

# Heritability of High Reading Ability and its Interaction with Parental Education

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**Abstract** Moderation of the level of genetic influence on children's high reading ability by environmental influences associated with parental education was explored in two independent samples of identical and fraternal twins from the United States and Great Britain. For both samples, the heritability of high reading performance increased significantly with lower levels of parental education. Thus, resilience (high reading ability despite lower environmental support) is more strongly influenced by genotype than is

high reading ability with higher environmental support. This result provides a coherent account when considered alongside results of previous research showing that heritability for low reading ability decreased with lower levels of parental education.

**Keywords** High reading ability · Gene-by-environment interaction · Twins · Resilience

## Introduction

The overall goal of this study was to test whether the heritability of high reading ability was moderated by parent education. We predict, based on the work by Pennington et al. (2008), that moderation of group heritability for high reading should take the form of a resilience interaction in which genes play a greater role in a good outcome when there is less environmental support for that outcome than when there is greater environmental support for a good reading outcome. In what follows, we review previous research that has motivated the present study. DeFries and Fulker (1985, 1988) proposed a multiple regression model for the analyses of twin data that estimates group heritability specific to low or high levels of a trait in samples selected from the high or low tails of normally distributed phenotypes, such as reading. Previous research has shown that group heritability for both low reading ability (DeFries and Alarcón 1996; Gayán and Olson 2001; Harlaar et al. 2005) and high reading ability (Boada et al. 2002) is substantial, accounting for over 50% of extreme group membership. However, there may be significant variation in the level of heritability for individuals within the extreme groups that interacts with family environment. In other words, there may be a gene-by-environment ( $G \times E$ ) interaction in that the effect of genotype for high reading ability is moderated by environmental

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support. This line of research is important because reading is a basic skill that is essential for high academic achievement. Understanding how genetic and environmental influences interact for group membership in the high tail of reading ability can provide new insight about individual differences within the high literacy group.

Recently Friend et al. (2008) explored the interaction between low reading heritability and the twins' reading environment in a sample of 545 twin pairs, as indexed by their parents' mean years of education. Higher levels of parental education are associated with greater investment in children's performance in school and their educational attainment (Craig 2006), and with performance on cognitive measures and health outcomes (Bradley and Corwyn 2002). Of specific relevance to individual differences in early reading development, parental education is correlated with child print environment in preschool (Samuelsson et al. 2005), and with the mean Colorado state testing score of the school that children are attending (Olson et al. 2009). These studies suggest that parental education may be a good indicator of environmental risk and support factors influencing reading development. However, parental education may also be indicative of genetic influence on parents' education that is shared with their children's reading ability and reading support in the home. To control for this potential genotype-environment correlation ( $r_{GE}$ ), Friend et al. (2008) used a residual parental education moderator that was uncorrelated with probands' scores on reading and then tested for the interaction between heritability of low reading ability and parental education. This residualization facilitates unbiased regression-based tests for  $G \times E$  interactions (Purcell 2002; G. Carey, personal communication).

Friend et al. (2008) found that heritability of low reading ability was significantly higher among children whose parents had higher levels of education in a sample of identical and fraternal twin pairs in which at least one proband had a school history of reading disability. In contrast, heritability was lower and shared family environment was relatively more important for twins whose parents had low levels of education. These results support the idea that on average, poor environmental support for reading may often be the main cause of low reading performance among children whose parents have less education, while genes may be more important as a cause of the low reading performance among children who fail in reading in spite of greater environmental support.

In this paper, we turn our attention to the group heritability of high reading ability and its interaction with parents' years of education. Pennington et al. (2008) recently investigated whether parental education moderated heritability of above average reading ability in the Colorado Learning Disabilities Research Center (CLDRC) twin sample. They used a cutoff of .5 SD above the population mean on a standardized

measure of reading ability. Their hypothesis was that children with above average reading ability and lower environmental support for reading should demonstrate a resilience that is more strongly influenced by genes. The results demonstrated that consistent with this hypothesis, the heritability of above average reading performance decreased significantly with increasing levels of parental education. However, the interaction of heritability with parent education was not significant using more extreme selections for high reading, possibly due to small sample sizes.

