

Developmental Psychology

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Jasmin Wertz, Jay Belsky, Terrie E. Moffitt, Daniel W. Belsky, HonaLee Harrington, Reut Avinun, Richie Poulton, Sandhya Ramrakha, and Avshalom Caspi

Online First Publication, March 28, 2019. <http://dx.doi.org/10.1037/dev0000709>

CITATION

Wertz, J., Belsky, J., Moffitt, T. E., Belsky, D. W., Harrington, H., Avinun, R., Poulton, R., Ramrakha, S., & Caspi, A. (2019, March 28). Genetics of Nurture: A Test of the Hypothesis That Parents' Genetics Predict Their Observed Caregiving. *Developmental Psychology*. Advance online publication. <http://dx.doi.org/10.1037/dev0000709>

Genetics of Nurture: A Test of the Hypothesis That Parents' Genetics Predict Their Observed Caregiving

Jasmin Wertz
Duke University

Jay Belsky
University of California, Davis

Terrie E. Moffitt
Duke University and King's College London

Daniel W. Belsky, HonaLee Harrington,
and Reut Avinun
Duke University

Richie Poulton and Sandhya Ramrakha
University of Otago

Avshalom Caspi
Duke University and King's College London

Twin studies have documented that parenting behavior is partly heritable, but it is unclear how parents' genetics shape their caregiving. Using tools of molecular genetics, the present study investigated this process by testing hypotheses about associations between a genome-wide polygenic score for educational attainment and parental caregiving in 702 members of the Dunedin Study, a population-representative birth cohort. Data have been prospectively collected from when Study members were born through to midlife, and include assessments of the caregiving they provided once they became parents. Results showed that parents' polygenic scores predicted warm, sensitive, and stimulating caregiving, both in personal interactions with their young children (as captured on video) and through the home environments they created for their families (as observed by home visitors). The magnitude of this effect was small. Polygenic-score associations were independent of well-established predictors of parenting, such as parents' own childhood experiences of parenting and the age at which they became parents. Polygenic-score associations were mediated by parents' early-emerging cognitive abilities and self-control skills. Findings have implications for theory and research about genetic influences on caregiving and child development.

Keywords: educational attainment, gene–environment correlation, parenting, polygenic score

A remarkable discovery revealed by developmental behavior genetics research is that genetic influences affect not only individuals' behavior, but also the kinds of environments they experience (Plomin & Bergeman, 1991). Genetic influences on measures of the environment indicate that individuals select, create, or other-

wise end up in environments that are correlated with their genetically influenced proclivities (Rutter, Moffitt, & Caspi, 2006). The result is a link between individuals' genotypes and the environments they inhabit; a gene–environment correlation (Scarr & McCartney, 1983).

Jasmin Wertz, Department of Psychology & Neuroscience, Duke University; Jay Belsky, Department of Human Ecology, University of California, Davis; Terrie E. Moffitt, Department of Psychology & Neuroscience, Duke University, and Social, Genetic & Developmental Psychiatry Centre, King's College London; Daniel W. Belsky, HonaLee Harrington, and Reut Avinun, Department of Psychology & Neuroscience, Duke University; Richie Poulton and Sandhya Ramrakha, Dunedin Multidisciplinary Health and Development Research Unit, University of Otago; Avshalom Caspi, Department of Psychology & Neuroscience, Duke University, and Social, Genetic & Developmental Psychiatry Centre, King's College London.

The Dunedin Multidisciplinary Health and Development Research Unit is supported by the New Zealand Health Research Council and the New Zealand Ministry of Business, Innovation and Employment (MBIE). This research received support from the U.S. National Institute on Aging (Grant R01AG032282 and R01AG049789), United Kingdom Medical Research

Council (Grant MR/P005918/1), and the Jacobs Foundation. The Dunedin Parenting Study was supported by U.S. Eunice Kennedy Shriver National Institute of Child Health and Human Development Grant 5R01HD32948 and a New Zealand Health Research Council Next Generation Study grant. This work used a high-performance computing facility partially supported by Grant 2016-IDG-1013 ("HARDAC+: Reproducible HPC for Next-generation Genomics") from the North Carolina Biotechnology Center. We thank the Dunedin Study members, their parents and children, Unit research staff, Bob Hancox, and Study founder Phil Silva. We also thank Robert Bradley, David L. Corcoran, Joseph A. Prinz, Karen Sugden, and Benjamin Williams. The study protocol was approved by the institutional ethical review boards of the participating universities. Study members gave informed consent before participating.

Correspondence concerning this article should be addressed to Jasmin Wertz, Department of Psychology & Neuroscience, Duke University, Box 104410, Durham, NC 27708. E-mail: jasmin.wertz@duke.edu

Most research about gene–environment correlations focuses on how individuals’ genotypes affect the kinds of environments they themselves experience (Boivin et al., 2013; Harden, Hill, Turkheimer, & Emery, 2008). However, as people grow up, their genotypes also increasingly influence the kinds of environments *others* are exposed to. One of the most striking examples of this process occurs once people become parents and their genotypes affect the environment they provide to their children (Reiss, 2005). For example, studies of adult twins reveal that many measures of parenting are heritable; that is, genetically identical monozygotic twins are more similar in their parenting behavior than dizygotic twins (Klahr & Burt, 2014; Neiderhiser et al., 2004). Understanding how parents’ genotypes affect the kinds of family environments they create is important because the family environment is the greenhouse in which a new generation grows (Collins, Maccoby, Steinberg, Hetherington, & Bornstein, 2000). Here we studied this process by examining genetic influences, summarized in a genome-wide polygenic score, on parents’ caregiving.

