, Green, and Shachar 2003; Green and Shachar 2000; Miller and Shanks 1996; Plutzer 2004; Verba and Nie 1972
  - Previously interpreted as reinforcement learning
  - Large genetic component suggests inherent variability
  - Could be due in part to MAOA and 5HTT

Reinterpreting Turnout Theory

- Consistent with *D* & *E* terms $PB + D + E > C$

  Riker and Ordeshook 1968; Schuessler 2000

  - But variation in taste for voting may be heritable
- Consistent with new models of *ethical* voters

  Feddersen and Sandroni 2006

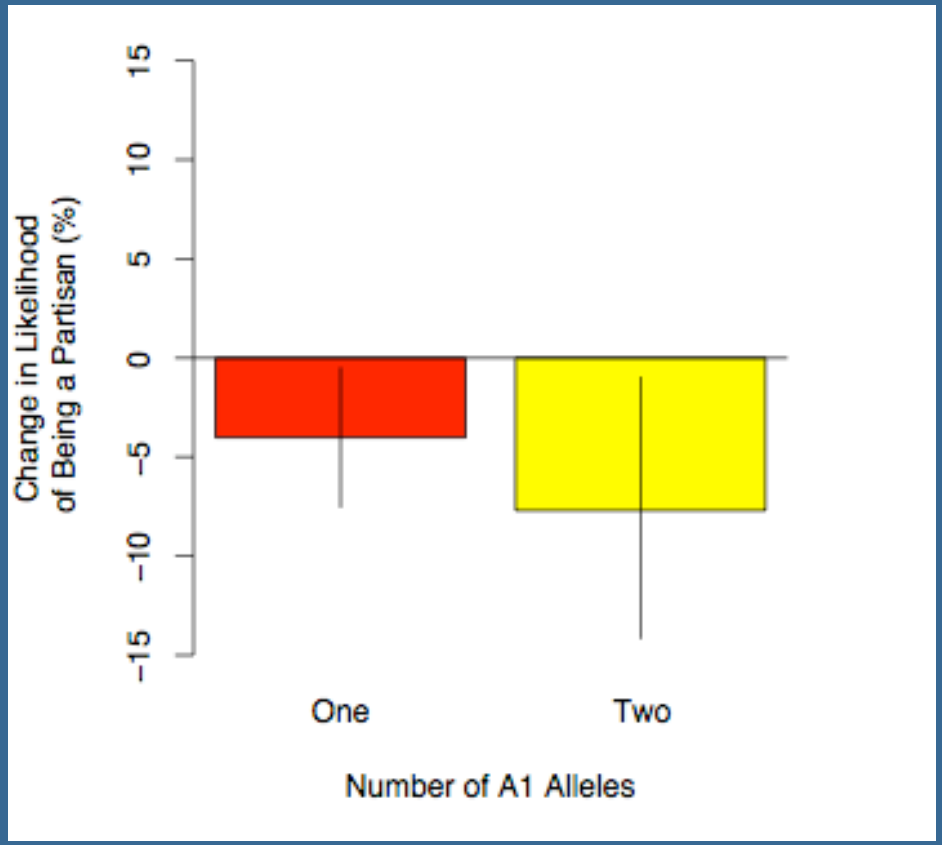
  - But *genetic* variation suggests voting behavior may result from evolutionary adaptation instead of rational optimizing behavior

Summary

- Five tests from four different samples of twins suggest significant heritability of political participation
- “High” MAOA allele increases turnout by about 5%
- “Long” 5HTT allele increases turnout by about 10% among religious attendees
  - suggests sensitivity to negative social experiences plays a role in effect of religious attendance on turnout

Preview: Dopamine, Partisanship and Genes

- Significant association between the D2 dopamine transporter gene (DRD2) and
  - partisanship
  - voter turnout
- Partisanship partially *mediates* the gene's influence on voter turnout



Parting Thoughts

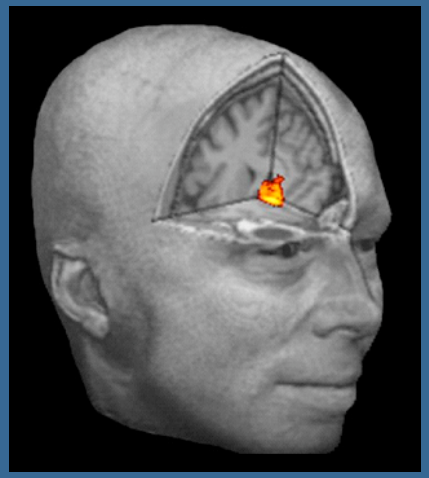
- Association studies require replication
  - Study of schizophrenia yielded several dead-ends
  - *Nature* and *Science* now require replication for publication
- Further work is needed to understand the difference between the MAOA and 5HTT results
  - Could have different impacts on the brain
  - Could result from multipurpose nature of MAOA
- Genes are the institutions of the human body