In the present study, we estimated the heritability of high reading ability (at least one standard deviation above the population mean) and its interaction with parent education. This cut-off point yielded a sample size with sufficient power to detect  $G \times E$  interaction within a group of high ability readers who were all well above the population mean. High reading probands were selected from two independent longitudinally assessed population samples of twins from the US (Colorado) and the UK. In the Colorado sample, we analyzed data from children with high reading ability collected at the end of kindergarten, first, and second grade. In the UK sample (Twins' Early Development Study; TEDS), we analyzed data from children with high reading ability collected in the first and 6th grades. These data allowed us to assess relationships between parents' education and the heritability of high reading ability across the early grades when children are learning to read and in 6th grade when children are reading to learn.

## Method

### Colorado sample

#### Participants

Progress in early literacy development for the Colorado twin sample was assessed in 489 monozygotic and same sex dizygotic twin children recruited in the last year prior to kindergarten from the Colorado Twin Registry. Ninety percent of families initially approached when the twins were in preschool agreed to participate, with a very low level of attrition (1%) through second grade. Their reading ability was assessed at the end of kindergarten, first, and second grade. All of the twins were native English speakers. Zygosity was determined by DNA analysis from cheek swab collection, or, in a minority of cases, by selected items from the questionnaire by Nichols and Bilbro (1966).

**Proband selection** Probands were selected if they scored a minimum of 1 SD above the sample mean. At the end of kindergarten this selection yielded a sample of 114 twin pairs (MZ = 38, DZ = 76, mean age 6.3 years, SD = .33, 47%

male). At end of first and second grades, this selection yielded samples of 112 twin pairs (MZ = 49, DZ = 63, mean age 7.5 years, SD = .33, 50% male) and 105 twin pairs (MZ = 40, DZ = 65, mean age 8.4 years, SD = .32, 49% male), respectively. Although this is a longitudinal sample, probands were selected independently at each test occasion based on a plus 1 SD cut-off. However, the samples were largely overlapping across grade level due to high longitudinal correlations between grades for our reading measure.

### Measures

**Reading** Reading skills in kindergarten, first grade, and second grade were measured by the word and nonword subtests from the Test of Word Reading Efficiency (TOWRE; Torgesen et al. 1999), with both forms A and B administered and averaged to increase reliability (test-retest reliability for children aged 6–9 years is .97 for word and .90 for nonword standard scores). Children were directed to read from a list of words and a list of nonwords as quickly as possible. Their scores for the word list and the nonword list were based on the number of items read correctly in 45 s. Each twin's reading was tested separately in their home by different testers. A standardized composite measure of reading skill was created from combining the highly correlated word and nonword scores at kindergarten ( $r = .85$ ), first grade ( $r = .89$ ), and second grade ( $r = .83$ ). Outliers were truncated to  $\pm 3$  SD. Trimming scores in this way, which is typical in unselected samples, reduces effects of extreme outliers.

**Parental education** Parents provided their years of education as part of a larger questionnaire. Data on parents' years of education was available for all families in this study (mean = 15.87, SD = 1.97, range = 11–21 years). A mean score was created from parental education when information was available from both parents (99%). In a minority of cases, the years of education from the one available parent (usually the mother) was used. Mean parental education was significantly correlated with probands' reading at .198 in kindergarten, .214 in first grade, and .226 in second grade. This mean parental education variable was adjusted for its correlation with probands' reading scores at each grade level separately. Standardized residual mean parental education scores were used in all analyses for this sample.

### TEDS sample

### Participants

The Twins' Early Development Study is a large-scale longitudinal study of twins that has multiple measures on

twins assessed at 2, 3, 4, 7, 9, 10, 12, and 14 years of age. Participants were identified from birth records of twins born in the UK between 1994 and 1996 (Oliver and Plomin 2007). Data used in the present study were obtained from a population sample of 4,987 twin pairs at age 7 (first grade), and 3,772 twin pairs at age 12 (sixth grade). Twins with serious medical or perinatal problems were excluded. Despite attrition from ages 7 to 12, the overall TEDS sample is representative of the population from which twins were drawn (Oliver and Plomin 2007). The samples include data from identical, same sex, and opposite sex twins. We combined these groups in the present analysis because (qualitative) sex differences were not the focus of the study.