It may seem surprising to suggest that parents’ caregiving is influenced by genetics. However, research shows that what parents do is partly shaped by their personal characteristics and resources, including their cognitive skills, personality traits, and educational attainment (Barrett & Fleming, 2011; Belsky, 1984; Belsky & Jaffee, 2006), all of which are themselves genetically influenced (Polderman et al., 2015). Findings from twin, adoption, and candidate-gene studies indicate that genetic differences between parents contribute to individual differences in parenting (Bakermans-Kranenburg & van Ijzendoorn, 2008; Elam et al., 2016; Klahr & Burt, 2014). Here we extended this research by studying genetic influences on parenting with a novel molecular-genetic approach, based on discoveries of genome-wide association studies (GWAS; Visscher et al., 2017). GWAS scan the entire genomes of large samples of individuals to identify genetic variants associated with a phenotype. GWAS results can be used as a scoring algorithm to aggregate the effects of millions of variants across the genome into a summary measure, a *polygenic score*, which captures part of a person’s genetic proclivity to a particular trait or behavior (Dudbridge, 2013). Polygenic score methods are a promising new approach to studying gene–environment correlation, because they allow measurement of individuals’ genetic propensities at the level of DNA while their aggregate nature reflects the polygenic architecture of complex traits (Plomin & von Stumm, 2018).

Perhaps the polygenic score most relevant to the study of parenting is the one derived from a GWAS of educational attainment, the largest GWAS in the social and behavioral sciences to date, with a sample size of more than one million (Lee et al., 2018). The polygenic score accounts for approximately 10% of individual differences in educational attainment and it is associated with differential educational attainment even among siblings growing up within the same family (Lee et al., 2018). The education polygenic score predicts not only how far people go in school, but also many of the choices and opportunities in their own life as they enter adulthood (Belsky et al., 2016). An important question is how these genetic differences, observed in one generation, shape experiences and opportunities in the next generation. Here we extend research about the nomological network of the polygenic score for educational attainment by asking: How does it shape the way adults parent their offspring?

The education polygenic score is hypothesized to be associated with parental caregiving for several reasons. First, educational attainment reflects people’s position in a hierarchical social structure, which is fundamental to how they parent (Hoff, Laursen, & Tardif, 2002). Second, research suggests that part of the reason why the education polygenic score predicts attainment is because it is associated with early-emerging cognitive and behavioral skills that are known to shape life-course development more broadly (Belsky et al., 2016; Wertz et al., 2018). These same skills are also associated with parents’ caregiving (Crandall, Deater-Deckard, & Riley, 2015; Johnston, Mash, Miller, & Ninowski, 2012). Third, children’s polygenic scores for educational attainment were shown to be associated with features of the home a child grows up in, such as socioeconomic status (Krapohl et al., 2017), suggesting that the polygenic score is associated with the caregiving environment parents create.

The present study had three aims. The first was to test the hypothesis that parents’ polygenic scores for educational attainment are associated with warm, sensitive, and stimulating caregiving of their children. We tested this hypothesis in a population-representative birth cohort, the Dunedin Study (Poulton, Moffitt, & Silva, 2015). Data have been prospectively collected from when participants were born through to midlife, and include assessments of participants’ own caregiving once they had children. Parents’ warm, sensitive, and stimulating caregiving was assessed using previously developed, objective measures, including videotaped interactions of parents with their children and observations of the home environment (Belsky, Hancox, Sligo, & Poulton, 2012; Belsky, Jaffee, Sligo, Woodward, & Silva, 2005). We further differentiated between cognitively stimulating and warm-sensitive caregiving, to test the possibility that the education polygenic score would be more strongly associated with aspects of caregiving that reflect cognitive stimulation versus warmth and sensitivity.

The second aim was to test whether parents’ polygenic scores predicted caregiving over and above parents’ own experienced-parenting and the age at which they first became parents. We conducted this test because genetic effects on caregiving are unlikely to materialize in a vacuum, detached from a parent’s previous experiences. We chose to examine parents’ own experienced-parenting because there is a wealth of evidence indicating intergenerational transmission of parenting: that is, that the parenting a person experienced when they were young affects the caregiving they provide to their own children once they become parents (Belsky, Conger, & Capaldi, 2009; Madden et al., 2015). We chose to examine parents’ age-at-entry to parenthood because research indicates that individuals who become parents at an early age provide less effective caregiving to their children (Hoffman & Maynard, 2008; Jaffee, Caspi, Moffitt, Belsky, & Silva, 2001). A finding that the polygenic score predicts caregiving over and above these factors would support the hypothesis that the score carries incremental value in addition to these well-established predictors of parenting. It would also indicate that high polygenic scores positively affect parents’ caregiving despite adverse circumstances, pointing to polygenic scores as a possible engine of *upward parenting mobility*. This is often described as breaking the cycle of poor parenting.

Our third aim was to test hypotheses about possible mediators of the association between the polygenic score for educational attainment and parental caregiving. There are at least two hypotheses

about why a polygenic score for educational attainment may predict parenting. First, individuals with higher polygenic scores stay in school for a longer period of time, and it may be the credential bestowed by education, or the knowledge acquired through education, that improves their caregiving skills. Second, a higher education polygenic score may influence personal characteristics that help individuals go further in their education, and also become more effective parents once they have children. Indeed, previous research (Belsky et al., 2016) shows that the education polygenic score predicts individual characteristics that are also known to positively affect caregiving, including cognitive and self-control skills (Crandall et al., 2015; Johnston et al., 2012). Simply controlling for educational attainment does not differentiate between the two hypotheses. Furthermore, controlling for education may be problematic because individuals with lower polygenic scores may have children earlier (Barban et al., 2016), and having children early may disrupt education (Levine & Painter, 2003). However, the design of the Dunedin study makes it possible to go back to people's childhoods, and test the role of personal characteristics that people already had before they completed their education or became parents. A finding that these characteristics mediate the association would suggest that characteristics already present before individuals complete their education explain why parents with higher polygenic scores display more warm, sensitive, stimulating parenting. We tested the hypothesis that these skills connect genetic differences between parents to their caregiving, thus serving as mediators of the polygenic effect.

