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Generalist genes and high cognitive abilities

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Abstract

The concept of generalist genes operating across diverse domains of cognitive abilities is now widely accepted. Much less is known about the etiology of the high extreme of performance. Is there more specialization at the high extreme? Using a representative sample of 4000 12-year-old twin pairs from the UK Twins Early Development Study, we investigated the genetic and environmental overlap between web-based tests of general cognitive ability, reading, mathematics and language performance for the top 15% of the distribution using DF extremes analysis. Generalist genes are just as evident at the high extremes of performance as they are for the entire distribution of abilities and for cognitive disabilities. However, a smaller proportion of the phenotypic intercorrelations appears to be explained by genetic influences for high abilities.

One way in which behavioral genetics has gone beyond the rudimentary question of the relative influence of nature and nurture is to use multivariate genetic analysis to investigate the genetic and environmental etiologies of covariance between traits (Plomin, DeFries, McClearn, & McGuffin, 2008). Multivariate genetic analysis yields a key statistic called the *genetic correlation* that indexes the extent to which genetic influences on one trait also affect another trait (Neale & Maes, 2003). A high genetic correlation implies that if a gene were associated with one trait, there is a good chance that this gene would also be associated with the other trait.

A surprising finding from multivariate genetic analysis within the domain of cognitive abilities is that there is substantial genetic overlap between diverse cognitive abilities such as tests of verbal, spatial and memory abilities. Genetic correlations are consistently greater than 0.50 and often near 1.0 across different cognitive abilities (Deary, Spinath, & Bates, 2006; Petrill, 2002; Plomin & Spinath, 2002). Similar findings have also emerged from multivariate genetic research on learning abilities: genetic correlations vary from 0.67 to 1.0 between reading and language (five studies), 0.47 to 0.98 between reading and mathematics (three studies), and 0.59 to 0.98 between language and mathematics (two studies) (Plomin & Kovas, 2005). The average genetic correlation across all of these studies is about 0.70. Moreover, genetic correlations are also substantial between general cognitive ability and learning abilities. A recent review of a dozen such studies suggests a genetic correlation of

about 0.60 between general cognitive ability and learning abilities (Plomin & Kovas, 2005), which is similar to the results of several subsequent studies (Davis et al., 2008; Davis, Haworth & Plomin, in press; Harlaar, Hayiou-Thomas, & Plomin, 2005; Haworth, Kovas, Dale, & Plomin, 2008; Kovas, Haworth, Dale, & Plomin, 2007a).

These findings of substantial genetic correlations among diverse cognitive abilities have led to a *Generalist Genes* hypothesis which predicts that the same set of genes largely affects all cognitive abilities (Kovas & Plomin, 2007; Plomin & Kovas, 2005). The Generalist Genes hypothesis has far-reaching implications for molecular genetics and neuroscience (Kovas & Plomin, 2006).

Nearly all of this multivariate genetic research has focused on the normal range of variation. One reason to suspect that the Generalist Genes hypothesis might not apply equally to high cognitive abilities is a body of data consisting of more than one hundred studies suggesting that phenotypic correlations among cognitive tests may be lower at the high end of the ability distribution than at the low end of the distribution (Deary et al., 1996; Hartmann, 2006), although more recent studies provide little support for this hypothesis (Arden & Plomin, 2007; Hartmann & Reuter, 2006; Saklofske, Yang, Zhu, & Austin, 2008). In other words, the general cognitive ability ('g') factor (Jensen, 1998) appears to account for less variance at the high end as compared to the low end of the distribution of 'g'. The weaker strength of phenotypic 'g' for high cognitive ability might reflect weaker genetic underpinnings. That is, to the extent that genes are less generalist in their effect on high ability, phenotypic correlations will be reduced.

