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A genetic two-factor model of the covariation among a subset of Multidimensional Aptitude Battery and Wechsler Adult Intelligence Scale—Revised subtests

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Abstract

The phenotypic and genetic factor structure of performance on five Multidimensional Aptitude Battery (MAB) subtests and one Wechsler Adult Intelligence Scale—Revised (WAIS-R) subtest was explored in 390 adolescent twin pairs (184 monozygotic [MZ]; 206 dizygotic (DZ)). The temporal stability of these measures was derived from a subsample of 49 twin pairs, with test–retest correlations ranging from .67 to .85. A phenotypic factor model, in which performance and verbal factors were correlated, provided a good fit to the data. Genetic modeling was based on the phenotypic factor structure, but also took into account the additive genetic (*A*), common environmental (*C*), and unique environmental (*E*) parameters derived from a fully saturated *ACE* model. The best fitting model was characterized by a genetic correlated two-factor structure with specific effects, a general common environmental factor, and overlapping unique environmental effects. Results are compared to multivariate genetic models reported in children and adults, with the most notable difference being the growing importance of common genes influencing diverse abilities in adolescence.

Keywords: MAB; WAIS-R; Multivariate genetic analysis; Twin study; Cognitive ability

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1. Introduction

The large contribution of genes ($\sim$50%) to the variation in IQ test scores or first principal component derived from a battery of IQ subtest scores is well established (see reviews by McCartney, Harris, & Bernieri, 1990; Plomin, DeFries, McClearn, & McGuffin, 2001). It is now important to establish the pattern of genetic relationships among IQ subtests, which is possible through multivariate genetic analysis (Petrill, 1997). This type of analysis provides a more informative decomposition of the structure of genetic and environmental effects because general, group, and specific variance factors can be explored (e.g., Cardon & Fulker, 1994; Casto, DeFries, & Fulker, 1995; Martin & Eaves, 1977; Tambs, Sundet, & Magnus, 1986). Such analysis might also be helpful in the search for quantitative trait loci (QTLs) influencing intelligence, since genes may show pleiotropic effects (the same gene influencing different cognitive abilities). As multivariate quantitative genetic analysis of IQ subtest scores can identify which groups of subtests have the strongest genetic relationships, this will improve the selection of cognitive phenotypes for use in multivariate genetic linkage analyses.

The partitioning of genetic and environmental components of variance in a trait is possible through twin, family, and adoption studies that assess the correlations of diverse pairings of relatives (on the trait) in relation to the expected correlations based on Mendelian laws of inheritance. In the classical twin design, which is used in this study, monozygotic (MZ) twin pairs who share 100% of their genes are compared with dizygotic (DZ) twins who share roughly 50% of their segregating genes. If the causes of familial similarity are the additive genes (transmissible from parent to child), the correlation of MZ co-twin's IQ scores is expected to be twice that of DZ co-twins. An underlying assumption is that environmental influences on cognitive ability are equivalent in MZ and DZ twins (e.g., Kendler, Neale, Kessler, Heath, & Eaves, 1993). Multivariate genetic modeling is simply an extension of the univariate case, where MZ and DZ cross-correlations (Twin 1's score on one measure is correlated with Twin 2's score on a different measure) are compared instead of correlations on the same measure (Plomin, 1986). Various multivariate genetic models have been applied to the covariance among IQ subtest scores.

An independent pathways model, that specifies a general and specific factors (parameterized as genetic and/or environmental) corresponds to a general factor view of intelligence (e.g., Spearman, 1904) and has been demonstrated in an analysis of four Wechsler Adult Intelligence Scale—Revised (WAIS-R) subtests in American and Swedish samples (Finkel, Pedersen, McGue, & McClearn, 1995). In the American sample (age 27–88), a genetic general factor explained the most variance (49%) in Block Design (cf. Information, 39%; Digit Symbol, 24%; Digit Span, 16%), while genetic specific effects were largest for Digit Span (39%) and lowest for Block Design (24%). In the Swedish young to middle age adult sample (age 27–65), a genetic general factor explained the most variance (51%) in Block Design (cf. Digit Symbol, 41%; Information, 33%; Digit Span, 27%); the genetic specific effects were largest for Information (42%) and again lowest for Block Design (23%). The major disparity between these results was in the estimates of genetic variance for Digit Symbol, but this could be explained by differences between the versions used; one required writing unusual symbols to match digits, while the other (Swedish task) required the reverse. It was claimed that digits were easier to write than novel symbols and, hence, the Swedish task was a purer measure of perceptual speed, with the result of higher loadings from the genetic general factor.