Method

Sample

The participants in this study were members of the Dunedin Multidisciplinary Health and Development Study, a longitudinal investigation of health and behavior in a birth cohort. Dunedin participants ($N = 1,037$; 91% of eligible births; 52% male) were all individuals born between April 1972 and March 1973 in Dunedin, New Zealand, who were eligible on the basis of residence in the province and who participated in the first assessment at age 3. Full details about the sample are reported elsewhere (Poulton et al., 2015). The cohort represented the full range of socioeconomic status (SES) in the general population of New Zealand's South Island. On adult health, the cohort matches the New Zealand National Health and Nutrition Surveys on key health indicators (e.g., body mass index, smoking, visits to the doctor). Assessments with Dunedin participants were carried out at birth and ages 3, 5, 7, 9, 11, 13, 15, 18, 21, 26, 32, and, most recently, 38 years. All but one of the assessments have enjoyed participation rates well above 90% (Poulton et al., 2015). The study was approved by the New Zealand Southern Health and Disability Ethics Committee (Reference 17/STH/25: "A Lifecourse Study on Aging Processes to Inform Early Intervention Strategies") and the Duke Campus Institutional Review Board (Protocol 1604: "The Dunedin Multidisciplinary Health and Development Study"). Written informed consent was obtained from all participants.

The Dunedin Participants as Parents

In 1994, when Dunedin participants were between 21 and 22 years old, a study of their parenting behavior was initiated (the Parenting Study; Belsky et al., 2005). By 2017, when Dunedin participants were 44–45 years old, $N = 702$ had participated in the parenting study, of $N = 738$ cohort members eligible for participation based on their having a 3-year-old child (participation rate: 95%). For the majority of participants, the child they participated in the study with was their first-born (91%) biological child (97%). Dunedin study participant-parents and their children were visited in their home by an interviewer who conducted systematic observations of the home environment and who videotaped the parent interacting with his or her child. Children were observed when they were on average 3.3 years old, with 59% seen within 2 months of their third birthday ($SD = 0.5$ years; range 2.1–6.8 years). On average, parents were 33 years old at the time of the assessment ($SD = 5.7$ years; range 21.5–44.7 years). All dyad pairs (i.e., mother/son, mother/daughter, father/son, father/daughter) were equally represented. Parents were paid NZ\$40 for their participation.

Video Observations of Caregiving

During the home visit, each participating parent–child dyad was videotaped in three, increasingly demanding, semistructured situations, each lasting 10 min. The procedure has previously been described in detail (Belsky et al., 2005). Briefly, the first situation involved free play, with the parent instructed to engage their child using a varied set of age-appropriate toys. The second was a competing-task situation which involved the parent sitting on a chair while (a) completing a questionnaire and (b) not permitting the child to engage a second set of toys that was clearly (and purposefully) visible nearby. The third task was a teaching task and involved parent and child seated together, with the parent asked to provide whatever assistance the child needed to complete a set of activities that had been provided.

Each of the three situations was rated by trained coders using a set of 7-point scales developed for the NICHD Study of Early Child Care (NICHD Early Child Care Research Network, 1999). Six scales were used to evaluate parental behavior: sensitive responsiveness, intrusiveness/overcontrol, detachment/disengagement, stimulation of cognitive development, positive regard for the child, and negative regard for the child. Scores for each scale were summed across the interaction episodes to create across-episode total scores. To assess intercoder reliability, 15% of the videotapes were randomly selected and coded by a second coder. Interrater agreement ranged from .77 to .96 across ratings.

Evidence for the validity of these measurements comes from NICHD Study findings linking individual differences in parenting with children's cognitive-linguistic and socioemotional functioning (NICHD Early Child Care Research Network, 1999, 2002). We analyzed a previously developed summary measure comprising all the video observation rating scales of parenting (Belsky et al., 2005). We also separately examined cognitively stimulating parenting, as indexed by the stimulation of cognitive development subscale, versus warm, sensitive parenting, as indexed by an averaged measure of the remaining subscales (i.e., sensitive responsiveness, reverse-coded intrusiveness/overcontrol, reverse-coded detachment/disengagement, positive regard for the child, and reverse-coded neg-

ative regard for the child). Video observations of cognitively stimulating and warm, sensitive parenting were correlated with each other, $r = .61$.

Interviewers' Impressions of the Caregiving Environment

Following the home visit, the interviewer rated each family on the Infant/Toddler Home Observation for Measurement of the Environment (HOME; Caldwell & Bradley, 1984). The HOME measures the quality and quantity of stimulation and support available to the child in the home environment. Home interviewers indicated the absence (0) or presence (1) of each of 45 items pertaining to features of the home and family environment. Following previous research using the HOME (Bradley & Corwyn, 2005), we constructed a summary measure reflecting a warm-sensitive-stimulating home environment, omitting 10 items that assessed other aspects of the home environment, such as whether the family had a pet. This measure had an internal consistency reliability of .81. Parallel to the video assessment of parenting we also constructed separate measures reflecting the degree to which home environments were cognitively stimulating and warm-sensitive. The cognitive stimulation measure was an average score across 21 items reflecting the availability of learning materials and direct attempts by parents to teach skills and concepts (example items: "Parent provides toys that challenge child to develop new skills" and "Child has three or more books of his or her own") ($\alpha = .77$). The warm-sensitive measure was an average score of 14 items reflecting parental expressions of warmth, affection and sensitivity toward their child (example items: "Parents voice conveys positive feelings towards child"; "Parent does not express overt annoyance with or hostility to child") ($\alpha = .66$). These two home environment measures were correlated with each other, $r = .42$.

Dunedin Participant-Parents Own Experienced-Parenting

Measures reflecting the Dunedin participants' experienced-parenting during early (ages 3 and 5 years) and middle childhood (ages 7 and 9 years) were available in the study archives. These included the Parental Attitude Research Instrument (PARI; Schaefer & Bell, 1958) at ages 3 and 5 years, assessing mothers' openness to communications from her child and their authoritarian parenting; an interview with mothers at ages 7 and 9 years, assessing their practices disciplining the child; the Family Relations Index of the Family Environment Scales (FES; Moos & Moos, 1981) at ages 7 and 9 years, assessing family atmosphere; and maternal reports on the activities and experiences of the child at home (such as being read to and dressing up) and away from home (such as zoo, farm, train, beach) at all ages. For use in the Dunedin Parenting Study, Belsky et al. (2005) created reliable and valid averaged composite measures reflecting 'positive' and 'negative' parenting. To reduce the risk of multiple testing in our analyses, we averaged the measures (after reverse-coding negative parenting), to create an overall measure of positive experienced-parenting in childhood.

