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META-ANALYSIS OF TWIN STUDIES HIGHLIGHTS THE IMPORTANTCE OF GENETIC VARIATION IN PRIMARY SCHOOL EDUCATIONAL ACHIEVEMENT

Based on Eveline L. de Zeeuw, Eco J. C. de Geus and Dorret I. Boomsma. Meta-analysis of twin studies highlights the importance of genetic variation in primary school educational achievement. *Trends in Neuroscience and Education*. Submitted.

Children differ in their ability to learn what is taught at school. Evidence from twin studies suggests that genetic effects contribute to such differences. The aim of the present study was to meta-analyze the existing literature on twin studies on educational achievement in primary school children. The meta-analysis includes 61 studies from 11 different cohorts and is based on up to 5330 MZ and 7084 DZ twin pairs. Heritability is estimated at 70% for reading, 50% for reading comprehension, 57% for mathematics, 44% for spelling, and 66% for educational achievement). The importance of genetic effects on educational achievement differed between countries. In general, heritability was consistently high in the Netherlands, while for the USA and UK heritability for some educational domains was moderate or even low. It can be concluded that genetic variation is an important contributor to the individual differences in educational achievement, with evidence for interaction with country.

INTRODUCTION

Educational achievement in children can be defined as the extent to which a child has achieved the educational goals corresponding to his or her grade level. Lower educational achievement has an adverse effect on access to higher education and is negatively related to numerous other outcomes later in life, including earnings (Julian & Kominski, 2011), health and wellbeing (Mackenbach et al., 1997). Research into the causes of individual differences has tended to focus on environmental factors, such as parental educational level, socio-economic status (SES) and quality of education. Yet, even children from a similar background, attending the same school and taught by the same teacher, can differ greatly in their performance at school. This introduces genetic effects as an important additional source of variation in educational achievement. Moreover, parts of the child's environment, like parental educational level, can themselves be influenced by genes (Rietveld et al., 2013; Vinkhuyzen et al., 2010). In keeping, general cognitive ability is the most important predictor of educational achievement (Deary et al., 2007), explaining roughly half of the variation (Frey & Detterman, 2004). A major role for genetic effects on general cognitive ability is well recognized (Plomin, 2004). Here we systematically review twin studies on educational achievement of children in primary school, aiming to provide, based on the existing literature, an estimate of the heritability and the influence of the environment by meta-analyzing the twin correlations.

Twin studies are the most often used design to analyze the causes of variation in complex phenotypes such as educational achievement (Boomsma et al., 2002). Monozygotic (MZ) twin pairs are genetically (nearly) identical while dizygotic

(DZ) twin pairs share approximately 50 per cent of their segregating genes (Plomin R. et al., 2008). If the larger genetic resemblance of MZ twin pairs is mirrored in a larger resemblance for a phenotype, i.e. when the correlation between MZ twin pairs is higher than between DZ twin pairs, this observation is consistent with the phenotype being influenced by genetic effects. Genetic effects are the sum of the effects of all genetic variants with an influence on educational achievement. Environmental effects often are distinguished into common environmental and unique environmental effects. Common environmental effects are influences that are shared between twins or siblings who grow up in the same environment, e.g. SES, and enhance their similarity beyond the similarity due to shared genes. There are other effects that also make offspring from the same parents more similar, including the effects of assortative mating, the similarity between spouses, which will in the classical twin design also be detected as common environment (Evans, Gillespie & Martin, 2002). When the correlation between DZ twin pairs is more than half the correlation between MZ twin pairs there is an indication for the influence of the common environment. Unique environmental effects are influences that are not shared between twins, and make children less similar. When the correlation between MZ twin pairs is not equal to unity the unique environment has an influence. The unique environmental effects also include measurement error, for instance when teacher's reports on achievement test results are incorrect, e.g. wrong child, wrong test.

The twin method assumes that MZ twins are more similar in educational achievement than DZ twins because of their larger genetic resemblance and not because MZ twins are treated more alike than DZ twins. The equal environment assumption can be violated if similarity in treatment relates to similarity in a phenotype, however, MZ twins may be exposed to more similar treatment because of their larger genetic resemblance. For instance, if smart children get treated differently than less smart children, the higher genetic resemblance in cognitive ability of MZ twins causes them to experience more similar environments than DZ twins, as a secondary effect of the genetic effects on cognitive ability. In contrast, when there is a similar environment unrelated to the genetic make-up of the twins, e.g. MZ twins are dressed more alike than DZ twins this could lead to a violation of the assumption, if dress similarity relates to similarity in the outcome. Such violations of the equal environments assumption have been tested by empirical approaches in large scale studies (Evans & Martin, 2000; Loehlin, 1989; van den Oord, Boomsma & Verhulst, 2000) which show that the assumption holds for general cognitive ability, educational achievement and childhood behavioral problems.

In order to generalize the outcome of twin studies to the general population, twins should be representative of the general population for the phenotype of interest. With regard to most characteristics, this assumption will be met as twins are born in all strata of society (Hoekstra et al., 2010). Nonetheless, twins differ from singletons with regard to birth conditions. Twins are born, on average, 3-4 weeks prematurely and have ~1 kg lower birth weights (Martin et al., 2010). These differences dissipate fairly early on, however, and, already in childhood, twins and singletons have very similar body composition (Estourgievan Burk et al., 2010), general cognitive ability (Webbink et al., 2008) and educational achievement (Cohen et al., 2002), especial when birth order within family is taken into account (Boomsma et al., 2008; de Zeeuw et al., 2012).

The heritability of general cognitive ability as measured by psychometric IQ tests has been studied extensively. A large meta-analysis of twin studies from different countries established that heritability increases linearly from childhood to adulthood from .41 in childhood to .66 in young adulthood. Simultaneously, a decrease from .33 to .16 was seen for the influence of the common environment shared by children growing up in the same family (Haworth et al., 2010; Molenaar et al., 2013). Even during the short period of primary school, heritability of general cognitive ability increased from .38 to .49 (Kovas et al., 2013) and there is a substantial genetic correlation across age (Davis et al., 2008). One explanation that has been suggested for this consistent finding of increasing heritability with age is that children, when they grow up, can more and more select their own environment and experiences based on their genotype (Haworth et al., 2010).

General cognitive ability and educational achievement are positively associated with a correlation of approximately 0.50 (Bartels et al., 2003). Multivariate twin methods (Boomsma, 2014) have been used to analyze the etiology of this association. In childhood, a large part of this association is due to correlated genetic effects, i.e. genes that influence general cognitive ability also influence educational achievement (Bartels et al., 2002; Calvin et al., 2012). General cognitive ability is often seen as a predisposition while educational achievement is perceived as the outcome of education, which leads to expectations that heritability of educational achievement would be lower than for general cognitive ability (Kovas et al., 2013). However, in a study in primary school children literacy and numeracy were more heritable than general cognitive ability (Kovas et al., 2013). One hypothesis for this difference is that the homogeneity of education reduces differences in the environment and, as a result, individual differences between children in educational achievement can to a greater extent be explained by genes (Heath et al., 1985).

Twin studies have mainly focused on reading and, more recently, mathematics. Most studies are from English speaking countries, such as the USA, UK and Australia. Studies from other countries with different educational systems are relatively scarce (Bartels et al., 2002; Byrne et al., 2009; Chow et al., 2011). Studies are characterized by differences in age, sample size, cohort and measurement instrument. Therefore, it is difficult to draw clear conclusions regarding the relative contribution of genetic and environmental influences on educational achievement. Here we aim to provide a review of all studies that addressed the heritability of educational achievement in primary school and carry out a meta-analysis of the correlations in mono- and dizygotic twins. This review does not include twin studies of selected samples (low or high performance) or of learning disabilities, such as dyslexia and dyscalculia, as there are excellent recent reviews (e.g. (Grigorenko, 2004; Schulte-Körne, 2001; Wadsworth, Olson & Defries, 2010; Willcutt et al., 2010)).

METHODS

A search of the published literature was conducted in PubMed to find all relevant papers describing twin studies on the heritability of educational achievement in primary school children published before September 2014. Searches were performed to find any paper in English that contained the words genetics, heritability and twin study combined with educational achievement, educational attainment, school achievement, academic achievement, scholastic achievement, school performance and academic performance as well as with reading, mathematics, arithmetic, spelling and science in its title, key words, abstract or main text. Abstracts of these search results were evaluated and relevant full text articles were retrieved from the internet. The reference lists of all these papers were examined to identify additional studies that had not been located in the initial database search and searches on names of authors who previously published twin studies on educational achievement were performed. Criteria for inclusion were determined a priori and assessed. Only original research reports published in peer-reviewed journals were included in the review. Twin studies including a sample of primary school aged children (6-13 years) were selected. Studies were included when they contained information on heritability estimates for a measure of educational achievement in a specific educational domain, for example, reading or mathematics, or a measure of general educational achievement. Studies were selected when they used standardized tests or teacher assessments to measure educational achievement. Studies reporting on estimates from univariate analyses as well as studies containing univariate estimates from multivariate analyses were included. Only twin studies from unselected genetically sensitive samples were included. From

each study, when available, the first author, year of publication, country, cohort, age, sample size, measurement instrument, educational domain and heritability estimates were extracted.

A meta-analysis of studies that provided a description of sample size, with the numbers of MZ and DZ twins, and twin correlations was conducted for both educational achievement in specific educational domains and general educational achievement. The meta-analysis was carried out to estimate heritability across multiple datasets when at least two independent studies from different cohorts reported information on twin correlations and sample size. The decision which study to select and include in the analysis when studies reported twin correlations from the same cohort was based on the largest sample size. The meta-analyses did not make a distinction for gender as almost no studies reported twin correlations separately for boys and girls.

