

Research Article

A QUANTITATIVE GENETIC ANALYSIS OF COGNITIVE ABILITIES DURING THE SECOND HALF OF THE LIFE SPAN

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Abstract—Little is known about the importance of genetic effects on individual differences in cognitive abilities late in life. We present the first report from the Swedish Adoption/Twin Study of Aging (SATSA) for cognitive data, including general cognitive ability and 13 tests of specific cognitive abilities. The adoption/twin design consists of identical twins separated at an early age and reared apart (46 pairs), identical twins reared together (67 pairs), fraternal twins reared apart (100 pairs), and fraternal twins reared together (89 pairs); average age was 65 years. Heritability of general cognitive ability in these twins was much higher (about 80%) than estimates typically found earlier in life (about 50%). Consistent with the literature, heritabilities of specific cognitive abilities were lower than the heritability of general cognitive ability but nonetheless substantial. Average heritabilities for verbal, spatial, perceptual speed, and memory tests were, respectively, 58%, 46%, 58%, and 38%.

Evidence of a genetic influence on cognitive function has accumulated rapidly in the last few decades. There is still some disagreement about the magnitude of the genetic effect, but it appears to be very substantial indeed: Results from dozens of twin and adoption studies converge on the conclusion that about half of the variance of general cognitive ability (IQ) can be accounted for by genetic factors (Bouchard & McGue, 1981; Chipuer, Rovine, & Plomin, 1990; Loehlin, 1989). Although less is known about the genetics of specific cognitive abilities—such as verbal ability, spatial ability, perceptual speed, and memory—two trends have emerged: Specific cognitive abilities appear to yield estimates of genetic influence that are significant but lower than estimates for IQ, and memory tests appear to be subject to less genetic influence than other tests of specific cognitive abilities (Plomin, 1988).

The conclusion that significant and substantial genetic influence contributes to the variability of scores on cognitive tests is much nearer the beginning than the end of the story of genetics and cognitive abilities (Plomin & Neiderhiser, in press). One gap in our understanding about genetic influence on cognitive abilities is the virtual absence of information for the entire second half of the life course.

In this article, we present the first report of a quantitative genetic investigation of cognitive abilities in the second half of the life span. The study, the Swedish Adoption/Twin Study of Aging (SATSA), uses the powerful combination of adoption and twin designs in that it includes identical and fraternal twins

reared apart in addition to the traditional twin design involving twins reared together.

One of the most basic developmental questions is whether the relative importance of genetic variance (heritability) differs with age. The proportional importance of genetic and environmental factors could change throughout the life span for a number of reasons. Although we are born with a full complement of genes, not all are operating at any one time. Genes may be “turned on” only at specific stages during the life span, while others may be inactivated. Temporal genes may be involved in the timing of specific age-related events (Farrer, 1987; Paigen, 1980). Thus, changes in the activity of genes could result in differences in genetic variance at various points during the life span.

It is perhaps more obvious that environmental influences vary throughout the life span. Some life span developmental theorists predict that total variance increases as one accumulates experiences. Thus, it would be reasonable to assume that heritability decreases during early development as experiences accumulate or that environmental influence becomes increasingly important later in life (Horn & Cattell, 1966), with the accumulation of wounds from life’s “slings and arrows of outrageous fortune.” The net effect on heritability estimates (i.e., the relative importance of genetic variance) will, of course, depend on whether total phenotypic variance is changing, and whether the effects of genetic or environmental factors are accumulated over time or are occasion-specific. If a single set of genes operates throughout development and information from the environment is “stored over time,” heritability will decrease over time (Eaves, Long, & Heath, 1986). However, if environmental effects are occasion-specific, heritability will increase with age.

Although early twin studies focused on age differences in twin resemblance for cognitive ability (Merriman, 1924; Thorndike, 1905), interest in developmental issues disappeared until the past decade (Plomin, 1986). Contrary to expectations of proportionally increasing environmental variance during development, research in early childhood suggests a steady increase in the heritability of IQ scores, at least up until the early school years (Fulker, DeFries, & Plomin, 1988; McCartney, Harris, & Bernieri, 1990). Whether heritability of general and specific cognitive abilities changes during adolescence is less clear, and very little is known about this issue during adulthood or old age.

The only previous behavioral genetic study of cognitive abilities in late life is the New York State Psychiatric Institute Study of Aging Twins, which was concerned primarily with biological aging (Kallmann & Sander, 1948). Six cognitive tests were administered to a subsample of 75 identical and 45 frater-

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nal twin pairs between the ages of 60 and 89 (Kallmann, Feingold, & Bondy, 1951). Unfortunately, twin correlations were not reported, and thus it has not been possible to use the results of this study to estimate the magnitude of genetic influence on cognitive abilities late in life. Mean twin intrapair differences were reported, and these suggest genetic influence in that identical twins yielded smaller intrapair differences than did fraternal twins, except in the case of a test of digit memory (Jarvik & Bank, 1983).