Dunedin Participant-Parents' Educational Attainment

Participant-parents' educational attainment was measured as the highest degree completed by the time of participation in the Parenting Study. For the parents in our cohort, compulsory education ended at age 15 years, at which point students could elect to sit for a School Leaving Certificate exam. By the time of their participation in the Parenting Study, 13% of parents had obtained no educational credential; 11% had obtained the School Leaving Certificate but did not progress further, 46% had completed qualifications roughly equivalent to a full high school diploma in the United States, such as 6th form or Bursary Certificates, and 31% had completed a university degree.

Dunedin Participant-Parents' Childhood Cognitive and Self-Control Skills

Participant-parents' cognitive ability was individually assessed when they were ages 7, 9, 11 and 13 years old, using the Wechsler Intelligence Scale for Children-Revised (WISC-R; Wechsler, 1974). Scores were averaged across age and standardized to $M = 0$, $SD = 1$. Participant-parents' low self-control was measured using multiple measures of self-control as previously described (Moffitt et al., 2011): observational ratings of participants' lack of control (ages 3 and 5) and parent, teacher, and self-reports of impulsive aggression, overactivity, lack of persistence, inattention, and impulsivity (ages 5, 7, 9, and 11). Based on principal components analysis, the standardized measures were averaged into a single composite score ($M = 0$, $SD = 1$; Moffitt et al., 2011), and coded so that a high score reflects high self-control.

Genotyping and Imputation

We used Illumina HumanOmni Express 12 BeadChip arrays (Version 1.1; Illumina, Hayward, CA) to assay common single-nucleotide polymorphism (SNP) variation in the genomes of Dunedin study participant-parents. Commercially available genotyping arrays measure only a subset of all SNPs. It is possible to use imputation to infer genotypes for additional, unmeasured SNPs. Imputation in genetics is different from imputation in the social and behavioral sciences. Genotype sequences are inherited in *chunks* (i.e., spatially proximate genotypes tend to be inherited together). If several base pair genotypes are known, the surrounding base pair genotypes can be imputed with high accuracy. Imputation is a standard practice in genetics research (Marchini & Howie, 2010) and is recommended by the consortium that published the GWAS of educational attainment that we used to compute the education polygenic score for this study (Lee et al., 2018). We therefore imputed SNPs, using the IMPUTE2 software (Version 2.3.1, https://mathgen.stats.ox.ac.uk/impute/impute_v2.html; Howie, Donnelly, & Marchini, 2009) and the 1000 Genomes Phase 3 reference panel (Abecasis et al., 2012). Imputation was conducted on SNPs appearing in dbSNP (Version 140; <http://www.ncbi.nlm.nih.gov/SNP/>; Sherry et al., 2001) that were called in more than 98% of the samples. Invariant SNPs were excluded. Prephasing and imputation were conducted using a 50-million-base-pair sliding window. We used only SNPs imputed with >90% confidence of a specific genotype to compute the polygenic score. In general, polygenic scores computed from imputed SNP data are

highly correlated with polygenic scores computed from genotype-only data (within our own data, $r = .89$ between imputed and genotyped-only polygenic scores) and are similarly predictive in phenotype association analysis (Ware et al., 2017).

We restricted our analyses to European-descent members of the Dunedin cohort because allele frequencies, linkage disequilibrium patterns, and environmental moderators of associations may vary across populations (Martin et al., 2017). Genotype data were available for $n = 654$ (93%) of the $n = 702$ participating in the Parenting Study. We analyzed SNPs in Hardy-Weinberg equilibrium ($p > .01$).

Polygenic Scoring

Polygenic scoring was conducted following the method described by Dudbridge (Dudbridge, 2013) using PRSice (Euesden, Lewis, & O'Reilly, 2015). Briefly, SNPs reported in the most recent GWAS results released by the Social Science Genetic Association Consortium (Lee et al., 2018) were matched with SNPs in the Dunedin database. For each SNP, the count of education-associated alleles was weighted according to the effect estimated in the GWAS. Weighted counts were averaged across SNPs to compute polygenic scores. We used all matched SNPs to compute polygenic scores irrespective of nominal significance for their association with educational attainment and linkage disequilibrium between SNPs. The education polygenic score computed in our sample includes approximately 6,512,686 SNPs of which approximately 5,921,145 were imputed. To control for possible population stratification, we conducted a principal components analysis of our genome-wide SNP database using PLINK v1.9 (Chang et al., 2015). The 10 principal components explained 1.2% of variance in the education polygenic score. We residualized polygenic scores for the first 10 principal components estimated from the genome-wide SNP data. The residualized score was normally distributed. We standardized residuals to $M = 0$, $SD = 1$ for analysis.

Statistical Analysis

We used linear regression analyses to test whether the polygenic score for educational attainment predicted participant-parents' caregiving. Mothers and fathers did not differ in their polygenic scores or in their provision of warm-sensitive parenting, but mothers provided more cognitively stimulating parenting than fathers; we therefore adjusted for sex in all models. Regression models were extended to include additional covariates as described in the Results; for example, to test whether the polygenic score predicted caregiving over and above own experienced-parenting and whether educational attainment and early-emerging cognitive and self-control skills mediated genetic associations with caregiving. All continuous measures were standardized to $M = 0$, $SD = 1$. All analyses were conducted using Stata Version 14.2 (StataCorp, 2015).

Results

Do Parents' Polygenic Scores for Educational Attainment Predict the Caregiving They Provide to Their Children?