To our knowledge, no multivariate genetic research has been reported for high cognitive abilities. However, four multivariate genetic studies have investigated the low end of the ability distribution, specifically reading and mathematics disabilities. The first study focused on children selected for reading disability who were then selected for mathematics disability (Light & DeFries, 1995). Substantial genetic overlap was found between reading disability and mathematics ability but no genetic correlation could be calculated because the twins were all selected for reading disability. In a follow-up analysis, twins were selected both for reading disability and mathematics disability (Knopik, Alarcón, & DeFries, 1997). The genetic correlation between reading disability and mathematics disability was estimated as 0.53. The other two studies are based on the Twins Early Development Study (TEDS; Oliver & Plomin, 2007) on which the present study is also based. A multivariate genetic analysis of a web-based battery of reading and mathematics tests for 10-year-old twins with the lowest 15% scores on reading or mathematics yielded a genetic correlation of 0.67 (Kovas et al., 2007b), which is close to the average genetic correlation of 0.70 mentioned above for studies of normal variation. The fourth study is the mirror image of the present study in that it examined the lowest 15% scores on general cognitive ability and language as well as reading and mathematics using a web-based battery for 12-year-old twins in TEDS (Haworth et al., in pressb). The multivariate genetic analyses yielded an average genetic correlation of 0.67 between low ability in the four domains, which is comparable to the average genetic correlation of 0.68 that emerged in multivariate genetic analysis of the entire sample. All four studies used a bivariate extension of DF extremes analysis (DeFries &

Fulker, 1988), which is explained in the Methods section below. These four studies provide consistent evidence for generalist genes for low cognitive abilities.

Univariate estimates of genetic and environmental influence for high ability are typically similar to those found in the whole distribution, for example for general cognitive ability in young twins (Ronald, Spinath & Plomin, 2002), and also for science performance compared to science excellence (Haworth, Dale & Plomin, in pressa). However, we do not know whether the multivariate relationship between different domains will be the same at the high extreme, compared to the whole distribution of scores.

The goal of the present study is to conduct the first multivariate genetic analyses of high cognitive abilities in order to test the Generalist Genes hypothesis for high cognitive abilities. Although our focus is on testing the Generalist Genes hypothesis for high cognitive abilities, multivariate genetic analyses also yield correlations for shared environmental influences which tend to be substantial for cognitive abilities and for non-shared environmental correlations which are low (Kovas et al., 2007a). In other words, for the normal range of variation, the same set of generalist genes and the same set of shared environmental factors largely affect different cognitive abilities, mathematical and reading disabilities. The dissociation between cognitive abilities occurs largely due to independent non-shared environmental influences. We will explore the extent to which similar results are found for high cognitive abilities. As mentioned above, we conducted multivariate genetic analyses of high cognitive abilities using data from a web-based battery of tests of general cognitive ability, reading, mathematics and language performance for the TEDS sample of 4000 12-year-old twin pairs, the same dataset used in our previous multivariate genetic analyses of low cognitive abilities (Haworth et al., in pressb). In the Discussion we compare our present results for high cognitive abilities with our previously reported results from multivariate genetic analyses of low cognitive abilities and the normal distribution.

Methods

Sample

The sampling frame for the present study was the Twins Early Development Study (TEDS), a study of twins born in England and Wales in 1994, 1995, and 1996 (Oliver & Plomin, 2007; Trouton, Spinath, & Plomin, 2002). The TEDS sample has been shown to be reasonably representative of the general population in terms of parental education, ethnicity and employment status (Kovas et al., 2007a). Zygosity was assessed through a parent questionnaire of physical similarity, which has been shown to be over 95% accurate when compared to DNA testing (Price et al., 2000). For cases where zygosity was unclear from this questionnaire, DNA testing was conducted.

At age 12, twins born in 1994, 1995 and 1996 were invited to participate. The twins completed our internet cognitive test battery (Haworth et al., 2007). 10,875 individuals participated (completed at least one test) in our web battery. This is the same sample and dataset in which we previously reported results for low cognitive abilities (Haworth et al., in pressb), where further details about the sample and measures can be found.