The only other data relevant to late life come from a report of a pilot study for SATSA based on 12 cognitive tests administered to 34 pairs of fraternal twins who had been reared apart and were 59 years old on average (Pedersen, McClearn, Plomin, & Friberg, 1985). A measure of general cognitive ability, an unrotated first principal component score based on the 12 cognitive tests, yielded a twin correlation of .52 for this small sample, after the effects of age, age at separation, and differences in the twins' degree of separation were partialled out. This correlation is consistent with a hypothesis of substantial genetic influence. However, the 95% confidence interval for the correlation is from .19 to .75, which suggests caution should be exercised in estimating heritability from these data.

Two twin studies of cognitive abilities in the middle adult years (average age of 40) also found heritabilities for cognitive abilities that greatly exceed the estimates of 50% typically found earlier in the life course. For example, heritability of IQ was estimated as 80% in a Norwegian study of 40 pairs each of identical and fraternal twins from 30 to 57 years of age (Tambis, Sundet, & Magnus, 1984). In a report of about 45 pairs of identical twins who had been reared apart and ranged in age from 19 to 68 years, heritability of IQ was estimated at 75% (Bouchard, Lykken, McGue, Segal, & Tellegen, 1990).

Based on the evidence from midlife and later life and the substantial corpus of studies in adolescence and young adulthood, we hypothesized not only that cognitive abilities later in life would show genetic influence but also that heritabilities might be higher than the heritabilities of 50% typically found in adolescence and young adulthood. We also predicted that specific cognitive abilities would show results similar to those found earlier in life: The magnitude of genetic influence for tests of specific cognitive abilities was expected to be lower than for general cognitive ability, and genetic influence was expected to be lower for memory tests than for other specific cognitive abilities.

METHOD

Sample

The SATSA sample consists of a subset of twins from the population-based Swedish Twin Registry (Cederlöf & Lorch, 1978). The base population is composed of all pairs of twins who indicated that they had been separated before the age of 11 and reared apart (TRA) and a sample of twins reared together (TRT) matched on the basis of gender and date and county of birth (Pedersen, Friberg, Floderus-Myrhed, McClearn, & Plomin, 1984). When SATSA was initiated in 1984, both members of 591 TRA and 627 TRT pairs were alive. The first occasion of data collection in SATSA began in October 1984, with a two-part mail-out questionnaire (Q1). A subset of the TRA and TRT

pairs in which both members responded to Q1 was invited to participate in an examination which included health evaluation and administration of cognitive tests. Both members of 291 pairs 50 years of age or older and 12 pairs under 50 years participated in this in-person testing (IPT) phase. The average age at time of testing was 65.6 years ($SD = 8.4$); 60% of the twins were female. The present analyses include 46 pairs of monozygotic twins reared apart (MZA), 67 pairs of monozygotic twins reared together (MZT), 100 dizygotic pairs reared apart (DZA), and 89 dizygotic pairs reared together (DZT). Zygosity diagnoses were first made on the basis of physical similarity and confirmed on the basis of serological assay. (For further details of the procedures, sample, and design of SATSA, see Pedersen et al., 1991.)

By definition, the twins reared apart were separated by the age of 11. However, the distribution of age at separation was highly skewed. Fifty-two percent of these twins were separated before their first birthday, 69% by their second birthday, and 82% by the age of 5. Two additional measures describing separation were computed. Degree of separation is a composite of items concerning biological relatedness of rearing parents of one twin to rearing parents of the co-twin, whether the co-twins ever met one another, whether they ever moved back together again, the extent to which they spent weekends and vacations together, whether they attended the same school, their contact by letter, and their contact by telephone. A high score means a greater degree of separation (minimum = 0, maximum = 8). The mean value for degree of separation was 5.24 ($SD = 1.4$); 75% of the pairs had values of 4 or greater. The number of years separated was calculated by subtracting age at separation from age at first contact after separation. The number of years separated varied greatly, from less than a year to over 70 years. The mean was 10.9 years ($SD = 14.8$). Reasons for separation varied; the majority of twins reared apart were separated because of the death of one or both parents, economic hardship, or both.

Procedures and Measures

IPT examinations were performed by registered nurses trained specifically to administer the IPT measures in a standardized fashion. The twins were tested at locations close to their homes; for the most part, district nurses' offices, health care schools, and long-term care clinics were used. If both members of a pair lived in the same area, they were discouraged from scheduling their examinations on the same day. In any case, different nurses tested the individuals within each pair. Most subjects (67%) were tested in the morning. The cognitive testing followed a health examination and light breakfast. An average IPT session took 4 hr.