Results supported our hypothesis that parents' polygenic scores predict their caregiving. Parents with higher education polygenic scores provided more warm, sensitive, stimulating caregiving, as assessed by both video observations and the HOME ($\beta = .12$, 95% CI [.04, .19], $p < .01$ for video observations and $\beta = .16$, 95% CI [.09, .24], $p < .01$ for the HOME; Figure 1). The modest effect sizes indicate that a parents' high polygenic score did not always go along with warm, sensitive, and stimulating caregiving, and that many parents with low polygenic scores provided warm, sensitive, stimulating caregiving to their children. This finding is illustrated by comparing the proportion of parents providing a high level of warm, sensitive, stimulating caregiving (operationally defined as falling above the median of caregiving) among those with high

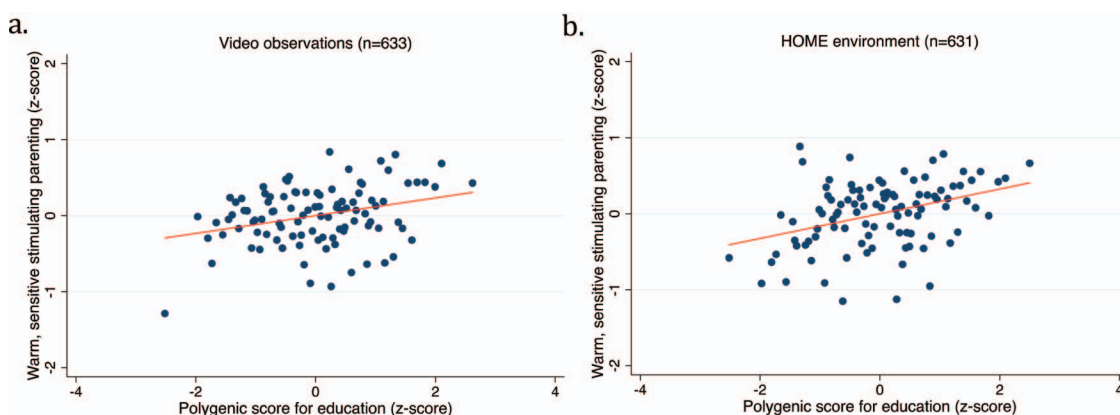


Figure 1. The polygenic score for educational attainment is associated with warm, sensitive, stimulating caregiving across different methods of assessment. The scatterplots show associations between the polygenic score for educational attainment and caregiving provided by parents, as measured through video observations (a) and observations of the home environment (b). Each plotted point represents the mean x and y coordinates for a bin of about 6 parents. The solid lines are the best-fitting regression lines. See the online article for the color version of this figure.

(>1 *SD* above the mean) versus low (<1 *SD* below the mean) education polygenic scores (the proportions were 63% vs. 45% for the video observations and 60% vs. 36% for the HOME).

Do Parents' Polygenic Scores for Educational Attainment Differentially Predict Cognitively Stimulating Versus Warm, Sensitive Parenting?

Results did not support specificity of genetic associations with different aspects of caregiving. We tested this possibility by examining genetic associations with subscales of video observations and the HOME that reflected cognitively stimulating versus warm, sensitive caregiving and testing whether associations differed. This was not the case; parents' polygenic scores predicted cognitively stimulating as well as warm, sensitive caregiving, across both data-collection methods (see Figure 2).

Based on the finding that genetic associations were similar across both assessment methods (video observations and HOME) as well as both aspects of caregiving (cognitively stimulating vs. warm, sensitive caregiving), we created an overall measure of warm, sensitive, stimulating parenting averaged across assessment methods and subscales of caregiving. The association between the polygenic score and this overall measure was $\beta = .16$ (95% CI [.08, .23], $p < .01$). Effect sizes were similar for mothers and fathers ($\beta = .18$, 95% CI [.07, .29], $p < .01$ for mothers' and $\beta = .13$, 95% CI [.02, .24], $p < .05$ for fathers' caregiving).

Do Genetic Associations With Parenting Reflect Evocative Effects of Children?

Results did not support the possibility that associations between parents' polygenic scores and caregiving reflect evocative effects of children. This possibility arises because parents' and children's genetics are correlated because of their relatedness, and children's genetic differences have been shown to evoke differences in parenting (Avinun & Knafo, 2014). Associations between parents' polygenic scores and caregiving might therefore pick up on effects of children's genetics. Although children's genomes were not

measured, children's behavior during the videotaped parent-child interaction tasks was coded on four scales (positive mood, negative mood, activity level, and sustained attention, as described previously; Belsky et al., 2005; NICHD Early Child Care Research Network, 1999). Adjusting for children's behavior did not change associations between parents' polygenic scores and the caregiving they provided (adjusted $\beta = .15$, 95% CI [.08, .22], $p < .01$).

Are Parents' Polygenic Scores Associated With Their Warm, Sensitive, Stimulating Caregiving Over and Above Their Own Experienced-Parenting?

Findings supported the hypothesis that the polygenic score for educational attainment predicted parenting independently of parents' own experienced-parenting. Parents who had themselves received more positive parenting when they were young tended to go on to provide more warm, sensitive, stimulating caregiving to their own children, indicating intergenerational transmission of positive parenting ($\beta = .32$, 95% CI [.25, .40], $p < .01$). Furthermore, there was a gene-environment correlation whereby parents with higher polygenic scores had received more positive parenting when they were children ($\beta = .12$, 95% CI [.04, .20], $p < .01$). However, parents' polygenic scores predicted their warm, sensitive, stimulating caregiving, over and above the parenting they themselves had received ($\beta = .12$, 95% CI [.05, .19], $p < .01$). Figure 3 shows associations between the polygenic score and warm, sensitive, stimulating caregiving in groups of parents within the bottom, middle, and top tertile for own experienced-parenting.

Do Polygenic Scores Predict Caregiving Over and Above Parents' Age at Entry to Parenthood?

Findings supported the hypothesis that the polygenic score for educational attainment predicted parenting independently of the age at which participants first became parents. Parents were on average 29 years old ($SD = 6$ years, range 15–42 years) when they had their first child. Those who had become parents at older ages provided more warm, sensitive, stimulating caregiving to their

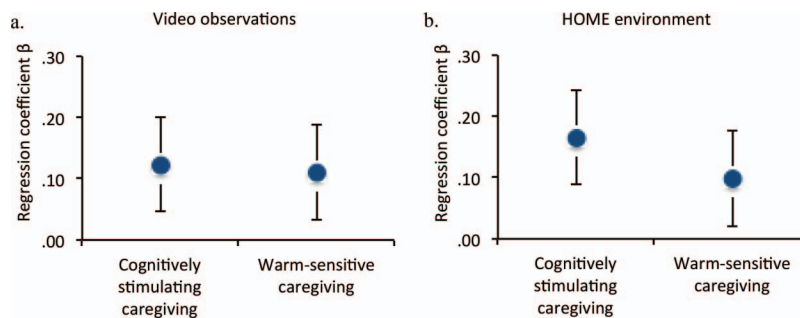


Figure 2. The polygenic score for educational attainment is associated both with cognitively stimulating and warm-sensitive caregiving. The figure shows associations (indicated by standardized regression coefficients) between the polygenic score and cognitively stimulating versus warm-sensitive caregiving assessed using video observations (a) and observations of the home environment (b). All associations are adjusted for parents' sex. Error bars indicate 95% confidence intervals. Effect sizes of associations between cognitively stimulating and warm, sensitive caregiving were not significantly different from each other, neither for video observations ($p = .83$) nor for observations of the home environment ($p = .22$). See the online article for the color version of this figure.