Measures

We have shown that our web-based cognitive test battery is a reliable and valid method for collecting cognitive data on children as young as 10 years old (Haworth et al., 2007). More than 80% of the TEDS sample has access to the internet at home and most children without access to the internet at home have access in their schools and local libraries. At 12 years we collected information relating to four main cognitive domains: general cognitive ability, reading, mathematics and language. These domains are moderately correlated phenotypically: g with reading, math and language $r = 0.54, 0.65$ and 0.65 ; reading with math and language $r = 0.57$ and 0.57 ; and math with language $r = 0.58$.

General cognitive ability (g)—At age 12, the twins were tested on two verbal tests, WISC-III-PI Multiple Choice Information (General Knowledge) and Vocabulary Multiple Choice subtests (Wechsler, 1992), and two non-verbal reasoning tests, the WISC-III-UK Picture Completion (Wechsler, 1992) and Raven's Standard and Advanced Progressive Matrices (Raven, Court, & Raven, 1996; Raven, Court, & Raven, 1998). These tests show good internal consistency reliability with Cronbach's alphas of .81 for general knowledge; .88 for vocabulary; .73 for picture completion; and .75 for Raven's. We calculated a mean composite g scale using these four tests.

Reading—Four measures of reading ability were used at 12 years: two measures of reading comprehension and a measure of reading fluency presented on the Web, and a fourth measure administered over the telephone.

Reading comprehension: At age 12, the twins completed an adaptation of the reading comprehension subtest of the Peabody Individual Achievement Test (Markwardt, 1997), which we will refer to as PIAT_{rc}. The PIAT_{rc} assesses literal comprehension of sentences. The sentences were presented individually on the computer screen. Children were required to read each sentence and were then shown four pictures. Using the mouse, they selected the picture that best matched the sentence they had read. All children started with the same items, but an adaptive algorithm modified item order and test discontinuation depending on the performance of the participant. The internet-based adaptation of the PIAT_{rc} contained the same practice items, test items and instructions as the original published test.

As well as the PIAT_{rc}, we assessed reading comprehension at age 12 using the GOAL Formative Assessment in Literacy for Key Stage 3 (GOAL plc, 2002). The GOAL is a test of reading achievement that is linked to the literacy goals for children at Key Stage 3 of the UK National Curriculum. Questions are grouped into three categories: Assessing Knowledge and Understanding (e.g. identifying information, use of punctuation and syntax), Comprehension (e.g. grasping meaning, predicting consequences), and Evaluation and Analysis (e.g. comparing and discriminating between ideas). Within each category, questions about words, sentences, and short paragraphs are asked. Because we were primarily interested in comprehension skills, we used questions from the two relevant categories, Comprehension, and Evaluation and Analysis, with 20 items from each category. Correct answers were summed to give a total comprehension score.

Reading fluency: At 12 years, reading fluency was assessed using an adaptation of the Woodcock-Johnson III Reading Fluency Test (Woodcock, McGrew, & Mather, 2001) and the Test of Word Reading Efficiency (TOWRE, Form B; Torgesen, Wagner, & Rashotte, 1999). The Woodcock-Johnson is a measure of reading speed and rate that requires the ability to read and comprehend simple sentences quickly e.g. "A flower grows in the sky? - Yes/No". The online adaptation consists of 98 yes/no statements; children need to indicate yes or no for each statement as quickly as possible. There is a time limit of 3 minutes for this test. Correct answers were summed to give a total fluency score.

The TOWRE, a standardized measure of fluency and accuracy in word reading skills, includes two subtests, each printed on a single sheet: A graded list of 85 words, called Sight-word Efficiency (SWE), which assesses the ability to read aloud real words; and a graded list of 54 non-words, called Phonemic Decoding Efficiency (PDE), which assesses the ability to read aloud pronounceable printed non-words (Torgesen et al., 1999). The child is given 45 seconds to read as many words as possible. Twins were individually assessed by telephone using test stimuli that had been mailed to families in a sealed package with separate instructions that the package should not be opened until the time of testing. The same tester, who was blind to zygosity, assessed both twins in a pair within the same test session.