**Proband selection** Probands were selected if they scored a minimum of 1 SD above the population mean. At first grade (mean age = 7.1, SD = .24) and sixth grade (mean age = 11.5, SD = .62), this selection yielded samples of 1,155 twin pairs (MZ = 348, DZ = 807, 29% male, 42% female, 29% opposite sex) and 830 twin pairs (MZ = 266, DZ = 564, 29% male, 37% female, 34% opposite sex), respectively.

### Measures

**Reading** At both waves in first and sixth grade, reading ability was assessed by telephone using form A of the TOWRE (Torgesen et al. 1999) that was administered in person in the Colorado sample. The telephone-adaptation of the TOWRE retained the original test materials and the administration procedure was identical to the standard face-to-face procedure. Subtest item lists were mailed to families in a sealed envelope prior to the test sessions with separate instructions that the envelope should not be opened until the time of testing. Twins in each pair were tested within the same test session and by the same tester, who was blind to zygosity. A standardized composite measure of reading skill was created from word and nonword reading at each grade level, and outliers were trimmed to  $\pm 3$  SD prior the present analysis. Trimming scores in this way, which is typical in unselected samples, reduces effects of extreme outliers that may be quite unrepresentative of our high reading group.

**Parental education** Mothers were asked to indicate their highest educational qualification, using a 7-point scale. Response options ranged from 'no qualifications' to 'A/S level' (equivalent to completing a high school education) to 'Postgraduate qualification' (e.g., Masters, Ph.D). For the purpose of the current analysis, we dichotomized the scale. Individuals whose highest qualifications were CSEs (Certificate of Secondary Education), O-levels (Ordinary level of

qualification for a particular subject), or GCSEs (General Certificate of Secondary Education), or who had no qualifications, were classified as having ‘lower’ education levels. This cut-off was used because CSEs, O-levels, and GCSEs are taken in the last year of compulsory education (16 years) in the UK and are typically the minimum educational qualification required by UK employers and higher education institutions. Individuals who had qualifications beyond CSEs, O-levels, or GCSEs—for example, whose highest qualifications were A-levels (Advanced level of qualification for a particular subject used for entrance into a university), an undergraduate degree or a postgraduate degree—were classified as having ‘high’ education levels. At the age 7 assessments, 61.4% of mothers could be classified as having ‘lower’ education levels, and 38.6% had ‘high’ education levels. At the age 12 assessment, 54.1% of mothers had ‘lower’ education levels, and 45.9% had ‘high’ education levels. These data were available for 98.1% of first grade probands and 97.3% of sixth grade probands.

Mothers’ qualification was significantly correlated with probands’ reading in the TEDS twin sample at .158 in first grade and .169 in sixth grade.

This maternal education variable was adjusted for its correlation with probands’ reading scores at each grade level separately. Standardized residual mean scores were used in all analyses for this sample, which were derived by residualizing out a continuous variable (proband scores on reading) from a dichotomous variable (maternal education).

## Analysis

### *DF regression analyses of linear $G \times E$ interactions*

The DeFries-Fulker (DF) regression (DeFries and Fulker 1985, 1988) allows for the estimation of genetic and environmental influences on group membership at the extreme tails of continuous normally distributed phenotypes such as word recognition. Proband group heritability estimates are derived from the differential regression toward the population mean of identical (MZ) cotwins, who share all of their segregating alleles, and fraternal (DZ) cotwins, who share half of their segregating alleles on average. The extension of this method tests whether a moderator significantly influences heritability for extreme group membership.

**Transformation of data** Proband and cotwin  $z$ -scores were transformed prior to analysis by subtracting the population mean (0) from each score and then dividing that total by the difference between the proband mean and the population mean. This transformation yields a mean of 1 for probands and a mean somewhere between 0 and 1 for cotwins because they have not been selected and their

scores tend to be less extreme than proband scores. The transformed proband and cotwin scores are then analyzed using the extended DF regression model.

