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Paternal Age is Negatively Associated with Religious Behavior in a Post-60s But Not a Pre-60s US Birth Cohort: Testing a Prediction from the Social Epistasis Amplification Model

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Abstract

Participation in social behaviors that enhance group-level fitness may be influenced by mutations that affect patterns of social epistasis in human populations. Mutations that cause individuals to not participate in these behaviors may weaken the ability of members of a group to coordinate and regulate behavior, which may in turn negatively affect fitness. To investigate the possibility that de novo mutations degrade these adaptive social behaviors, we examine the effect of paternal age (as a well-established proxy for de novo mutation load) on one such social behavior, namely religious observance, since religiosity may be a group-level cultural adaptation facilitating enhanced social coordination. Using two large samples (Wisconsin Longitudinal Study and AddHealth), each of a different US birth cohort, paternal age was used to hierarchically predict respondent's level of church attendance after controlling for multiple covariates. The effect is absent in WLS ($\beta = .007$, *ns*, $N = 4560$); however, it is present in AddHealth ($\beta = -.046$, $p < .05$, $N = 4873$) increasing the adjusted model R^2 by .005. The WLS respondents were (mostly) born in the 1930s, whereas the AddHealth respondents were (mostly) born in the 1970s. This may indicate that social-epistatic regulation of behavior has weakened historically in the USA, which might stem from and enhance the ability for de novo mutations to influence behavior among more recently born cohorts—paralleling the secular rise in the heritability of age at sexual debut after the sexual revolution.

Keywords Church attendance · Paternal age effect · Religious behavior · Social epistasis amplification model

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Introduction

Social epistasis is a type of social genetic effect, specifically one by which the genome of one organism (or more than one organism) affects the gene expression of another organism (or more than one organism). The term was first used in Linksvayer's (2007) research on social insects; he reported evidence, from an experiment that used three ant species, that "adult worker size was determined by an interaction between the genotypes of developing brood and care-giving workers," a phenomenon that he calls "intergenomic social epistasis": "[W]ith intergenomic epistasis, phenotypes are determined by combinations of interacting genes expressed in different individuals" (p. 1). Although social epistasis is now (relatively) well studied in non-human organisms (Baud et al. 2017; Linksvayer 2007; Teseo et al. 2014), direct examination of the process in humans, through the use of genetic data, has only recently been attempted (Domingue et al. 2018).

The social epistasis amplification model (SEAM) builds on non-human social epistasis research and shows its potential relevance to human populations (Sarraf and Woodley of Menie 2017; Woodley of Menie et al. 2017). The SEAM predicts that social-epistatic transactions among genomes have the potential to amplify the fitness costs of certain deleterious mutations, such that their fitness-depressing effects may, at least in some cases, extend far beyond the carriers of those mutations. This amplification may occur because a mutation present in one individual can influence the gene expression, and therefore the phenotype and fitness, of other organisms via social epistasis. As most mutations that are non-neutral are harmful to their carriers, their effects on genomes with which they socially transact are likely to also be harmful. Deleterious mutations with fitness-reducing social-epistatic effects have been termed *spiteful mutations*, given that they are harmful to both their carriers and those organisms social-epistatically influenced by them. Mathematical modeling has offered evidence that relatively few of these "spiteful mutations" are needed to overwhelm a population of fitness co-dependent genotypes and induce population collapse (Woodley of Menie et al. 2017).

It has been predicted that spiteful mutations, in human groups, should have their most pronounced negative effects on *group-selected*[1] adaptations (Woodley of Menie et al. 2017). Among these adaptations are those aspects of culture that limit variability with respect to certain fitness-salient behaviors, compressing phenotypic variance around adaptive means that promote group fitness (Sarraf et al. 2019; see also MacDonald 1994; Wilson 2002 for information about some prospective group-selected adaptations in humans). Such adaptations may include aspects of culture that promote loyalty to one's in-group (e.g., patriotism) and fertility-enhancing

[1] It should be noted that the reality of group selection is a controversial matter (see Bahar 2018). Nevertheless, some of the most quantitatively sophisticated evolutionary theorists of recent times have provided a great deal of support for the view that group selection does operate, or at least has operated, in human populations (e.g., Bowles and Gintis 2011; Jones 2018; see also: Salter and Harpending 2013). Individual and gene-level selection theorists who oppose group-selection theories have failed to provide any compelling basis on which to doubt the results of such research, so we freely avail ourselves of the concept of group selection.

behaviors (e.g., early marriage). By engaging in behavior that is at odds with what is optimal for group fitness, the carriers of spiteful mutations might (if socially influential) be able to subvert these cultural adaptations. They might, for example, promulgate alternative, maladaptive cultural practices that displace adaptive ones. This would tend to promote fitness loss at both the group level and, by extension, the individual level (see Bowles and Gintis 2011 on the connection between group and individual fitness; Woodley of Menie et al. 2017). It has been predicted that humans have evolved specialized *social epistasis control modules* that have the effect of protecting groups against the fitness threat that spiteful mutations pose, e.g., by triggering hostile reactions to behaviors that threaten group-level fitness, but these modules likely will not have their ordinary effects when a population is excessively burdened by spiteful mutations, and/or when harmful mutations have undermined the modules themselves (Sarraf et al. 2019).