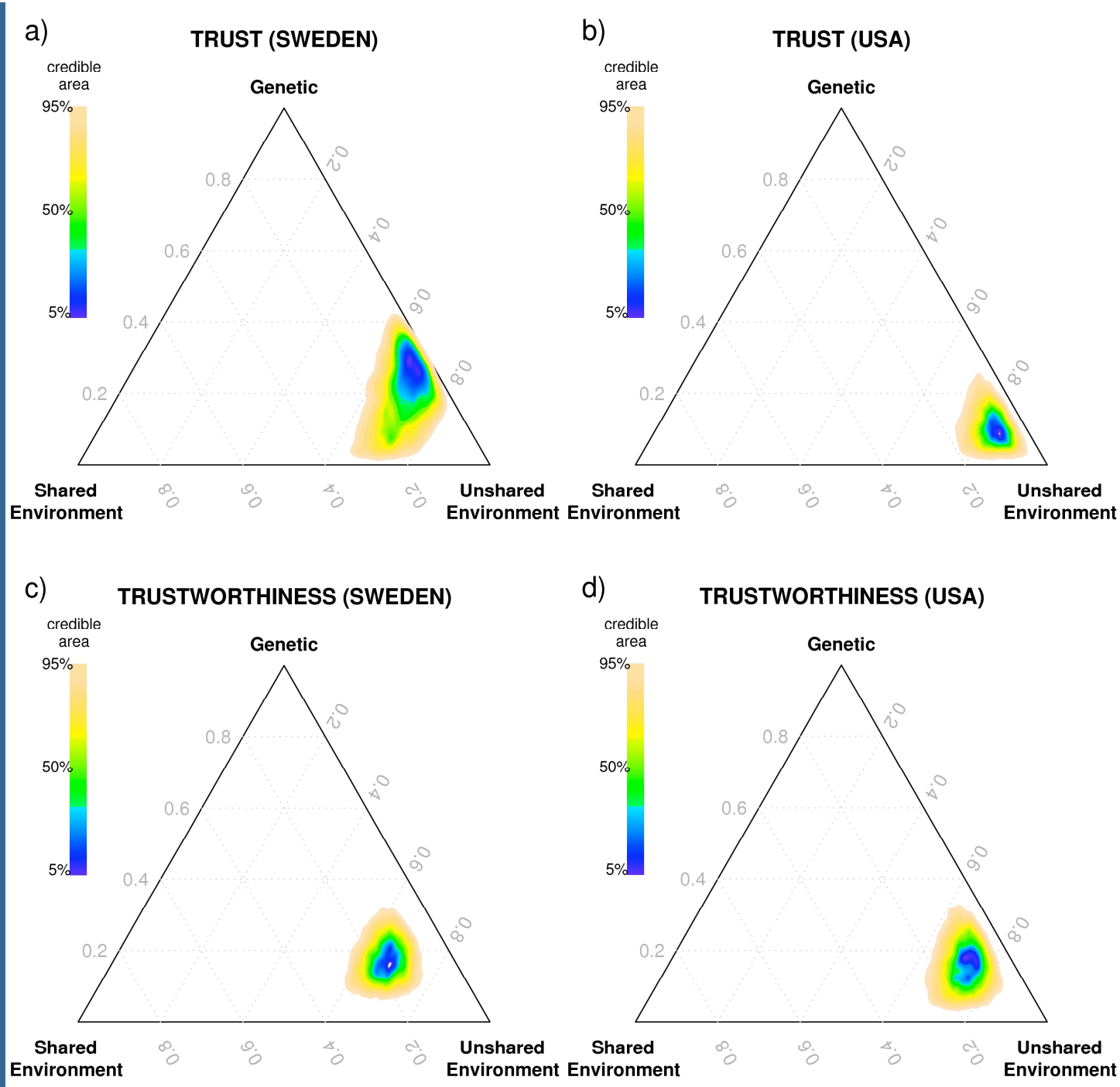
Acknowledgements

- Chris Dawes
- Laura Baker and the Southern California Twin Project staff
- Add Health team
- Matt McGue and the Minnesota Center for Twin and Family Research
- Twins Days Festival
- National Science Foundation grant SES-0719404
- University of California Institute of Government Affairs

