



Genetic and environmental influences on the Verbal-Perceptual-Image Rotation (VPR) model of the structure of mental abilities in the Minnesota study of twins reared apart

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Abstract

In previous papers [Johnson, W., & Bouchard Jr., T. J. (2005a). Constructive Replication of the Visual-Perceptual-Image Rotation (VPR) Model in Thurstone's (1941) Battery of 60 Tests of Mental Ability. *Intelligence*, 33, 417–430.] [Johnson, W., & Bouchard Jr., T. J. (2005b). The Structure of Human Intelligence: It's Verbal, perceptual, and image rotation (VPR), not Fluid and Crystallized. *Intelligence*, 33, 393–416.] we have proposed the Verbal, perceptual, and image rotation (VPR) model of the structure of mental abilities. The VPR model is hierarchical, with a *g* factor that contributes strongly to broad verbal, perceptual, and image rotation abilities, which in turn contribute to 8 more specialized abilities. The verbal and perceptual abilities, though separable, are highly correlated, as are the perceptual and mental rotation abilities. The verbal and mental rotation abilities are much less correlated. In this study we used the twin sample in the Minnesota Study of Twins Reared Apart to estimate the genetic and environmental influences and the correlations among them at each order of the VPR model. Genetic influences accounted for 67–79% of the variance throughout the model, with the exception of the second-stratum Content Memory factor, which showed 33% genetic influence. These influences could not be attributed to assessed similarity of rearing environment. Genetic correlations closely mirrored the phenotypic correlations. Together, these findings substantiate the theory that the entire structure of mental abilities is strongly influenced by genes.

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We recently demonstrated (Johnson & Bouchard, 2005a,b; Johnson, te Nijenhuis, & Bouchard, in press) that the Verbal-Perceptual-Image Rotation (VPR) model

of the structure of human intellectual abilities offers a more theoretically satisfactory description of that structure than the major competing theories. Based most closely on the ideas of Vernon (1964, 1965), the VPR model has firm roots in both ongoing discussions of theories regarding the nature and structure of intelligence since Spearman (1904) introduced the concept of *g*, and practical applications and observations

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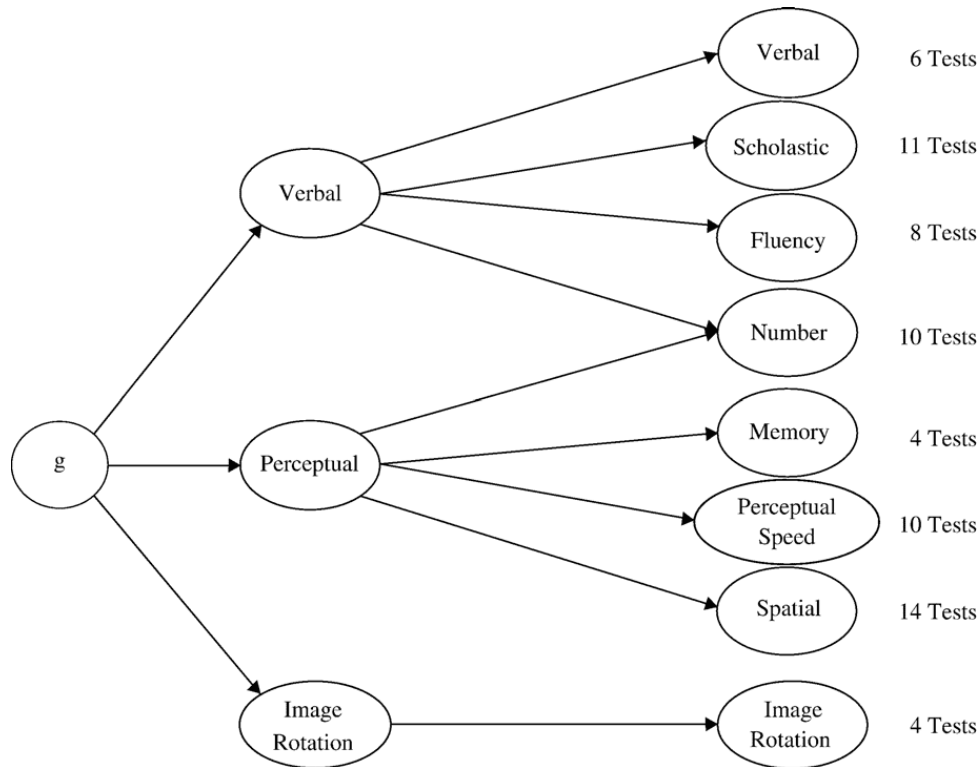


Fig. 1. Structural portion of verbal-perceptual-rotation (VPR) model.

related to occupational and academic aptitudes (Gottfredson, 2002; Humphreys & Lubinski, 1996). It includes a fourth stratum (Carroll, 1993) *g* factor that contributes strongly to broad third-stratum verbal, perceptual, and image rotation abilities. These contribute to 8 second-stratum factors representing more specialized abilities, which, in turn, contribute to specific test performance. The model is articulated in detail in Johnson and Bouchard (2005a), but we show it in Fig. 1 as well. In this implementation, the third-stratum verbal and perceptual abilities, though separable, were highly correlated (.80), as were the perceptual and image rotation abilities (.85). The verbal and image rotation abilities, however, were much less correlated (.41), though *g* contributed similarly to all of them. The third-stratum Verbal factor contributed to more specialized Verbal, Scholastic, Fluency, and Numerical abilities. The third-stratum Perceptual factor contributed to more specialized Numerical, Content Memory, Perceptual Speed, and Spatial abilities. Thus both the third-stratum Verbal and Perceptual Ability factors contributed to the specialized Numerical Ability factor, with Verbal Ability making the larger contribution. The third-stratum Image Rotation factor represented three-dimensional image rotation abilities.

This is the first formally presented four-stratum model in the intelligence domain. and some investiga-

tors have doubted the need for a fourth stratum (Jensen, 1998, pp. 67–68). Consequently we have carried out a number of replications (Johnson & Bouchard, 2005a,b). More recently we again constructively replicated the model using one of the largest data sets in the world. It consisted of a battery of 46 mental ability tests completed by 500 young Dutch seamen homogeneous in age and socioeconomic background. (Johnson et al., in press).

The purpose of this study was to make use of the twin pairs from the sample used to develop the VPR model to estimate the proportions of variance attributable to genetic and environmental influences and the relations among them at each factor level. This is important for several reasons. First, though the existence and relative magnitudes of genetic and environmental influences on both specialized and more general mental abilities as reflected in test scores are well established (Boomsma, Busjahn, & Peltonen, 2002; Bouchard, 1998; Devlin, Daniels, & Roeder, 1997; Jacobs et al., 2001; McClearn et al., 1997; Segal, 2000a; Segal & Hershberger, 2005; Teasdale & Owen, 1984; Toga & Thompson, 2005), we know much less about the relative magnitude of such influences on higher-order factors in the structure of mental abilities. That is, studies that have addressed the existence of genetic and environmental influences on mental ability structure have tended to limit the analysis

to the first and second strata of mental ability and have not addressed the existence of genetic and environmental influences on g and other higher-order abilities. One exception is [Rijsdijk, Vernon, and Boomsma \(2002\)](#), who examined the structure of the WAIS supplemented by the Raven, with the conclusion that there were strong links among the genetic influences throughout the hierarchical structure.

This is of interest because g can be seen as a unitary or molar process that contributes to performance on all cognitive tasks, or as the collective action of many independent modular processes that contribute in varying degrees to performance on any specific cognitive task. [Pettrill \(1997\)](#) termed this the molar-versus-modular debate in intelligence research, though of course the two are not mutually exclusive. He outlined how understanding the associations among genetic and environmental influences on the various levels of hierarchical models of intelligence could help to resolve this debate. Genetic influences on the higher-order strata and associations among genetic and environmental influences throughout the strata lend support to the molar hypothesis, while less than complete correlations among the genetic and environmental influences on the various lower-order strata lend support to the modular hypothesis. From this perspective, any model of the structure of abilities that fits a given data set will do; the use of the VPR model is not important. What is important is the degree to which the genetic influences are consistent throughout the hierarchy.

Second, the ultimate goal of all research into the structure of mental abilities is to understand how the biochemical processes in the organic brain produce intellectual performance, and here the specific model used becomes critical. The VPR model provides a description of the structure of observed or phenotypic mental abilities superior to those of competing models ([Johnson & Bouchard, 2005a,b](#); [Johnson et al., in press](#)), but this does not necessarily mean that it has theoretical or causal relevance to actual brain structure or function. Demonstration that substantive genetic factors influence higher-order abilities as well as lower-order abilities, that the patterns of associations among the genetic factors parallel existing knowledge about brain structure and function, and that these relations parallel the phenotypic structure provides evidence that the model has some biological relevance and helps to generate further testable hypotheses about brain organization. Estimates of these relations also provide information about the degree to which we can expect the same genetic and environmental influences to be associated with different mental abilities. There is compelling evidence in other domains that the structure of genetic

and environmental correlations mimic each other ([Krueger, 2000](#); [Markon, Krueger, Bouchard, & Gottesman, 2002](#)).