A variance decomposition model was fitted to the twin correlations, weighted by sample size, to estimate the influence of genetic and common environmental effects (Bartels et al., 2003; van Beijsterveldt & Van Baal, 2002; Verweij et al., 2010) on educational achievement using the structural equation modelling program Mx (Neale et al., 1999). With Mx it is possible to analyze the twin correlations from multiple studies in a multi-group analysis and obtain a maximum likelihood estimate of heritability across all studies. It was tested whether the heritability estimate could be constrained to be equal across studies. The difference in goodness of fit between the nested models was assessed with hierarchic chi-squared tests. The difference in the χ^2 -statistic is evaluated with the difference in the number of estimated parameters between the nested models as degrees of freedom. A p-value smaller than 0.01 was considered significant.

RESULTS

The PubMed search retrieved 61 studies that were published between 1991 and 2014. Table S1 summarizes the characteristics and results of these twin studies from 6 different, mostly English speaking, countries (mainly Northern Europe, UK and US, but also Australia and China). The studies include heritability estimates for a number of specific educational domains, i.e. reading, reading comprehension, mathematics, spelling, language and science, and general educational achievement. Table S1 gives an overview of the results for the heritability estimates as reported by the included studies. Studies providing separate estimates for the heritability in boys and girls did not report any gender differences (de Zeeuw et al., 2015; Harlaar et al., 2005; Haworth, Dale & Plomin, 2008; Kovas et al., 2007b; Petrill & Thompson, 1994; Reynolds et al., 1996). Some

studies used teacher assessments or standardized tests taken at school while others were based on results from tests that had been administered by the researchers through the internet, telephone or during a home-visit. Teacher assessments were based on the evaluation by the teacher of the overall proficiency of a student or on criteria that are listed in national guidelines regarding what a student should be able to do or know regarding a certain educational domain. Some studies took into account that the members of a twin pair could be assessed by the same or different teachers and reported separate heritability estimates for these groups (Harlaar, Dale & Plomin, 2005; Walker et al., 2004).

The cohorts that are described in the studies were the Colorado Learning Disabilities Research Center (CLDRC), UK government's Department of Children, Schools and Families (DSCF), Environmental Risk Longitudinal Twin Study (ERLTS), Florida Twin Project (FTP), International Longitudinal Twin Study (ILTS), Netherlands Twin Register (NTR), Primair Onderwijs en Speciaal Onderwijs Cohort (PRIMA), Virginia Twin Study of Adolescent Behavioral Development (VTSABD) and the Western Reserve Twin Project (WRTP). Most of the studies focused on the so called core educational domains, i.e. reading and mathematics. Other educational domains that we came across in the literature search and that are included in the review are reading comprehension, spelling, language and science. Some of the studies used a measure of general educational achievement. The instruments used to measure educational achievement differ across country and cohort.

Estimates of the heritability of reading (.10-.94), reading comprehension (.32-.87), mathematics (.04-.75), spelling (.33-.84), language (.21-.81), science (.32-.64) and general educational achievement (.27-.57) varied considerably across the studies reported in this review. The same is true for the environmental effects on reading (.00-.74), reading comprehension (.00-.50), mathematics (.00-.81), spelling (.00-.46), language (.10-.25), science (.08-.39) and general educational achievement (.08-.67). Reported heritability estimates may vary due to considerable differences in sample sizes, different countries, different age groups and a large variation in measurement instruments. We explore some of these explanations in the meta-analysis.

A meta-analysis was carried out for reading, reading comprehension, mathematics, spelling and general educational achievement. The MZ and DZ correlations of all studies included in the meta-analyses are given in Table 1. The number of included studies in the meta-analysis was 11 for reading with a total of 5330 MZ and 7084 DZ twin pairs. For reading comprehension a total of 6 studies provided data on 3042 MZ and 5218 DZ twin pairs. For mathematics and spelling, there were fewer studies. Three studies on mathematics included a

total of 3419 MZ and 6247 DZ twin pairs and the 3 studies for spelling had 1093 MZ and 1692 DZ twin pairs. In primary school aged children we retrieved 2 studies for general educational achievement with large sample sizes, totaling 4341 MZ and 7808 DZ twin pairs. The heritability estimates reported by the studies included in the meta-analyses and the mean estimate of the heritability based on all available studies are displayed in Figure 1.

We next investigated the heterogeneity between studies for heritability estimates by comparing the fit of the meta-analysis models in which all estimates across studies were constrained to be equal to a model in which all estimates were free. The differences in chi-squared statistics for reading ($\Delta\chi^2 = 25.46$, $\Delta df = 20$, $p = .184$) and general educational achievement ($\Delta\chi^2 = 6.68$, $\Delta df = 2$, $p = .035$) were not significant. For the educational domains reading comprehension ($\Delta\chi^2 = 73.76$, $\Delta df = 14$, $p < .001$), mathematics ($\Delta\chi^2 = 15.58$, $\Delta df = 4$, $p = .004$) and spelling ($\Delta\chi^2 = 30.74$, $\Delta df = 8$, $p < .001$) the constrained model fitted worse, pointing to heterogeneity. The contributions of the included studies to the difference in the chi-squared statistics between the models with all estimates freely estimated and the models where the estimates were constrained to be equal across the different studies are displayed in Table 1 and inform on the degree and sources of heterogeneity across the different samples. A study from the Netherlands (de Zeeuw et al., 2015) and a study from the UK (Trzesniewski et al., 2006) both contribute the most to the increase in the chi square statistic for reading. More than 40 per cent of the increase in the chi square test statistic for reading comprehension is caused by a study in twins from the USA (Hart et al., 2013) and a sample from Australia (Byrne et al., 2009) contributes for nearly half the increase in the chi square statistic for spelling. The included studies contribute approximately the same to the increase in chi square statistic for mathematics and general educational achievement.

The studies included in the meta-analyses are mainly from cohorts from the USA, UK and the Netherlands (NL), providing the opportunity to explore gene-environment (GxE) interaction across those countries for the educational domains with studies available from those three countries, i.e. reading, reading comprehension and mathematics (Table 2). These countries have different teaching methods, educational systems and societies and the expression of the genotype could depend on differences in the environment (Eaves, 1984). Heritability and the influence of the common environment, respectively, was first estimated separately for each country. The fit of the model did not deteriorate significantly after equating the estimates across countries for reading ($\Delta\chi^2 = 10.55$, $\Delta df = 4$, $p = .032$), but did so for reading comprehension ($\Delta\chi^2 = 49.80$, $\Delta df = 4$, $p < .001$) and mathematics ($\Delta\chi^2 = 15.58$, $\Delta df = 4$, $p = .004$).

DISCUSSION

The current paper presents a review of the heritability of educational achievement of children in primary school estimated from twin studies. Heritability estimates varied considerably across studies as did the influence of the environmental effects. The small sample sizes, different countries, different age groups and the variety of measurement instruments are probably the main reasons for the broad range of estimates observed in this review. For example, the smallest sample size was 32 MZ and 28 DZ twin pairs (Hohnen & Stevenson, 1999) and the largest was 2292 MZ and 4184 DZ twin pairs (Harlaar, Hayiou-Thomas & Plomin, 2005). It is noteworthy that studies estimating the magnitude of the effects for genes and the environment separately for boys and girls did not find any evidence for quantitative nor qualitative gender differences. This means that in primary school the extent to which genes influence educational achievement is similar across boys and girls and the same genes are involved in educational achievement for boys and girls.

A meta-analysis of twin correlations was performed for reading, reading comprehension, mathematics, spelling and general educational achievement. Many of the studies included in the review used data from the same cohorts. Consequently, the meta-analysis of twin correlations for most educational domains was based on only a few studies. It was not possible to equate the estimates across the studies included in the meta-analyses without a significant drop in model fit for reading comprehension, mathematics and spelling. If we nevertheless averaged the heritability across studies, 73% of the variation in reading, 49% in reading comprehension, 57% in mathematics, 44% in spelling and 66% in general educational achievement could be explained by genetic effects. Common environmental effects explained 10% of the variation in reading, 13% in reading comprehension, 10% in mathematics, 23% in spelling and 12% in general educational achievement. The only selection criteria for the meta-analyses was the largest sample size when studies from the same cohort reported on the same educational achievement domain and this must be kept in mind when evaluating the mean heritability estimates. Overall, the results suggest that educational achievement of the different educational domains is moderate to highly heritable and that the common environment has a small influence.

Further analyses indicated that the heritability of educational achievement in reading comprehension and mathematics, but not reading, is moderated by the country, i.e. USA, UK and the Netherlands, in which children attend school. Heritability of reading was equally high across countries, but heritability of reading comprehension was larger in the Netherlands and the USA compared to the UK and heritability of mathematics was low in the USA, moderate in the UK

and large in the Netherlands. Furthermore, the influence of the common environment was larger in the USA and UK compared to the Netherlands. It must be noted that the sample sizes included in the studies from the USA are much smaller, making the estimates less reliable. In general, the heritability estimates are consistently high in the Netherlands while this is not true for the USA and UK. The inequality in educational opportunity, income and circumstances under which children grow up is larger in the USA and the UK compared to the Netherlands. It seems that equal opportunities in the relatively homogenous education environment in the Netherlands reduce environmental variation, making differences in educational achievement between children to a greater extent due to genetic differences. Several studies have already found that the heritability of general cognitive ability is larger in children from middle and upper class families while environmental effects have a larger influence in children from lower income families (Scarr-Salapatek, 1971; Turkheimer et al., 2003).