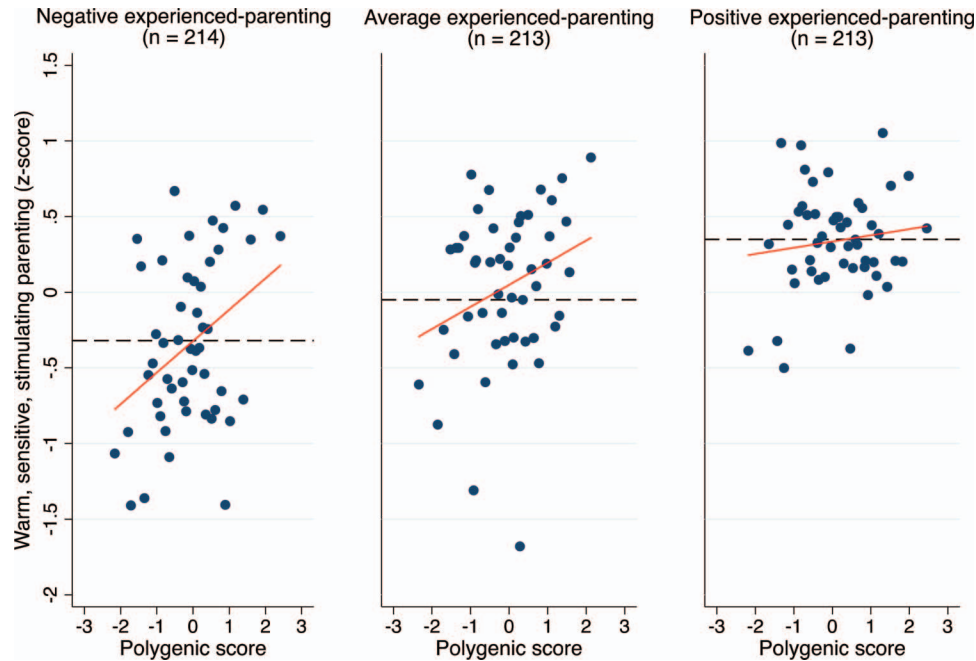


Figure 3. Parents' polygenic scores for educational attainment predicted their warm, sensitive, stimulating caregiving over and above the quality of their own experienced-parenting. The scatterplots show the association between parents' polygenic scores (z scores) and an overall measure of warm, sensitive, stimulating caregiving (z score), separately for participants within the bottom, middle and top tertile for own experienced-parenting (a categorized version of the continuous measure of own experienced-parenting used in the analyses). Each plotted point represents the mean x and y coordinates for a bin of about five parents. The solid lines are the best-fitting regression lines. The dashed lines show the mean level of warm, sensitive, stimulating caregiving for each subgroup. The polygenic score tended to predict own parenting better among people who had experienced more negative parenting in their family of origin (left panel above); however, this association was not statistically significant with our sample size (p value for the interaction was $p = .06$). See the online article for the color version of this figure.

children, compared with their cohort peers who became parents at younger ages ($\beta = .39$, 95% CI [.32, .47], $p < .01$). Parents with higher polygenic scores tended to have their child at a later age ($\beta = .07$, 95% CI [-.01, .15], $p = .08$). However, parents' polygenic scores predicted their caregiving regardless of when they had their first child ($\beta = .13$, 95% CI [.06, .20], $p < .01$).

Can Parents' Early-Emerging Cognitive and Self-Control Skills Explain Genetic Associations With Their Caregiving?

As outlined in the Introduction, the education polygenic score may be associated with parenting because individuals with high polygenic scores completed more education, or because they possess characteristics that made them go further in their education and become more effective parents once they had children. We first tested whether educational attainment mediated genetic associations with caregiving. As expected, individuals with higher polygenic scores completed more education ($\beta = .25$, 95% CI [.17, .32], $p < .01$) and individuals who completed more education provided more warm, sensitive, stimulating caregiving ($\beta = .45$, 95% CI [.38, .52], $p < .01$). Parents' educational attainment was a statistically significant mediator of the effect of parents' polygenic scores on caregiving, reducing the polygenic-score association

with caregiving by approximately two thirds (see Table 1). However, this analysis does not differentiate between the two possible explanations. Furthermore, individuals with lower polygenic scores tended to have their children earlier, and early childbearing may have disrupted these individuals' education. The longitudinal design of the Dunedin study made it possible to test the role of personal characteristics that participants already had before completing their education or becoming parents. As expected, parents with higher polygenic scores for educational attainment displayed greater cognitive and self-control skills when they were youngsters ($\beta = .27$, 95% CI [.19, .34], $p < .01$ for cognitive skills and $\beta = .19$, 95% CI [.11, .26], $p < .01$ for self-control skills). Those with greater cognitive and self-control skills went on to provide more warm, sensitive, stimulating caregiving to their children once they became parents ($\beta = .39$, 95% CI [.32, .46], $p < .01$ for cognitive skills and $\beta = .33$, 95% CI [.26, .41], $p < .01$ for self-control skills). Cognitive and self-control skills were both statistically significant mediators of the effect of parents' polygenic scores on caregiving ($p < .01$ for both; Table 1). Together, they accounted for approximately 71% of the polygenic-score association with caregiving (see Table 1). These results indicate that parents with higher polygenic scores for educational attainment provide greater warm, sensitive, stimulating caregiving in large part because they