Third, it is likely that there are substantive correlations between genetic and environmental influences on mental abilities. That is, it is likely that both people seek environments that provide levels of intellectual stimulation appropriate to their intellectual ability (cf., [Bouchard, 1997](#); [Raine, Reynolds, Venables, & Mednick, 2002](#); [Scarr, 1996](#)) and that people are provided with intellectual opportunities commensurate with the level of ability others perceive them to have ([Plomin, DeFries, & Loehlin, 1977](#)). It is also all but certain that there may be genetically influenced differences in sensitivity to environmental influences in the domain of mental abilities, just as there are in other domains ([Moffitt, Caspi, & Rutter, 2006](#)). Standard models for decomposing variance into components reflecting genetic and environmental influences are based on the assumption that such genetic and environmental correlations, as well as more complex interactions, do not exist. When they do, they render the estimates applicable only on an overall average, population level basis, and they introduce certain systematic distortions in the estimates. At the same time, because such gene–environment interactions and correlations are inherently multivariate, the first step in searching for their existence is to estimate the genetic and environmental proportions of variance in a multivariate context. Such designs make it possible to get some sense of the interrelations that might be involved, and the presence in the model of the other variables mathematically smoothes any peculiarities that may exist in the covariances for one variable. The estimates we provide in this study thus help to clarify the organization of higher-strata mental abilities and to suggest ways in which biological variables transact with environmental experiences to produce manifest performance on tests of mental abilities.

1. Method

1.1. Research participants

The participants for this study came from the Minnesota Study of Twins Reared Apart (MISTRA).¹ The full sample of 436 individuals consists of adult

¹ Informed consent was obtained from all participants and the data were gathered with the approval of the University of Minnesota Institutional Review Board.

twins who were reared apart, along with many of their spouses, partners, adoptive and biological family members, and friends. It is a sample of opportunity, and was not sought systematically. The sample used for this study included 126 twin pairs (74 monozygotic, 52 dizygotic)² only. Most of the pairs were separated early in life, reared in adoptive families, and reunited only in adulthood. A few were separated early in life but reared by different biological family members. The twins were primarily from North America, Great Britain, and Australia, though several came from other countries and a few had been raised in different countries. They ranged in age from 18 to 79 years (mean=42.7, SD=13.6). Their educational backgrounds varied from less than high school to post-graduate experience, and occupations ranged accordingly.

MISTRA was initiated in 1979 and continued to recruit reared apart twin pairs until 2000. The assessment consisted of a battery of tests evaluating medical/dental and physical traits as well as psychological (cognitive abilities, personality, interests, attitudes, etc.) characteristics administered over the course of a week. Bouchard, Lykken, McGue, Segal, and Tellegen (1990) and Segal (2000b, 2005) report further details on recruitment and assessment. Most of the mental ability tests were administered in blocks lasting 60 to 90 min throughout the full week of assessment. The tests relevant to this study included three cognitive ability batteries. In addition to these tests of performance, we made use of retrospective reports of childhood rearing environment. We describe the three cognitive ability batteries and the retrospective reports of rearing environment below.

1.2. Measures

1.2.1. Comprehensive Ability Battery (CAB)

The CAB was developed by Hakstian and Cattell (1975). It consists of 20 brief (5–6 min each) primary ability tests intended to measure a broad range of well-replicated primary abilities. Six of the CAB tests (Auditory Ability, Originality, Representational Draw-

ing, Aiming, Spontaneous Flexibility, and Ideational Fluency) were not administered to MISTRA participants in order to maximize use of available time by avoiding duplication of tasks in the extensive assessment. In addition, we omitted the test of Esthetic Judgment from this analysis, as we deemed it at best indirectly relevant to cognitive ability. Hakstian and Cattell (1978) reported split-half and retest reliabilities for the tests ranging from .64 for Perceptual Speed and Accuracy to .96 for Memory Span. The Verbal Ability test consists of 2 completely different tasks, multiple choice vocabulary and proverb interpretation exercises. We thus tabulated the scores on these 2 parts separately. We thus used a total of 14 test scores from the CAB.

1.2.2. The Hawaii Battery, including Raven's progressive matrices (HB)

The HB was developed to assess familial resemblance in cognitive ability in the Hawaii Family Study of Cognition (DeFries et al., 1974; Kuse, 1977). It consists of 15 tests of primary abilities. The tests require 3 to 10 min for administration. Two tests in this battery were not administered (Number Comparison and Social Perception) in order to maximize use of available time by avoiding duplication of tasks in the other batteries. The battery was supplemented, however, with 4 tests from the Educational Testing Services (Cubes, Paper Folding, Identical Pictures, and Different Uses) to provide better definition of the spatial, perceptual speed and fluency factors hypothesized to underlie the test scores. There were thus a total of 17 tests in the battery. The original HB included a shortened printed version of the Raven (1941). In MISTRA, the Raven was presented via slides in a psychophysiology laboratory (Lykken, 1982), and administered on an untimed basis. DeFries et al. (1974) reported internal consistency and retest reliabilities for the HB tests ranging from .58 for Immediate Visual Memory to .96 for Vocabulary.

1.2.3. The Wechsler Adult Intelligence Scale (WAIS)

The WAIS (Wechsler, 1955) is probably the best known and most widely used individually administered test of general intellectual ability. It includes 11 subtests organized into Verbal and Performance subcomponents. Many of the subtests require overt verbal articulation of reasoning based on factual knowledge. Thus, for example, the WAIS similarities subtest requires the examinee to articulate his/her own reasons for similarities between the concepts presented. Internal consistency reliabilities range from .79 for Comprehension to .94 for Vocabulary (Wechsler, 1955). Average WAIS full-scale IQ for this sample was 109.6 (range 79–140) when

² The full twin sample included 128 twin pairs and 2 sets of triplets. Consistent with MISTRA practice we included only twin pairs over the age of 18 at the time of assessment, thus deleting 3 pairs. We also deleted one pair that was very discrepant in size and stature. The smaller twin had cardiovascular problems and other serious medical ailments going back to childhood. The medical information about the lifelong nature of the medical problems was provided by a source other than the twin. We presume that this is a case of twin transfusion syndrome. We used 2 members of each of the triplet pairs to form 2 twin pairs.

Table 1
Tests included in the 3 batteries

Test	Assessment activity
<i>Comprehensive Ability Battery</i>	
1. Numerical Ability	Computations including fractions, decimal divisions, square roots, etc.
2. Spatial Ability	Interpretation of 2-dimensional figural rotation or reversal.
3. Memory Span	Recall of digits presented aurally.
4. Flexibility of Closure	Identification of embedded figures.
5. Mechanical ability	Identification of mechanical principles and tools.
6. Speed of closure	Completion of gestalt.
7. Perceptual Speed	Evaluation of symbol pairs.
8. Word fluency	Production of anagrams.
9. Inductive reasoning	Identification of pattern in sequences of letter sets.
10. Associative memory	Rote memorization of meaningless pairings.
11. Meaningful memory	Rote memorization of meaningful pairings.
12. Verbal-vocabulary	Multiple choice among possible synonyms.
13. Verbal-proverbs	Interpretation of proverbs.
14. Spelling	Multiple choice identification of misspellings.
<i>Hawaii Battery with Raven</i>	
15. Card rotations	Matching of rotated alternatives to probe.
16. Mental rotation	Identification of rotated versions of 2-dimensional representation of 3-dimensional objects.
17. Paper form board	Outline of cutting instructions to form the target figure.
18. Hidden patterns	Identification of probe figures in more complex patterns.
19. Cubes	Identification of matched figures after rotation.
20. Paper folding	Identification of unfolded version of a folded probe.
21. Raven	Identification of analogous figure to follow a sequence of figures.
22. Vocabulary	Multiple choice among possible meanings.
23. Subtraction/multiplication	Completion of 2-digit subtractions and 2-digit by 1-digit multiplications.
24. Word beginnings/endings	Generation of words beginning and ending with specified letters.
25. Pedigrees	Identification of familial relationships within a family tree.
26. Things categories	Generation of things that share assigned characteristics.
27. Different uses	Generation of novel uses for specified objects.
28. Immediate Visual Memory	Recall of illustrations of common objects immediately following presentation.
29. Delayed Visual Memory	Recall of illustrations of same common objects after delay.
30. Lines and dots	Trace of a path through a grid of dots.
31. Identical pictures	Identification of alternative identical to probe.
<i>Wechsler Adult Intelligence Scale</i>	
32. Information	Recall of factual knowledge.
33. Comprehension	Explanation of practical circumstances.
34. Vocabulary	Free definition.
35. Coding	Identification of symbol-number pairings.
36. Arithmetic	Mental calculation of problems presented verbally.
37. Similarities	Explanation of likenesses between objects or concepts.
38. Digit span	Recall of spans of digits presented aurally, both forwards and backwards.
39. Picture completion	Identification of parts missing in pictures of common objects.
40. Block design	Reproduction of 2-dimensional designs using 3-dimensional blocks.
41. Picture arrangement	Chronological sequencing of pictures.
42. Object assembly	Reassembly of cut-up figures.