The consequence of the homogeneity in an educational system is that it will highlight the innate individual differences between children as reflected in the high heritability (Harlaar et al., 2012; Kovas et al., 2013). What must be kept in mind is that this heritability does not equal determinism. The variance between children may be heritable, but the mean can be positively influenced by a school environment of good quality. High heritability in a homogeneous school environment means that children with a predisposition for lower educational achievement will have to struggle while children with a genetic advantage can excel at school without ever tapping their full potential. Heritability does support the role of differentiation in teaching. The double challenge for primary school teachers is to make sure that children, who have more difficulty at school, will learn how to read, write and perform calculations, but that those who have it easy are still sufficiently challenged. Classroom teaching might not be the best method to achieve this goal and a more personalized approach to learning will be necessary.

The next question is whether there is a common set of genes that is influencing educational achievement across different educational domains. A number of studies have demonstrated that a large proportion of the genes that are responsible for the achievements of children in different educational domains are the same (Kovas et al., 2007a). For example, with a genetic correlation of .74 there is a substantial part of the genes with an influence that is shared between mathematics and reading. There is also about one third of the genetic variation that is specific to mathematics and reading (Kovas et al., 2005). The genetic correlation between mathematics and reading comprehension (.76) was significantly larger than between mathematics and word recognition (.50),

which suggests that the association with mathematics partly differs between these two components of reading (Harlaar et al., 2012). The genetic correlation between reading and reading comprehension is high, but there are also genetic effects for reading comprehension that are independent from those on reading and vice versa (Betjemann et al., 2008). Although science is less heritable than other educational domains it does share a genetic link with, amongst others, language and mathematics (Haworth et al., 2008). In general, the similarity between the performance of a child in different educational domains is due to genetic rather than environmental effects. Most environmental effects are specific to a certain educational domain and are the cause of individual differences between domains (Kovas et al., 2005).

This is in agreement with the generalist genes hypothesis which holds that many genes associated with one educational domain also influence other domains, that genes associated with educational achievement in the normal range also influence learning disabilities and that genes that influence one aspect of a certain educational domain are largely the same as those that influence other aspects (Plomin & Kovas, 2005). The hypothesis is also supported by multiple studies that have established that learning disabilities are the low end of a continuum and are influenced by the same genetic and environmental effects as normal educational achievement (Hensler et al., 2010; Knopik & DeFries, 1999; Oliver et al., 2004). Heritability estimates of learning disabilities seem to be roughly similar to those for learning abilities (Plomin & Kovas, 2005). Whether high ability is the high end of a continuum of normal variation has been studied less, but seems to be supported for reading (Friend et al., 2009) and mathematics (Petrill et al., 2009).

The same genes are also for a large extent responsible for the performance of children at different ages. Continuity is largely due to the same genetic effects with only some new genes coming into play when a child grows older while environmental effects are responsible for change. For example, heritability of reading at age 7, 9 and 10 was rather similar and the stability across age was primarily genetically mediated with some genes specific to a certain age (Harlaar, Dale & Plomin, 2007b). The longitudinal correlation between mathematics at age 7 and age 9 was for 80 per cent genetically mediated (Haworth et al., 2007). The pattern observed for science is somewhat different since heritability decreased from 9 to 12 years while the shared environmental effects became increasingly important. The genetic correlation of .50 suggests that different genes influence science at these ages (Haworth, Dale & Plomin, 2009).

The phenotypic association between general cognitive ability and educational achievement during the primary school years is largely due to shared genes

while differences between the two phenotypes are due to environmental differences. For example, the genetic correlation in a small sample of 6 to 12-year-old twins was very high (.92) while the common unique environmental correlation was only .16 (Petrill & Thompson, 1993). In a study from the Netherlands, the genetic correlation between general cognitive ability and educational achievement in 12-year-olds was somewhat lower (.47) and equal to the unique environmental correlation (Bartels et al., 2002). Genes also explained the largest part of the association between general cognitive ability and specific educational domains, i.e. language and mathematics and to a lesser extent for science (Calvin et al., 2012).

Having established that educational achievement is relatively highly heritable in primary school age children, even more so than general cognitive ability at the same age (Kovas et al., 2013), it is somewhat surprising that no specific genetic variants involved in educational achievement in children have been found. Molecular genetic research towards the lower end of the distribution of reading is most extensive and has yielded promising findings. For recent reviews of the molecular genetic findings for dyslexia see (Carrion-Castillo, Franke & Fisher and Kere (Carrion-Castillo, Franke & Fisher, 2013; Kere, 2014)). In contrast, studies using samples of unselected children are rather scarce and have not yet resulted in conclusive evidence for an association with specific genetic variants. A genome-wide association (GWA) study for reading and spelling including a cohort of 5472 children aged 8 and 9 years from the UK and 1177 older children from Australia (12-25 years) did not find any genetic variants (single nucleotide polymorphisms (SNPs)) associated at a genome-wide significance level. The top results indicated the strongest association with genetic variants in the pseudo gene *ABCC13* and the gene *DAZAP1*. Subsequent gene-based analyses pointed to the genes *CD2L1*, *CDC2L2* and *RCAN3* (Luciano et al., 2013). Another GWA study selected the 300 lowest and highest scoring children on mathematics from the 10-year-old TEDS cohort and validated the suggestive associations from this sample in an unselected sample of 2356 children. None of the genetic variants reached genome-wide significance, but genetic variants located within the *MMP7*, *GRIK1* and *DNAH5* genes were implicated. The largest effect size observed explained 0.58 per cent of the variance in mathematical performance (Docherty et al., 2010).

The explanation for this lack of significant findings with regard to specific genes influencing educational achievement may be that it is a highly complex phenotype that is caused by many common genetic variants with small effects. The non-significant measured genetic variants in the GWA studies probably did capture relevant genetic variation, but sample sizes have not been large enough to detect these small effects (Flint & Munafo, 2013). This has been confirmed by

the observation that polygenic scores including information from all genetic variants, also the non-significant ones, and their effect sizes observed in a meta-analysis of educational attainment in adults actually explained part of the variance in educational achievement in a sample of children (de Zeeuw et al., 2014; Ward et al., 2014).

There are several limitations of this review of the literature about educational achievement in primary school children that should be noted. A rather large number of studies included in the review suffer from a lack of power which has an effect on the reliability of the obtained heritability estimates in these studies. Another limitation is the heterogeneity in the age of the samples and in the measures used to assess educational achievement. Teacher assessments are used to assess educational achievement in some studies while others use objective tests. Although the association between teacher assessments and standardized tests is relatively strong they are likely measuring partly different aspects of a child's educational achievement. Furthermore, the number of studies included in the meta-analyses was rather small compared to the number of studies included in this review due to the fact that many studies were based on the same population cohort.

To summarize, the heritability of educational achievement in primary school was moderate to high with a small influence of the common environment, which means that most environmental effects were unique. There is some indication for GxE interaction for educational achievement across country. The overlap between educational achievement in different educational domains is mainly due to shared genes while the environmental effects are specific per educational domain. Continuity of educational achievement across primary school is mostly due to the same genes while environmental effects are responsible for change. The association between general cognitive ability and educational achievement is largely due to a shared genetic component. Even though conclusive evidence for an association between specific genetic variants and educational achievement has not yet been found, educational achievement across the normal range remains a promising target for molecular genetic research.

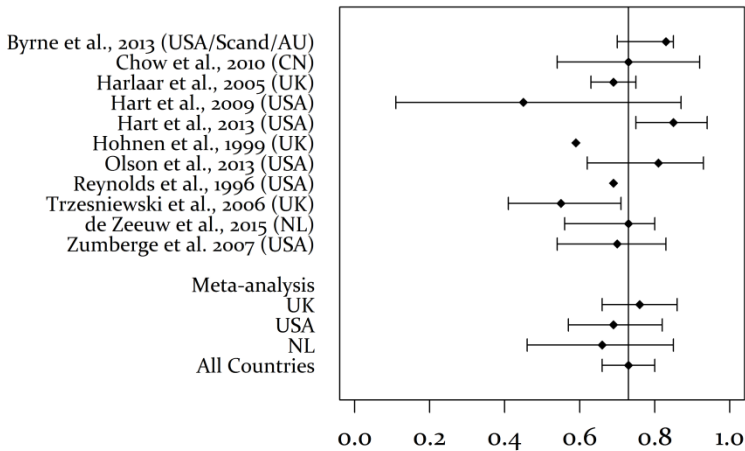
TABLE 1 Descriptives of the studies included in the meta-analyses

Study	Country	Mean Age	Sample Size	MZ correlation	DZ correlation	ΔX^2 (df)
Reading						
Byrne et al., 2013	USA	8	433 MZ + 437 DZ	.81	.43	1.51 (2)
	Scandinavia					
Chow et al., 2011	Australia	-	228 MZ + 84 DZ	.90	.54	1.70 (2)
	China	7	1067 MZ + 1039 DZ (boys)	.86	.52	0.59 (6)
Harlaar et al., 2005	UK	7	1225 MZ + 1111 DZ (girls)	.84	.51	
			2034 DOS		.37/.46	
Hart et al., 2009	USA	6	128 MZ + 175 DZ	.82	.50	0.45 (2)
Hart et al., 2013	USA	7	486 MZ + 468 DZ	.82	.47	0.23 (3)
			442 DOS		.45	
Hohnen & Stevenson, 1999	UK	7	34 MZ + 32 DZ	.92	.61	1.41 (2)
Olson et al., 2013	USA	11	81 MZ + 189 DZ	.91	.50	0.83 (2)
	USA	11	292 MZ + 179 DZ (boys)	.79	.44	1.40 (5)
Reynolds et al., 1996	USA		380 MZ + 184 DZ (girls)	.81	.52	
			284 DOS		.39	
Trzesniewski et al., 2006	UK	7	285 MZ + 244 DZ	.88	.59	7.81 (2)
	The Netherlands	8	199 MZ + 182 DZ (boys)	.73	.38	8.49 (5)
de Zeeuw et al., 2015			215 MZ + 174 DZ (girls)	.75	.48	
			369 DOS		.39	
Zumberge et al., 2007	USA	10	139 MZ + 84 DZ (boys)	.80	.50	1.05 (5)
			138 MZ + 97 DZ (girls)	.78	.52	
			147 DOS		.43	