It is likely that deleterious mutations have been accumulating in populations that have industrialized and achieved a high level of modernization,[2] primarily because of the near-abolition of reproductively relevant mortality in these populations (see Kondrashov 2017; Lynch 2016; Rühli and Henneberg 2017; Sarraf et al. 2019); the accumulation of spiteful mutations in particular following industrialization in the West has been proposed as a possible and *partial* cause of the seemingly very rapid and (likely) maladaptive reductions of fertility in Western populations. Thus, the SEAM may figure in a complete explanation of the *demographic transition* (Sarraf et al. 2019; Woodley of Menie et al. 2017).

Intriguingly, an 80-year-long secular increase in the USA of certain potentially pathological traits—which might reflect the direct action of, and/or influence stemming from, spiteful mutations—has been found to completely mediate the effect of increases in a factor of proxies for mutation load on large secular declines in a factor of fitness indicators of the US population, consistent with the central prediction of the SEAM (Sarraf et al. 2019). More direct tests of the SEAM have been conducted using mice (see Bachmann et al. 2018; see also the closely related work of Cross 2019; Kalbassi et al. 2017; the commentary of Sarraf and Woodley of Menie 2017). Among the striking findings of this research is that mice with deletion of the gene *Nlgn3*, a deletion that is positively related to autistic-like behaviors, appear to induce pathological behaviors consistent with that mutation in mice that *have* the *Nlgn3* gene (Kalbassi et al. 2017). More recent tests have found strong evidence that a social-epistatic effect underlies this behavioral change (Cross 2019).

Testing Certain Predictions of the SEAM Relevant to Humans

Comprehensive tests of the SEAM in human populations would require the use of ethically problematical forms of gene manipulation; therefore, only indirect tests

[2] For molecular-genetic evidence of mutation accumulation in some European populations over many thousands of years, see Aris-Brosou (2019). But note that there is little reason to think that *relaxed selection* is relevant to the mutation accumulation detected except for that in "recent times" (Aris-Brosou 2019, p. 7), as mutation-accumulation theories stressing the role of industrialization would predict.

have been possible (specifically relying on secular trend analysis of phenotype-only data; Sarraf et al. 2019). Despite this, it is possible to identify specific predictions of the SEAM that could be tested by exploiting natural human variability. One of the key predictions of the SEAM is that religiosity constitutes a group-level adaptation that may be a significant target for spiteful mutations (Woodley of Menie et al. 2017). Religion seems to have been historically important to regulation of the behavior of human groups, especially in times of conflict, as behavioral policing of faith and devotion has been posited as a solution to the problem of controlling free riders, or those who benefit from exploiting the altruism of others and thereby threaten to undermine altruistic behavior generally (MacDonald 1994; Wilson 2002). Religiosity may be a consequence of evolution toward improved prefrontal cortex functioning (Henneberg and Saniotis 2009), especially as the prefrontal cortex has been found to be associated with social cognition and moral judgment (Forbes and Grafman 2010). More broadly, there appears to be a strong alignment of religiosity and prosociality in human populations (Norenzayan and Sharif 2008), which further evidences its adaptive basis (Sela et al. 2015; *cf* Boyer 2001).

Religiosity may be related to a matrix of fitness-enhancing social-epistatic effects, since it is evidently positively associated with a large number of beneficial physical and mental health outcomes (Koenig et al. 2012). Irreligiosity, on the other hand, may be associated with a matrix of harmful social-epistatic effects, since irreligiosity has been tied to elevated levels of psychopathy (Jack et al. 2016), low social effectiveness, as indicated by low levels of the General Factor of Personality (Dunkel et al. 2015), and autistic-like personality (Dutton et al. in Press; Norenzayan et al. 2012). It may also positively correlate with higher rates of sinistrality (Dutton et al. 2018)—a physiological marker of developmental instability—which is potentially positively associated with burdens of (certain) deleterious mutations (Lalumiere et al. 2000).

Given these findings, it might be the case that religious behaviors are related to variables that track mutation load, insofar as irreligious individuals may tend toward higher average mutation load than religious individuals (other factors held equal). A fairly direct test of this possibility can be conducted using individual differences in paternal age to predict variation in offspring religious behavior. Paternal age is associated with larger burdens of new or de novo mutations in sperm, such that older fathers on average bequeath larger burdens of de novo mutations to their offspring than younger ones (approximately 1.38 de novo mutations per gamete per year of paternal age; Moorjani et al. 2016). Consistent with this, paternal age effects have been found on fitness-salient offspring characteristics, such as measures of other-rated physical attractiveness (Huber and Fieder 2014; Woodley of Menie and Kanazawa 2017), certain clinical manifestations of personality, such as attention-deficit/hyperactive disorder (D'Onofrio et al. 2014) and autistic-like personality (Michaelson et al. 2012), and on fitness itself (Arslan et al. 2017; Fieder and Huber 2015).