Using a general and group factor approach, Rijsdijk, Vernon, and Boomsma (1998) investigated the underlying genetic structure of the covariation among WAIS subtests and reaction time measures in an adolescent twin sample with a mean age of 16.1 ± 0.6 years on first test occasion. A genetic general factor explained between 7% and 49% of variance in the IQ subtest scores, while respective genetic performance (Block Design, Picture Arrangement, and Object Assembly) and verbal (Information, Comprehension, Arithmetic, Similarities, and Vocabulary) group factors explained between 1–28% and 1–44% of variance in subtest scores. Genetic test-specific influences were also significant for all subtests except Similarities and Block Design. Unique environment had a generalized effect on most subtests (not Information, Digit Span, or Coding) and substantial specific effects.

Genetic models have also been specified in accordance with the established Cohen (1957) factor structure (verbal comprehension, perceptual organization, and freedom from distractibility) of the WAIS. In a twin study (80 pairs) of adults aged from 30 to 57 years, Tambs et al. (1986) found that a model specifying a genetic general and Cohen factors showed improvement over a WAIS subtest model that specified a genetic general and subtest-specific factors. The genetic general factor had the largest loadings (~ .60 to .67) on Comprehension, Similarities, and Vocabulary and the smallest loadings on Digit Span (.08) and Digit Symbol (.22), with intermediate loadings (.40 to .50) on the other subtests (Arithmetic was excluded from the analysis due to its nonconforming phenotypic factor loadings). A further analysis of the Cohen factors, using composite scores, showed that the genetic general factor had the largest influence on verbal comprehension, followed by perceptual organization; and lastly, freedom from distraction. The only substantial composite-specific genetic loading was for freedom from distraction (explaining 35% of variance). Effects of common and unique environment were specific to each Cohen factor rather than overlapping. The analysis of Cohen factors was later investigated in children aged between 7 and 16 years, but the factor scores were analyzed instead of the individual subtests or composite scores (Casto et al., 1995). In contrast to the study by Tambs et al. (1986), the genetic general factor was less important than the individual genetic influences on each factor score, with variance components ranging from 14% to 24% for the general factor compared with unique genetic variance components of 26% (verbal comprehension), 35% (freedom from distractibility), and 26% (perceptual organization). These results suggest that the pleiotropic effects of genes on cognitive abilities develop with age; this idea is further supported by a study of verbal and nonverbal abilities in infants that showed that less than half of the phenotypic correlation between the abilities was genetic in origin (Price et al., 2000).

A method of analyzing the covariance among tests that follow a hierarchical factor structure is to specify an oblique factor model, but then transform the solution so that the genetic and environmental contributions to the general factor and uncorrelated group factors can be derived (see Cardon, Fulker, DeFries, & Plomin, 1992). Genetic hierarchical modeling of Wechsler Intelligence Scale for Children—Revised (WISC-R) and specific cognitive ability subtests by Cardon et al. (1992) in a sample of children (mean age 7.4 years) showed that, in addition to a genetic general factor, there were independent genetic group factors for verbal, spatial, and memory abilities, but not for perceptual speed. Genetic group factors showed the largest influence on verbal and memory abilities, while the genetic contribution to the variance in perceptual speed was only through the genetic general factor. Genetic general and group factors affected spatial ability to a similar extent. In a battery of WISC-R subtests, Luo, Petrill, and Thompson (1994) reported that genes and common environment were equally important in influencing the general factor (sample age range 6–12 years). This finding is in line with univariate findings of IQ (McCartney et al., 1990; McClearn et al., 1997; Wilson, 1986), which show environmental influences to be substantial in childhood but lessen during adolescence and adulthood. A further result from this study was that verbal subtests generally displayed higher phenotypic, genetic, and common environmental general factor loadings than the performance subtests.

Multivariate genetic analyses of the WAIS and WISC-R subtests thus support the presence of genetic general, group, and specific factors. This study will test whether these factors generalize to subtests of the Multidimensional Aptitude Battery (MAB), which is patterned after the WAIS-R, and in a sample of adolescents. Like the WAIS-R, the MAB shows the presence of a verbal and performance factor, with a statistical comparison of their factor structures demonstrating correlation coefficients of .97 and .96 for verbal and performance factors, respectively (Jackson, 1984). As the Cohen (1957) factors have not been related to the MAB and as a short version of the MAB is administered in our study, the analysis of the IQ subtests will initially be directed toward a general factor model with test-specific variance. Subsequently, the fit of a simplified two-factor model based on the verbal-performance dichotomy found by Jackson (1998) will be examined. Test–retest reliability analysis of the IQ measures will be performed on a subsample, with estimates expected to be in the range between .88 and .97 as reported by Jackson. The test–retest reliability also acts as an upper bound estimate of heritability since the MZ co-twin correlation cannot exceed it. IQ data are collected in the context of a larger study, which aims to find QTLs influencing diverse cognitive abilities (e.g., processing speed, working memory, and IQ). Determining the genetic correlation structure among the IQ subtests will enable separation of genetic general and group factors and this will allow the appropriate specification of multivariate models using the other cognitive measures (and including the effect of a QTL).