normed at the 1955 level, with a standard deviation of 11.8. Because of secular changes (Flynn, 1998), it is necessary to adjust IQ scores based on tests with old norms. Jensen (1998, p. 319) summarized average rates of change in WAIS scores over time. We used these rates to adjust the sample's scores for secular change. The average adjusted WAIS full-scale IQ for the sample was 101.2 (range 61.1–139.9), with a standard deviation of

14.8. The adjustment increased the standard deviation because IQ was *positively* correlated with age in this sample.³ The WAIS was administered in almost all

³ To estimate change in full-scale IQ, we weighted the rates of change for verbal and performance IQ .6 and .4 respectively. We individually adjusted scores downward from date of assessment to 1955 and upward by age at assessment in excess of 25. Other adjustment terms yielded similar results.

instances to each twin, at about the same time, by different neuropsychologists at the University of Minnesota Medical School.

Table 1 briefly describes the mental ability tests administered to MISTRA participants from the three batteries.

1.2.4. Retrospective reports of childhood rearing environment

As part of a life history interview, each participant reported data on rearing father's and mother's occupations during the participant's childhood, rearing father's and mother's best jobs during their lifetimes, and rearing father's and mother's level of education. We coded the reports of parental occupation using the recommendations of Mueller and Parcel (1981). We report estimates of the socioeconomic status of the rearing home in terms of the Duncan Socioeconomic Index (SEI). Participants also reported rearing family size and completed the Physical Facilities Checklist (PFC). The PFC, developed for MISTRA, lists 41 different physical objects or facilities that people sometimes keep in their homes. Items on the checklist included a library of at least 200 books, telescopes and other scientific equipment, photographic equipment, guns, pets, boats, musical instruments, carpentry tools, cookbooks, and sports equipment. The scale yielded 4 factors labeled material (TV, 2 or more cars, etc.), cultural (art reproductions, sports equipment, etc.), scientific/technical (photographic darkroom, stopwatch, etc., and mechanical/outdoor equipment (garden, automotive tools, etc.) possessions (see McGue & Bouchard, 1989 for a full list and factor analysis). Finally, participants completed the Family Environment Scale (FES; Moos & Moos, 1994), a true–false self-report inventory developed to tap interpersonal and environmental aspects of the rearing home. The FES consists of 10 scales that assess family relationship (Cohesion, Expressiveness, Conflict), personal growth (Independence, Achievement Orientation, Intellectual–Cultural Orientation, Active-Recreational Orientation, and Moral–Religious Emphasis), and system maintenance (Organization and Control) dimensions.

1.3. Statistical analyses

1.3.1. Factor analysis used to develop the VPR model

The VPR model (Johnson & Bouchard, 2005b) was developed as an extension to the verbal-perceptual model proposed by Vernon (1964, 1965). Vernon hypothesized that general intelligence contributes to all mental abilities, but suggested that, after consideration of

general intelligence, the residual abilities tended to fall in two main groups. One group consists of verbal and educational abilities, and the other of spatial, practical, and mechanical abilities. We used maximum likelihood confirmatory factor analysis to implement Vernon's verbal-perceptual model using data from the full MISTRA sample consisting of the reared apart twins and their relatives. The resulting model fit considerably better than the alternative models to which we compared it, but it did not meet the fit criteria we had established (Johnson & Bouchard, 2005b).

We thus modified the Vernon model based primarily on two theoretical and empirical considerations. First, Vernon (1964) suggested that memory demands tend to be distributed relatively evenly over the other abilities, and thus omitted an explicit memory factor from his model. We believe, however, that subsequent research has shown that memory tasks can be distinguished from other kinds of tasks, and inclusion of a memory factor in the model at the second-stratum significantly improved its fit. In addition, we had noted persistent and significant negative cross-loadings involving tests explicitly involving verbal and mental rotation abilities. These negative cross-loadings could be resolved by including in the model a mental rotation factor of the same hierarchical order as Vernon's verbal and perceptual factors. The factor analysis used to develop the VPR model and its relations with the theoretical conceptualizations of other researchers are described in greater detail in Johnson and Bouchard (2005b). For this study, we implemented the VPR model by freely estimating path coefficients for all paths specified in that previous study and constraining all other paths to 0.

1.3.2. Estimation of genetic and environmental influences

The standard quantitative genetic model for a trait is based on the assumption that the observed or phenotypic variance (V_p) in the trait of interest is a linear additive function of additive genetic (A) and shared (C) and nonshared (E) environmental variance, respectively. Symbolically, this can be expressed as,

$$V_p = A + C + E.$$

In a sample of twins reared apart, the monozygotic (MZ) twins share 100% of their additive genetic influences, the dizygotic (DZ) twins share 50% of their additive genetic influences. Here, because we were dealing with twins reared in different environments after their adoption, we assumed that there were no shared

environmental influences resulting from common rearing and therefore set C to 0. Thus, the phenotypic covariance for MZ twins could be expressed symbolically as,

$$\text{Cov}_{\text{MZ}} = A,$$

and that for DZ twins could be expressed as,

$$\text{Cov}_{\text{DZ}} = .5 * A.$$

Under this model, we made several other assumptions. As discussed above, we assumed that the variance components are independent of each other, which implies that there are no correlations or interactions between genetic and environmental components of variance. We also assumed, contrary to evidence, that there was no assortative mating for the trait, and that the genetic influences were additive. Genetic variance can be additive in the sense that multiple genetic influences act independently of each other. It can also be nonadditive, reflecting coordinated multiple genetic influences such as dominance and other interactive polygenic and epistatic effects. We could estimate nonadditive genetic influences, but we did not do so due to the modest size of the twin sample, the complexity of the VPR model, and the relative instability of estimates of nonadditive genetic influences in general (Bouchard & McGue, 2003).

These assumptions are generally oversimplifications of the actual situation, and their violation can introduce systematic distortions in the estimates. The presence of unmeasured shared environmental influences tends to inflate estimates of genetic influence. Where MZ twins elicit more similar experiences from their environments than DZ twins due to the greater genetic similarity of the MZ twins, however, this is generally considered to be an expression of their genetically influenced characteristics rather than an unmeasured shared environmental influence. The presence of assortative mating, known to be relatively strong at least for overall cognitive ability (Bouchard & McGue, 1981; Vandenberg, 1972), tends to inflate DZ twin correlations, inflating or creating the appearance of shared environmental influences on the trait in question. Interaction between genetic and shared environmental influences acts to increase estimates of genetic influence; interaction between genetic and nonshared environmental influences acts to increase estimates of nonshared environmental influence. Correlation between genetic and shared environmental influences acts to increase estimates of shared environmental influence; correlation between genetic and nonshared environmental influences acts to increase estimates of genetic influence (Purcell, 2002). Thus violations in the underlying assumptions have varied effects, and several combinations of violations of

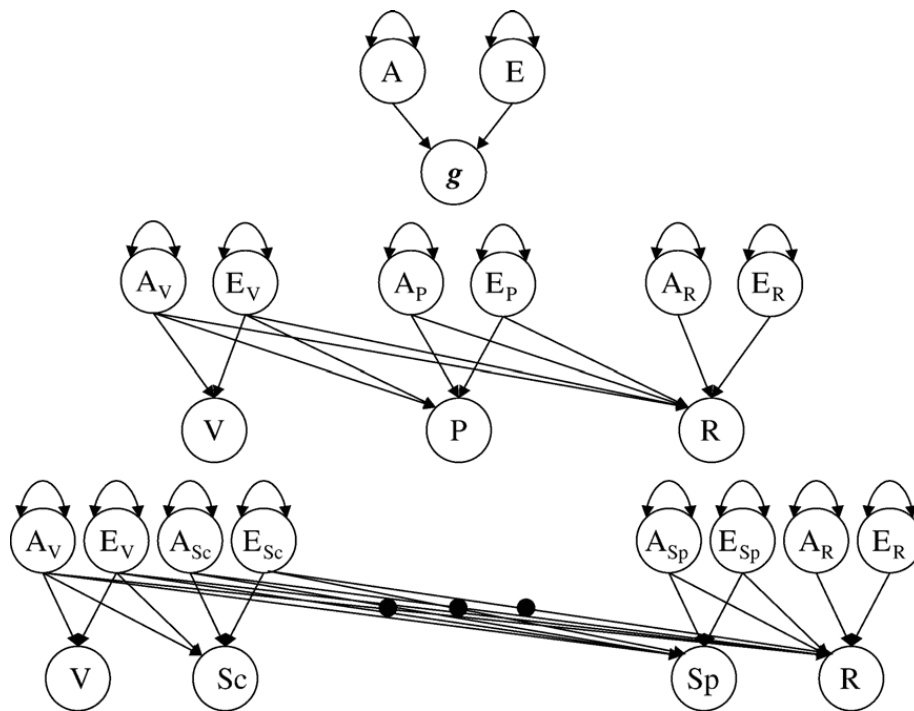


Fig. 2. Cholesky models of the VPR strata. V = Verbal, P = Perceptual, R = Rotation, Sc = Scholastic, Sp = Spatial, A = additive genetic influences, E = environmental influences. We omit the four factors shown in the middle of Fig. 1 to simplify the presentation of the model.

assumptions can act to offset each other. In this light, our results should be considered approximate. Under the model we used, error variance in the test scores due to unreliability of measurement is attributed to nonshared environmental influences.