Establishing a direct and negative effect of paternal age on offspring religious behavior would strengthen the view that irreligious behavior (specifically church absenteeism) indexes negative social epistasis (Sarraf et al. 2019): If those whose genomes carry on average higher burdens of de novo mutations, and therefore, in all probability, spiteful mutations, are more likely to be irreligious, then they are more

likely to exert negative social-epistatic effects on religiosity in others. We expect this process to be especially pronounced when behavioral irreligiosity occurs with traits that promote social success (e.g., high levels of intelligence). For socially successful individuals are more likely to be effective in influencing others. These observations lead us to predict that the offspring of older fathers are more likely to be behaviorally irreligious owing to higher burdens of (spiteful) de novo mutations, when covariates are statistically controlled. With statistical controls applied, we also test for the possibility that the behaviorally irreligious have higher average IQ.

Methods

Data

WLS

The Wisconsin Longitudinal Study (WLS) is a longitudinal, mixed-sex sample of 10,317 individuals sourced from the graduate population of the Wisconsin high school system and first surveyed in 1957. The study tracks the development of a large array of measures, including those tracking physical and mental health and well-being, along with morbidity and mortality and family functioning, starting in late adolescence, and continuing through to 2011 (the date of the most recent data collection; for further sample details, see Herd et al. 2014).

AddHealth

The National Longitudinal Study of Adolescent Health (AddHealth) is a large, nationally representative and prospectively longitudinal study of young Americans. A sample of 20,745 adolescents were personally interviewed in their homes in 1994–1995 (Wave I; mean age = 15.6 years). They were again interviewed in 1996 (Wave II; $N = 14{,}738$; mean age = 16.2 years), in 2001–2002 (Wave III; $N = 15{,}197$; mean age = 22.0 years), and in 2007–2008 (Wave IV; $N = 15{,}701$; mean age = 29.1 years). Additional details of sampling and study design are provided at http://www.cpc.unc.edu/projects/addhealth/design.

Variables

Dependent Variable: Church Attendance

Both WLS and AddHealth contain measures of religiosity (self-rated level of religiousness); however, it is well known that attitudes are not necessarily indicative of underlying behavior, and that people can espouse "socially desirable" attitudes, while behaving in a completely contradictory way (e.g., LaPiere 1934). Moreover, self-reported religiosity likely suffers from measurement invariance issues when cohorts from different time periods are compared (different levels of religiosity are

evaluated relative to a baseline, which may shift in time). Specific labels may mean different things also, i.e., atheism might historically have been associated with an extreme rejection of God possibly stemming form the holding of politically extreme values (such as Marxism), whereas today the label is used by many more moderate individuals, including those who potentially embrace anomic (Godless) forms of spirituality. Church attendance is therefore prospectively measurement invariant (it describes a specific unit of behavior, expressed in terms of an integer value, or range of values), therefore making it a potentially more stable measure of the actual social–behavioral trait of interest (i.e., religious engagement).

To track the positively social-epistatic behaviors of interest a measure of the respondent's self-reported frequency of church/religious attendance within the last year was therefore selected. This constitutes a measure of the degree to which individuals actively seek out and participate in the behavioral ecology associated with religious ceremony.

WLS measured the respondent's frequency of religious service attendance in the last year in 1975 using an 11-point Likert scale (1 = "one time per week" to 11 = "never") and church attendance in the last year in 1992 using a 6-point Likert scale (1 = "one time per week" to 6 = "never").

AddHealth measured the respondent's frequency of church attendance in the past year at Wave III on a 7-point Likert scale (0 = "never" to 6 = "more than once a week") and at Wave IV on a 6-point Likert scale (0 = "never" to 5 = "more than once a week").

We computed a unit-weighted factor for frequency of church attendance in the past 12 months, combining the measures at both ages in both datasets, by first standardizing the measure of church attendance within each wave and then taking the arithmetic mean of the two standardized factors (see Gorsuch 1983).

Independent Variables

Main Predictor: Father's Age at Birth In WLS, father's age at birth (measured in terms of calendar years) was computed by subtracting year of father's birth from the respondent's year of birth. The encoding of parental birth years in WLS is unusual as birth years from 1900 to 1929 are encoded as 000-029 and birth years from 1870 to 1899 are encoded as 070-099. This had to be taken into account in calculating father's age at birth. These data were collected in 1992–1993.

In AddHealth, father's age at birth was measured in calendar years at Wave I.

Control Variable: Mother's Age at Birth Maternal age at birth has been found to have independent and sometimes even opposing effects on traits in previous studies of paternal age effects (e.g., Woodley of Menie and Kanazawa 2017). In WLS, mother's age at birth was computed (in calendar years) in the same fashion as father's age at birth. These data were collected in 1992–1993.

In AddHealth mother's age at respondent's birth was measured in calendar years at Wave 1.