Heritability of Cooperation in the Trust Game, *PNAS* 2008

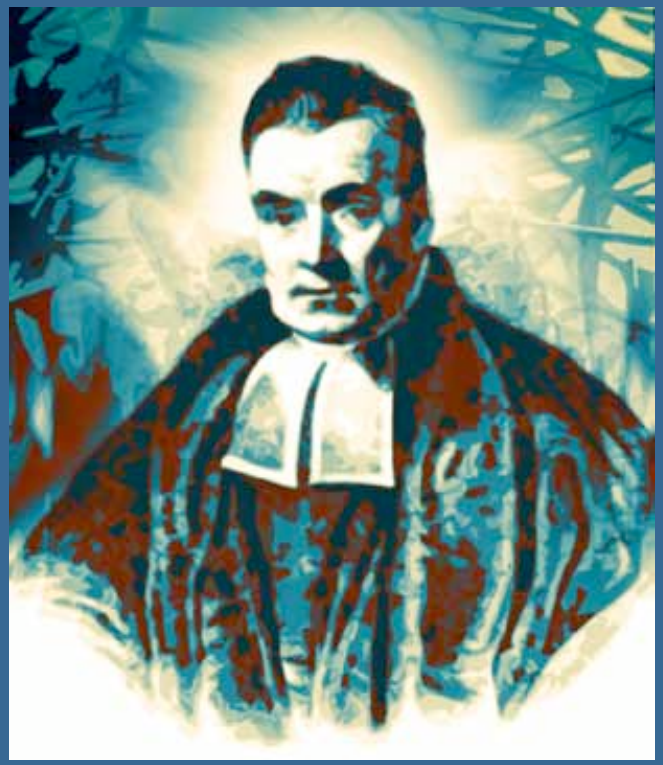
- Trust Game (Berg, et al. 1995)
  - P1 gets $10, chooses how much to send to P2
  - Each dollar sent is tripled
  - P2 chooses how much to send back
- Yields measures of *trust* and *trustworthiness*
- Used to study cooperation
  - fMRI (de Quervain 2004)
  - oxytocin experiments (Zak 2007)




a)
TRUST (SWEDEN)
credible area
95%
50%
5%
Genetic
0.8
0.6
0.4
0.2
Shared Environment
Unshared Environment
b)
TRUST (USA)
c)
TRUSTWORTHINESS (SWEDEN)
d)
TRUSTWORTHINESS (USA)

Bayesian Markov Chain Monte Carlo (MCMC)

- Evaluate high-dimension integrals using random draws
- Also allows use of singleton data
- Performs better than SEM for recovering parameter estimates in simulated data (van den Berg, et al 2006)



Bayesian Inference in Genetic Models

- Recent studies have successfully applied Bayesian methods to
  - binary data (van den Berg, et al. 2006)
  - survival analysis (Do et al. 2000)
  - GxE interaction (Eaves and Erkanli 2003)
  - item response theory (Eaves et al. 2005)
  - longitudinal models (Burton et al. 2005)
  - multivariate ordinal models (van den Berg et al. 2006)

The ACE Mixed-Effects Model

$$\Pr\left(T_{ijk}=1\right)=\Psi\left(\beta_k\tau_{ij}-\alpha_k\right)$$

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

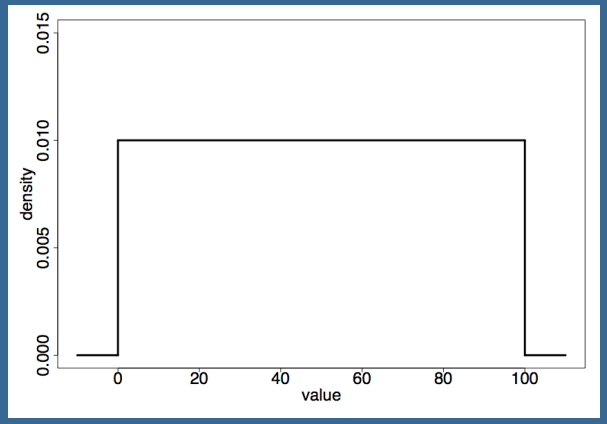
- Subject *j* is a member of family *i* and voting in election *k*
- Ψ = a logit function
- α = election-specific threshold in voter turnout
- β = election-specific factor loading
- τ = latent propensity to vote
- A, A_1, A_2 = genetic effects
- C = shared environmental effect
- E = unshared environmental effect