**Extended DF regression** Equation 1 shows the extended DF regression model, which includes a main effect of parent education and its interactions.

$$C = \beta_1 P + \beta_2 R + \beta_3 ED + \beta_4 P \times ED + \beta_5 R \times ED + K \quad (1)$$

The cotwin’s score ( $C$ ) is regressed on the proband’s score ( $P$ ), the coefficient of relationship ( $R$ ), parental education ( $ED$ ), two interaction terms ( $P \times ED$  and  $R \times ED$ ), and a constant ( $K$ ). The  $\beta_5$  partial regression coefficient tests, by way of the interaction ( $\beta_5$ ) between a moderator ( $\beta_3$ ) and the coefficient of relationship ( $\beta_2$ ) for the differential linear change in heritability as a function of parental education.

**Mx.** We employed the Purcell and Sham (2003) implementation of the DF analysis using the Mx software package (Neale et al. 2003). This method also uses transformed proband and cotwin scores. Scores are single entered along with an additional variable for each twin in a pair indicating proband status. The DF method in Mx parses the variance from MZ and DZ transformed means and covariances for probands and cotwins into additive genetic effects ( $A$ ), shared environment effects ( $C$ ) and non-shared environment effects ( $E$ ) and includes confidence intervals for extreme group membership. A median split was used to estimate  $A$ ,  $C$ , and  $E$  for low and high parental education for each sample and grade level.

## Results

### High reading group membership

Estimates of heritability, shared environment (environmental influence that is common to both members of twin pairs), and nonshared environment (environmental influence that is unique to each member of a pair and/or measurement error) for high reading group membership (1 SD or more above the population mean) are presented by sample and grade level in Table 1. In the Colorado sample, heritability for high reading group membership was significant and substantial at the end of kindergarten ( $h_g^2 = .72$ ), first grade ( $h_g^2 = .72$ ), and second grade ( $h_g^2 = .52$ ). Shared environment influences were not significant at any grade level, and non-shared environment influences were significant at all grade levels.

In the TEDS sample, estimates of group heritability for high reading ability were significant in first ( $h_g^2 = .50$ ) and

**Table 1** Additive genetic influence, shared environment influence, and nonshared environment influence on high reading ability by sample, and grade level

Sample	$h_g^2$ (CI)	$c_g^2$ (CI)	$e_g^2$ (CI)
<i>Colorado</i>			
Kindergarten	.72 (.49, .80)	.00 (.00, .18)	.28 (.20, .37)
First grade	.72 (.49, .84)	.04 (.00, .21)	.24 (.16, .32)
Second grade	.52 (.08, .82)	.17 (.00, .47)	.31 (.11, .50)
<i>TEDS</i>			
First grade	.50 (.30, .59)	.17 (.10, .24)	.34 (.30, .38)
Sixth grade	.59 (.48, .68)	.05 (.00, .13)	.36 (.32, .41)

*Note:* Colorado Sample of twins recruited from the Colorado Twin Registry, TEDS Twins' early development study. Probandes were selected for high reading ability if their scores on word recognition were a minimum of 1 SD above the population mean at each grade level and sample

sixth grade ( $h_g^3 = .59$ ). Shared environmental influence was statistically significant in first grade ( $c_g^2 = .17$ ) but not in sixth grade ( $c_g^2 = .05$ ). Non-shared environment was significant in both first and sixth grades.

Thus, in both the Colorado and TEDS samples, group heritability for high reading is substantially influenced by genes and by nonshared environment (including measurement error). Influences from shared environment were generally not significant, except for the modest influence that was present in the TEDS sample in the first grade.

#### High group heritability interactions with parent education

Transformed cotwin means for high reading ability, which demonstrate regression toward the population mean, are presented by grade level and parental education in Table 2. The pattern of MZ cotwin means was similar across grades, parental education, and samples, ranging from .79 to .91 in the Colorado Sample and from .74 to .88 in the TEDS sample. On the other hand, there was greater variance among the DZ cotwin means. DZ cotwin means tended to be lower for low parent education than for high parent education in both the Colorado and TEDS samples, which is consistent with the hypothesis that heritability varies as a function of parental education.