All of the reading tests demonstrated good internal consistency reliability with Cronbach's alphas of .94 for the PIAT_{RC}; .89 for the GOAL; .96 for reading fluency; and .85 for the TOWRE. We calculated a mean composite reading scale using these four tests.

Mathematics—In order to assess mathematics, we developed an internet-based battery that included questions from three components of mathematics. The items were based on the National Foundation for Educational Research 5–14 Mathematics Series, which is linked closely to curriculum requirements in the UK and the English Numeracy Strategy (InferNelson, 1999). The presentation of items was streamed, so that items from different categories were mixed, but the data recording and branching were done within each category. The items were drawn from the following three categories: Understanding Number, Non-Numerical Processes and Computation and Knowledge. The mathematics battery is described in more detail elsewhere (Kovas, Haworth, Petrill, & Plomin, 2007). All of the math tests showed good internal consistency reliability with Cronbach's alphas of .90, .87 and .93 for the three math subtests. We calculated a mean composite mathematics scale using these three tests.

Language—In order to assess receptive spoken language, standardized tests were selected that would discriminate children with language disability as well as being sensitive to individual differences across the full range of ability. Furthermore, an aspect of language that becomes increasingly important in adolescence – and which shows interesting variability at this age -- is metalinguistic ability, which is knowledge about language itself (Nippold, 1998). For this reason, the three measures selected for testing included one with low metalinguistic demands designed to assess syntax (*Listening Grammar*) and two with higher demands that assess semantics (*Figurative Language*) and pragmatics (*Making Inferences*).

Syntax: Syntax was assessed using the *Listening Grammar* subtest of the Test of Adolescent and Adult Language (TOAL-3) (Hammill, Brown, Larsen, & Wiederholt, 1994). This test requires the child to select two sentences that have nearly the same meaning, out of three options. The sentences are presented orally only.

Semantics: Semantics were assessed using Level 2 of the *Figurative Language* subtest of the Test of Language Competence (Wiig, Secord, & Sabers, 1989), which assesses the interpretation of idioms and metaphors; correct understanding of such non-literal language requires rich semantic representations. The child hears a sentence orally and chooses one of four answers, presented in both written and oral form.

Pragmatics: Level 2 of the *Making Inferences* subtest of the Test of Language Competence (Wiig et al., 1989) assessed an aspect of pragmatic language, requiring participants to make permissible inferences on the basis of existing (but incomplete) causal relationships presented in short paragraphs. The child hears the paragraphs orally and chooses two of four responses, presented in both written and oral form.

The language tests each showed good internal consistency reliability with Cronbach's alphas of .94 for the TOAL; .67 for figurative language; and .57 for making inferences. We calculated a mean composite language scale using these three tests.

Analyses

Univariate and bivariate DF extremes analyses were used to investigate the genetic and environmental correlations for high performance. Individuals scoring in the top 15% of the distribution for each domain were classified as high performers (probands). We are interested in the etiology of high cognitive ability as compared to normal performance, not in the etiology of individual differences among high performers. Probandwise concordance (number of probands in concordant pairs as a ratio of the total number of probands) was calculated which indicates the risk that a co-twin of a proband also meets criteria for high performance. Greater MZ than DZ concordances suggest genetic influence, but unlike twin correlations, twin concordances cannot be used to estimate genetic and environmental parameters because they do not in themselves include information about population incidence.