The standard model for a single trait can be extended to multivariate situations by modeling the covariance between one twin's score on one variable and the other twin's score on another variable in a manner directly analogous to the case for a single trait. To do this for the 42 test scores included in the VPR model as implemented in Johnson and Bouchard (2005b), we made use of three Cholesky factor models implemented in the structural modeling program Mx (Neale, Boker, Xie, & Maes, 1999). Each Cholesky factor model decomposed the factor variances at one of the second, third, and fourth strata of the VPR model into genetic and nonshared environmental components, providing estimates of the proportions of variance attributable to each component for each factor at each stratum of the model and of the corresponding associations between components. Fig. 2 shows the basic schematic design of the model for each stratum. Latent genetic and environmental influences contribute to the latent factors in each stratum, and the coefficients we estimated for each path document the extent of those influences. The model reflected the phenotypic structure imposed by the framework of the VPR model, but it imposed no underlying structure on the genetic and environmental influences, simply recounting the extent of their interrelations. The first latent factor of each type (genetic or nonshared environmental) loaded on all the latent phenotypic ability factors, the second on all the variables except the first, the third on all the variables except the first 2, and so on. The order of the latent phenotypic ability variables was chosen for convenience of presenting the model only, and the measurements of the covariances, correlations, and proportions of variance would have been the same no matter what order was used.

Substantial associations among genetically influenced components of variance in the various factors provide evidence that genetic effects on one factor also contribute to genetic effects on others, and similar statements can be made for nonshared environmental associations. We examined these associations in two ways. First, we estimated genetic and environmental correlations, which reflect the extent to which influences on a given pair of traits arise from common genetic or environmental sources. These correlations range from -1 to 1 and can be considered to account for common variance in the manner usual to correlations. Second, we examined the proportions of the observed correlations

that can be attributed to genetic and environmental influences common to the two variables. These proportions are sometimes called bivariate genetic and environmental influences.

As noted above, we assumed that there were no shared effects due to common rearing in this sample of twins reared apart. This is consistent with empirical data from both twin and adoption samples indicating little or no shared environmental influence on mental abilities assessed in adulthood, even among family members who have shared a common rearing environment (Bouchard, 1998). It is nevertheless important to evaluate the appropriateness of this assumption both in terms of the accuracy of the assumption of no shared effects due to common rearing and the relative importance of any shared effects we might be overlooking on mental abilities assessed in adulthood. In this study, we had no direct way of evaluating the accuracy of the assumption that there were no shared effects due to common rearing. We could, however, evaluate the similarity of the twins on the environmental measures, by way of addressing possible sources of shared environmental influences on mental abilities.

We could also address the question of whether any shared effects we might have overlooked were important in generating twin similarity in general mental ability in this sample of reared-apart twins and we did so in two ways. Because all differences between monozygotic twins are environmental or stochastic in origin we correlated the MZA pair differences in general mental ability with pair differences in the environmental measures, using the MZA's reared in adoptive homes

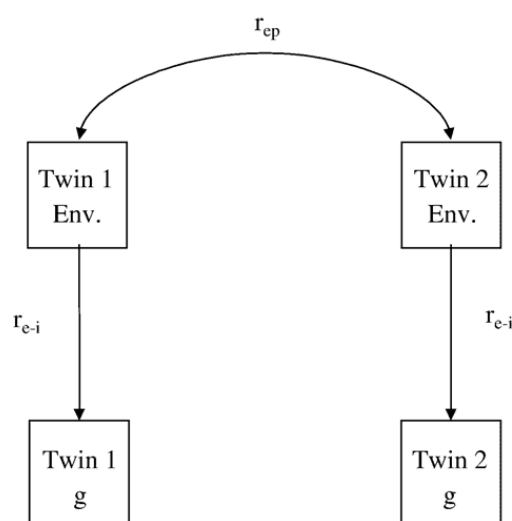


Fig. 3. Effects of environmental similarity on phenotypic similarity between twins. Env. Refers to Environment, g to general mental ability, r_{ep} to the correlation between the twins' environments, and r_{e-i} to the correlation between the environment and general mental ability.

Table 2
Standardized factor pattern matrix of the VPR model

	Verbal	Scholastic	Fluency	Number	Content Memory	Perceptual Speed	Spatial	Image rotation	Verbal	Perceptual	Image	<i>g</i>
CAB verbal-proverbs	.79											
HB Vocabulary	.88											
Spelling	.36		.50									
CAB verbal-vocabulary	.86											
WAIS vocabulary	.35	.53										
Information		.78										
Comprehension		.74										
Similarities		.78										
Arithmetic	.36			.52								
Different uses	.33		.31									
Things	.20		.43									
Word fluency			.78			.13						
Word beginnings/endings			.81									
Digit span			.17	.42								
Memory span			.26	.41								
Meaningful memory		.49			.33							
Associative memory				.37	.22							
Immediate Visual Memory					.66							
Delayed visual memory					.66							
Speed of Closure			.59									
Subtraction/multiplication				.79								
Numerical Ability				.85								
Pedigrees	.54					.28	.19					
Coding				.40		.35						
Perceptual Speed				.29		.47						
Identical pictures						.78						
Lines and dots						.44						
Picture completion		.33					.34					
Inductive reasoning				.43			.38					
Raven		.30					.47					
Picture arrangement		.21					.34					
Flexibility of closure				.44			.35					
Paper Form Board						.19	.54					
Hidden patterns						.48	.40					
Object assembly							.65					
Mechanical ability							.54					
Paper folding							.66					
Block design							.82					
Spatial ability								.75				
Card rotations								.44				
Cubes							.34	.36				
Mental rotation							.29	.36				
Verbal									.78			
Scholastic									.50			
Fluency									.69			
Number									.67	.26		
Content Memory										.13		
Perceptual Speed										.66		
Spatial										.41		
Rotation											.72	
Verbal												.80
Perceptual												.39
Image rotation												.40

Note: HB refers to the Hawaii Battery. Loadings not reported were fixed to 0 in the confirmatory factor model.

in order to remove the possibility of genetic and environmental correlation caused by genetic influences on the home environments created by the parents. In addition, in the adopted-away twins, pair correlations on the environmental measures reflect the maximum extent to which there was possible selective placement for similarity on those environmental dimensions. (It is the maximum extent of possible selective placement because twin similarity on environmental dimensions could result from retrospective bias in reporting on childhood environments and/or from direct influence of the individual on the rearing environment, as well as from selective placement.) If, in turn, the environmental measures are associated with general mental ability assessed in an adoption sample, then shared environmental influences may be indicated. The extent of the contribution of environmental effects to the twin correlation can be estimated as

$$r_{e-i}^2 * r_{ep},$$

where r_{e-i} is the correlation between the environmental measure and the measure of general mental ability, and r_{ep} is the correlation between adopted-away twins on the environmental measure. Figs. 2 and 3 diagram the associations involved in the formula. We used two measures of general mental ability: the first principal components factor score from the full set of 42 mental ability tests, and WAIS IQ.

Given the wide age range in our sample and the presence of sex effects on many of the tests, we adjusted all mental ability test scores to remove the effects of age, age², sex, sex × age, and sex × age² (McGue & Bouchard, 1984). To be certain that we considered all possible effects of our measures of environmental influences, we did not adjust the environmental measures for age and sex effects. Some participants were missing data for some tests, so we read the raw data into the Mx program, using maximum likelihood to estimate the model parameters allowing for the absence of small amounts of data. This method relies on the assumptions that the variables are normally distributed and that the unavailable data are missing at random (Little & Rubin, 1987). These assumptions were reasonable for the test scores. We evaluated model fit by comparing our models decomposing variance into genetic and environmental components to models in which the variance was not decomposed.