Model Specifics

- Random effects are normally distributed:
  - $A \sim N(0, \sigma_A^2)$ MZ shared genetic effect
  - $A_1 \sim N(0, \sigma_A^2/2)$ DZ shared genetic effect
  - $A_2 \sim N(0, \sigma_A^2/2)$ DZ unshared genetic effect
  - $C \sim N(0, \sigma_C^2)$ common environment effect
  - $E \sim N(0, \sigma_E^2)$ unshared environment

Model Specifics

- Vague priors
  - α , $\beta \sim N(0,1000000)$
  - $1/\sigma_A$, $1/\sigma_C \sim$ Pareto(0.01,0.01) (also tried U(0,100), Γ(0.01,0.01)

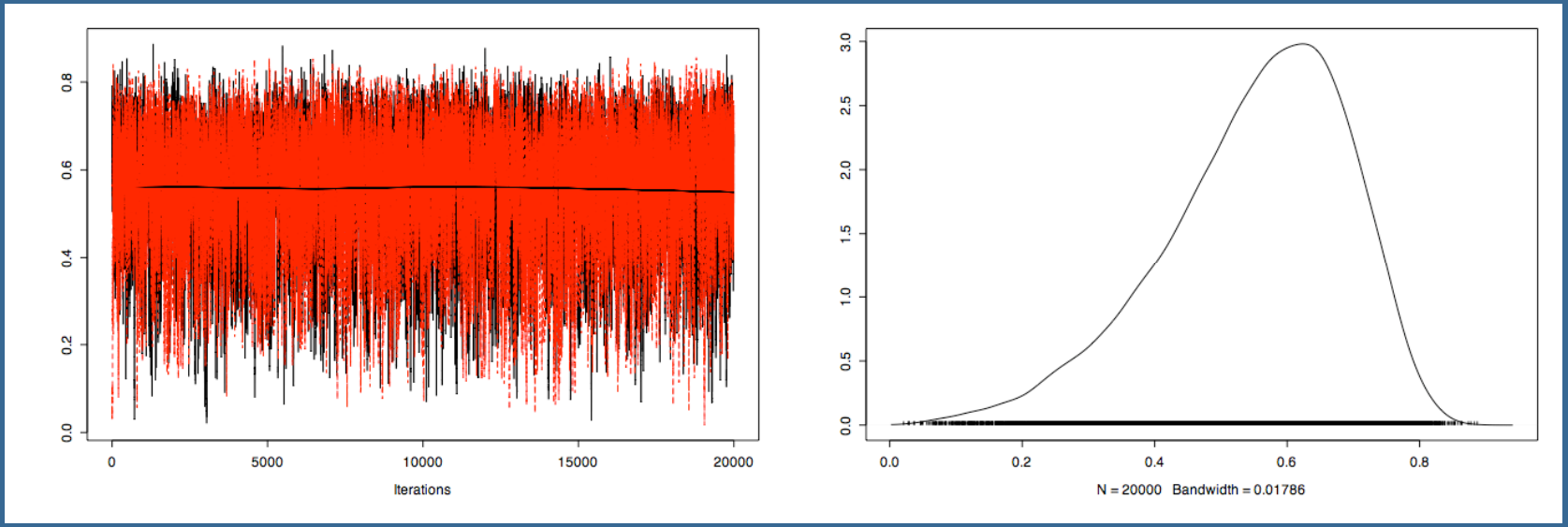


- To identify the model
  - We fix $\sigma_E^2 = 1$ and then use estimates of σ_A^2 and σ_C^2 to derive the proportion of variance generated by each factor

$$h^2 = \sigma_A^2 / \left(\sigma_A^2 + \sigma_C^2 + 1\right) \quad c^2 = \sigma_C^2 / \left(\sigma_A^2 + \sigma_C^2 + 1\right) \quad e^2 = 1 / \left(\sigma_A^2 + \sigma_C^2 + 1\right)$$

  - For AE model fix $\sigma_C^2 = 0$

Model Specifics



- Convergence
  - We ran two MCMC chains for each model
  - Brooks-Gelman (1998) test shows 'potential scale reduction factors' reduced to 1.1 or less by 10,000th draw
  - Severe autocorrelation requires 2 million draws
- Sample
  - Thin second half and keep 10,000 thinned draws from each of the two chains for analysis