Rather than dichotomizing each trait for 'cases' versus 'controls' and analyzing concordance (or polychoric correlations in the case of liability/threshold models), we used DeFries-Fulker (DF) extremes analysis (DeFries & Fulker, 1988) which incorporates quantitative trait information from the co-twins of selected probands. DF extremes analysis assesses twin similarity as the extent to which the mean standardized quantitative trait score of co-twins of the selected extreme probands is above the population mean and approaches the mean standardized score of those probands (see Plomin & Kovas, 2005). This measure of twin similarity is called a *group* twin correlation (or *transformed co-twin mean*) in DF extremes analysis because it focuses on the mean quantitative trait score of co-twins rather than individual differences. Genetic influence is implied if group twin correlations are greater for MZ than for DZ twins, that is, if the mean standardized score of the co-twins is higher for MZ pairs than for DZ pairs. Doubling the difference between MZ and DZ group twin

correlations estimates the genetic contribution to the average phenotypic difference between the probands and the population. The ratio between this genetic estimate and the phenotypic difference between the probands and the population is called *group heritability*. It should be noted that group heritability does not refer to individual differences among the probands – the question is not why one proband scores slightly higher than another but rather why the probands as a group have higher scores than the rest of the population.

Although DF extremes group heritability can be estimated by doubling the difference in MZ and DZ group twin correlations (Plomin, 1991), DF extremes analysis is more properly conducted using a regression model (DeFries & Fulker, 1988). The DF extremes model fits standardized scores for MZ and DZ twins to the regression equation:

$$C(X) = B_1 P(X) + B_2 R + A$$

where the co-twins' scores ($C(X)$) are predicted from the probands' scores ($P(X)$) and the coefficient of relatedness (R), which is 1.0 for MZ (genetically identical) and 0.5 for DZ twins (who are on average 50% similar genetically), and A is the regression constant. B_1 is the partial regression of the co-twin score on the proband, an index of average MZ and DZ twin resemblance independent of B_2 . The focus of DF extremes analysis is on B_2 . B_2 is the partial regression of the co-twin score on R independent of B_1 . It is equivalent to twice the difference between the means for MZ and DZ co-twins adjusted for differences between MZ and DZ probands. In other words, B_2 is the genetic contribution to the phenotypic mean difference between the probands and the population. Group heritability is estimated by dividing B_2 by the difference between the means for probands and the population.

In contrast to univariate DF extremes analysis which selects probands as extreme on X and compares the quantitative scores of their MZ and DZ co-twins on X , bivariate DF extremes analysis selects probands on X and compares the quantitative scores of their co-twins on Y , a cross-trait twin group correlation. The genetic contribution to the phenotypic difference between the means of the probands on trait X and the population on Y can be estimated by doubling the difference between the cross-trait twin group correlations for MZ and DZ twins. Bivariate group heritability is the ratio between this genetic estimate and the phenotypic difference between the probands on trait X and the population on Y . Unlike bivariate analysis of individual differences in unselected samples, such as those mentioned above, bivariate DF extremes analysis is directional in the sense that selecting probands on X and examining quantitative scores of co-twins on Y could yield different results as compared with selecting probands on Y and examining quantitative scores of co-twins on X . A group genetic correlation can be derived from four group parameter estimates: bivariate group heritability estimated by selecting probands for X and assessing co-twins on Y , bivariate group heritability estimated by selecting probands for Y and assessing co-twins on X , and univariate group heritability estimates for X and for Y :

$$r_{g(xy)} = \sqrt{\frac{(B_{2xy})(B_{2yx})}{(B_{2x})(B_{2y})}}$$

where B_{2xy} is the group heritability from x to y (e.g., from g to reading) and B_{2yx} is the group heritability from y to x (e.g., from reading to g), B_{2x} is the group heritability at x (e.g., univariate group heritability of g) and B_{2y} is the group heritability at y (e.g., univariate group heritability of reading) (see Knopik et al., 1997 for further details).

Results

Probandwise concordances and group twin correlations were higher in MZ than DZ pairs for each scale, indicating that genetic influences are important which is confirmed by ACE estimates from DF extremes analysis (Table 1). Results from the bivariate DF extremes analyses (performed in both directions for each bivariate comparison of the scales) can be found in Table 2. MZ cross-concordances and group cross-twin correlations were greater than DZ pairs, indicating that genetic factors contribute to the co-morbidity for each bivariate comparison. The bivariate DF estimate of group heritability (Biv A in Table 2) indicates that genetic factors contribute significantly to the group phenotypic correlation (shown in the last column of Table 2)

Genetic and environmental correlations were calculated from the bivariate DF extremes analyses (Table 3). All of the genetic correlations are substantial, varying only from 0.52 to 0.63.