2. Results

The standardized factor loadings for the upper three strata of the full VPR model are shown in Table 2. We

specified the same loadings as in Johnson and Bouchard (2005b) but estimated them freely for this sample, so they were similar to, though differing slightly from, those given for the full sample because they are based on the twin sample alone. To establish baseline data about genetic and environmental influences, Table 3 shows the intraclass correlations for MZA and DZA twins, along with estimates of proportions of variance attributable to genetic and environmental influences and their 95% confidence intervals from the standard univariate quantitative genetic model described above, as operationalized in Mx. In a sample of this size, we expected random fluctuations in the data to create variability in the ratios of DZA to MZA correlations around the one-half mark that is consistent with their relative percentages of shared genes;⁴ thus the average correlations were of some importance, though it is important to keep in mind that there is no a priori reason that the same genetic mechanisms would have to underlie all the tests. As indicated by these averages, there was some tendency for the correlations for DZ twins to be more than half the MZ correlations. The relatively high DZ correlations were consistent with those from other samples (Bouchard & McGue, 1981; Bouchard, Lykken, McGue, Segal, & Tellegen, 1990). We attributed the excess to assortative mating.⁵ At the same time, some of the tests had DZA correlations that were less than half the MZA correlations. To the extent that this was systematic rather than random, it indicated the existence of nonadditive genetic influences due to dominance or epistatic effects.

The twin correlations generally indicated genetic influences on all the tests because the MZA correlations were in almost all cases larger than the DZA correlations. Use of the univariate quantitative genetic models, however, tends to provide more accurate estimates of genetic and environmental influences than do the twin

⁴ For 4 tests, DZ correlations actually exceeded MZ correlations, a situation we attribute to sampling variability. In such situations, Mx gives greater weight to the larger MZ than DZ sample, providing estimates of genetic influence based primarily on the MZ correlations. The anomalous pattern of correlations is reflected in poor model fit.

⁵ Though we had no data available on the extent of assortative mating for mental ability by the twins' parents, there was substantial assortative mating for *g* and IQ by the twins themselves: spousal correlations ($N=116$ couples) were .38 for *g*, .42 for WAIS IQ, and .52 for WAIS IQ as adjusted for the Flynn Effect. To assess the effect of assortative mating on our estimates of genetic and environmental influences on the VPR model, we estimated the genetic and environmental influences on these three measures of general mental ability with and without provision for the level of assortative mating by the twins. Inclusion of the provision for assortative mating changed the estimates of genetic influence by less than 1%.

Table 3
Intraclass twin correlations, and estimated genetic and environmental influences and their confidence intervals for the tests in the three batteries

Test	MZA correlation	DZA correlation	Estimated genetic influence	95% Confidence interval	Estimated environmental influence	95% Confidence interval
<i>Comprehensive Ability Battery</i>						
1. Numerical Ability	.58	.45	.58	(.43–.69)	.42	(.31–.57)
2. Spatial Ability	.51	.53	.57	(.41–.68)	.43	(.32–.59)
3. Memory Span	.35	.49	.44	(.25–.59)	.56	(.41–.75)
4. Flexibility of closure	.27	.22	.31	(.09–.50)	.69	(.51–.91)
5. Mechanical ability	.52	.11	.48	(.28–.63)	.52	(.37–.72)
6. Speed of closure	.48	.34	.50	(.31–.65)	.50	(.35–.69)
7. Perceptual speed	.57	.32	.42	(.23–.57)	.58	(.43–.77)
8. Word fluency	.58	.41	.64	(.48–.75)	.36	(.25–.52)
9. Inductive reasoning	.45	.28	.49	(.31–.64)	.51	(.36–.69)
10. Associative memory	.46	.21	.46	(.26–.61)	.54	(.39–.74)
11. Meaningful memory	.38	.28	.44	(.22–.61)	.56	(.39–.78)
12. Verbal-Vocabulary	.55	.46	.60	(.44–.72)	.40	(.28–.56)
13. Verbal-Proverbs	.42	.33	.43	(.24–.59)	.57	(.41–.76)
14. Spelling	.73	.52	.72	(.61–.81)	.28	(.19–.39)
<i>Hawaii Battery with Raven</i>						
15. Card rotations	.66	.45	.67	(.54–.77)	.33	(.23–.46)
16. Mental rotation	.50	.24	.54	(.36–.68)	.46	(.32–.64)
17. Paper form board	.57	.24	.55	(.38–.68)	.45	(.32–.62)
18. Hidden patterns	.60	.43	.59	(.44–.70)	.41	(.30–.56)
19. Cubes	.47	.23	.48	(.29–.63)	.52	(.37–.71)
20. Paper folding	.45	.36	.47	(.29–.61)	.53	(.39–.71)
21. Raven	.55	.42	.58	(.42–.71)	.42	(.29–.58)
22. Vocabulary	.75	.45	.76	(.65–.83)	.24	(.17–.35)
23. Subtraction/multiplication	.63	.44	.64	(.51–.74)	.36	(.26–.49)
24. Word beginnings/endings	.53	.52	.59	(.43–.70)	.41	(.30–.57)
25. Pedigrees	.64	.52	.66	(.53–.76)	.34	(.24–.47)
26. Things categories	.45	.55	.51	(.35–.64)	.49	(.36–.65)
27. Different uses	.61	.21	.61	(.45–.73)	.39	(.27–.55)
28. Immediate visual memory	.19	.00	.16	(.00–.37)	.84	(.63–1.00)
29. Delayed visual memory	.28	.20	.32	(.10–.50)	.68	(.50–.90)
30. Lines and dots	.26	.19	.26	(.06–.44)	.74	(.56–.94)
31. Identical pictures	.67	.34	.64	(.51–.75)	.36	(.25–.49)
<i>Wechsler Adult Intelligence Scale</i>						
32. Information	.57	.64	.65	(.51–.75)	.35	(.25–.49)
33. Comprehension	.48	.30	.49	(.31–.64)	.51	(.36–.69)
34. Vocabulary	.68	.41	.62	(.47–.73)	.38	(.27–.53)
35. Coding	.38	.38	.64	(.49–.75)	.36	(.25–.51)
36. Arithmetic	.62	.26	.67	(.54–.77)	.33	(.23–.46)
37. Similarities	.59	.52	.45	(.26–.60)	.55	(.40–.74)
38. Digit span	.65	.31	.61	(.44–.73)	.39	(.27–.56)
39. Picture completion	.33	.18	.31	(.11–.48)	.69	(.52–.89)
40. Block design	.61	.37	.59	(.44–.71)	.41	(.29–.56)
41. Picture arrangement	.49	.22	.48	(.30–.63)	.52	(.37–.70)
42. Object assembly	.55	–.06	.50	(.30–.65)	.50	(.35–.70)
Average:	.51	.34	.53		.47	

Note: MZA is monozygotic, reared apart; DZA is dizygotic, reared apart.

correlations. These models smooth out some of the effects of random fluctuations in the twin correlations because they make use of covariances rather than correlations and independently consider the data provided by the MZA and DZA covariances, differentially weighting them based on sample size. Where the DZA correlation was

greater than half the MZA correlation, this occasionally created estimates of genetic influence that were greater than the MZA correlations. With the possible exception of Immediate Visual Memory for which the bottom end of the 95% confidence interval was 0, each individual test showed significant and substantial genetic influence.

Table 4

Residual variance as proportion of total variance, and its decomposition into components attributable to genetic and environmental influences

Test	Proportion of variance that is residual	Proportion of residual variance that is genetic	Proportion of residual variance that is environmental
CAB verbal-proverbs	.39	.00	1.00
HB vocabulary	.21	.09	.91
Spelling	.34	.40	.60
CAB verbal-vocabulary	.24	.11	.89
WAIS vocabulary	.21	.20	.80
Information	.50	.40	.60
Comprehension	.59	.10	.90
Similarities	.60	.32	.68
Arithmetic	.70	.46	.54
Different uses	.57	.28	.72
Things	.55	.30	.70
Word fluency	.32	.15	.85
Word beginnings/endings	.37	.17	.83
Digit span	.50	.27	.73
Memory span	.62	.27	.73
Meaningful memory	.77	.22	.78
Associative memory	.73	.27	.73
Immediate Visual Memory	.83	.04	.96
Delayed Visual Memory	.83	.27	.73
Speed of closure	.54	.33	.67
Subtraction/multiplication	.46	.48	.52
Numerical Ability	.55	.13	.87
Pedigrees	.39	.40	.60
Coding	.44	.30	.70
Perceptual Speed	.51	.02	.98
Identical pictures	.38	.51	.49
Lines and dots	.54	.14	.86
Picture completion	.71	.18	.82
Inductive reasoning	.70	.06	.94
Raven	.66	.33	.67
Picture arrangement	.75	.13	.87
Flexibility of closure	.74	.00	1.00
Paper form board	.49	.12	.88
Hidden patterns	.46	.25	.75
Object assembly	.74	.14	.86
Mechanical ability	.74	.21	.79
Paper folding	.66	.16	.84
Block design	.58	.31	.69
Spatial ability	.49	.24	.76
Card rotations	.30	.52	.48
Cubes	.54	.11	.89
Mental rotation	.44	.16	.84
Average	.54	.23	.77