2. Method

2.1. Participants

Three hundred and ninety twin pairs (97 MZ females, 87 MZ males, 52 DZ females, 48 DZ males, 106 DZ opposite sex pairs) were tested in the ongoing Brisbane Memory, Attention, and Problem-Solving (MAPS) twin study (Wright, De Geus, et al., 2001). Most had participated in a melanocytic naevi study 2 years earlier (Zhu et al., 1999) and others were ascertained through mail-outs to secondary schools in the Brisbane region. Zygosity was determined by ABO, MN, and Rh blood groups and by nine independent polymorphic DNA markers, and could be assigned with a probability of error less than 10^{-3}. Twin pairs were excluded if either co-twin had a history of significant head injury, neurological or psychiatric illness, substance dependence, or if they were currently taking long term medications with central nervous system effects (25 twin pairs were excluded on this basis). All participants had normal or corrected-to-normal vision (better than 6/12 Snellen equivalent). They were mostly in their penultimate year of secondary school, and aged between 15 and 18 years (16.17 years, S.D. = 0.34). Written informed consent was obtained from each participant and their parent/guardian prior to testing.

2.2. Experimental protocol

The MAB and WAIS-R subtests were part of a psychometric battery, which also included a choice reaction (Luciano et al., 2001a) and inspection time task (Luciano et al., 2001b) and two reading tests. The session approximated 1.5 hours in length and was either preceded or followed by a testing session of similar duration that involved the measurement of event-related potentials during a delayed response task (Hansell et al., 2001; Wright, Hansell, et al., 2001).

One twin completed the psychometric session while the other completed the alternate session. The order of session testing was counterbalanced between twin pairs based on the birth order of the twins. A full description of the protocol is given in Wright, De Geus, et al. (2001).

A subsample of twins (49 pairs) returned for retesting approximately 3 months (1–5 months) after their initial test session. This sample comprised 23 MZ and 26 DZ pairs (57 females, 41 males). An identical battery of tests was administered on both occasions. To minimize confound effects, the participants performed the sessions in the same order on retest.

2.3. IQ battery

A shortened version of the MAB was used, which included three verbal subtests, (Information, Arithmetic, and Vocabulary) and two performance subtests (Spatial and Object Assembly). The Information subtest examined general knowledge of persons, places, and common phenomena. Arithmetic tested quantitative ability by presenting mathematics problems within a verbal framework. The Vocabulary subtest measured knowledge of word meaning. In the Spatial subtest, participants were required to perform spatial rotations of various shaped figures, and Object Assembly required reassembling disjointed pieces of an object to form its regular shape. The five subtests were chosen to obtain maximal differentiation between verbal and performance scales, as the Information, Arithmetic, and Vocabulary subtests correlate only moderately with Spatial and Object Assembly (Jackson, 1984). Thus, these subtests had high factor loadings on their respective verbal and performance scales.

A computerized version of the MAB verbal subtests was used for all participants, and for the MAB performance subtests 326 twin pairs were tested using a paper-and-pencil version, with the remainder tested on the computerized version, which became available later in the study. All MAB subtests had a multiple-choice format and were timed at 7 minutes each. Participants were not penalized for guessing and were verbally encouraged by the research assistant to answer every item within the time period, in accord with the administration instructions of the manual (Jackson, 1984). Task-specific instructions were provided on screen and scoring was computerized.

The Digit Symbol Substitution test, a performance subtest of the WAIS-R (Wechsler, 1981), was administered in paper and pencil form by the examiner following completion of the MAB. This test required the participant to pair random digits with their matching symbols (nine different digit–symbol pairs) for 93 items in 90 s. The total number of correct digit–symbol matches within the time constraint indexed performance on this task. As the Digit Symbol test was introduced at a later stage in the study to supplement the measurement of performance IQ, data were not available for the first 34 twin pairs. The raw scores from each subtest (MAB and Digit Symbol) were analyzed.

Twins were tested as closely as possible to their 16th birthday, resulting in differential completion of months of schooling between pairs. As the MAB was primarily tapping crystallized ability, the effect of schooling was tested in the multivariate data analysis. Months of schooling was measured by calculating how many months had passed since the individual had commenced Grade 10 (the lowest school grade in the sample). For those not at school (12 co-twins; 3 twin pairs), months of schooling since year 10 was estimated as the grade they would be in had they remained at school, using the age at which they first started school.