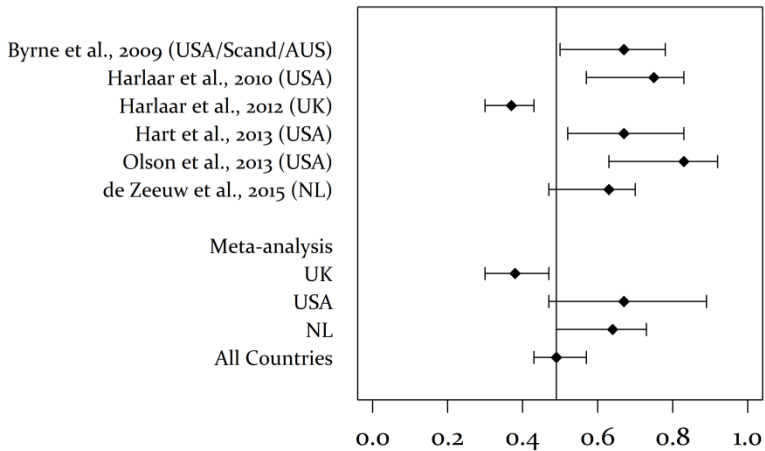
Reading Comprehension									
Reading Comprehension Byrne et al., 2009	USA	8	185 MZ + 220 DZ	.72	.45	4.88 (2)			
	Australia		86 MZ + 49 DZ	.71	.33	1.06 (2)			
	Scandinavia		32 MZ + 43 DZ	.76	.46	1.37 (2)			
	USA	10	89 MZ + 131 DZ	.73	.25	7.37 (2)			
	UK	12	1748 MZ + 3117 DZ	.56	.37	12.85 (2)			
	USA	8	189 MZ + 388 DZ	.83	.53	31.23 (2)			
	USA	11	81 MZ + 189 DZ	.88	.47	9.42 (2)			
	The Netherlands	8	305 MZ + 285 DZ (boys)	.67	.41	5.58 (5)			
			327 MZ + 261 DZ (girls)	.67	.30				
			535 DOS		.34				
			1627 MZ + 2902 DZ	.62	.39	5.52 (2)			
Mathematics Harlaar et al., 2012 Hart et al., 2009 de Zeeuw et al., 2015	UK	11	128 MZ + 175 DZ	.58	.45	3.47 (2)			
	USA	8	757 MZ + 787 DZ (boys)	.70	.37	6.59 (5)			
	The Netherlands	12	907 MZ + 765 DZ (girls)	.76	.41				
			1618 DOS		.37				
			185 MZ + 220 DZ	.79	.41	3.63 (2)			
Spelling Byrne et al., 2009	USA	8	86 MZ + 49 DZ	.74	.10	12.79 (2)			
	Australia		32 MZ + 43 DZ	.68	.24	3.92 (2)			
	Scandinavia		81 MZ + 189 DZ	.91	.48	4.96 (2)			
	USA	11	344 MZ + 316 DZ (boys)	.62	.40	5.43 (5)			
	The Netherlands	6	365 MZ + 281 DZ (girls)	.57	.40				
			594 DOS		.53				
Educational Achievement Haworth et al., 2011 de Zeeuw et al., 2015	UK	12	1892 MZ + 3250 DZ	.75	.47	3.85 (2)			
	The Netherlands	12	1112 MZ + 1129 DZ (boys)	.80	.47	2.83 (5)			
			1337 MZ + 1149 DZ (girls)	.83	.43				
			2280 DOS		.44				

FIGURE 1 Heritability estimates (95% Confidence Intervals) as reported by the studies included in the meta-analysis and the estimated mean heritability by country for reading (A), reading comprehension (B), mathematics (C), spelling (D) and educational achievement (E)

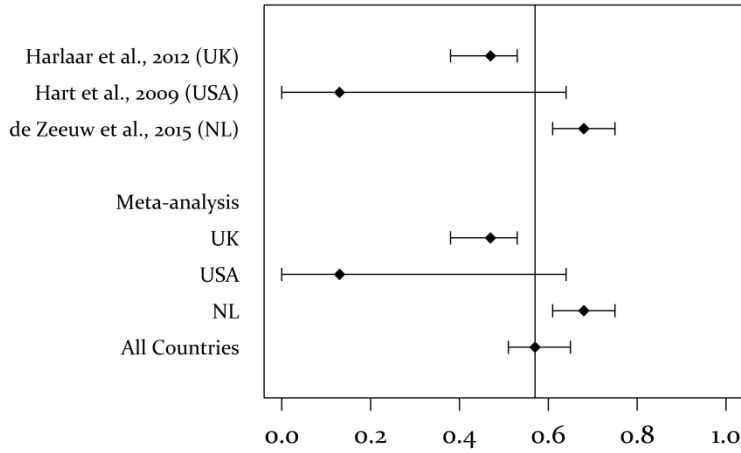
A.



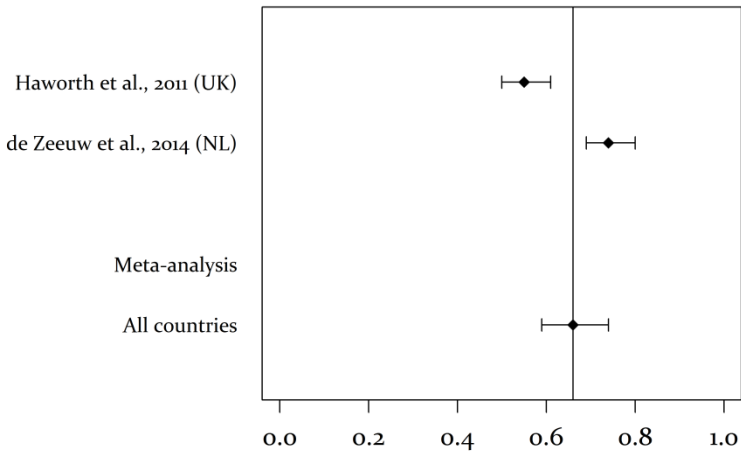
B.



C.



D.



E.

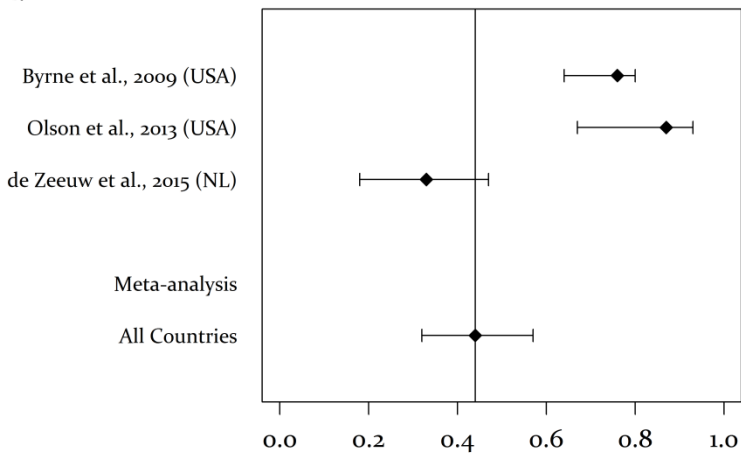


FIGURE 2 Heritability estimates from the meta-analysis of reading, reading comprehension, mathematics, spelling and general educational achievement