The models decomposing variance into components attributable to genetic and environmental influences for the third and fourth strata of the VPR model fit well. We judged this by comparing the models decomposing variance and covariance into genetic and environmental components to the saturated models allowing free phenotypic variances and covariances for MZ and DZ twins at each stratum. The change in $-2 \times \log$ likelihood for the third-stratum was 27.77 on 26 degrees of freedom, which was not significant. For the fourth stratum, the corresponding statistic was 5.78 on 6 degrees of free-

dom, which also was not significant. For the second-stratum, the model decomposing the variance into genetic and environmental components actually fit better than the saturated model: the $-2 \times \log$ likelihood for the saturated model was 22,016.67 on 9661 degrees of freedom. For the variance decomposition model, the $-2 \times \log$ likelihood was 21,931.30 on 9853 degrees of freedom. The difference of 85.37 on 192 degrees of freedom, however, was not significant.

Table 4 shows the residual variances, or the proportions of total variance in each test that remained after

Table 5
Higher-order factor variances, and proportions attributable to genetic and environmental influences

Second-stratum factors	Factor variance	Proportion genetic	95% Confidence interval	Proportion environmental	95% Confidence interval
Verbal	.62	.79	(.68–.87)	.21	(.13–.32)
Scholastic	.28	.69	(.53–.81)	.31	(.19–.47)
Fluency	.61	.79	(.66–.88)	.21	(.12–.34)
Number	.18	.72	(.59–.82)	.28	(.18–.41)
Content Memory	.11	.33	(.02–.52)	.67	(.48–.98)
Perceptual Speed	.61	.67	(.49–.80)	.27	(.20–.51)
Spatial	.22	.76	(.63–.85)	.22	(.15–.37)
Rotation	.56	.75	(.35–.1.00)	.25	(0–.65)
<i>Third-stratum factors</i>					
Verbal	.61	.78	(.67–.85)	.22	(.15–.33)
Perceptual	.07	.77	(.65–.86)	.23	(.14–.35)
Image rotation	.52	.76	(.58–.88)	.24	(.12–.42)
<i>Fourth stratum factor</i>					
<i>g</i>	–	.77	(.66–.84)	.23	(.16–.34)

variances contained in the factor structure (variances due to *g*, 3 third-stratum factors and 8 second-stratum factors) was removed, and the proportions of this residual variance attributable to genetic and environmental influences unique to each test. As would be expected, most of the tests showed substantial unique variance, though there was also considerable variability in the degree to which this was true (range .21 to .83). The tests with the largest unique variances tended to be the least reliable, as test error variance was included in the residual variances. Consistent with the fact that the error variances were attributed in the variance decomposition to nonshared environmental influences, the proportions of unique variance attributable to genetic influences were relatively modest (range 0–.52). There was, however, no significant correlation between the proportions of residual variance and the proportions of residual variance attributable to genetic influences. This indicated that some of the unique variance of some of the tests was systematic. Card Rotations and Identical Pictures, both of which showed relatively little total residual variance (and had high reliabilities), showed the greatest genetic influences on residual variance. Flexibility of Closure and Proverbs, with relatively large and small amounts of total residual variance, respectively (but still very good reliabilities), both showed no genetic influences on residual variance.

Table 5 shows the factor variances and the proportions of factor variance attributable to genetic and environmental influences for the second, third, and fourth strata of the VPR model. The factors at the second-stratum could be divided into two groups based on the magnitudes of the factor variances: the Verbal, Fluency, Perceptual Speed, and Image Rotation factors had factor

variances of around .6, while the variances of the Scholastic, Number, Content Memory, and Spatial factors were much smaller, more like .2. The proportions of variance attributable to genetic and environmental influences, however, were highly consistent from factor to factor, with Content Memory being the single exception. For the other second-stratum factors, genetic influences accounted for 69–79% of variance. Genetic influences accounted for only 33% of variance for Content Memory. At the third-stratum, the factor variances for the Verbal and Image Rotation factors were similar in size to those of the larger variance group at the second-stratum. The Perceptual factor, however, had a much smaller variance of only .07. Again, the proportions of variance attributable to genetic and environmental influences were highly consistent across the three factors. Genetic influences accounted for 76–78% of the variance. At the fourth stratum, factor variance in *g* was .64. Genetic influences accounted for 77% of this variance.

The phenotypic, genetic, and environmental correlations among the 8 second-stratum factors of the VPR model are shown in Table 6, along with the bivariate genetic influences. Due to the extensive amounts of computer time (weeks) involved in calculating confidence intervals for the correlations, we estimated them only for selected genetic and environmental correlations. In general, the genetic correlations were strikingly similar to or slightly higher than the observed phenotypic correlations, indicating that, at this level of the model, the genetic structure of mental abilities very closely paralleled the phenotypic structure. The biggest differences between the genetic and phenotypic correlations involved Content Memory and its relations with

Table 6
Phenotypic, genetic and environmental correlations and bivariate genetic influences among the second-stratum VPR factors

Phenotypic (and bivariate genetic)	1	2	3	4	5	6	7	8
1. Verbal	1.00							
2. Scholastic	.90 (.92)	1.00						
3. Fluency	.80 (.95)	.74 (.92)	1.00					
4. Number	.73 (.92)	.64 (.86)	.84 (.91)	1.00				
5. Content Memory	.38 (1.00)	.32 (1.00)	.32 (.96)	.28 (1.00)	1.00			
6. Perceptual Speed	.53 (.90)	.43 (.82)	.54 (.91)	.67 (.88)	.31 (.49)	1.00		
7. Spatial	.56 (.93)	.58 (.84)	.51 (.94)	.51 (.91)	.36 (.29)	.62 (.90)	1.00	
8. Rotation	.28 (.92)	.23 (.94)	.31 (.92)	.35 (.93)	.27 (.41)	.68 (.91)	.66 (.98)	1.00
<i>Genetic</i>								
1. Verbal	1.00							
2. Scholastic	.92 (.83–.98)	1.00						
3. Fluency	.86 (.75–.95)	.83 (.67–.96)	1.00					
4. Number	.74 (.61–.85)	.68 (.50–.83)	.80	1.00				
5. Content Memory	.72 (.59–.83)	.83 (.60–.98)	.54	.57 (.33–.82)	1.00			
6. Perceptual Speed	.49 (.29–.66)	.41	.52 (.32–.68)	.67	.43	1.00		
7. Spatial	.56 (.39–.70)	.56	.51	.53	.33	.62	1.00	
8. Rotation	.27 (.05–.48)	.29	.30 (.06–.51)	.39	.33 (–.11–.68)	.71	.81 (.64–.96)	1.00
<i>Environmental</i>								
1. Verbal	1.00							
2. Scholastic	.86 (.68–.96)	1.00						
3. Fluency	.60	.48 (.17–.72)	1.00					
4. Number	.71 (.49–.85)	.56	.96	1.00				
5. Content Memory	.03	–.15	.13	.00	1.00			
6. Perceptual Speed	.65 (.34–.91)	.48	.64 (.33–.89)	.66 (.37–.88)	.25	1.00		
7. Spatial	.57	.67	.48	.43	.51	.62	1.00	
8. Rotation	.30	.10 (–.23–.41)	.35	.22	.28	.59	.15 (–.19–.50)	1.00

Note: 95% Confidence intervals are in parentheses below the genetic and environmental correlations. We did not estimate all confidence intervals due to large computer time requirements. Bivariate genetic influences are in parentheses following the phenotypic correlations. Bivariate environmental influence is the difference between 1.00 and the bivariate genetic influence.

the factors loading on the third-stratum Verbal factor — its genetic correlations with these factors were substantially stronger than its phenotypic correlations. The environmental correlations also closely paralleled the phenotypic correlations, again primarily with the exception of the correlations involving Content Memory. The environmental correlations involving Content Memory were substantially weaker than the phenotypic correlations.