2.4. Statistical procedure

2.4.1. Test–retest analysis

A consequence of the twin design with respect to test–retest reliability analysis (subsample of 49 twin pairs) was the relatedness of individuals in the sample. Structural equation models, which tested hypotheses concerning means, variances, and covariances enabled the calculation of test–retest reliability coefficients through a maximum likelihood estimation (MLE) procedure. The aim of the modeling was to constrain parameters (means/variances) across birth order and zygosity group so that a single parameter could describe the four groups now composed of independent individuals. Other parameters for each twin group included mean sex deviations at test and retest and a mean deviation for the effect of practice. Co-twin correlations at test and retest were equated within zygosity groups (MZ vs. DZ), and similarly, the co-twin correlations across test occasion (e.g., Twin 1, test-Twin 2, retest) were equated within zygosity group. Finally, differences in test–retest correlations (r) across birth order and zygosity were tested (i.e., MZ Twin 1 r = MZ Twin 2 r = DZ Twin 1 r = DZ Twin 2 r). The structure of this correlation matrix is presented in Table 1.

The fit of each submodel was compared to the one within which it was nested, by a likelihood ratio chi-square test (Neale & Cardon, 1992). The difference in minus two log likelihood ($-2LL$) between the models is compared to the critical value (α=.05) of the chi-square distribution for the degrees of freedom difference. A nonsignificant chi-square indicates that there is no difference between the full model and the reduced model. The statistical program, Mx version 1.50 (Neale, 2000), was used for all analyses.

Table 1
Predicted correlation structure where the correlation (r) is equated across birth order and zygosity, and cross twin and cross twin–cross test occasion correlations are equated within zygosity group

	Twin 1		Twin 2	
	Test	Retest	Test	Retest
Twin 1				
Test	1			
Retest	Retest$_r$	1		
Twin 2				
Test	DZ$_r$/MZ$_r$	DZ$_r$/MZ$_r$	1	
Retest	DZ$_r$/MZ$_r$	DZ$_r$/MZ$_r$	Retest$_r$	1

2.4.2. Means, variances, and covariances

In the full sample (first testing occasion only), means and variances were tested for equality across birth order and zygosity. In this procedure, each of the twin groups (MZ female, MZ male, DZ female, DZ male, DZ opposite sex first born female, and DZ opposite sex first born male) has two means (one each for Twins 1 and 2), two variances, and one covariance. Sex differences were also tested by specifying a female mean and male deviation from that mean but otherwise made no restrictions on the size of variances and covariances of twins (i.e., one additional parameter). A weighted regression parameter, which tested effects of differential months of schooling, was also specified as the twin pairs were tested at different times during the school year. First, a saturated model is fitted estimating all parameters, then progressively simplified models are compared to the full model and assessed by the likelihood ratio chi-square test.

MLEs of the correlations for each zygosity group were estimated with means and variances constrained to be equal but including a deviation in the means model for any sex effects (sex differences in the means can inflate twin resemblance for same sex twins) and months of schooling effects. The equality of co-twin correlations across male and female MZ pairs and across DZ same- and opposite-sex pairs was tested to evaluate the presence of sex differences in genetic effects on IQ subtest scores.

2.4.3. Phenotypic factor analysis

MLEs of the phenotypic correlations among IQ variables were derived separately for females and males after a correction for any significant sex and schooling effects. A phenotypic factor analysis of the six IQ subtests was initially carried out to provide a base for the genetic modeling. Test models were compared against a baseline model where no covariance was specified amongst the variables. As the baseline model was more restrictive than the test models, a procedure of model comparison was adopted whereby a significant change in chi-square from the baseline to the hypothesized model indicated a better fit of the hypothesized model, which meant that the more restrictive model was highly unlikely to be true (Bollen, 1989).

Three test models were formulated based on prominent factor theories of intelligence, these were (1) a general factor model with test-specific components, (2) an uncorrelated two-factor model with test-specific components, and (3) a correlated two factor model with test-specific components (this model is equivalent to a hierarchical model in which the pathways from the second order factor to the two factors have been constrained equal—a necessary condition for model identification). The two group factors were specified according to Jackson's (1998) orthogonally derived solution of a performance and verbal scale.

2.4.4. Genetic modeling

A fully saturated model (Cholesky decomposition) in which there were as many factors as variables for each source of variance (additive genetic, A; common environment, C; and unique environment, E) was initially specified and served as the base model for comparison. The path coefficients for each source of variance were inspected, and where the factor loading patterns appeared congruent with the phenotypic factor models, A, C, and E, sources of variance were then sequentially specified in terms of the appropriate factor structure and tested for significance. Model fit was assessed by the chi-squared difference test; as models progressed from least restrictive (Cholesky) to more restrictive (based on simplified phenotypic models), a nonsignificant chi-square value indicated that the submodel provided a more parsimonious fit to the data than the model in which it was nested.

3. Results

3.1. Preliminary analyses

Computer or experimenter error resulted in the loss of IQ data from six participants (0.76%) All variables were normally distributed. Univariate outliers (z score < -3 or >3) were identified in the following subtests: Information (1), Arithmetic (1), Vocabulary (6), Spatial (1), and Digit Symbol (3); analyses were performed excluding these outliers.