Control Variable: Birth Year Birth year potentially captures variance associated with temporal trends toward secularization and reduced religious engagement, with younger cohorts possibly being less engaged than older ones (Dillon 2003). In WLS, birth year was measured for all respondents in 1975, and for a small number of cases where the variable was not reported, it was collected in 1993. It varies from 1937 to 1940. In AddHealth the respondent's birth year was measured in calendar years at Wave I. It varies from 1974 to 1983.

Control Variable: Sex There are data indicating a sex difference in religiosity, with females typically reporting higher levels of religious engagement and belief than males (see Ellis et al. 2016 and references therein). In WLS, respondent' sex was measured in 1957 (1 = male, 2 = female). In AddHealth, the respondent's sex was measured at Wave I (0 = female, 1 = male).

Control Variable: Race There are documented race differences in levels of religious engagement (Pew Research Center 2015). In the public release of WLS, the respondent's race was not recorded; however, the sample is overwhelmingly non-Hispanic White (Herd et al. 2014). In AddHealth, the respondent's race was measured at Wave I with three dummies for Black, Asian, and Native American, with White as the reference category.

Control Variable: Father's and Mother's Education High levels of educational attainment are negatively associated with religious engagement and belief (Meisenberg et al. 2012). Parental level of education might therefore confound offspring religious engagement, as growing up in a more highly educated environment might present fewer opportunities for religious engagement. In WLS, the respondent's father's education and mother's education were measured in calendar years of attained education in 1975. In AddHealth, both father's education and mother's education were measured at Wave I with a 9-point Likert scale (0 = "no education" to 9 = "post-graduate education").

Father's and Mother's Religiosity The behaviors undergirding religious engagement and belief are heritable (Bradshaw and Ellison 2008; Bouchard 2004; Kendler and Myers 2009); furthermore, the parental environment will also influence the respondent's opportunity for religious engagement, with more religious parents providing their offspring with more opportunities to attend church. These data were only recorded for WLS and are available as a combined parental religiosity variable recorded with a five-point Likert scale (1 = "not religious" to 5 = "very religious"). These data were collected in 2004.

Father's and Mother's Income As with higher levels of education, higher-income households may be less religious (Meisenberg et al. 2012), providing fewer opportunities to the offspring for religious engagement. This variable was only measured in WLS and was scaled in terms of tens of thousands of dollars. The variable exhibited high skewness ($z > 2$)—therefore, it was natural log-transformed prior to use in the

regression analysis. These data were collected in 1975, but the question asks about income in 1957.

Control Variable: IQ IQ is robustly negatively correlated with religious engagement and belief (Zuckerman et al. 2019); this may confound the paternal age effect of interest as those with higher IQ are likely to be the offspring of older fathers as there is a positive correlation between IQ and age at first birth (Rindermann 2018). In WLS, the respondents' IQ was measured in 1957 using the Henmon-Nelson test. In AddHealth the respondent's IQ was measured at Wave I with an abbreviated version of the Peabody Picture Vocabulary Test. In both cases, the raw scores were standardized to have a mean of 100 and a standard deviation of 15.

Control Variable: Education Like IQ, educational attainment is associated with lower religiosity (Meisenberg et al. 2012), and also more advanced age at first birth, thus more highly educated respondents are likely to be the offspring of older fathers, who will typically be more highly educated themselves (Rindermann 2018). In WLS, the respondent's educational attainment was measured in 1964 and was scaled in terms of the number of years of education.

In AddHealth, the respondent's education was measured at Wave I as the number of years of *forma*l education (for example, high school graduation = 12, bachelor's degree = 16, five or more years of graduate school = 22).

Control Variable: Income In WLS, the respondent's annual income is scaled in terms of tens of thousands of dollars in 1975. In AddHealth, the respondent's annual income was measured in tranches of $1 K at Wave III. In both datasets, this variable exhibited high skewness ($z > 2$); thus, for the regression analysis, we took the natural log of the annual income. In both datasets unemployed respondents (who reported 0 income) were given a value equivalent to one cent in order to permit transformation.

Control Variable: Political Attitudes Political orientation is confounded to an extent with religious engagement and belief, as those with leftist/liberal political values tend toward lower levels of religiosity (Piurko et al. 2011); therefore, to separate the effects of this variable from that of religious engagement the former was controlled. In WLS, the respondent's political orientation was measured in 2004 on a 7-point Likert scale ranging from 1 = "very liberal" to "7 = "very conservative." In AddHealth, the respondent's political attitude was measured at Wave III on a 5-point Likert scale ranging from 1 = "very conservative" to 5 = "very liberal."

Control Variable: Birth Order Birth order effects can confound paternal age effects as they may reflect the action of sources of within-family variance that do not vary between families (such as the unique environmental influences stemming from positional effects within a family, e.g., being a "middle child") (Sulloway 1998). There are furthermore indications that individuals with higher birth ordinals are more likely to be irreligious (e.g., Chou and Elison 2014). Controlling for any effect of birth order strengthens the case for paternal age as a source of purely

between family variance impacting a predictor (e.g., D'Onofrio et al. 2014). Birth order also serves as a good proxy for the fertility of the respondent's parents' generation—with higher birth ordinals being associated with larger families. Family size positively tracks religiosity (Norenzayan et al. 2016) and may therefore additionally confound the direct effect of paternal age.