The bivariate genetic influences were generally in excess of 90%, indicating that the phenotypic correla-

tions were primarily genetically mediated. There were a few bivariate genetic influences in the 80–90% range, mostly involving the Scholastic factor, but these were very minor differences from the overall pattern. The bivariate genetic influences involving the Content Memory factor, however, did differ somewhat. At the phenotypic level, the Content Memory factor was least closely linked to the other factors overall: no phenotypic correlation exceeded .38. These correlations with the other second-stratum factors loading on the third-stratum Verbal factor were essentially completely

Table 7
Phenotypic, genetic, and environmental correlations and bivariate genetic influences among the third-stratum VPR factors

Phenotypic			
1. Verbal	1.00		
2. Perceptual	.63 (.91)	1.00	
3. Image rotation	.28 (.93)	.74 (.96)	1.00
Genetic			
1. Verbal	1.00		
2. Perceptual	.60 (.45–.72)	1.00	
3. Image rotation	.29 (.06–.49)	.86 (.70–.98)	1.00
Environmental			
1. Verbal	1.00		
2. Perceptual	.74 (.54–.88)	1.00	
3. Image rotation	.24 (.00–.53)	.35 (.02–.65)	1.00

Note: 95% Confidence intervals are in parentheses. Bivariate genetic influences are in parentheses following the phenotypic correlations.

genetically mediated, however, while the correlations with the other second-stratum factors loading on the third-stratum Perceptual and Image Rotation factors

were mediated to a greater degree by environmental than by genetic influences.

Table 7 shows the phenotypic, genetic, and environmental correlations among the 3 third-stratum factors, again along with the bivariate genetic influences. Once again, the genetic correlations were strikingly similar to the phenotypic correlations. The environmental correlation between the Verbal and Perceptual factors was slightly higher than the phenotypic correlation (though the confidence intervals overlapped), while the environmental correlation between the Perceptual and Image Rotation factors was substantially lower, though still significantly different from 0. The bivariate genetic influences, all in excess of 90%, again indicated that the phenotypic correlations were primarily genetically mediated.

We show the means and standard deviations of the environmental measures in twins reared in adoptive and biological families in Table 8. The twins reared in adoptive families tended to have grown up in homes with somewhat higher SES than did the twins reared in biological families. There were, however, no significant differences in general intelligence (either WAIS IQ or *g*) associated with adoptive vs. biological family rearing

Table 8
Means, standard deviations, and ranges of environmental measures in twins reared by adoptive and biological parents

	Adoptive rearing			Biological rearing		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
<i>Environmental measure</i>						
Family size	3.9*	1.2	240	5.5*	1.9	134
Rearing father best occupation	41.8*	21.2	246	36.1*	18.8	138
Rearing father occupation in childhood	39.6*	21.2	242	31.4*	16.8	141
Rearing mother best occupation	35.8*	16.8	230	28.6*	14.1	139
Rearing mother occupation in childhood	34.9*	18.9	247	26.5*	15.2	149
Rearing father education	10.8	4.0	224	10.2	3.1	122
Rearing mother education	10.4	3.4	229	10.2	2.6	123
Total physical possessions in childhood home	18.3	7.8	221	16.7	7.3	137
Material possessions in childhood home	6.8	4.3	221	5.9	4.1	137
Cultural possessions in childhood home	7.2	2.5	221	6.7	2.6	137
Mechanical possessions in childhood home	3.5	1.7	221	3.5	1.7	137
Scientific possessions in childhood home	.9	1.3	221	.5	1.3	137
<i>Family environmental scale</i>						
Cohesion	5.6	2.8	229	5.8	2.8	136
Expressiveness	3.1	2.3	229	3.8	2.3	136
Conflict	3.0	2.7	229	3.4	2.7	136
Independence	5.1*	2.1	229	5.9*	1.8	136
Achievement Orientation	5.0	2.3	229	5.0	2.1	136
Intellectual–Cultural Orientation	3.9	2.4	229	3.9	2.4	136
Active–Recreational Orientation	3.7	2.3	229	3.9	2.4	136
Moral–Religious Emphasis	5.7	2.2	229	5.5	2.3	136
Organization	7.0	2.0	229	6.4	2.2	136
Control	6.2	2.1	229	5.8	2.1	136

Note: * Adoptive and biological means are different at $p < .01$, stated without explicit correction for multiple tests.

status, and the mean SES for both groups would be considered lower middle class. Twins reared in biological families rated their families substantially higher in encouraging independence – about .4 standard deviation – but this was the only other difference in environmental measures associated with family rearing status. The FES scale means for both groups differed considerably from those given in the FES manual for normal families (Moos & Moos, 1994). Both groups of twins scored lower than the norms for the first 7 FES scales, but especially for Expressiveness, Intellectual–Cultural Orientation, and Active Recreational Orientation. Both groups of twins scored considerably higher than the norms for the last 3 FES scales. In addition, the scale variances in both of our sample groups were considerably higher than those in the norm group: the average variance in our sample groups was 5.4, while that in the normative data was 3.0. We have no ready explanation for the differences in our means from those

in the norm group. The differences, however, did not appear to be due to the twin status of the sample, as there was only one significant difference between the means for the twins in our sample and those of their spouses and other family members. That difference was again for Independence, with twins scoring about a third of a standard deviation lower than their spouses and other family members. Whatever the reason for the differences between the means in our sample and those in the norm data, the greater variances in our sample increase the possibility of detecting correlations between the FES scales and general intelligence. We note that there is no restriction of range on our environmental measures for the adoptive group relative to the biological group (Stoolmiller, 1998).

The twin correlations for the environmental measures were generally modest and few were statistically significant. Among the measures of parental occupation and education, only mother's best occupation and

Table 9
Estimated effects of shared environmental influences on measures of general mental ability in adopted-away twins reared separately

	Correlations					Implied effect on <i>g</i>	Implied effect on IQ
	MZA		All twins				
	Difference in <i>g</i>	Difference in IQ	<i>g</i> component	WAIS IQ	Placement effect		
<i>Environmental measure</i>							
Family size	-.39 (.004)	-.29 (.03)	-.08	-.10	-.11	.00	.00
Rearing father best occupation	-.07	.08	.14	.14	.09	.00	.00
Rearing father occupation in childhood	.14	.14	.22	.22	.16	.01	.01
Rearing mother best occupation	.04	.20	.15	.04	.22	.00	.00
Rearing mother occupation in childhood	.08	.02	.01	-.04	.22	.00	.00
Rearing father education	.05	.20	.11	.05	.23	.00	.00
Rearing mother education	.06	.08	.07	-.01	.22	.00	.00
Total physical possessions in childhood home	-.12	-.04	.12	.01	.54	.01	.00
Material possessions in childhood home	-.10	-.05	.06	-.09	.63	.00	.01
Cultural possessions in childhood home	.08	.13	.29	.23	.28	.02	.01
Mechanical possessions in childhood home	-.29 (.04)	-.32 (.02)	-.12	-.16	.21	.00	.01
Scientific possessions in childhood home	-.16	.09	.13	.12	.49	.01	.01
<i>Family Environmental Scale</i>							
Cohesion	.06	.04	.00	-.02	.19	.00	.00
Expressiveness	-.02	-.16	-.03	.07	.09	.00	.00
Conflict	-.10	.04	-.03	-.01	.23	.00	.00
Independence	-.18	-.13	.06	.09	.26	.00	.00
Achievement Orientation	-.10	.03	.07	.03	-.04	.00	.00
Intellectual–Cultural Orientation	.11	.18	.13	.12	.22	.00	.00
Active-Recreational Orientation	-.12	.01	.09	.10	.19	.00	.00
Moral–Religious Emphasis	.10	.12	.00	-.04	.17	.00	.00
Organization	.21	.13	.06	.06	-.03	.00	.00
Control	.06	.16	-.07	-.05	.00	.00	.00

Note: Total numbers of adopted twin pairs with available data ranged from 75–92. Numbers of adopted MZ twin pairs ranged from 47–61. *P*-values of correlations, when .05 or less (without correction for multiple tests) are given in parentheses. Difference correlations are between pair difference in intelligence and pair difference in environmental measures. Implied effects on intelligence are the squares of the correlations between the environmental measures and intelligence × the placement effect. MZA is monozygotic, reared apart.

education showed any correlation in excess of .10, and only in DZA twins: the correlations were .35 and .19 respectively. The measures of physical facilities showed rather consistent correlations in MZA twins, ranging from .26 to .46, but with one exception (.25) they were less than .10 in DZA twins. The higher MZA than DZA correlations suggest that genetic influences on retrospective recall played some role, but Family Size showed the same pattern: it was correlated .26 in MZA twins, but only .05 in DZA twins. Among the FES scales, there were 6 correlations in excess of .1 in MZA twins: Cohesion (.32), Conflict (.28), Independence (.30), Intellectual–Cultural (.13), Active-Recreational (.11), and Moral–Religious (.24). DZA twins showed only 2: Conflict (.14) and Active-Recreational (.16). There was thus some evidence that these environmental measures might capture some shared environmental effects, but the question of importance was whether such shared environmental effects had any influence on intelligence.