The results from the extended DF regressions used to test the moderation of parental education on group heritability for high reading ability are presented in Table 3. One-tailed *P*-values are reported here based on the resilience hypothesis and previous data indicating the direction of the effect. We found a consistent interaction for kindergarten, first grade and second grade ( $P = .029$ ,  $P = .033$ , and  $P = .012$ , respectively) in the Colorado samples. In the TEDS samples, although the direction of the interaction was consistent across first and sixth grade, only the interaction in sixth grade

**Table 2** Transformed Cotwin means for high reading ability by sample, grade level, parental education, and zygosity

Sample	MZ cotwins	DZ cotwins
<i>Colorado (low parent education)</i>		
Kindergarten	.85	.36
First grade	.90	.25
Second grade	.86	.21
<i>Colorado (high parent education)</i>		
Kindergarten	.91	.60
First grade	.89	.54
Second grade	.79	.53
<i>TEDS (low maternal education)</i>		
First grade	.79	.41
Sixth grade	.74	.27
<i>TEDS (high maternal education)</i>		
First grade	.88	.55
Sixth grade	.77	.46

*Note:* Colorado Sample of twins recruited from the Colorado Twin Registry, TEDS Twins' early development study. Probandes were selected for high reading ability if their scores on reading were a minimum of 1 SD above the population mean at each grade level and sample

**Table 3** Extended DF regression results by sample and grade level

Sample	No. pairs	Interaction coefficient	<i>t</i> value <sup>a</sup>	<i>P</i> value
<i>Colorado</i>				
Kindergarten	91	-.403	-1.919	.029
First grade	114	-.370	-1.864	.033
Second grade	105	-.499	-2.281	.012
<i>TEDS</i>				
First grade	1,155	-.048	-0.828	.245
Sixth grade	830	-.153	-1.964	.025

*Note:* Colorado Sample of twins recruited from the Colorado Twin Registry, TEDS Twins' early development study. Probandes were selected for high reading ability if their scores on reading were a minimum of 1 SD above the population mean at each grade level and sample

<sup>a</sup> Negative interaction coefficients and *t* values indicate that heritability decreased in each sample as parental education increased

reached significance ( $P = .025$ ). Overall, the data from the Colorado and TEDS samples support a strong genetic influence on resilience from environmental disadvantage, such that heritability for high reading ability increases as parental education decreases.

Estimates of additive genetic influence ( $h_g^2$ ), shared environment ( $c_g^2$ ) and nonshared environment ( $e_g^2$ ) and confidence intervals are presented by parental education, grade level, and sample for high reading group membership in Table 4. The confidence intervals were large. However, it is important to note that the high and low parent



**Table 4** Additive Genetic Influence, Shared Environment Influence, and Nonshared Environment Influence on High Reading Ability by Sample, Parental Ed. Median Split and Grade Level

Sample	$h_g^2$ (CI)	$c_g^2$ (CI)	$e_g^2$ (CI)
<i>Colorado (low parental education)</i>			
Kindergarten	.67 (.52, .84)	.00 (.00, .10)	.33 (.19, .46)
First grade	.78 (.43, .89)	.00 (.00, .28)	.26 (.15, .38)
Second grade	.73 (.44, .88)	.01 (.00, .25)	.26 (.19, .48)
<i>Colorado (high parental education)</i>			
Kindergarten	.46 (.15, .78)	.23 (.00, .48)	.31 (.20, .42)
First grade	.67 (.37, .84)	.07 (.00, .30)	.21 (.10, .34)
Second grade	.29 (.00, .53)	.34 (.11, .41)	.37 (.29, .53)
<i>TEDS (low maternal education)</i>			
First grade	.54 (.39, .69)	.10 (.00, .21)	.36 (.30, .42)
Sixth grade	.60 (.50, .66)	.00 (.00, .06)	.40 (.34, .46)
<i>TEDS (high maternal education)</i>			
First grade	.46 (.33, .60)	.22 (.12, .31)	.32 (.26, .38)
Sixth grade	.48 (.34, .63)	.15 (.05, .26)	.36 (.30, .42)