In WLS, birth order was measured in 1975 (1 = first born, 2 = second born, etc.). In AddHealth, birth order was measured at Wave I and is scaled the same way as in WLS, with later-born respondents getting higher birth ordinals. Children without siblings were assigned a value of one.

Analysis

The data were analyzed using bivariate correlations and linear regression. The analyses were carried out in SPSS (v.25). The variance inflation factors were < 3 for all variables used in these regressions, indicating that there was no problematic multicollinearity among the predictors (values < 10 are considered indicative of non-excessive multicollinearity: Kutner et al. 2005). Cases containing missing values on any of the variables to be analyzed were eliminated, yielding an N of 4993 for WLS and 4873 for AddHealth.

Results

Computing bivariate correlations between the church/religious attendance measure and father's age at respondent's birth in WLS yields a correlation of $r = -.003$, $p = .779$ for the combined sample ($N = 7926$), $r = .018$, $p = .240$ for the females ($N = 4234$), and $r = -.024$, $p = .129$ for the males ($N = 3690$). The results are graphed in Fig. 1.

In the AddHealth sample, the bivariate correlation between church attendance and father's age at respondent's birth is $r = .006$, $p = .572$ for the combined sample ($N = 7585$), $r = -.013$, $p = .421$ for the females ($N = 3978$), and $r = .029$, $p = .085$ for the males ($N = 3607$). These results are graphed in Fig. 2.

Table 1 presents the results of the hierarchical linear regression analysis for the WLS sample, $N = 4560$. Model 1 was run without paternal age, and Model 2 was run with the addition of paternal age.

Significant effects on church attendance were found for education (higher levels predict lower levels of church/religious ceremony attendance), income (higher levels predict lower levels of church/religious ceremony attendance), and parental religiosity (higher levels predict higher levels of church/religious ceremony attendance). There is no significant effect of father's age at respondent's birth on level of church attendance when this is added hierarchically to the regression, with no increase in model goodness of fit ($\Delta R^2 = .000$).

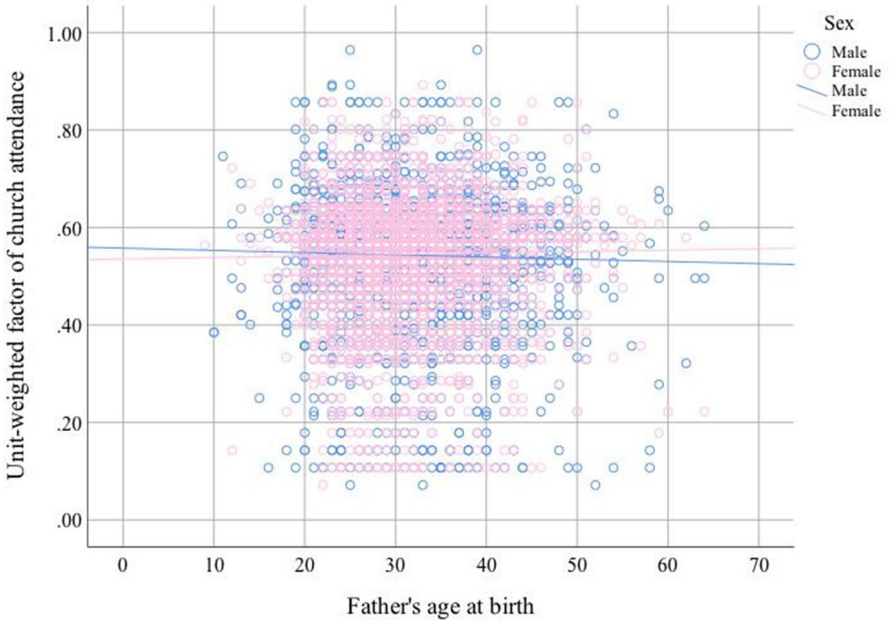

Fig. 1 Scatter plot of unit-weighted church/religious attendance versus father's age at respondent's birth in WLS, for both males (blue) and females (pink), $N = 7926$ (Color figure online)