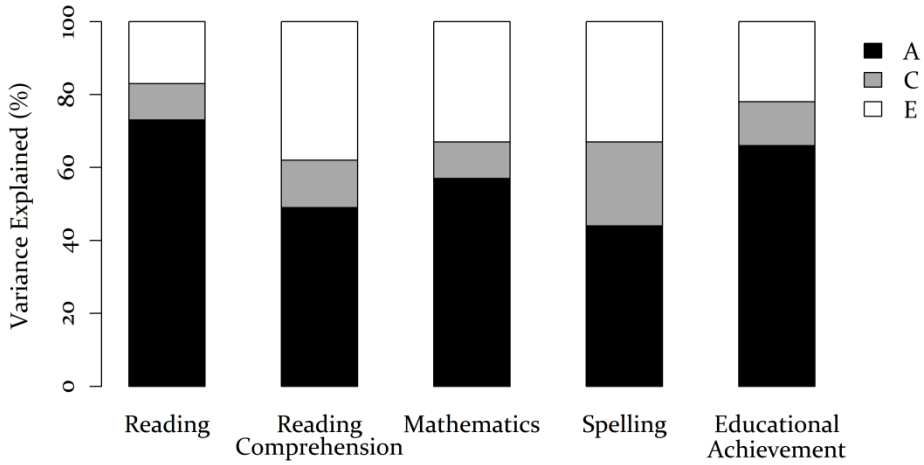


TABLE S1 Twin studies on educational achievement in primary school children

Authors	Country	Study	Study Sample (pairs)	Age (SD) Range	Educational Domain	Test	Subtest	Heritability Estimates
Bartels et al., 2002	The Netherlands	NTR	313 MZ 490 DZ	~12	Educational Achievement	CITO	Total Score	$a^2 = .57$ $c^2 = .27$ $e^2 = .16$
	USA Australia	ILTS	172 MZ 153 DZ	~6	Reading Spelling	TOWRE -	- -	$a^2 = .70$ $c^2 = .22$ $e^2 = .07$ $a^2 = .39$ $c^2 = .40$ $e^2 = .20$
Byrne et al., 2006	USA Australia Scandinavia	ILTS	213 MZ 209 DZ		Reading Spelling	TOWRE -	- -	$a^2 = .70$ $c^2 = .22$ $e^2 = .07$ $a^2 = .39$ $c^2 = .40$ $e^2 = .20$
	USA Australia	ILTS	167 MZ 152 DZ	~7	Reading Reading Comprehension	TOWRE WJ	- Passage Comprehension	$a^2 = .82$ $c^2 = .00$ $e^2 = .18$ $a^2 = .76$ $c^2 = .03$ $e^2 = .21$
Byrne et al., 2008	USA Australia	ILTS	225 MZ 214 DZ	8.3 (.4)	Spelling Spelling	WJ WRAT	Spelling Spelling	$a^2 = .71$ $c^2 = .07$ $e^2 = .22$ $a^2 = .74$ $c^2 = .03$ $e^2 = .23$
	USA Australia Scandinavia	ILTS	303 MZ 312 DZ	~8	Reading	TOWRE	Sight Word	$a^2 = .84$ $c^2 = .00$ $e^2 = .16$
Byrne et al., 2009 ^{2,4}	USA Australia Scandinavia				Reading Comprehension	WJ	Phonemic Decoding Total -	$a^2 = .74$ $c^2 = .07$ $e^2 = .19$ $a^2 = .82$ $c^2 = .03$ $e^2 = .14$ $a^2 = .67$ $c^2 = .07$ $e^2 = .26$
	USA Australia Scandinavia	ILTS	433 MZ 437 DZ	~8	Spelling Reading	WRAT TOWRE	Spelling Sight Word Phonemic Decoding	$a^2 = .76$ $c^2 = .00$ $e^2 = .24$ $a^2 = .83$ $c^2 = .00$ $e^2 = .17$ $a^2 = .81$ $c^2 = .01$ $e^2 = .18$

Calvin et al., 2012	UK	DCSF	1056 SS 495 OS	ii.2	Educational Achievement	NC-TA	Total	$a^2 = .75$
					Language	NC-TA	English	$a^2 = .81$
					Mathematics	NC-TA	Mathematics	$a^2 = .66$
					Science	NC-TA	Science	$a^2 = .51$
					Language	CITO	-	$a^2 = .74$
	The Netherlands	PRIMA	785 SS 327 OS	~8	Mathematics	CITO	Arithmetic	$a^2 = .67$
				~10	Language	CITO	-	$a^2 = .43$
				~12	Mathematics	CITO	Arithmetic	$a^2 = .73$
					Language	CITO	-	$a^2 = .53$
					Mathematics	CITO	Arithmetic	$a^2 = .36$
Chow et al., 2011 ¹	China	-	228 MZ 84 DZ	3-II	Reading	HKT	Word Reading Word Attack	$a^2 = .73$ $c^2 = .18$ $e^2 = .09$ $a^2 = .38$ $c^2 = .60$ $e^2 = .02$
Christopher et al., 2013	USA	ILTS	224 MZ 263 DZ	6.3 (.3) 5.5-7.1 7.4 (.3) 6.6-8.7	Reading	TOWRE	Sight Word Phonemic Decoding Sight Word	$a^2 = .68$ $c^2 = .22$ $e^2 = .10$ $a^2 = .62$ $c^2 = .12$ $e^2 = .26$ $a^2 = .84$ $c^2 = .02$ $e^2 = .14$
				8.5 (.3)	Reading	TOWRE	Phonemic Decoding Sight Word	$a^2 = .82$ $c^2 = .00$ $e^2 = .18$ $a^2 = .73$ $c^2 = .07$ $e^2 = .20$
				7.7-9.5	Reading	TOWRE	Phonemic Decoding Sight Word	$a^2 = .40$ $c^2 = .33$ $e^2 = .27$ $a^2 = .74$ $c^2 = .13$ $e^2 = .13$
	Australia	ILTS	152 MZ 115 DZ	6.1 (.4) 5.3-6.8 7.0 (.4) 6.2-7.8 8.0 (.4) 7.3-8.7	Reading	TOWRE	Phonemic Decoding Sight Word Phonemic Decoding Sight Word	$a^2 = .83$ $c^2 = .00$ $e^2 = .77$ $a^2 = .83$ $c^2 = .00$ $e^2 = .17$ $a^2 = .60$ $c^2 = .15$ $e^2 = .26$ $a^2 = .40$ $c^2 = .33$ $e^2 = .27$ $a^2 = .81$ $c^2 = .00$ $e^2 = .19$

Scandinavia	ILTS	138 MZ	6.8 (.3)	Reading	TOWRE	Sight Word	$a^2 = .46$	$c^2 = .43$	$e^2 = .11$
		142 DZ	6.2-7.7			Phonemic Decoding	$a^2 = .42$	$c^2 = .45$	$e^2 = .13$
	ILTS	210 MZ 254 DZ	6.3 5.5-7.1	Reading	TOWRE	Sight Word	$a^2 = .80$	$c^2 = .03$	$e^2 = .17$
						Phonemic Decoding	$a^2 = .67$	$c^2 = .12$	$e^2 = .22$
						Sight Word	$a^2 = .78$	$c^2 = .00$	$e^2 = .22$
	ILTS	210 MZ 254 DZ	6.3 5.5-7.1	Reading	TOWRE	Phonemic Decoding	$a^2 = .71$	$c^2 = .02$	$e^2 = .26$
						Sight Word	$a^2 = .68$	$c^2 = .22$	$e^2 = .10$
						Phonemic Decoding	$a^2 = .63$	$c^2 = .12$	$e^2 = .25$
	ILTS	210 MZ 254 DZ	7.4 6.6-8.7	Reading	TOWRE	Sight Word	$a^2 = .84$	$c^2 = .02$	$e^2 = .14$
						Phonemic Decoding	$a^2 = .82$	$c^2 = .00$	$e^2 = .18$
Passage						$a^2 = .71$	$c^2 = .10$	$e^2 = .20$	
USA	ILTS	210 MZ 254 DZ	6.3 5.5-7.1	Reading	WRMT	Comprehension	$a^2 = .68$	$c^2 = .10$	$e^2 = .23$
						Spelling	$a^2 = .73$	$c^2 = .08$	$e^2 = .19$
	ILTS	210 MZ 254 DZ	8.5 7.7-9.5	Reading	TOWRE	Phonemic Decoding	$a^2 = .75$	$c^2 = .04$	$e^2 = .21$
						Passage	$a^2 = .59$	$c^2 = .14$	$e^2 = .27$
						Comprehension	$a^2 = .81$	$c^2 = .00$	$e^2 = .19$
	ILTS	210 MZ 254 DZ	10.5 9.7-11.7	Reading	WRAT	Spelling	$a^2 = .57$	$c^2 = .15$	$e^2 = .29$
						Reading	$a^2 = .74$	$c^2 = .03$	$e^2 = .22$
						Comprehension	$a^2 = .68$	$c^2 = .04$	$e^2 = .28$

Christopher et al.,
2013

Davis et al., 2008	UK	TEDS	919 MZ 1622 DZ	~10	Mathematics	NFER	Mathematics	$a^2 = .49$ $c^2 = .23$ $e^2 = .29$
Davis et al., 2014	UK	TEDS	2794	~12	Reading Reading	PIAT PIAT	Reading Reading Comprehension	$a^2 = .38$ $c^2 = .25$ $e^2 = .37$ $a^2 = .66$ $c^2 = .14$ $e^2 = .20$
						GOAL	Reading Comprehension	
						TOWRE	Reading Fluency	
					Mathematics	NFER	Numbers	$a^2 = .51$ $c^2 = .21$ $e^2 = .27$
							Non-Numerical Processes Computation & Knowledge	
Gayán and Olson, 2003	USA	CLDRC	257 MZ 183 DZ	10.6 7.8-18.6	Reading	PIAT	World Recognition	$a^2 = .85$ $c^2 = .04$ $e^2 = .11$
Greven et al., 2009	UK	TEDS	1217 MZ 1070 DZ	9.0 (3)	Educational Achievement	NC-TA	English Mathematics Science	$a^2 = .70$ $c^2 = .19$ $e^2 = .11$
							English Mathematics Science	
					Educational Achievement	NC-TA	English Mathematics Science	$a^2 = .51$ $c^2 = .35$ $e^2 = .14$
Greven et al., 2014	UK	TEDS	2191 MZ 3930 DZ	~12	Mathematics	NFER	-	$a^2 = .46$ $c^2 = .23$ $e^2 = .31$
					Reading	TOWRE	-	$a^2 = .56$ $c^2 = .21$ $e^2 = .23$
						PIAT	Reading Comprehension	
						WJ	Reading Fluency	
						GOAL	-	