*Note:* Colorado Sample of twins recruited from the Colorado Twin Registry, TEDS Twins' Early Development Study. Probands were selected for high reading ability if their scores on reading were a minimum of 1 SD above the population mean at each grade level and sample

education sample sizes were half that of the overall sample used in the extended DF regressions. For low parental education in the Colorado sample, heritability estimates were quite similar ranging from .67 to .78, shared environment was consistently estimated at or close to zero, and nonshared environment was also similar ranging from .26 to .33. For high parental education in the Colorado sample, the estimates were less consistent. Heritability ranged from .29 to .67, shared environment from .07 to .34 and nonshared environment ranged from .21 to .37. Heritability estimates here were somewhat lower than twice the difference between MZ and DZ cotwin means because this method constrains  $c^2$  to be equal to or greater than zero.

In the TEDS data, the heritabilities for the low parental education groups were similar across first and sixth grade levels (.54 and .60, respectively), which were higher than the same estimates for the high parental education groups (.46 and .48, respectively). Shared environment was consistently higher for high parental education groups than for the low parental education groups (.22 and .15 vs. .10 and .00, respectively) and nonshared environment was consistent across both grade level and parental education groups ranging from .32 to .40. Consistent with the extended DF regression interaction results, all of the heritability estimates for the high parental education groups were lower than the heritability estimates for the low parental education groups.

## Discussion

The present study investigated group heritability for high reading ability and its interaction with parental education in

twins selected from two independent longitudinal population samples. Group heritability for high reading ability (at least one SD above the population mean) was substantial, ranging from .50 to .72 across grades in the two samples. These results are consistent with those of Boada et al. (2002), who estimated the heritability of above average reading ability at .54.

However, in the present study, the group heritability estimates for high reading varied across levels of parental education. In the extended DF regression analysis, we found a significant linear interaction between parental education and group heritability for high reading in the Colorado and the TEDS samples. In both samples, children whose parents had lower levels of education tended to have stronger genetic influence on their high reading ability compared to children whose parents had higher levels of education. Conversely, this study also suggests that a familial environment that supports literacy development as indexed by high parental education acts to make twins more similar to each other. However, nonshared environment, which are environmental influences that are independent for members of twin pairs, does not change as function of parental education, demonstrating that the trade-off is between genetic influences and shared environmental influences for high reading ability. Thus, this study suggests that continued emphasis on literacy support positively influences high reading ability.

To understand better the basis for the significant linear interaction in the extended DF model, we split the samples into low and high parental education groups and observed the group differences in cotwin mean regression toward the population mean. In the present study of group heritability

for high reading, the MZ cotwin means were similar across education groups, indicating similar levels of influence from nonshared environment. However, DZ cotwin means were substantially lower in the low parental education groups than in the high parental education groups, and this was the basis for the significant interaction between high group heritability and parent education in the extended DF model. The possibility of non-additive genetic influence (i.e., dominance and/or epistasis) for the low parent education groups was suggested by DZ cotwin means that were less than half of the MZ cotwin means, but these deviations from additivity were not statistically significant.

Differences in the type of moderator (mean parental education versus a categorical measure of maternal qualifications) may influence the effect sizes for the interactions across the two studies. If differences at the extremes of the educational range are important for differences in literacy support, a variable such as mothers' qualifications may be less sensitive to capture that variance than a more continuous variable like parental education. However, it is important to note that accumulating an additional year of schooling may be a stronger index of environmental support at certain thresholds such as completing or not completing high school or college than the difference between 8 and 10 years of education or the difference between a masters and a Ph.D for indexing environmental support for literacy development. Therefore, a measure such as the mother's qualifications may be capturing a critical threshold even if it is less sensitive at the extremes.