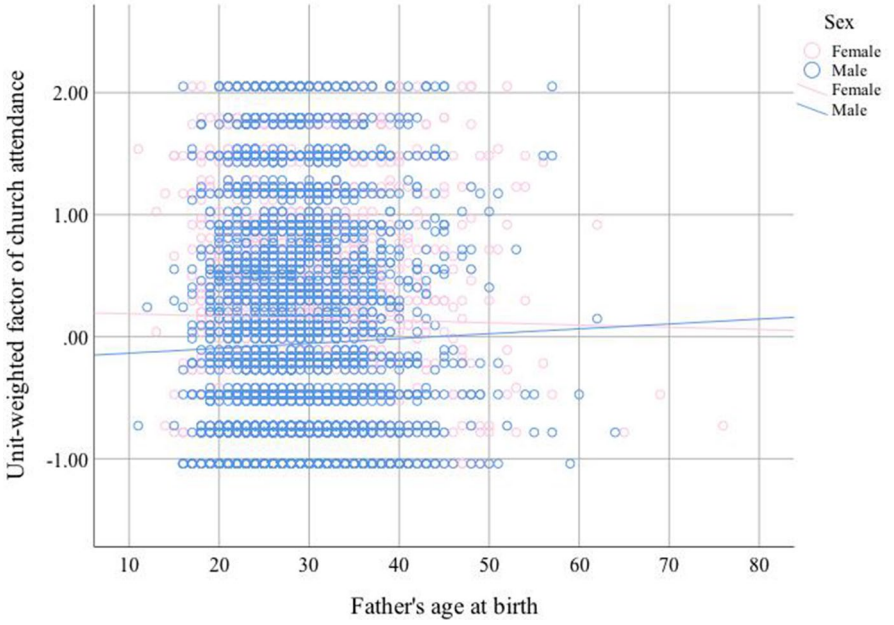

Fig. 2 Scatter plot of unit-weighted church attendance versus father's age at respondent's birth in AddHealth for both males (blue) and females (pink), $N = 7585$ (Color figure online)

Table 1 The hierarchical effect of father's age at birth on church/religious ceremony attendance: WLS. Model 1 = without father's age, Model 2 = father's age added

	(1)	(2)
Father's age at birth		−.000
		(.000)
		−.007
Mother's age at birth	−.000	−.000
	(.000)	(.000)
	−.023	*−.018*
Birth year	.003	.003
	(.004)	(.004)
	.010	*.010*
Sex	−.004	−.004
	(.005)	(.005)
	−.016	*−.016*
Father's education	.000	.000
	(.001)	(.001)
	.014	*.013*
Mother's education	.002*	.002*
	(.001)	(.001)
	.035	*.035*
IQ	.000	.000
	(.000)	(.000)
	.010	*.009*
Education	.005***	.005***
	(.001)	(.001)
	.070	*.070*
Income	.004***	.004***
	(.001)	(.001)
	.075	*.075*
Political attitude	.001	.001
	(.001)	(.001)
	.014	*.014*
Birth order	.003*	.003*
	(.001)	(.001)
	.044	*.046*
Parental income	−.005	−.005
	(.003)	(.003)
	−.028	*−.029*
Parental religiosity	−.008***	−.008***
	(.002)	(.002)
	−.068	*−.068*
Intercept	.188	.187
	(.151)	(.151)
Adjusted R^2	.021	.021
Number of cases	4560	4560

Main entries are unstandardized regression coefficients. Entries in parentheses are standard errors. Italicized entries are standardized regression coefficients

*$p < .05$ **$p < .01$ ***$p < .001$

Table 2 presents the results of the linear regression analysis for the AddHealth sample, $N = 4560$. Model 1 was run without paternal age, and Model 2 was run with the addition of paternal age.

Significant effects on church attendance were found for father's age (more advanced father's age predicts lower levels of church attendance), once this term was entered hierarchically. The addition of this term also increased model goodness of fit ($\Delta R^2 = .005$). Net of this, sex was a significant predictor (females have higher levels of church attendance than males), as was self-identifying as Black (positively predicts church attendance), father's education (higher levels predict higher levels of church attendance), IQ (higher IQ predicts lower levels of church attendance), respondent's education (higher levels predict higher levels of church attendance), political orientation (more liberal values predict lower levels of church attendance), and birth order (being a later-born offspring [having higher birth order] is associated with higher levels of church attendance).

Interaction effects between sex and paternal age were also estimated separately for each dataset, and these were not statistically significant in either case however.

Discussion

The bivariate correlations reveal no direct association between the measure of church attendance and father's age at respondent's birth in WLS. In AddHealth, there is also no significant association between the variables. In the regressions, only the effect of paternal age in AddHealth attained conventional statistical significance. Also, only in AddHealth was sex a significant predictor. Specifically, it was found that females attended church more frequently than males. Further, greater liberalism/leftism was associated with lower church attendance. Father's education is associated with higher levels of church attendance in AddHealth, but only once paternal age is estimated hierarchically. This estimation step also reduces the magnitude of the effect of maternal education to non-significance in AddHealth. In WLS, maternal, but not paternal, education is a significant positive predictor of respondents' church/religious behavior, as was expected.

Income in WLS predicts lower levels of church attendance in the expected direction (higher income goes with lower church attendance), but not in AddHealth. Respondents' education reduces church attendance, and IQ has no independent effect in WLS, but in AddHealth, educational attainment promotes church attendance and IQ suppresses it. Birth order was a significant positive predictor in AddHealth (meaning that a high birth ordinal goes with higher church attendance) and in WLS (meaning a higher birth ordinal goes with lower church/religious ceremony attendance). The direction of the effect in WLS is consistent with previous findings (e.g., Chou and Elison 2014), suggesting a role for within-family environments (such as discriminative parental solicitude) that might reduce religious behavior among the younger born, but not in AddHealth. It might be that in AddHealth, the finding stems instead from a fertility effect—those exhibiting higher birth ordinals should come from bigger families, and larger families are more likely to be religious (Norenzayan et al. 2016).