Hanscombe et al., 2011	UK	UK	TEDS	3843	~12	Language Mathematics	NC	English	$a^2 = .56$ $c^2 = .25$ $e^2 = .19$
Harlaar, Dale, & Plomin, 2005	UK	UK	TEDS	1019 MZ 948 DZ	7.1 (.2)	Reading	TOWRE	Mathematics	$a^2 = .49$ $c^2 = .48$ $e^2 = .23$
								Science	$a^2 = .44$ $c^2 = .34$ $e^2 = .22$
Harlaar, Dale, & Plomin, 2005	UK	UK	TEDS	2292 MZ 4184 DZ	7.1 (.2)	Reading	TOWRE	Sight Word	same: $a^2 = .63$ $c^2 = .22$ $e^2 = .15$
								Phonemic Decoding	different: $a^2 = .74$ $c^2 = .09$ $e^2 = .17$
Harlaar, Hayiou-Thomas, & Plomin, 2005 ¹	UK	UK	TEDS	1396 MZ 2513 DZ	7.1 (.2)	Reading	TOWRE	Sight Word	same: $a^2 = .65$ $c^2 = .18$ $e^2 = .17$
								Phonemic Decoding	different: $a^2 = .66$ $c^2 = .04$ $e^2 = .30$
Harlaar, Dale, & Plomin, 2007	UK	UK	TEDS	1237 MZ 2179 DZ	~7	Reading	NC-TA	-	$a^2 = .69$ $c^2 = .16$ $e^2 = .15$
								Reading	girls: $a^2 = .67$ $c^2 = .17$ $e^2 = .16$
Harlaar, Dale, & Plomin, 2007	UK	UK	TEDS	899 MZ 1579 DZ	~9	Reading	NC-TA	-	boys: $a^2 = .65$ $c^2 = .19$ $e^2 = .16$
								Reading	$a^2 = .67$ $c^2 = .11$ $e^2 = .22$
Harlaar, Dale, & Plomin, 2007	UK	UK	TEDS	921 MZ 1651 DZ	~10	Reading	NC-TA	-	$a^2 = .65$ $c^2 = .10$ $e^2 = .25$
								Reading	$a^2 = .57$ $c^2 = .17$ $e^2 = .26$
Harlaar, Dale, & Plomin, 2010 ²	USA	USA	WRTP	89 MZ 131 DZ	9.9 (.9)	Reading	TOWRE	-	$a^2 = .65$ $c^2 = .09$ $e^2 = .15$
								Word Attack	$a^2 = .10$ $c^2 = .49$ $e^2 = .41$
Harlaar et al., 2010 ²	USA	USA	WRTP	89 MZ 131 DZ	9.9 (.9)	Reading	TOWRE	-	$a^2 = .67$ $c^2 = .10$ $e^2 = .23$
								Word Attack	$a^2 = .73$ $c^2 = .11$ $e^2 = .16$
Harlaar et al., 2010 ²	USA	USA	WRTP	89 MZ 131 DZ	9.9 (.9)	Reading	TOWRE	-	$a^2 = .81$ $c^2 = .03$ $e^2 = .17$
								Word Attack	$a^2 = .71$ $c^2 = .10$ $e^2 = .19$
Harlaar et al., 2010 ²	USA	USA	WRTP	89 MZ 131 DZ	9.9 (.9)	Reading	TOWRE	-	$a^2 = .78$ $c^2 = .00$ $e^2 = .22$
								Word Attack	$a^2 = .78$ $c^2 = .00$ $e^2 = .22$

Harlaar et al., 2012 ²	UK	TEDS	1844 MZ 3318 DZ	11-9 (.6) 11-12	Mathematics	NER	Reading Comprehension	WRMT	Passage	$a^2 = .75$	$c^2 = .00$	$e^2 = .25$		
							Comprehension		Comprehension					
								PIAT	Reading		$a^2 = .58$	$c^2 = .00$	$e^2 = .42$	
									Comprehension					
									Understanding		$a^2 = .47$	$c^2 = .16$	$e^2 = .37$	
									Numbers					
									Non-Numerical		$a^2 = .42$	$c^2 = .15$	$e^2 = .44$	
									Processes					
									Computation & Knowledge		$a^2 = .50$	$c^2 = .08$	$e^2 = .42$	
									Word Reading	TOWRE				
									Reading Fluency	PIAT		$a^2 = .74$	$c^2 = .02$	$e^2 = .24$
									Reading	PIAT		$a^2 = .64$	$c^2 = .08$	$e^2 = .28$
									Comprehension			$a^2 = .34$	$c^2 = .13$	$e^2 = .53$
										GOAL	Reading	$a^2 = .37$	$c^2 = .18$	$e^2 = .45$
							Hart et al., 2009 ¹³	USA	WRTP	128 MZ 175 DZ	6.1 (.7) 4-3-8.3	Reading	WRMT	Reading Comprehension
		Word												
		Identification												
		Passage												
		Comprehension												
		Word	WRMT		$a^2 = .76$	$c^2 = .07$								$e^2 = .15$
		Identification												
		Passage												
		Comprehension												
		Word	WRMT		$a^2 = .81$	$c^2 = .00$								$e^2 = .17$
		Identification												
		Passage												
		Comprehension												

Hart, Petrill, & Thompson, 2010	USA	94 MZ 134 DZ	WRTP	9-9 (0.9)	Mathematics	WJ	Calculation	$a^2 = .04$	$c^2 = .50$	$e^2 = .44$
							Fluency	$a^2 = .63$	$c^2 = .15$	$e^2 = .21$
							Applied Problems	$a^2 = .14$	$c^2 = .49$	$e^2 = .37$
							Quantitative	$a^2 = .00$	$c^2 = .50$	$e^2 = .50$
	WRMT	Reading	9-9 (.8) (8.0-12.1)	WRMT	WRAT	$a^2 = .13$	$c^2 = .46$	$e^2 = .42$		
					Word Identification	$a^2 = .94$	$c^2 = .00$	$e^2 = .12$		
					Passage					
					Comprehension					
	WRMT	Mathematics	9-9 (0.9)	WRMT	Calculation	$a^2 = .44$	$c^2 = .29$	$e^2 = .26$		
					Fluency	$a^2 = .47$	$c^2 = .36$	$e^2 = .14$		
					Applied Problems	$a^2 = .54$	$c^2 = .24$	$e^2 = .22$		
					Quantitative	$a^2 = .29$	$c^2 = .52$	$e^2 = .23$		
	WRMT	Reading	9-9 (0.9)	WRMT	WRAT	$a^2 = .35$	$c^2 = .34$	$e^2 = .32$		
					Applied Problems	$a^2 = .41$	$c^2 = .37$	$e^2 = .22$		
					Quantitative	$a^2 = .49$	$c^2 = .32$	$e^2 = .19$		
					Concepts					
WRMT	Reading	9-9 (0.9)	WRMT	Calculation	$a^2 = .35$	$c^2 = .39$	$e^2 = .25$			
				Fluency	$a^2 = .34$	$c^2 = .46$	$e^2 = .19$			
				Word Attack	$a^2 = .74$	$c^2 = .00$	$e^2 = .27$			
				Word Identification	$a^2 = .80$	$c^2 = .03$	$e^2 = .17$			
WRMT	Comprehension	9-9 (0.9)	WRMT	DIBELS	$a^2 = .82$	$c^2 = .00$	$e^2 = .17$			
				TOWRE	$a^2 = .84$	$c^2 = .00$	$e^2 = .17$			
				Sight Word						
				Phonemic Decoding						
WRMT	Reading	9-9 (0.9)	WRMT	Passage	$a^2 = .79$	$c^2 = .00$	$e^2 = .26$			
				Comprehension						

Hart et al., 2010	USA	WRT P	112 MZ 159 DZ	9.8 (1.0)	Reading	PIAT	Reading Comprehension Word Identification Word Attack	$a^2 = .68$ $c^2 = .00$ $e^2 = .42$
Hart et al., 2013a ¹	USA	FTP	824 MZ 1546 DZ	6.7 (.5)	Reading	DIBELS	Applied Problems Quantitative Concepts Calculation Fluency	$a^2 = .63$ $c^2 = .35$ $e^2 = .03$
Hart et al., 2013 ²	USA	FTP	189 MZ 388 DZ	8.2 (1.3)	Reading Comprehension	FCAT	-	$a^2 = .18$ $c^2 = .81$ $e^2 = .01$
Haworth et al., 2007 ³	UK	TEDS	1146 MZ 1032 DZ 893 MZ 820 DZ	7.1 6.5-8.0 9.0 8.5-10.5	Mathematics Mathematics	NC-TA NC-TA	Composite Using & Applying	grade 1: $a^2 = .85$ grade 2: $a^2 = .63$ grade 3: $a^2 = .56$ grade 4: $a^2 = .65$ grade 5: $a^2 = .71$ $c^2 = .16$ $c^2 = .22$ $c^2 = .28$ $c^2 = .16$ $c^2 = .09$ $c^2 = .17$ $e^2 = .14$ $e^2 = .15$ $e^2 = .16$ $e^2 = .19$ $e^2 = .20$ $e^2 = .15$
Haworth et al., 2008	UK	TEDS	929 MZ 1650 DZ	10.1 (.3)	Language Mathematics Science	NC-TA NC-TA NC-TA	Composite English Mathematics Science	$a^2 = .62$ $c^2 = .16$ $e^2 = .22$ $a^2 = .64$ $c^2 = .09$ $e^2 = .27$ $a^2 = .62$ $c^2 = .09$ $e^2 = .29$ $a^2 = .62$ $c^2 = .11$ $e^2 = .27$ $a^2 = .68$ $c^2 = .09$ $e^2 = .23$ $a^2 = .59$ $c^2 = .20$ $e^2 = .21$ $a^2 = .62$ $c^2 = .14$ $e^2 = .24$ $a^2 = .49$ $c^2 = .27$ $e^2 = .24$