Assumptions concerning means, variances, and covariances across birth order and zygosities (and test occasion for the retest sample) were generally met. Where inequalities were found, they mostly pertained to a single group (e.g., higher mean for male MZ first born twins), rather than being a consistent effect of birth order or zygosity. Significant mean sex differences were found for all variables except Vocabulary. In the MAB subtests, males outperformed females, whereas in the WAIS-R Digit Symbol subtest, the reverse was observed. In addition, months of schooling effects were significant in all subtests with the exception of Object Assembly, so that those participants who had completed more months of school tended to perform better. The regression deviations ranged from .098 (Arithmetic) to .235 (Digit Symbol), with the effect that each month of schooling increased the grand mean score by this amount, for example, a person with 12 months of schooling would have a score 1.18 points (0.098×12) above the grand mean for Arithmetic. Co-twin correlations were equal between DZ same- and opposite-sex groups for all variables, indicating that a sex-limited model was not appropriate for the data and therefore the same multivariate genetic structure was fitted for males and females. Descriptive statistics (grouped by sex) of the IQ variables on first test and their test–retest correlations derived from the subsample are displayed in Table 2.

Table 2
Sample size, mean (S.D.), and range of the IQ variables on first test for male and female participants

	Males			Females			r (95% CI)
	N	Mean (S.D.)	Range	N	Mean (S.D.)	Range	
Verbal							
Information	370	21.14 (5.82)	6–32	402	19.87 (5.13)	6–35	.83 (.75–.89)
Arithmetic	372	12.48 (3.06)	5–19	403	11.84 (2.61)	5–20	.67 (.54–.78)
Vocabulary	369	17.19 (4.72)	4–32	398	17.26 (4.74)	3–30	.77 (.34–.72)
Performance							
Spatial	374	31.74 (8.83)	3–50	403	28.43 (9.32)	3–50	.77 (.67–.84)
Object Assembly	376	13.09 (3.81)	3–20	404	12.33 (3.78)	3–20	.67 (.54–.77)
Digit Symbol	332	55.22 (10.16)	39–87	375	63.50 (9.59)	30–86	.85 (.79–.90)

Maximum likelihood estimates of test–retest correlations (r) are displayed with 95% confidence intervals (CI).

MLE of the phenotypic correlations among the IQ subtests were obtained separately for females and males, although overlapping confidence intervals indicated that the estimates did not significantly differ between sexes. Intercorrelations among the IQ subtest scores ranged from .28 (Vocabulary–Digit Symbol) to .68 (Vocabulary–Information).

Phenotypic model fitting results are presented in Table 3. A correlated two-factor model (verbal and performance group factors) provided the best account of the data as it was the least restrictive model tested with a significant P value. The standardized path coefficients of this model are presented in Table 4. Verbal and performance factors were correlated at .64. Factor loadings on the verbal factor ranged from .64 to .88 and loadings on the performance factor ranged from .49 to .78.

3.2. Multivariate genetic modeling

The standardized path coefficients for the fully saturated Cholesky decomposition of IQ variables are shown in Table 5. As additive genetic effects (A) were largely overlapping, a test

Table 3
Model fitting results of phenotypic factor models applied to IQ subtest scores via MLE

Model	vs.	-2LL	df	$\Delta -2$LL	Δdf	P value
I. Null: All specifics (22 parameters)		28,259.57	4556			
II. One general factor + specifics	I	27,035.42	4550	1224.14	6	< .01
III. Two orthogonal group factors (performance, verbal) + specifics	II	27,085.59	4550	1173.98	6	< .01
IV. Two oblique group factors (performance, verbal) + specifics	**III**	**26,865.42**	**4549**	**220.17**	**1**	**< .01**

Best fitting model is in bold.
As models are compared to a more restrictive model, a better fitting model is indicated by a significant probability value.

Table 4
Standardized factor loadings for the correlated two-factor model of IQ subtests

	v	p	s
Information	.88	–	.48
Arithmetic	.64	–	.77
Vocabulary	.75	–	.66
Spatial	–	.72	.69
Object Assembly	–	.78	.63
Digit Symbol	–	.49	.87

The correlation between verbal and performance factors is .64.
v = verbal group factor; p = performance group factor; s = specific factors.

of the fit of the correlated two factor model with specific components (obtained in the phenotypic analyses) was performed. This model provided acceptable fit (see Table 6). A test of whether the correlation between verbal and performance factors could be fixed to zero was significant. The Cholesky decomposition showed that C effects were considerable for the first factor and relatively small or zero for the remaining five factors. Hence, C effects were parameterized as a single general factor and compared to the previous model; this model

Table 5
Standardized factor loadings for the additive genetic, common environmental, and unique environmental sources of variance in the Cholesky decomposition of IQ subtests