Table 2 The hierarchical effect of father's age at birth on church attendance: AddHealth. Model 1 = without father's age, Model 2 = father's age added

	(1)	(2)
Father's age at birth		−.007* (.003) *−.046*
Mother's age at birth	.001 (.002) *.005*	.002 (.004) *.011*
Birth year	.011 (.007) *.021*	.007 (.008) *.013*
Sex	−.181*** (.021) *−.102*	−.194*** (.024) *−.108*
Race		
Black	.440*** (.030) *.177*	.483*** (.037) *.180*
Asian	.028 (.043) *.008*	.009 (.046) *.003*
Native American	−.084 (.056) *−.018*	−.033 (.065) *−.007*
Father's education	.009 (.007) *.021*	.016* (.008) *.038*
Mother's education	.015* (.007) *.032*	.005 (.008) *.010*
IQ	−.003*** (.001) *−.053*	−.003** (.001) *−.047*
Education	.071*** (.006) *.160*	.066*** (.007) *.144*
ln(earnings)	−.001 (.002) *−.008*	−.000 (.003) *−.002*
Political attitude	−.288*** (.014) *−.250*	−.315*** (.016) *−.271*
Birth order	.041*** (.010) *.054*	.053*** (.012) *.070*
Intercept	−21.723 (12.903)	−13.477 (14.939)
Adjusted R^2	.136	.141
Number of cases	6244	4873

Main entries are unstandardized regression coefficients. Entries in parentheses are standard errors. Italicized entries are standardized regression coefficients

*$p < .05$ ** $p < .01$ ***$p < .001$

It could be argued that some of the differences between these analyses may be due to differences in the patterns of covariates used. For example, we were able to control for both parental religiosity and income in WLS, but not in AddHealth. It should be noted, however, that the inclusion of these covariates did not suppress an effect of father's age at respondent's birth on church attendance level. Running a restricted regression using WLS, in which both parental income and religiosity are excluded, thus bringing the covariates into conjunction with those used in AddHealth, did not lead to any kind of a difference in the effect of father's age at respondent's birth ($b_{(restricted\ model)} = .000$, $SE = .000$, $p = .812$).

The magnitude of the effect size is very small (i.e. $< .10$; Cohen 1988), but they are consistent with those reported in other studies of paternal age effects on other phenotypes (such as offspring physical attractiveness; see Fieder and Huber 2015; Woodley of Menie and Kanazawa 2017). Moreover, we note that in the AddHealth sample, the effect of paternal age on church attendance net of covariates is virtually equal in magnitude to the effect of IQ ($\beta_{(\text{paternal age})} = -.046$ vs. $\beta_{(\text{IQ})} -.047$), and that IQ has a very well-established negative association with religiosity (Zuckerman et al. 2019). That both paternal age and IQ should co-equally predict church attendance in AddHealth raises the possibility that the coupling of higher burdens of prospectively spiteful mutations (as indexed by advanced paternal age at birth) with greater potential for social success (as indexed by higher IQ) presents a pathway for substantial amplification of the costs of these mutations via the tendency for lower-status individuals to imitate the (in this instance irreligious) behaviors of those with higher status (elite imitation effects are well studied in sociology, see e.g.: Simmel 1957).

For comparative purposes, it should be noted that both the direct effects of paternal age and IQ on church attendance are nevertheless much smaller in magnitude than that of leftist political attitudes ($\beta_{(\text{political attitudes}) =} -.271$), which are strongly expected to predict religious engagement due to the close alignment between secularism and these attitudes in contemporary populations (Piurko et al. 2011).

The practical effects of even very small effect sizes can be quite pronounced when the extremes of distributions in large populations are considered, but there are reasons to doubt that the true effect sizes are as small as was found here. One possibility is *overcontrolling* in regression for the effects of variables that share variance with the predictor, thus partitioning the variance via regression will remove variance that is legitimately shared among predictors, in addition to that which is genuinely confounding the associations (this would be an example of what Garret Jones has termed the "Everest regression problem," or the observation that when controlled for atmospheric pressure, Mt. Everest's height above sea level is 0 m). Another potential problem stems from the imperfect validity

and reliability of the variables used in the regression. Adjusting effect sizes for these reduces error yielding larger effects (Schmidt and Hunter 2015). The best way to interpret these associations is therefore as indications of the presence of effects, which emerge consistent with predictions, and which offer a *conservative* estimate of the magnitude of the effects.