Haworth, Dale, & Plomin, 2008	UK	TEDS	1846 MZ	9.0	Science	NC-TA	Composite	$a^2 = .62$	$c^2 = .14$	$e^2 = .23$
			3273 DZ	8.5-10.5						
Haworth, Dale, & Plomin, 2009	UK	TEDS	910 MZ	9.0 (3)	Science	NC-TA	Scientific Enquiry	$a^2 = .56$	$c^2 = .17$	$e^2 = .27$
			1626 DZ				Life Processes	$a^2 = .64$	$c^2 = .11$	$e^2 = .25$
Haworth et al., 2011	UK	TEDS	1175 MZ	11.5 (3)	Science	NC-TA	Physical Processes	$a^2 = .62$	$c^2 = .12$	$e^2 = .26$
			1980 DZ				Scientific Enquiry	$a^2 = .32$	$c^2 = .39$	$e^2 = .29$
							Life Processes	$a^2 = .40$	$c^2 = .33$	$e^2 = .27$
							Physical Processes	$a^2 = .36$	$c^2 = .37$	$e^2 = .27$
							Materials Properties	$a^2 = .40$	$c^2 = .33$	$e^2 = .27$
							Arithmetic	$a^2 = .52$	$c^2 = .30$	$e^2 = .17$
Hohnen and Stevenson, 1999 ¹	UK	-	32 MZ	5.8	Reading	NC	Reading	$a^2 = .55$	$c^2 = .20$	$e^2 = .25$
			28 DZ	5.7-6.1			Reading			
Hohnen and Stevenson, 1999 ¹	UK	-	32 MZ	5.8	Reading	BAS	Comprehension	$a^2 = .60$	$c^2 = .36$	$e^2 = .04$
			28 DZ	5.7-6.1		SST	Mathematics			
			34 MZ	7.0	Reading	NARA				
			32 DZ	6.8-7.3		BAS				
					SST		$a^2 = .59$	$c^2 = .32$	$e^2 = .08$	
					NARA					

Keenan et al., 2006	USA	CLDRC	70 MZ	~11	Reading	WJ	Passage	$a^2 = .51$	$c^2 = .18$	$e^2 = .31$
			61 DZ	8-17	Comprehension		Comprehension			
Kovas et al., 2005	UK	TEDS	1500 MZ	~7	Reading	PIAT	Comprehension	$a^2 = .66$	$c^2 = .11$	$e^2 = .23$
					Mathematics	NC-TA	Mathematics	$a^2 = .67$	$c^2 = .09$	$e^2 = .24$
					Reading	TOWRE	-	$a^2 = .69$	$c^2 = .17$	$e^2 = .15$
					Reading	NC-TA	-	$a^2 = .68$	$c^2 = .07$	$e^2 = .25$
					Reading	TOWRE	Sight Word	$a^2 = .69$	$c^2 = .15$	$e^2 = .17$
Kovas et al., 2007	UK	TEDS	-	~7	Word Decoding		Word Decoding	$a^2 = .67$	$c^2 = .13$	$e^2 = .20$
					Total		Total	$a^2 = .70$	$c^2 = .15$	$e^2 = .15$
					Mathematics	NC-TA	Using & Applying	$a^2 = .65$	$c^2 = .07$	$e^2 = .28$
							Numbers &	$a^2 = .64$	$c^2 = .06$	$e^2 = .30$
							Algebra			
					Shapes, Space &		Shapes, Space &	$a^2 = .66$	$c^2 = .09$	$e^2 = .25$
					Measures		Measures			
					Composite		Composite	$a^2 = .68$	$c^2 = .09$	$e^2 = .22$
					-		-	$a^2 = .64$	$c^2 = .10$	$e^2 = .25$
					-		-	$a^2 = .39$	$c^2 = .25$	$e^2 = .36$
					Using & Applying		Using & Applying	$a^2 = .73$	$c^2 = .01$	$e^2 = .26$
					Numbers &		Numbers &	$a^2 = .67$	$c^2 = .04$	$e^2 = .29$
					Algebra		Algebra			
					Shapes, Space &		Shapes, Space &	$a^2 = .63$	$c^2 = .09$	$e^2 = .28$
					Measures		Measures			
					Composite		Composite	$a^2 = .72$	$c^2 = .04$	$e^2 = .23$

Kovas, Petrill, & Plomin, 2007	UK	TEDS	470 MZ 781 DZ	~10	Mathematics	NFER	Mathematical	$a^2 = .30$	$c^2 = .30$	$e^2 = .41$
							Application			
							Understanding	$a^2 = .42$	$c^2 = .15$	$e^2 = .44$
							Numbers			
							Mathematical	$a^2 = .42$	$c^2 = .10$	$e^2 = .48$
							Interpretation			
							Computation & Knowledge	$a^2 = .35$	$c^2 = .08$	$e^2 = .56$
							Non-Numerical	$a^2 = .45$	$c^2 = .11$	$e^2 = .44$
							Processes			
							Numbers	$a^2 = .66$	$c^2 = .16$	$e^2 = .17$
Kovas et al., 2013	UK	TEDS	2415 MZ 2251 DZ	~7	Mathematics	NFER	Using & Applying			
							Shapes, Space & Knowledge			
							-			
							Reading Fluency	$a^2 = .68$	$c^2 = .22$	$e^2 = .10$
							Reading			
							Comprehension			
							-			
							Total			
							Numbers	$a^2 = .73$	$c^2 = .08$	$e^2 = .19$
							Using & Applying			
Kovas et al., 2013	UK	TEDS	1294 MZ 1152 DZ	~9	Mathematics	NFER	Shapes, Space & Knowledge			
							-			
							Reading Fluency	$a^2 = .77$	$c^2 = .10$	$e^2 = .13$
							Reading			
							Comprehension			
							-			
							Total			
							Numbers			
							Using & Applying			
							Shapes, Space & Knowledge			

Study	Year	Country	Sample Size	Grade	Subject	Assessment	Outcome	a^2	c^2	e^2																																		
1942 MZ 2192 DZ	~12	USA		Mathematics	Non-Numerical Processes	NFER		$a^2 = .56$	$c^2 = .21$	$e^2 = .24$																																		
											Understanding Numbers	Computation & Knowledge																																
													Reading	NC-TA	$a^2 = .65$	$c^2 = .24$	$e^2 = .12$																											
																		WRMT	Reading Fluency																									
																				PIAT	Passage																							
																						GOAL	Comprehension																					
																								TOWRE	Total																			
																										WRMT	Word Identification																	
																												WRTP	Reading	grade 1: $a^2 = .20$	$c^2 = .74$	$e^2 = .06$												
																																	213 DZ	6.1 (.7)	grade 2: $a^2 = .33$	$c^2 = .60$	$e^2 = .07$							
5.2-7.9	12.2 (1.0)	grade 3: $a^2 = .40$	$c^2 = .50$	$e^2 = .10$																																								
					10.0-14.6		grade 4: $a^2 = .59$	$c^2 = .25$	$e^2 = .16$																																			
												grade 5: $a^2 = .66$	$c^2 = .15$	$e^2 = .24$																														
																	grade 6: $a^2 = .82$	$c^2 = .00$	$e^2 = .18$																									
																																						grade 1: $a^2 = .30$	$c^2 = .58$	$e^2 = .12$				
																																									grade 2: $a^2 = .27$	$c^2 = .52$	$e^2 = .21$	
																																												grade 3: $a^2 = .58$
																														grade 5: $a^2 = .47$	$c^2 = .24$	$e^2 = .29$												
																																			grade 6: $a^2 = .71$	$c^2 = .01$	$e^2 = .28$							
Reading	WRMT	$a^2 = .39$	$c^2 = .39$	$e^2 = .22$																																								
					Comprehension	Comprehension	$a^2 = .44$	$c^2 = .47$	$e^2 = .09$																																			
												grade 3: $a^2 = .32$	$c^2 = .50$	$e^2 = .18$																														
																	grade 4: $a^2 = .72$	$c^2 = .05$	$e^2 = .23$																									
																																						grade 5: $a^2 = .55$	$c^2 = .23$	$e^2 = .12$				
																																									grade 6: $a^2 = .82$	$c^2 = .00$	$e^2 = .18$	

Luo et al., 2011	UK	TEDS	821 MZ 747 DZ	9.0 (.3)	Mathematics	NC-TA	-	$a^2 = .56$ $c^2 = .12$ $e^2 = .32$
			501 MZ 415 DZ	11.8 (.3)	Mathematics	NC-TA	-	$a^2 = .36$ $c^2 = .17$ $e^2 = .46$
Oliver et al., 2004	UK	TEDS	1146 MZ 1032 DZ	7.1 6.5-8.0	Mathematics	NC-TA	Using & Applying Numbers Shapes, Space & Measures Composite	$a^2 = .61$ $c^2 = .10$ $e^2 = .29$ $a^2 = .63$ $c^2 = .06$ $e^2 = .31$ $a^2 = .65$ $c^2 = .09$ $e^2 = .26$
Oliver, Dale, & Plomin, 2005	UK	TEDS	1565 MZ 1487 DZ	7.2 6.5-8.2	Reading	NC-TA	-	$a^2 = .66$ $c^2 = .09$ $e^2 = .25$ $a^2 = .59$ $c^2 = .18$ $e^2 = .23$
Olson et al., 2011	USA	ILTS	406 MZ 424 DZ	~8	Reading	TOWRE	Word Recognition Decoding Passage	$a^2 = .81$ $c^2 = .05$ $e^2 = .14$ $a^2 = .78$ $c^2 = .07$ $e^2 = .25$ $a^2 = .61$ $c^2 = .11$ $e^2 = .27$
	Australia Scandinavia				Reading Comprehension	WRMT	Comprehension	
	USA	ILTS	176 MZ 213 DZ	10.5 (.3)	Reading	TOWRE WJ	Word Recognition	$a^2 = .77$ $c^2 = .14$ $e^2 = .09$
					Reading	TOWRE	Phonemic Decoding	$a^2 = .78$ $c^2 = .09$ $e^2 = .14$
					Reading Comprehension	WRMT	Passage Comprehension	$a^2 = .86$ $c^2 = .09$ $e^2 = .04$
Olson et al., 2013 ^{1,2,4}	USA	CLDRC	81 MZ 189 DZ	12.0 (2.9) 8-18	Reading Reading Comprehension	PIAT WRMT	Word Recognition Reading Comprehension	$a^2 = .81$ $c^2 = .09$ $e^2 = .10$ $a^2 = .87$ $c^2 = .03$ $e^2 = .09$
					Spelling	PIAT	Reading Comprehension	
					Spelling	WRAT PIAT	Spelling Spelling	$a^2 = .83$ $c^2 = .05$ $e^2 = .12$