Table 1
Formal Tests of Parents' Childhood Cognitive and Self-Control Skills and Adult Educational Attainment as Mediators of Genetic Associations With Caregiving

Measure	Estimate [95% CI]
Total effect	.16 [.08, .23]
Educational attainment as mediator	
Direct effect	.05 [−.02, .12]
Indirect effect	.11 [.07, .14]
% Mediation	69%
Childhood cognitive skill as mediator	
Direct effect	.06 [−.02, .13]
Indirect effect	.10 [.07, .13]
% Mediation	63%
Childhood self-control as mediator	
Direct effect	.10 [.02, .18]
Total indirect effect	.06 [.03, .09]
% Mediation	38%
Childhood cognitive and self-control skill as mediators	
Direct effect	.04 [−.04, .12]
Total indirect effect	.12 [.08, .16]
% Mediation	75%
Educational attainment, childhood cognitive and self-control skill as mediators	
Direct effect	.01 [−.07, .08]
Total indirect effect	.15 [.11, .19]
% Mediation	94%

possessed better cognitive and noncognitive skills already before they completed their education and became parents.

Discussion

It has long been appreciated that parenting is multiply determined, including by individual differences that adults bring to bear on their caregiving (Belsky, 1984). Consistent with the idea that individual differences shape parenting, studies have shown that parenting is genetically influenced (Klahr & Burt, 2014). Here we extended prior work by conducting a molecular-genetic study to investigate whether—and how—parents' genotypes influence the kinds of caregiving environments they created for their offspring. Toward this end, we relied on a polygenic score derived from recent genome-wide association studies (GWAS) of educational attainment. To our knowledge, this is the first report examining associations between a GWAS-derived polygenic score and observed caregiving behavior in a cohort of mothers and fathers.

Findings revealed that parents with higher polygenic scores for educational attainment provided more warm, sensitive, and stimulating caregiving to their offspring, both in personal interactions with their young children (as captured on video) and through the home environments they created for their families (as observed by home visitors). Although the magnitude of this effect was small, three features stand out. First, parents' genetics predicted their caregiving irrespective of their own childhood experiences of parenting. Second, parents' genetics were associated with warm, sensitive and stimulating caregiving even when individuals began parenting under less than ideal circumstances, such as when they had children at a young age. Third, parents' genetics predicted their caregiving because they influenced the early development of personal characteristics that facilitated positive caregiving once

individuals became parents, including greater cognitive and self-control skills. Taken together, our findings illustrate how individuals' polygenic scores not only influence their own life-course development, but also the environments they create for their offspring.

Parents' educational attainment is known to predict their caregiving (Davis-Kean, 2005), so it may seem unsurprising that a polygenic score derived from a GWAS of educational attainment would be associated with parenting. However, there are three reasons why examining associations between an education polygenic score and parenting is informative over and above the known phenotypic associations between the two. First, genetic associations with parenting inform the interpretation of associations between parenting and children's educational attainment. Our findings show that genes that influence educational attainment also predict the kind of parenting that is linked with educational success. This finding suggests that genetic influences may create the false impression of a causal relationship between parenting and children's attainment (Knafo & Jaffee, 2013; Sherlock & Zietsch, 2018). Second, genetic associations with parenting inform the interpretation of findings from genome-wide association studies of educational attainment. Our findings indicate that GWAS of educational attainment partly capture aspects of children's environment, including the parenting that children receive. Previous polygenic-score studies have pointed to this possibility—in particular, studies have shown that parents' education-associated alleles predict children's educational attainment even if they are not passed on to children (Bates et al., 2018; Belsky et al., 2018; Kong et al., 2018). This finding suggests that education-associated genetics affect educational outcomes partly via the parenting children receive. Our study is a first step toward testing this hypothesis, by establishing whether parents' genetics are associated with parenting. Third, genetic associations with parenting inform our understanding about how genetic influences on parenting may operate. Our findings show that education-associated genetics predict parenting via early-emerging characteristics, extending research from twin and adoption studies, which do not reveal how parents' genetics shape their caregiving. In the absence of a GWAS for parenting, GWAS of phenotypes known to be related to parenting (such as educational attainment) can be used to study how parents' genetics influence their parenting.

Our findings illustrate how genetics may contribute to continuity of behaviors across generations. Intergenerational transmission has been vigorously studied in relation to the cycle of poverty (D'Addio, 2007) and the cycle of violence across generations (Widom & Wilson, 2015). Here we find that the same polygenic score that predicts greater educational and occupational attainment (Belsky et al., 2016) and lower antisocial behavior (Wertz et al., 2018) of individuals in their own lifetime also predicts the kind of caregiving—warm, sensitive and stimulating—that is known to affect these same outcomes in the next generation (Aunola & Nurmi, 2005; Rothbaum & Weisz, 1994). To the extent that genes are associated with behaviors, they may therefore contribute to intergenerational continuity both directly (via genetic inheritance) but also indirectly via nurture (i.e., by affecting the caregiving environment that shapes their offspring's outcomes). Although genetic influences will tend to promote continuity across generations on average, genes may also contribute to changes in behaviors across generations. Indeed, our finding that higher polygenic

scores were associated with positive caregiving among those with less supportive starting conditions into life as a parent suggests that genetic differences between individuals are implicated in the process by which individuals break the cycle of a negative early familial environment.

Our study went beyond showing an association between parents' polygenic scores and caregiving by conducting an initial test of the process by which genetic effects may be instantiated. Part of the reason why parents with higher polygenic scores provided more warm, sensitive, and stimulating caregiving was because they displayed, in childhood, personal characteristics that are known to be associated with more effective parenting, such as greater cognitive ability and higher self-control. These results are consistent with evidence that parents' personal-psychological attributes influence their parenting (Belsky & Jaffee, 2006; Prinzie, Stams, Deković, Reijntjes, & Belsky, 2009), although to our knowledge the Dunedin Study is the first to show that greater cognitive and self-control skills in childhood predict future parenting. Cognitive and noncognitive skills may promote future warm, sensitive and stimulating caregiving directly, for example by enabling parents to acquire more knowledge about effective parenting or by enabling them to avoid coercive conflicts in interaction with their child. Cognitive and noncognitive skills may also promote supportive caregiving more indirectly by enabling parents to accumulate assets that can make it easier to be a warm, sensitive, stimulating caregiver, such as economic security or a supportive partner (Belsky et al., 2016; Hoff et al., 2002).