Discussion

We found strong support for the Generalist Genes hypothesis for high cognitive abilities in that genetic ‘group’ correlations were substantial between g , reading, math and language. The average genetic correlation of 0.58 is comparable to genetic correlations found in multivariate genetic studies in unselected samples, which are about 0.60 between g and learning abilities and about 0.70 between cognitive abilities. A direct comparison can be made with our previous analyses of the entire distribution using the same sample, measures and methods as in the present analysis of high cognitive ability (Haworth et al., in pressb). In that report, we found that the average genetic correlation was 0.68 for the entire distribution. In addition, in our previous paper (Haworth et al., in pressb), we also analyzed low cognitive abilities (the lowest 15%) and found an average genetic correlation of 0.67. In other words, generalist genes appear to be almost as important at the high end of the distribution as they are for the rest of the distribution.

Although we have focused on the genetic aspect of the results in order to address the Generalist Genes hypothesis, these analyses also yield interesting results in relation to the environment. As shown in Table 3, shared environmental group correlations for high abilities are consistently very high, 0.93 on average, and the non-shared environmental group correlations are modest, 0.23 on average. Both findings are similar to previous studies of normal variation as mentioned in the Introduction. The findings are also similar to our previous report of analyses for the entire sample which yielded average correlations of 0.94 for shared environment and 0.23 for non-shared environment (Haworth et al., in pressb). These findings suggest that, similar to the whole distribution, at the high extreme shared environments are almost entirely generalists and non-shared environments are largely

specialists. Similar results were also found in our previous analyses of low ability: non-shared environmental group correlations were modest (0.23) indicating specialist effects of non-shared environmental influences for high and low performance, as well as performance across the full range of scores. Shared environmental results in our low ability analyses also indicated largely generalist effects for those domains that were influenced by the shared environment (Haworth et al., in pressb). One goal for future research could be to begin to identify the environmental factors responsible for these generalist and specialist effects for high ability. The similarity in results for high ability and the entire distribution suggests, but does not prove, that high ability differs quantitatively not qualitatively from the rest of the distribution in relation to these environmental effects.

Even though genetic correlations and environmental correlations are similar throughout the distributions of abilities, including the high and low ends of the distribution, these analyses suggest an intriguing but subtle difference between high and low ability: The genetic contributions to the phenotypic correlations among the cognitive domains may be less for high ability than for low ability. Bivariate heritability estimates the extent to which the phenotypic correlation is mediated genetically and is essentially the genetic correlation weighted by the relative heritabilities of the abilities (Plomin & DeFries, 1979). In Table 2, the genetic contribution to the group phenotypic correlation is shown in the 'Biv A' column (0.23 in the first row for 'g to reading'). The group phenotypic correlation is shown in the last column (0.51 for the first row). Group bivariate heritability for the first row is $0.23 \div 0.51 = 0.45$; that is, 45 percent of the group phenotypic correlation is mediated genetically. The average group bivariate heritability from the data in Table 2 is 0.42 for high abilities. We previously reported bivariate group heritabilities for low ability and for the entire distribution (Haworth et al., in pressb). In contrast to the average group bivariate heritability of 0.42 for high cognitive abilities, the average group bivariate heritability for low cognitive abilities was 0.69. The average bivariate heritability for the entire distribution is in between the result for the high and low performers: 0.58. The difference in group bivariate heritabilities for high and low performers is due in part to slightly lower group genetic correlations for high vs. low performers (0.58 vs. 0.67 on average) but the difference is mostly due to the lower univariate group heritabilities for the high vs. low performers (0.42 vs. 0.61). Nonetheless, to the extent that genes affect high performance, which may be less than the extent to which genes affect low performance, the genetic correlation of 0.58 provides strong support for Generalist Genes for high ability.