	A1	A2	A3	A4	A5	A6
Information	.67					
Arithmetic	.48	.49				
Vocabulary	.34	.16	.58			
Spatial	.54	.00	− .11	.16		
Object Assembly	.23	.36	.47	.33	− .03	
Digit Symbol	.18	.26	.15	.16	.67	.15
	C1	C2	C3	C4	C5	C6
Information	.54					
Arithmetic	.37	.10				
Vocabulary	.35	.21	.00			
Spatial	.45	.12	.00	.00		
Object Assembly	.26	.05	.00	.00	.00	
Digit Symbol	.21	.18	.00	.00	.00	.00
	E1	E2	E3	E4	E5	E6
Information	.50					
Arithmetic	.06	.62				
Vocabulary	.01	.06	.59			
Spatial	.14	.00	.06	.68		
Object Assembly	.10	.05	.09	.04	.62	
Digit Symbol	.15	.05	.06	.05	.04	.52

Table 6
Model fitting results for the genetic and environmental factorization of IQ subtests

Model	vs.	− 2LL	*df*	Δ − 2LL	Δ*df*	*P* value
I. *ACE* Cholesky decomposition		26,242.231	4499			
II. *A* (two oblique factors + specifics), *CE* (Cholesky)	I	26,253.491	4507	11.17	8	.19
III. *A* (two orthogonal factors + specifics), *CE* (Cholesky)	II	26,266.607	4508	13.12	1	< .01
IV. *A* (two oblique factors + specifics), *C* (general factor), *E* (Cholesky)	**II**	**26,262.318**	**4522**	**8.83**	**15**	**.89**
V. *A* (two oblique factors + specifics), *C* (general factor), *E* (two oblique factors + specifics)	IV	26,279.583	4530	17.26	8	.03

Best fitting model is in bold.

provided acceptable fit. Results of the Cholesky decomposition indicated that *E* effects were largely specific, although there was some covariation present on the first factor. A model in which *E* effects were specified to have correlated verbal and performance factors and specific factors did not show acceptable fit to the data. Due to potential overlapping measurement error among the IQ subtests, unique environmental effects were maintained in the form of a Cholesky factorization. This final model is presented as a path diagram in Fig. 1.

In this model, the genetic verbal factor (A_v) explained 61% of the variance in Information, 16% in Arithmetic, and 35% in Vocabulary, while the genetic performance factor (A_p) explained 21% of variance in Spatial, 49% in Object Assembly, and 4% in Digit Symbol. The

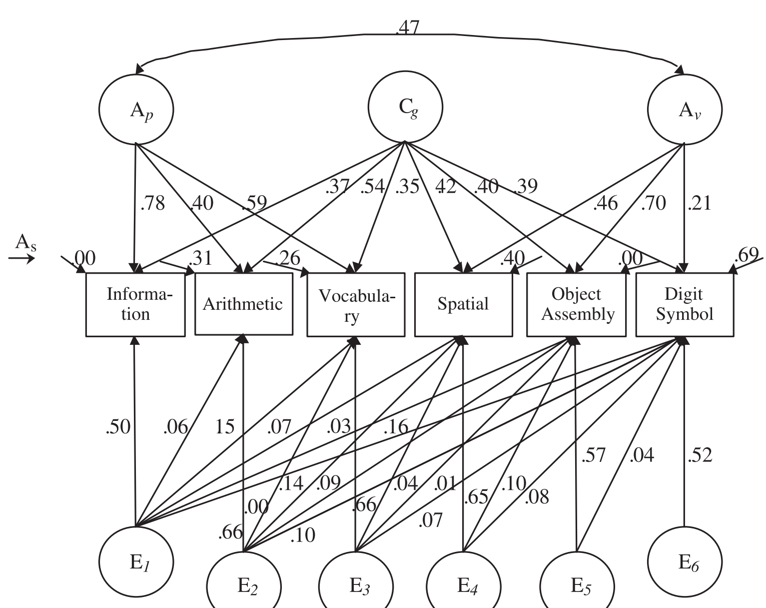

Fig. 1. Path diagram depicting the additive genetic, common environmental, and unique environmental factor loadings on the IQ subtests (Model IV in Table 6).

Table 7
Genetic (lower diagonal) and unique environment (upper diagonal) correlations between IQ subtest variables estimated from the best-fitting model

	Information	Arithmetic	Vocabulary	Spatial	Object Assembly	Digit Symbol
Information		.09	.23	.11	.04	.28
Arithmetic	.79		.01	.22	.16	.20
Vocabulary	.92	.72		.09	.02	.18
Spatial	.36	.28	.33		.21	.21
Object Assembly	.47	.37	.43	.75		.13
Digit Symbol	.14	.11	.13	.22	.29	

Common environment correlations between all IQ subtests were equal to unity.

general common environment factor (C_g) explained between 12% (Vocabulary) and 29% (Arithmetic) of variance. The first factor loading of each unique environmental factor (E_{1-6}) was particularly large, ranging from .50 (Information) to .66 (Arithmetic, Vocabulary). Genetic and environmental correlations among the variables, derived from the final model, are shown in Table 7. Genetic correlations ranged from .11 (Digit Symbol–Arithmetic) to .92 (Information–Vocabulary), while unique environmental correlations ranged between .01 (Arithmetic–Vocabulary) and .28 (Information–Digit Symbol). Common environmental correlations all equaled 1.