Table 9 shows the estimated effects of any shared environmental influences on these environmental variables on the measures of general mental ability. The correlations based on within-pair differences in MZA scores were small, and most were not significant. They did indicate that differences in family size might have some effect on differences in general mental ability, but the similarity in placement data did not replicate this effect. They also indicated that mechanical possessions in the childhood home might have some effect, but again the similarity in placement data did not replicate this effect. The similarity in placement data produced no indications of substantive influence.⁶ There was, overall, no real evidence for shared environmental influences on twin similarity in general mental ability.

3. Discussion

In this study, we estimated the proportions of variance attributable to genetic and environmental influences and the correlations among those influences in the VPR model. The results were highly consistent throughout the model: with the exception of the Content Memory factor, 67–79% of the variance could be attributed to genetic influences. For Content Memory, only 33% of the variance was under genetic influence.

⁶ Genetic influences on the phenotypic correlations between the general intelligence and environmental measures would indicate gene–environment correlation effects. It would be conceptually reasonable to evaluate whether any such genetic influences were present, but as the phenotypic correlations were low and insignificant, there was no power to do so in these data.

Even at the residual variance level there was meaningful genetic variance: on average 23% of the residual variance could be attributed to genetic influence. This figure, while modest compared to the genetic influence on higher stratum factors, is still approaching the medium range for effect sizes (Cohen, 1988). In addition to the strong and consistent genetic influences, the genetic correlations closely mirrored the phenotypic correlations, though they varied in magnitude. Finally, the phenotypic correlations among the VPR factors primarily resulted from genetic influence.

Coupled with the absence of evidence for shared environmental influences on general mental ability in adulthood that has emerged from other studies (Gottesman, 1997; McGue, Bouchard, Iacono, & Lykken, 1993; Plomin & Spinath, 2004; Teasdale & Owen, 1984), the generally consistent genetic influences throughout the model provide evidence for general intelligence as a unitary process that contributes to performance on all cognitive tasks. At the same time, the variation in the magnitudes of the genetic correlations provides evidence that there are independent influences on cognitive performance as well. Together, these clear findings substantiate the concept that the VPR model has a biological basis that may be useful in generating hypotheses that will help to link genes, biological function, endophenotypes, and mental ability.

The consistency of the proportions of genetic and environmental influences throughout the model is not a mathematical necessity. This is made clear by the much lower estimate of the proportion of genetic influence on the Content Memory factor. The degree to which the genetic associations among the factors paralleled the phenotypic structure is also not either mathematically or genetically inevitable (Searle, 1961). Both genetic and environmental correlations and bivariate genetic and environmental influences are independent of the phenotypic correlations. They are also both independent of the proportions of genetic and environmental influences on the two traits. That is, both kinds of associations between genetic influences on two traits can be great or small whether the phenotypic correlation between the two traits is great or small, and the same is true for environmental associations. At the same time, both kinds of associations between genetic influences on two traits may be great or small whether proportions of genetic influences on either trait are great or small. Bivariate genetic and environmental influences differ from genetic and environmental correlations, however, in that higher bivariate genetic influences imply lower environmental influences on a trait because their total must sum up to 1.00. No such relation exists between genetic and environmental correlations. In

addition, phenotypic correlations have no inherent relation to the magnitude of either bivariate genetic or environmental influences, but high phenotypic correlations do indicate that either or both genetic and environmental correlations will be high.

The substantial genetic correlations and high bivariate genetic influences we found should not be interpreted to imply that common sets of loci must necessarily be involved. Carey (1988) has called attention to the distinction between biological pleiotropism, in which the same genes underlie different traits, and statistical pleiotropism, in which genetic influences on one trait are correlated with those on another trait. Statistical pleiotropism is a more general situation that can arise for several reasons, only one of which is biological pleiotropism. Still, the existence of statistical pleiotropism shows where to look for biological pleiotropism, where to seek evidence for the involvement of specific common genetic loci. In addition, statistical and biological pleiotropism are more likely to be congruent when the underlying genetic structure involves multiple genes acting additively (Carey, 1988), as is likely to be the case particularly for more general mental abilities. Still, the conceptual distinction between the two is important to bear in mind.

Our results demonstrated high consistency between the environmental and phenotypic structure of mental ability as well as between the genetic and phenotypic structure. Although such comparability is not necessary and does not always occur, it would appear to be biologically efficient for correlated traits to respond similarly to genetic influences and environmental conditions (Hegmann & DeFries, 1970). The findings here suggest that efficiency of this nature pervades all levels of the structure of mental ability, from the most general to the rather specific. In particular, they identify a general intelligence factor contributing substantially to two components of ability, the third-stratum Verbal and Image Rotation factors, that could be considered independent or potentially negatively related absent the influence of the general factor. At the same time, each of these two components is closely associated with the third third-stratum Perceptual factor. This suggests a structure of abilities in which some general biological property such as neuronal plasticity (Garlick, 2002) contributes to all mental functioning. It also suggests a structure in which sensory perception plays a central role in the manifestation of abilities along a verbal-spatial dimension, reinforced by an educational and occupational environment that tends to separate tasks requiring verbal and spatial reasoning. Such a structure bears further investigation in future research.

As we noted in describing the assumptions underlying the models we employed, the models rely on the assumption that there are no interactions between genetic and environmental influences. Left unmodeled, the effects of such interactions will be reflected in the estimates of genetic influences, so that the estimates of genetic influences are overstated for some portions of the sample. It is of course possible that such interactions exist for genetic and environmental influences on all strata within the VPR model, and they could influence different strata and/or factors in different ways. There is some evidence for this in the form of moderating influences of socioeconomic status on the genetic and environmental influences on Wechsler full-scale, verbal, and perceptual IQ in young children (Turkheimer, Haley, Waldron, D'Onofrio, & Gottesman, 2003), but additional research is needed in this area.

Our results involving the second-stratum Content Memory factor were intriguing. The markedly lower proportion of genetic influence on this factor has been observed in other studies (e.g., Finkel, Pedersen, McGue, & McClearn, 1995; Pedersen, Plomin, Nesselrode, & McClearn, 1992), so it is reasonable to infer that our observation was not the result of something unique to our sample or combination of tests. In addition, the variance of this factor was smallest of all the factor variances. In part, this may have been because the Content Memory factor was less coherent, as indicated by the fact that its tests had larger residual variance, no doubt in part because they also had lower reliabilities. Still, the relatively small factor variance suggests that, at both the genetic and phenotypic levels, individual differences in memory ability are small relative to those of other abilities. It also suggests that the (still relatively small) individual differences that exist at the phenotypic level result to a much greater degree from environmental experience such as practice with similar memory tasks. At the same time, the memory tests in our batteries are not closely related to the kinds of tasks encountered in education, suggesting that the practice effects may result from use of perception and attention to a much greater degree than, for example, the environmental experience influencing performance on vocabulary tests. In fact, the pattern of bivariate genetic and environmental influences would appear to support this: the generally low phenotypic correlations between the Content Memory and other second-stratum factors loading on the third-stratum Verbal factor were essentially completely genetically rather than environmentally mediated, while the phenotypic correlations between the Content Memory factor and the other second-stratum factors loading on the Perceptual and Image Rotation

third-stratum factors showed substantial environmental mediation. This finding also warrants investigation in future research.

The battery of tests included in this study was compiled over 25 years ago when the MISTRA project commenced. Since that time, research in the area of memory has blossomed and tests for several additional aspects of memory, particularly semantic, episodic, and working memory have been devised. Researchers have begun to identify some of the specific genes involved in memory (de Quervain et al., 2003; Margolies, Tully, & Dubnao, 2005; Paunio et al., 2004; Tang et al., 1999). The literatures involving semantic and episodic memory tend to be rather distinct from the psychometric literature investigating the nature of intelligence, though working memory has been closely linked with general intelligence in both psychometric and neuroimaging studies (e.g., Colom, Rebollo, Palacios, Juan-Espinosa, & Kyllonen, 2004; Duncan et al., 2000). It is not clear how some of the more recently developed tests would perform if they were added to the battery of tests included here, though it seems unlikely their addition would alter the general conclusion that genetic influences are both substantial and consistent throughout the hierarchy of abilities. At the same time, the question is empirical, and future research should include the more recently developed memory tests.

In conclusion, we have presented evidence for a highly consistent pattern of genetic and environmental influences and the relations among them extending throughout the structure of mental ability. Our findings provide support for the conception of a biological structure organized around a general intelligence factor contributing to Verbal, perceptual, and image rotation abilities. The Verbal and Image Rotation abilities are, absent the influence of the general factor, independent or even potentially negatively related, though each is closely related to the Perceptual abilities. This structure has the potential to provide a useful framework for research exploring the dynamic framework linking genes, neurobiological systems, environments, and behavioral outcomes. Nevertheless, the applicability of this basic biological structure should be investigated in other samples and especially in other cultural contexts, using different but equally broad arrays of mental ability tests.

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