Finally, in addition to the genetic and environmental findings, the analyses yield a phenotypic result that is relevant to the issue mentioned in the Introduction about whether 'g' is weaker for high abilities. Along with other recent studies (Arden & Plomin, 2007; Hartmann & Reuter, 2006; Saklofske, Yang, Zhu, & Austin, 2008) that used different approaches to address this issue, we find that phenotypic 'g' is strong for high abilities. The last column of Table 2 lists the group phenotypic correlations for each bivariate comparison, which are between 0.51 and 0.72. Moreover, the average group phenotypic correlation of 0.56 for high abilities is similar to the average group phenotypic correlation of 0.58 for low abilities and the average Pearson correlation for the entire sample of 0.59.

Limitations of these analyses include the usual limitations of the classical twin design (Plomin et al., 2008). In addition there are at least five limitations specific to our study. First, power is limited to conduct multivariate genetic analyses on a subsample selected for high ability; we chose the moderate cut-off of the top 15% in order to balance selection for high ability against power. The cut-off of 15% is itself a limitation; however, we conducted the same analyses using a cut-off of the top 5% and found similar results taking into account the reduced power with the smaller sample (details available from first author). A third limitation is the age of the sample which was 12 years. Different results might be found at different ages; an interesting direction for future research is to explore the developmental course of generalist genes. A fourth potential limitation specific to our study is the novel use of web-based tests administered online in the home, although previous research indicates that these web-based tests are reliable and valid as compared to in-person testing (Haworth et al., 2007). Finally, the use of bivariate DF extremes analysis is a limitation; the rationale for using this method was discussed earlier and it is noteworthy that this method has been used in all previous research in this area. However, we also applied liability/threshold model fitting to the dichotomous data used to calculate the concordances in Tables 1 and 2. These analyses also led to conclusions supportive of the Generalist Genes hypothesis (details available from first author).

Definitive proof of the importance of generalist genes for high cognitive abilities will come from molecular genetic research. The prediction is clear: Most (but not all) genes found to be associated with a particular test or domain of cognitive ability will also be associated with other cognitive tests and domains. Moreover, the Generalist Genes hypothesis could facilitate the search for specific genes responsible for high cognitive ability. We have previously tested the Generalist Genes hypotheses using molecular genetic data from TEDS (Meaburn et al., 2007). We found that single nucleotide polymorphisms associated with reading, were also associated with performance in other literacy measures, math and general cognitive ability (Haworth, Meaburn, Harlaar & Plomin, 2007). Moreover, these 'reading SNPs' explained almost as much variance in these other cognitive domains as they did for reading. But these results refer to the whole distribution of scores; a very large sample with molecular genetic data would be required to assess the association with high ability. Even with our large sample, and using a cut-off of 85% we do not have sufficient power to reliably detect these associations.

Because the Generalist Genes hypothesis suggests that most of the genetic action in cognitive abilities lies in the co-action of genes across diverse domains, it recommends a multivariate approach that focuses on what is in common across domains rather than what is specific to each domain. In addition, because genetic correlations among cognitive domains are similar throughout the distribution of abilities, a quantitative trait locus (QTL) approach is defensible that increases the ratio of power to expense by comparing high and low performing individuals. Identifying more of these generalist genes will greatly accelerate research on general mechanisms at all levels of analysis from genes to brain to behavior.

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MZ and DZ probandwise concordances and results of univariate DF extremes analysis using an 85% cut-off

Table 1

	Probandwise concordance		Twin group correlation		DF estimates		
	MZ	DZ	MZ	DZ	h^2g (SE)	c^2g (SE)	e^2g (SE)
General Cognitive Ability	0.53	0.37	0.71	0.50	0.42 (.07)	0.30 (.05)	0.28 (.05)
Reading	0.62	0.39	0.79	0.50	0.59 (.07)	0.20 (.05)	0.21 (.04)
Math	0.52	0.43	0.73	0.57	0.32 (.07)	0.40 (.05)	0.28 (.04)
Language	0.47	0.35	0.64	0.47	0.34 (.07)	0.30 (.05)	0.36 (.05)

Note.