4. Discussion

Factor analysis of the selected MAB and WAIS-R subtests supported a phenotypic structure in which verbal and performance group factors were correlated; this model included test-specific influences. The separation of verbal and performance factors is in line with previous findings of the MAB (Jackson, 1998). Intercorrelations among the IQ subtests were, in general, slightly higher than those reported by the test's developer (Jackson, 1998) in a sample of 3121 students aged 16–19 years. Although the WAIS-R Digit Symbol test was used in preference to the MAB version, the correlations between the WAIS-R Digit Symbol and the MAB subtests were similar to the MAB version. Jackson's factor analytic study can only loosely be compared to that of the present study as his was based on 10 subtests and used an orthogonal rotation. However, there was consistency across studies in the relative magnitude of factor loadings between subtests on each factor (performance and verbal). For the verbal factor, the Arithmetic subtest showed the lowest loading in both studies, and likewise for the performance factor, the Digit Symbol subtest displayed the lowest loading (although this may be partially due to uncorrelated measurement error with the MAB subtests, which were computerized). In addition, across studies the loadings for Information and Vocabulary subtests were of similar magnitude and so too were the loadings for Spatial and Object Assembly subtests. Although Jackson does not report sex differences for the MAB, in this study, sex effects were present for all subtests except Vocabulary; while males outperformed females in the MAB subtests, the reverse was observed for Digit Symbol. These sex differences were commensurate with various findings of the WAIS-R subtests (e.g., Kaufman, McLean, & Reynolds, 1988; Lynn & Dai, 1993; Reynolds, Chastain, Kaufman, & McLean, 1987) and were subsequently factored into the genetic model through adjustments to the means.

The genetic effects mirrored the best-fitting phenotypic factor structure (correlated verbal and performance group factors and specific effects). Such a model suggests the overarching presence of a general factor (as previous results in adults confirm), in which the same genes influence all cognitive subtests to some extent, but further implies that particular genes have different levels of influence on diverse specific cognitive abilities, as well as completely unique effects on some individual subtests. It should be noted that a different battery of subtests (e.g., WAIS-III) or an increase in the number of subtests would likely produce a different factor structure, which may include a larger number of (genetic) group factors. The two genetic group factors in our study displayed moderate factor loadings on their respective IQ measures, although the performance factor loading on Digit Symbol (.21) was relatively low. This was not surprising since Digit Symbol has been shown to load on the freedom from distraction factor rather than the performance factor in WAIS-R analyses. Consequently, specific genetic effects were greater for Digit Symbol, but had a broader selection of tests been used another group factor related to perceptual speed/freedom from distraction would likely have emerged. Tambs et al. (1986) have also demonstrated the superiority of specific genetic effects over shared genetic effects for Digit Symbol (and the freedom from distraction composite score) in adults. Verbal and performance genetic group factors showed the largest influences, respectively, on Information and Object Assembly subtests. Interestingly, these subtests showed no influence from specific genetic effects, suggesting that the processes they tap bear heavily on the nature of general ability (implicated by the correlation of the group factors) underlying the six IQ subtests.

Additive genetic effects were substantially larger than common environmental effects for all measures, except Arithmetic, which was influenced by genes (25%) and common environment (29%) in roughly equal proportions. As a verbal subtest, Arithmetic, is obviously reliant on acculturalized learning (e.g., education in mathematics), although it is unclear why Information and Vocabulary, also verbal subtests, are less influenced by common environmental factors. The genetic correlations between variables were higher among subtests within each MAB scale. Digit Symbol showed larger genetic correlations with the MAB performance subtests than verbal subtests, perhaps reflecting their shared dependence on fluid ability.

As the correlation between genetic group factors in this study was .47, this indicates that the genes for verbal and performance abilities do not perfectly overlap, that is, various genes influencing verbal abilities do not influence performance abilities, and vice versa. Subtests for our study were selected so that maximal differentiation of verbal and performance abilities was attained, and hence it was not surprising that the correlation between genetic factors was of moderate size. Tambs et al. (1986) demonstrated in an adult sample that a model with a genetic general and Cohen factors of the WAIS gave a superior fit over a model specifying a genetic general and test-specific factors. Two of the Cohen factors represent verbal (i.e., verbal comprehension) and performance (i.e., perceptual organization) ability, hence our findings are consistent (except in their study specific genetic effects on perceptual organization were slight). In an adolescent sample, a genetic model with a general, verbal, performance, and test-specific factors showed a good fit to the data (Rijsdijk et al., 1998); the generality of genetic influences on verbal, spatial, perceptual speed, and to a lesser extent, memory abilities, has also been confirmed in adolescents (Alarcon, Plomin, Fulker, Corley, & DeFries, 1998). The presence of genetic verbal and performance factors has also been demonstrated in a sample of 5-year-old twins (Rietveld, van Baal, Dolan & Boomsma, 2000). However, in their analysis the correlation between verbal and performance factors could be fixed to zero, suggesting that during childhood, diverse cognitive abilities are genetically independent but during adolescence, they become dependent on the same genes in addition to unique genes. Pleiotropic effects continue into adulthood, but as common environmental influences decrease and additive genetic effects increase, genetic correlations between variables may also increase. This is because the original genes influencing abilities in adolescence (or new genetic influences emerging in adulthood) consume the covariation previously explained by common environmental effects.