The pattern of the results suggests that some of the differences between the two samples might be due to cohort/generational effects. For example, historically the association between IQ and educational attainment might have been stronger; hence, when the latter is controlled for the former, there is no independent effect of the latter. In the more modern cohort, the Flynn effect (the secular rise in specialized cognitive abilities amounting to about three IQ points per decade; Pietschnig and Voracek 2015) may have driven down the association between the two, causing educational attainment to reflect to a greater degree, behavioral traits that might promote religiosity, net of IQ (see e.g., Figueredo et al. 2007; Giosan 2006 for discussion of *K*-selected behavior and its relationship to religiosity and educational attainment). So in AddHealth, both offspring's educational attainment and father's educational attainment promote church attendance net of the other covariates, whereas IQ suppresses it. Similarly, higher IQ is known to be associated with a heightened ability to not only identify social norms and conform to them, but also with leadership roles and the generation and promulgation of novel social norms (Dutton and van der Linden 2015). The presence of negative associations between IQ and religiosity in the younger cohort might then reflect the increasing strength of secular norms, to which higher-IQ people are especially sensitive.

Also, the difference between the two samples in terms of the direction of the birth order effect suggests that within-family environmental factors that might make later-born offspring more "rebellious" (i.e., less rule-governed in their behavior) have been neutralized. This perhaps reflects a shift toward more equitable resource distribution with respect to smaller numbers of offspring. A cohort effect might also plausibly explain the observation that political orientation is not a predictor of church/religious attendance in WLS, whereas it is in AddHealth. This effect might stem from secular trends toward greater levels of political polarization within the USA (Turchin 2016; Twenge et al. 2016) and may be associated with an increasing alignment between leftist politics and secularism, especially since the 1960s.

There is certainly enough of a difference in terms of span of years between the birth years of the two samples for these cohort effects to have been consequential (the WLS respondents were mostly born in the 1930s, whereas the AddHealth respondents were mostly born in the 1970s). A cohort effect may therefore plausibly explain the presence of a paternal age effect upon respondents' church attendance in the younger of the two cohorts. In point of fact, this is consistent with the SEAM in that social epistasis is associated with the moderating influence of the social genome on the expression of genes within an individual's (or group's collective) genome (Domingue and Belsky 2017). The SEAM predicts that among human populations, the maintenance of social structures results partly from the action of social-epistatic influence on phenotypic development, optimizing the development of these phenotypes for participation in group-selected behaviors (Sarraf et al. 2019; Woodley of Menie et al. 2017). Where the social genome has a moderating effect on individual

gene expression, we might expect this effect to suppress the expressivity of genetic variants (including prospectively spiteful mutations) on individual behaviors, which would manifest as a null effect of paternal age on the social behaviors undergirding participation in religious behaviors. Where the strength of the moderation effect has been reduced, or where it ceases to alter patterns of gene expression in ways that enhance group-level fitness (perhaps as a consequence of the accumulation of spiteful and other prospectively deleterious mutations—especially among those who generate culture; Sarraf et al. 2019; Woodley of Menie et al. 2017), the expressivity of genetic variance, and new mutations, can manifest to a greater degree. This might be associated with an increase in the heritability of the social behaviors underlying religious observance over time—a trend comparable to that observed for age at sexual debut, the heritability of which rose in the decades following the sexual revolution (Dunne et al. 1997), perhaps reflecting the same breakdown of social-epistatic moderation on gene expression and behavior.

It should be noted that a temporal trend is only one explanation for the difference between these two cohorts. They are also not precisely matched in terms of sample characteristics, with the WLS being a representative sample of those living in Wisconsin in the 1950s, and AddHealth being more generally reflective of the US population as a whole. While efforts were made to homogenize the samples with respect to inequalities (e.g., race was controlled in the regressions involving AddHealth), other demographic differences between these two samples might have contributed variance to the difference in the effects above and beyond the effect of the passage of time.

In future research, potentially fruitful work might examine paternal age effects on other types of social and social-epistatically salient behavior that may be a target for spiteful mutations, specifically political behavior that orients individuals away from forms of cultural participation that optimize populations for inter-group competition, (potentially) such as those that reinforce "traditional" social roles (Faria 2017).

Generating latent social-epistatic "target" factors (e.g., by combining across a range of social–behavioral indicators that may present spiteful mutations with both direct and indirect targets) in future paternal age effect research might yield larger effects, given the prospectively higher validity that such a composite variable may have. Such a composite might also incorporate measures of fertility and childlessness, which have been found to track variation in paternal age in the WLS and other datasets (Arslan et al. 2017; Fieder and Huber 2015). Future research can furthermore examine the generalizability of the present findings by examining them in the context of the populations of other countries, some of which historically have had far lower rates of religious participation, such as the UK. Under such circumstances, being attracted to religious ceremony may reflect the action of mutations that make one defiant of secular cultural norms; thus, the offspring of older fathers may in fact be overrepresented among congregations in such cultures. Such mutations may even qualify as altruistic as opposed to spiteful in effect under such circumstances, given that the cost in terms of opportunity for social selection accrued to their carriers by virtue of rejection of prevailing secular norms will be offset by the group-level benefits that accrue from the spreading of religious behavior under such circumstances. Variation in the normativity of religiousness across populations may well therefore

have significant implications for the phenomena examined in this paper, insofar as it tracks differences in the nature of the cultural or social-epistatic mediation of individual-level genetic effects on positive social-epistatic manifestations of behavior.

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