MZ = monozygotic; DZ = dizygotic; h^2g = group heritability; c^2g = group shared environment; e^2g = group non-shared environment. Preliminary analyses revealed no significant sex differences, so to increase power we combined same-sex and opposite-sex dizygotic twins.
For each scale the number of complete twin pairs was as follows:

General cognitive ability: MZ = 1464; DZ = 2418. Reading: MZ = 1852; DZ = 3180. Math: MZ = 1696; DZ = 2896. Language: MZ = 1537; DZ = 2575.

MZ and DZ probandwise concordances and results of bivariate DF extremes analysis using an 85% cut-off

Table 2

	Probandwise cross-concordance		Twin group cross-correlation		Bivariate DF estimates			Group Phenotypic Correlation
	MZ	DZ	MZ	DZ	Biv A (SE)	Biv C (SE)	Biv E (SE)	
g to reading	0.38	0.28	0.47	0.35	0.23 (.08)	0.23 (.05)	0.05 (.05)	0.51
Reading to g	0.38	0.28	0.51	0.34	0.34 (.08)	0.17 (.05)	0.05 (.05)	0.56
g to math	0.41	0.36	0.55	0.42	0.25 (.07)	0.30 (.05)	0.08 (.04)	0.63
Math to g	0.39	0.36	0.61	0.51	0.20 (.09)	0.41 (.06)	0.11 (.05)	0.72
g to language	0.39	0.33	0.57	0.42	0.31 (.08)	0.26 (.05)	0.07 (.05)	0.64
Language to g	0.38	0.34	0.52	0.44	0.18 (.07)	0.35 (.05)	0.08 (.04)	0.61
Reading to math	0.37	0.32	0.47	0.34	0.26 (.07)	0.21 (.04)	0.05 (.04)	0.52
Math to reading	0.37	0.31	0.53	0.41	0.23 (.08)	0.30 (.05)	0.07 (.05)	0.60
Reading to language	0.39	0.30	0.53	0.37	0.32 (.08)	0.21 (.05)	0.05 (.05)	0.58
Language to reading	0.39	0.31	0.46	0.37	0.17 (.08)	0.29 (.05)	0.08 (.04)	0.54
Math to language	0.37	0.32	0.58	0.47	0.22 (.09)	0.35 (.06)	0.04 (.05)	0.61
Language to math	0.37	0.33	0.47	0.38	0.19 (.07)	0.29 (.04)	0.03 (.04)	0.51

Note.

MZ = monozygotic; DZ = dizygotic; Biv A = hxyrg; Biv C = cxyrg; Biv E = exeyre. Group phenotypic correlations are calculated by taking the mean proband score for x and dividing by the mean proband score for y. Bivariate heritability provides an estimate of the proportion of the phenotypic correlation that is accounted for by genetic influences. It is calculated by dividing the shared genetic contribution (hxyrg) by the phenotypic correlation. The same calculations were applied to the environmental contributions.

Table 3

Genetic and environmental correlations from DF extremes analysis using an 85% cut-off

	g and reading	g and math	g and language	Reading and math	Reading and language	Math and language
Gr _G	0.56	0.61	0.63	0.56	0.52	0.62
Gr _C	0.81	1.00 [±]	1.00 [±]	0.79	1.00 [±]	0.92
Gr _E	0.21	0.34	0.24	0.24	0.23	0.11

Note.

Gr_G= group genetic correlation; Gr_C= group shared environment correlation; Gr_E= group non-shared environment correlation. Three of the group shared environmental correlations exceed one (marked with [±]); this is a function of the equation for calculating the correlations, which does not restrict the correlation to fall between -1 and +1. Because correlations cannot exceed unity, we present these as correlations of 1.0.