Common environmental effects did not follow the best-fitting phenotypic IQ factor structure since only generalized effects were significant. This trend of generalized rather than specific common environmental influences on diverse mental abilities has been found by others (e.g., Martin, Jardine, & Eaves, 1984; Petrill, Luo, Thompson, & Detterman, 1996). In our study, the common environmental general factor showed similar effects across subtests (factor loadings ranged from .35 to .54). Eaves, Heath, and Martin (1984) interpret general common environmental influences in terms of a generalized effect of assortative mating (which is confounded with common environment in the classical twin design). They propose that individuals select mates on a general rather than specific latent factor, which may be general intelligence or correlated factors, such as educational achievement or socioeconomic background. The general factor is a linear combination of the additive effects of each specific cognitive ability, and this explains why the common environmental variation is general rather than specific.

Nonshared environmental effects were largely unique to each variable since the first loading from each Cholesky factor was substantially greater than the cross-variable loadings. The significant contribution of the unique environment to the variance in IQ subtest scores agrees with previous findings of IQ (Dunn & Plomin, 1990; Plomin, Chipuer, & Neiderhiser, 1994). Test-specific unique environmental effects may largely reflect measurement error (due to test unreliability) since the test–retest correlations were imperfect (for instance .67 for Arithmetic and Object Assembly). The stability coefficients for the MAB subtests were slightly lower than those reported by Harrell, Honaker, Hetu, and Oberwager (1987) and Jackson (1984), but the present study also used a longer retest interval. The retest reliability of the Digit Symbol subtest agreed with that reported in the WAIS-R manual (Wechsler, 1981).

The subtest to show the smallest influence from unique environmental effects was Information (25%), while Vocabulary (46%) showed the largest influence. It is reasonable that a test of word knowledge (Vocabulary) could be influenced so strongly by unique environmental factors, an obvious example being interindividual variation in extracurricular reading. The variation in one's general knowledge (Information) is seemingly not influenced substantially by nonshared environmental factors and instead is dependent to a greater extent on genes. Correlated unique environmental effects were smaller than respective genetic correlations, except for the correlations between Digit Symbol and the verbal subtests, which showed stronger unique environmental correlations. This was the result of a larger specific rather than group factor genetic influence on Digit Symbol. In general, unique environmental effects were largely uncorrelated.

The finding of genetic and common environmental covariation across all measures provides support for a molar view of cognitive functioning (i.e., a general process governing/integrating all abilities) although the genetic group factors hint at the possibility of modular subcomponents. These subcomponents may be defined by their greater reliance on specific brain systems. The verbal–performance abilities dichotomy found in our study is quite general, with a number of different systems contributing to the covariation in each factor; for instance, performance ability taps visuospatial, memory, and learning faculties. By including a much wider range and number of cognitive tests, it is likely that factors representing more individuated systems would emerge; a search for QTLs for each specific cognitive ability rather than for the general ability factor may be the ideal approach to identify genes for intelligence since specific abilities will be closer to each of the cognitive (brain) mechanisms that make up intelligence.

This study has demonstrated how the use of IQ subtest scores rather than a single index in a genetic analysis can provide a more comprehensive account of gene and environment effects on cognition. We found that the phenotypic factor structure of the IQ subtests could be described by a correlated verbal and performance group factor model with test-specific influences. Additive genetic effects mimicked this factor structure, but common environmental effects were generalized, while unique environmental effects overlapped to some extent. Specific genetic effects were most prominent for Digit Symbol and completely absent for Information and Object Assembly. Common environmental influences were of the same magnitude across subtests, and unique environmental contributions to variance were also similar for the varying subtests. The factor pattern of genetic, and common and unique environmental influences on the IQ subtests clearly differed from each other, with genetic effects demonstrating the best correspondence to the phenotypic factor structure. These results suggest that a search for QTLs at different levels of the cognitive ability hierarchy would be worthwhile, especially in samples of children/adolescents where specific cognitive abilities show greater genetic independence than in adulthood, where genetic *g* is most prominent. It is possible that the pleiotropic effects of a QTL act within specific cognitive ability domains (e.g., verbal and performance) as well as across general cognitive ability.

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