Our study has limitations. First, effect sizes were uniformly small, which is not surprising given the multiple determinants of parenting behavior. Nevertheless, it is notable that the polygenic score accounted for additional variance beyond other factors known to shape parenting, such as parents' own experiences of parenting in their family of origin. Furthermore, effect sizes of genetic associations are likely to increase as better polygenic scores, based on larger GWAS samples, are developed (Okbay et al., 2016; Plomin & von Stumm, 2018). Second, the findings cannot be generalized to individuals of non-European ancestry because allele frequencies, linkage disequilibrium patterns, and environmental moderators of the association may vary across populations (Martin et al., 2017). Third, we were unable to test hypotheses about how Dunedin Study members' parenting affected their children, because these data are being collected when each child reaches age 15, and insufficient numbers of children have reached this age to conduct the analyses at this time. Fourth, some of the apparent association between parental polygenic scores and caregiving may reflect evocative effects of children's genetics on the parenting they receive (Avinun & Knafo, 2014; Krapohl et al., 2017). We were unable to test this hypothesis, because we did not measure children's genomes. However, accounting for children's observed behavior did not change associations between parents' polygenic scores and the parenting they provided during the parent-child interaction tasks. Fifth, a general limitation of GWAS in the social sciences is that their target phenotypes—for example, educational attainment—are sensitive to cultural and historical influences, which may limit the generalizability of results. However, the GWAS on which the education polygenic score in this study is based consisted of samples representing a range of countries and historical periods (Lee et al., 2018). Furthermore, links between a polygenic score derived from

the GWAS of educational attainment and educational attainment have been widely replicated (Belsky et al., 2016; Rietveld, Conley, et al., 2014; Selzam et al., 2017). Sixth, we restricted our analyses of genetic associations to a polygenic score for educational attainment. As already noted, we chose this score because: educational attainment and its social and behavioral correlates are understood to be determinants of parenting; the score is based on the largest-ever GWAS of a social-behavior phenotype; and prior research links these genetics directly to putative determinants of parenting. However, this was only one polygenic score that represents only a fraction of all genetic influences on parenting. Until a GWAS for parenting is carried out, we and others will have to depend on such proxy-polygenic scores.

Our findings have implications for the interpretation of research on the effects of nature and nurture on child development. Genetic influences on home environments imply that a link between home environments and children's development cannot unambiguously be interpreted as reflecting a causal effect (Sherlock & Zietsch, 2018). The interpretive problem introduced by such genetic confounding has been well-described (Avinun & Knafo-Noam, 2015; Knafo & Jaffee, 2013; Moffitt, 2005). However, it is seldom appreciated that the reverse interpretive problem is also true. Genetic associations with caregiving environments complicate interpreting effects of polygenic scores on individuals' outcomes, because these effects may partly result from caregiving environments created through the same genetics in the parents. This phenomenon of genetic nurture could upwardly bias associations between polygenic scores and phenotypes (Bates et al., 2018; Koellinger & Harden, 2018; Kong et al., 2018). In other words, if the same genes that influence an outcome in the offspring generation also led parents to create caregiving environments that affect the outcome, it is difficult to interpret the effect of genes on that outcome as causal unless analyses take possible effects of parental genotype on caregiving environments into account. Thus, whereas parenting researchers need to pay attention to genetics, geneticists need to pay attention to the social context, including parenting, when estimating genetic influences on traits and behaviors (Domingue et al., 2018).

Our findings also have implications for our understanding of what the polygenic score for educational attainment represents. Some pundits were initially dubious about whether genetic discoveries from GWAS of a sociological variable such as educational attainment would be associated with meaningful individual differences. However, an ever-increasing number of studies now document the widespread influence of education-GWAS discoveries on many cognitive and behavioral traits, from IQ to antisocial behavior (Belsky et al., 2016; Plomin & von Stumm, 2018; Rietveld, Esko, et al., 2014; Wertz et al., 2018). The findings presented here further show that education-GWAS discoveries are also implicated in the environments that individuals create, for themselves and for their children. It is not yet clear whether education-GWAS discoveries will lead to a better understanding of the neurobiological basis of cognition and behavior (Boyle, Li, & Pritchard, 2017; Lee & McGue, 2016). What is apparent, however, is that education-GWAS discoveries lend themselves to use in research that seeks a better understanding of the developmental processes by which active gene-environment correlations are constructed in one generation and passive gene-environment correlations are created for the next generation (Scarr & McCartney, 1983). Understanding these processes is

fundamental to explaining how inequalities are created, sustained, and overcome.

Finally, genetic research in child development is often met with trepidation, perhaps because of fears that findings could be used to develop tests to predict children's outcomes, and because of the persistent myth that genetic influences imply nonmalleability. However, even in an age of ever-increasing GWAS samples, genetic prediction of behavioral outcomes is unlikely to reach the predictive power of measures that have been in the hands of psychologists for decades, such as assessments of a child's cognitive ability, personality or family history (Borghans, Duckworth, Heckman, & ter Weel, 2008; Deary, Whiteman, Starr, Whalley, & Fox, 2004; Milne et al., 2009; Roberts, Kuncel, Shiner, Caspi, & Goldberg, 2007). For caregiving specifically, our findings show that parents' cognitive and self-control skills, as well as their own experienced parenting, predict their future caregiving far better than their polygenic scores do. Because of these relatively small polygenic-score effect sizes, we do not believe that any recommendations for policy are currently warranted. However, if the findings presented here—for example, that parents' genetics contribute to positive caregiving and caregiving mobility via personal skills—replicate with larger effect sizes in future studies, they support what is known already: that interventions most effective at 'breaking the cycle' of disadvantage should target individuals when they are young and aim to improve their skills (Heckman, 2006; Heckman & García, 2017). Thus, although it is not possible to change the genes people are born with, it is possible to change behaviors that link genes with outcomes, thereby promoting healthy parent and child development in all families.

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Received June 3, 2018

Revision received December 21, 2018

Accepted January 11, 2019 ■