Petrill & Thompson, 1993	USA	WRTP	89 MZ	9.5 (1.8)	Educational Achievement	MAT	-	$a^2 = .27$	$c^2 = .67$	$e^2 = .06$
Petrill & Thompson, 1994	USA	WRTP	74 DZ	6-13	Reading	WRAT	-	$a^2 = .55$	$c^2 = .29$	$e^2 = .16$
			148 MZ	9.6 (1.8)	Spelling	MAT	-	$a^2 = .46$	$c^2 = .41$	$e^2 = .13$
			135 DZ	6-13	Mathematics	WRAT	-	$a^2 = .62$	$c^2 = .22$	$e^2 = .16$
						MAT	-	$a^2 = .53$	$c^2 = .19$	$e^2 = .28$
						WRAT	-	$a^2 = .28$	$c^2 = .51$	$e^2 = .21$
						MAT	-	$a^2 = .36$	$c^2 = .41$	$e^2 = .24$
						WRAT	-	$a^2 = .53$	$c^2 = .36$	$e^2 = .11$
						MAT	-			
Petrill et al., 2006	USA	WRTP	102 MZ	6.1 (.7)	Reading	WRMT	Word Identification	$a^2 = .68$	$c^2 = .22$	$e^2 = .10$
			140 DZ	4.3-7.9	Reading	WRMT	Word Attack	$a^2 = .48$	$c^2 = .32$	$e^2 = .20$
						WRMT	Word Identification	$a^2 = .59$	$c^2 = .31$	$e^2 = .10$
Petrill et al., 2006	USA	WRTP	118 MZ	6.1	Reading	WRMT	Word Knowledge	$a^2 = .55$	$c^2 = .34$	$e^2 = .11$
			163 DZ	4-7	Reading	WRMT	Passage	$a^2 = .58$	$c^2 = .33$	$e^2 = .09$
						WRMT	Comprehension			
						WRMT	Word Knowledge	$a^2 = .50$	$c^2 = .21$	$e^2 = .29$
						WRMT	Passage	$a^2 = .76$	$c^2 = .11$	$e^2 = .13$
						WRMT	Comprehension			
						SORT	-	$a^2 = .69$	$c^2 = .13$	$e^2 = .18$
Reynolds et al., 1996 ¹	USA	VTSABD	672 MZ	11.2 (2.5)	Reading	TOWRE	Word Decoding	$a^2 = .49$	$c^2 = .35$	$e^2 = .16$
			647 DZ		Spelling	-	-	$a^2 = .61$	$c^2 = .33$	$e^2 = .07$
Samuelsson et al., 2007	USA	ILTS	312	~6	Spelling	-	-	$a^2 = .34$	$c^2 = .46$	$e^2 = .20$

	Australia	ILTS	157	~6	Reading	TOWRE	Word Decoding	$a^2 = .88$
Samuelsson et al., 2008	USA	ILTS	224 MZ	6.3 (.3)	Spelling	-	Word Recognition	$a^2 = .91$
		ILTS	259 DZ		Reading	TOWRE		$a^2 = .84$
	Australia	ILTS	185 MZ	7.4 (.3)	Spelling	-		$a^2 = .68$
		ILTS	220 DZ	6.0 (.4)	Reading	TOWRE		$a^2 = .44$
Taylor & Schatschneider, 2010	USA	ILTS	98 MZ	7.0 (.4)	Reading	TOWRE		$a^2 = .83$
		ILTS	62 DZ	6.7 (.3)	Spelling	-		$a^2 = .62$
		ILTS	65 MZ	7.7 (.3)	Reading	TOWRE		$a^2 = .84$
		ILTS	73 DZ		Spelling	-		$a^2 = .74$
		ILTS	59 MZ	6.6 (.4)	Reading	TOWRE		$a^2 = .80$
		ILTS	66 DZ		Spelling	-		$a^2 = .79$
Thompson, Dettmerman & Plomin, 1991	USA	FTP	886 MZ	6.6 (.4)	Reading	PMRN	Oral Reading	$a^2 = .33$
		WRTP	1684 DZ	9.8	Spelling	-	Fluency	$a^2 = .46$
		WRTP	146 MZ	6-12	Reading	TOWRE		$a^2 = .79$
		WRTP	132 DZ		Spelling	-		$a^2 = .69$
Trzesniewski et al., 2006 ¹	UK	ERLTS	285 MZ	~7	Reading	MAT		$a^2 = .62$
		ERLTS	244 DZ		Reading	-		$a^2 = .29$
		ERLTS	244 DZ		Reading	-		$a^2 = .19$
Walker et al., 2004	UK	TEDS	434 MZ	~7	Mathematics	MAT		$a^2 = .21$
		TEDS	755 DZ		Language	MAT		$a^2 = .55$
						NC-TA	Total	same: $a^2 = .63$
						NC-TA	Total	different: $a^2 = .42$
						NC-TA	Total	$a^2 = .27$
						NC-TA	Total	$a^2 = .33$
						NC-TA	Total	$a^2 = .25$

de Zeeuw et al., 2015 ^{1,2,3,4,5}	The Netherlands	NTR	2451 MZ 4569 DZ	~12	Reading	NC-TA	English	same: $a^2 = .63$ $c^2 = .22$ $e^2 = .15$ different: $a^2 = .37$ $c^2 = .36$ $e^2 = .27$
						NC-TA	Mathematics	same: $a^2 = .69$ $c^2 = .22$ $e^2 = .09$ different: $a^2 = .46$ $c^2 = .30$ $e^2 = .24$ $a^2 = .74$ $c^2 = .08$ $e^2 = .18$
						CITO	Total Score	
						CITO	Arithmetic	$a^2 = .68$ $c^2 = .05$ $e^2 = .27$
						CITO	Language	$a^2 = .67$ $c^2 = .10$ $e^2 = .22$
						CITO	Arithmetic/ Mathematics	grade 1: $a^2 = .60$ $c^2 = .08$ $e^2 = .32$ grade 2: $a^2 = .66$ $c^2 = .00$ $e^2 = .34$ grade 3: $a^2 = .69$ $c^2 = .00$ $e^2 = .31$ grade 4: $a^2 = .61$ $c^2 = .07$ $e^2 = .32$ grade 5: $a^2 = .74$ $c^2 = .00$ $e^2 = .26$ grade 6: $a^2 = .65$ $c^2 = .04$ $e^2 = .31$
						CITO	DMT Reading	grade 2: $a^2 = .78$ $c^2 = .07$ $e^2 = .15$ grade 3: $a^2 = .73$ $c^2 = .03$ $e^2 = .24$ grade 4: $a^2 = .79$ $c^2 = .00$ $e^2 = .21$ grade 5: $a^2 = .82$ $c^2 = .00$ $e^2 = .18$ grade 3: $a^2 = .63$ $c^2 = .02$ $e^2 = .35$ grade 4: $a^2 = .59$ $c^2 = .08$ $e^2 = .32$ grade 5: $a^2 = .60$ $c^2 = .06$ $e^2 = .34$ grade 6: $a^2 = .54$ $c^2 = .12$ $e^2 = .35$
						CITO	Reading	grade 1: $a^2 = .33$ $c^2 = .28$ $e^2 = .39$
						CITO	Spelling	grade 2: $a^2 = .59$ $c^2 = .06$ $e^2 = .35$ grade 3: $a^2 = .70$ $c^2 = .00$ $e^2 = .30$ grade 4: $a^2 = .64$ $c^2 = .10$ $e^2 = .35$ grade 5: $a^2 = .58$ $c^2 = .11$ $e^2 = .31$ grade 6: $a^2 = .66$ $c^2 = .02$ $e^2 = .32$

Zumberge, Baker, & USA Manis, 2007 ²	-	277 MZ 328 DZ	9.6 (0.6)	Reading	WJ	Word Identification Word Attack	$a^2 = .70$ $c^2 = .11$ $e^2 = .19$
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BAS = British Ability Scales; CITO = Dutch National Educational Achievement Test; CLDRC = Colorado Learning Disabilities Research Center; DCSF = UK government's Department of Children, Schools and Families; DIBELS = Dynamic Indicators of Basic Early Literacy Skills; DMT = Three Minute Test; ERLTS = Environmental Risk (E-Risk) Longitudinal Twin Study; FCAT = Florida Comprehensive Achievement Test; FTP = Florida Twin Project; GOAL = Global Online Assessment for Learning; GORT = Gray Oral Reading Test; HKT = Hong Kong Test of Specific Learning Difficulties in Reading and Writing; ILTS = International Longitudinal Twin Study; MAT = Metropolitan Achievement Test; NARA = Neale Analysis of Reading Ability; NC = UK National Curriculum; NC-TA = UK National Curriculum Teacher Assessments; NFER = National Foundation for Educational Research 5-14; NTR = Netherlands Twin Register; PIAT = Peabody Individual Achievement Test; PMRN = Florida's Progress Monitoring and Reporting Network; PRIMA = Primair Onderwijs en Speciaal Onderwijs Cohort; QRI = Qualitative Reading Inventory; TOWRE = Word Reading Efficiency and Decoding Efficiency; SORT = Slosson Oral Reading Test; SST = Schonell Spelling Test; VTSABD = Virginia Twin Study of Adolescent Behavioral Development; WJ = Woodcock-Johnson III; WRMT = Woodcock Reading Mastery Tests; WRTP = Western Reserve Twin Project; WRAT = Wide-Range Achievement Test

¹ = included in meta-analysis of reading

² = included in meta-analysis of reading comprehension

³ = included in meta-analysis of mathematics

⁴ = included in meta-analysis of spelling

¹ = included in meta-analysis of educational achievement

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