Although we found a consistent interaction across the early grades in the Colorado data, and in sixth grade in the UK data, the interaction was not significant in first grade in the UK, which did have the largest sample size but the smallest effect size. However, it is important to note that the direction of the interaction was consistent. One potential factor influencing this difference in effect size could be due in part to differences in overall variance in the early educational environment across the two countries. Although there has been a push for creating accountability and promoting better reading outcomes in the US such as the "No Child Left Behind" legislation (107th Congress 2002), there is no national curriculum and schools may vary in how they apply state standards. On the other hand, the efforts to create and implement a national curriculum have been extensive in the UK.

A number of family literacy programs were instituted in the UK in the early 1990s, extending the focus on the teaching of early literacy from teachers to include families of young children (Hannon 2003). These types of programs may have positively influenced the environment in such a way as to reduce the gap in support that children from families with higher socioeconomic status (SES) have when compared to children from families with lower SES.

For example, Sammons et al. (2007) found that mother's highest qualification was a stronger predictor of cognitive outcomes at the key stage assessment at age 11 (test to ascertain if child has reached UK curriculum standards), than at key stage assessment at age 7. This result is consistent with our data demonstrating a significant resilience effect in sixth grade and a trend in first grade.

However, as with all studies looking at  $G \times E$  interaction, which is a differential effect of genotype that depends on environmental exposure, one potential confound is that genes related to the level of parental education may also influence child reading ability resulting in  $r_{GE}$  (Plomin et al. 2008). In other words, if  $r_{GE}$  is present, because some "environmental" variables may be genetically influenced (e.g., Kendler and Baker 2007; Plomin and Bergeman 1991), the association between the phenotype of the child and the measure of family environment (parental education) can be partially or completely due to the genotype of the parent. We have controlled for the potential influence of  $r_{GE}$  using the method introduced by Friend et al. (2008) for selected samples, wherein a residual parental education moderator that is uncorrelated with probands' scores is used to test for the  $G \times E$  interaction. If this potential confound is ignored, it can lead to biased estimates in the proportion of variance that is due to shared environment and genetic influence, resulting in a spurious  $G \times E$  interaction (Price and Jaffee 2008). Although parental education is a family-wide variable, it is not equally correlated with proband and cotwin scores. Probands scores have restricted variance because they are selected whereas cotwin scores can vary freely. Thus, a residual correlation between parental education and cotwin scores remains. This residual correlation is independent of the association between the high reading ability phenotype of the proband and parental education. Therefore, the interaction results presented here support a genotype by shared environment interaction (Medland et al. 2009) for high reading ability that is not confounded with  $r_{GE}$ .

A second potential confound is that our  $G \times E$  interaction results were driven by differences in environmental variance that were correlated with our moderator. For example, Kremen et al. (2005) found that parental education significantly moderated heritability of individual differences in reading in their sample of adult twins. Kremen et al. (2005) tested an alternative model to explain the pattern of results in their data where variance in shared environment decreased as a function of parental education. Kremen et al. suggested that if environmental variance were lower for higher parental education than for lower parental education, rather than the same throughout the range of parental education, then additive genetic influence would account for a larger proportion of the overall variance indicating a  $G \times E$  interaction. However, the

alternative model did not fit the data significantly better than the interaction model. Although this alternative model is consistent with findings for individual differences and group deficits in reading that show an increase in heritability as parental education increases, it would suggest that the same pattern of  $G \times E$  interaction should be found for high reading ability. This was not the case with the present results, which demonstrated higher group heritability for lower parental education than for higher parental education, thus indicating a strong genetic effect on resilience to environmental disadvantage.

Several studies on unselected population samples of identical and fraternal twins have reported that the degree of genetic influence on individual differences for cognitive and academic abilities increases as a function of family socioeconomic status (SES) and parental education (Harden et al. 2006; Turkheimer et al. 2003). Although, the underlying genetic mechanisms may be similar for extreme group performance and for individual differences across the phenotypic range,  $G \times E$  studies of unselected population samples and selected samples are asking theoretically different questions about  $G \times E$  interaction. Studies of unselected samples ask how the interaction of genes and environment influences individual differences regardless of where individuals are in the phenotypic distribution, whereas studies on extreme group membership ask how the interaction of genes and environment influences individual differences in the tails of the distribution.

Kovas and Plomin (2007) suggest that largely the same set of genes influence various measures of cognitive ability and that the environment is the differentiating factor. In other words, the same genes will function across the distribution of scores, such that genes influencing reading disability are likely the same genes influencing high reading ability. Therefore, molecular genetic studies of reading disability may provide the best hint of possible mechanisms involved in genetic resilience for high reading ability. For example, DCDC2 and KIAA0319 have been associated with reading disability in selected samples (Deffenbacher et al. 2004; Schumacher et al. 2006; Harold et al. 2006). These genes have been shown to modulate neuronal development in the brain (Meng et al. 2005; Paracchini et al. 2006). One hypothesis is that individuals with reading disability carry alleles that result in disrupted neuronal migration, which may negatively influence their reading ability (Paracchini et al. 2007). If these genes are examples of “generalist genes”, then individuals with high reading ability may carry alleles that result in optimal neuronal migration. Therefore, a possible future study could explore whether specific alleles for these genes are associated with high reading ability.

Studies on resilience to environmental disadvantage have typically focused on emotional resilience to trauma;

however, Rutter (2003) has argued that resilience (better outcome than what would be expected given a set of conditions) is not domain specific and is influenced by genetic factors, which suggests that resilience may also play a role in high cognitive ability. For example, Kim-Cohen et al. (2004) analyzed genetic and environmental components of resilience in IQ and vulnerability to socioeconomic deprivation. They found that 46% of the variance in a residual IQ score (difference in actual score from the expected score based on socioeconomic status) was accounted for by genetic factors. They also found that stimulating activities accounted for a significant proportion of the shared environment variance for resilience. However, the authors contended that stimulating activities provided by mothers may also be partially influenced by genes and that their model of resilience could not distinguish between genotype-environment ( $r_{GE}$ ) correlation and genotype-by-environment ( $G \times E$ ) interaction influences of such activities on resilience.

Child attributes, family aspects, and wider social environment have all been implicated in the development of resilience (Luthar et al. 2000). It is important to note that a finding of resilience in reading may not necessarily be indicative of other types of resilience such as emotional resilience. In fact, some researchers have suggested that it would be unlikely that resilient children would exhibit high functioning across many different types of domains when this has not been found for children who are not exposed to high-risk environmental factors (Luthar 2003).

Friend et al. (2008) found that heritability of low reading ability was significantly higher among children whose parents had higher levels of education in a sample of identical and fraternal twin pairs that included at least one proband with a school history of reading disability. These results support the idea that children who fail in reading despite adequate environmental support tend to have stronger genetic influences on their reading disability than children who fail in reading and lack good environmental support for reading. In contrast, the results of the present study are consistent with the hypothesis that genetic influences may be stronger for higher reading performance among children with lower environmental support, whereas shared family environmental influences may be relatively more important for higher reading performance among children with greater environmental support.

This study does not specify exactly what proximal shared environmental factors associated with high parental education are positively influencing high reading ability. These proximal factors could include children’s modeling of parents’ reading behavior, and parents’ shared book reading with their children. In the Colorado sample from which probands were selected for the present study, both of these factors were significantly correlated with parents’



years of education when the twins were in preschool (Samuelsson et al. 2005). Other proximal factors could include the amount and methods of instruction in the schools. We noted in the introduction that the mean Colorado state testing score of the school that the twins attend is significantly correlated with parental education. Unfortunately, there is no reliable information about variation in methods of instruction across the schools attended by twins in the Colorado sample. Therefore, what those strategies should be is beyond the scope of this article, except to say that we have made a case that genes for associative learning are implicated in literacy variance and that instruction needs to make allowance for this by affording many more opportunities for practice for compromised children (Byrne et al. 2008).

Taken together, the study by Friend et al. (2008) and the present study describe a coherent account of the interactions between environmental support and the heritability of extreme reading performance. When children's performance on reading deviates from environmental expectation (poor performance in the presence of higher environmental support for reading, and strong performance or resilience in the presence of lower environmental support for reading), then genetic influences are relatively more important than when reading ability is consistent with environmental expectations. In future research, it will be interesting to see if similar interactions between parent education and the heritability of high and low performance will be found for other academic and general cognitive skills.

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