The cognitive battery was selected to provide representation both of the domains of fluid and crystallized intelligence (Horn, 1982) and of specific abilities, and to include all major cognitive tests of the Gothenburg H-70 study of aging (Berg, 1980). Additional measures of spatial ability and perceptual speed were included so that specific cognitive abilities commonly analyzed in behavioral genetic research would be represented. The intended representation of domains and specific cognitive abili-

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ties (Nesselroade, Pedersen, McClearn, Plomin, & Bergeman, 1988), the sources of the tests, and reliabilities are reported in Table 1. Raw scores were used for descriptive and hierarchical multiple regression analyses, and scores residualized by gender (using a regression technique) were used in twin analyses.

Individuals' scores on the first principal component of the 13 tests were obtained and used as a measure of general cognitive ability. All tests except Digit Span Forward loaded higher than .50 on this first component, which accounted for 45% of the total variance.

Analyses

This section briefly reviews the logic underlying the use of intraclass correlations and model fitting for the determination of genetic and environmental influences. (For details, see Plomin, DeFries, & McClearn, 1990.)

The proportion of total variance due to genetic factors (heritability) can be estimated from twin intraclass correlations in several ways. However, in the absence of selective placement, the intraclass correlation for MZA twins provides a direct estimate. This estimate includes both additive (*Ga*) and nonadditive (*Gd*) components of genetic variance. The additive component is the sum of the average effects of all the genes that influence a character. Nonadditive effects result from interactions between alleles at a locus (dominance) or among genes at different loci (epistasis). If nonadditive effects are important for a trait, the expected correlation for dizygotic (DZ) twins is less than half that for monozygotic (MZ) twins.

The influence of shared rearing environments (*Es*) can be estimated by comparing correlations of twins reared apart with those for twins reared together. The effect of correlated environments (*Ec*) in an adoption/twin study refers to all twin sim-

ilarity which cannot be explained by genetic factors or shared rearing environments. *Ec* may reflect prenatal influences and similarities in adult life experiences, such as degree of contact as adults, and may be estimated by subtracting the estimate of heritability from the intraclass correlation for MZ twins. For twins reared apart, this estimate includes effects of selective placement.

Residual variance not explained by heredity, shared rearing environments, or correlated environments is attributed to non-shared environmental effects unique to the individual (*Ens*).

Examination of intraclass correlations provides valuable insights regarding the relative importance of genetic and environmental factors. However, it is difficult to estimate the importance of as many as five parameters (*Ga*, *Gd*, *Es*, *Ec*, and *Ens*) by separate comparisons of pairs of correlations. Model-fitting analyses are more powerful because the data from all four groups identified by zygosity status and rearing status (rearing-by-zygosity groups) are weighted appropriately, and tests of alternative models are permitted. The models to be fitted are based on quantitative genetic expectations of factors contributing to twin similarities and differences.

The model used in the present study, depicted in Figure 1, has been described in detail by Neale and Martin (1989). The model-fitting procedures are similar to those previously used in SATSA (Plomin, Pedersen, McClearn, Nesselroade, & Bergeman, 1988; Pedersen, Plomin, McClearn, & Friberg, 1988), except that age is also included in the model. This procedure is equivalent to removing the effects of age by a regression technique. Expected covariances and variances based on the model for the four rearing-by-zygosity groups were fitted to the observed covariance matrices using a maximum likelihood estimation procedure in LISREL VI (Jöreskog & Sörbom, 1986). *Ga*, *Gd*, *Ens*, *Es*, and age were included in the first complete

Table 1. Cognitive tests in SATSA

Test	Domain (crystallized vs. fluid)	Specific cognitive ability	Resource ^a	Reliability
Information	Crystallized	Verbal	CVB (modified WAIS)	.89
Synonyms ^b	Crystallized	Verbal	DS Battery	.95
Analogies	Fluid and crystallized	Verbal, reasoning	WIT-III	.82
Figure Logic ^b	Fluid	Spatial, reasoning	DS Battery	.87
Kohs Block Design ^b	Fluid	Spatial	DS Battery	.91
Card Rotations		Spatial	Educational Testing Service	.88
Digit Span (Forward and Backward) ^b		Memory	CVB (modified WAIS)	.92
Thurstone's Picture Memory ^b		Memory	DS Battery	.82
Names and Faces (Immediate and Delayed)		Memory	Colorado Adoption Project	.93
Digit Symbol		Perceptual speed	WAIS	.92
Figure Identification ^b		Perceptual speed	DS Battery	.96

^a WAIS = Wechsler Adult Intelligence Scale; DS Battery = Dureman-Sälde Battery. Sources are as follows: CVB—Jonsson & Molander, 1964; DS Battery—Dureman, Kebbon, & Osterberg, 1971; WIT-III—Westrin, 1969; Educational Testing Service—Ekstrom, French, & Harman, 1976; Colorado Adoption Project—DeFries, Plomin, Vandenberg, & Kuse, 1981; WAIS—Wechsler, 1972.

^b Test included in H-70 study of aging in Sweden (Berg, 1980).

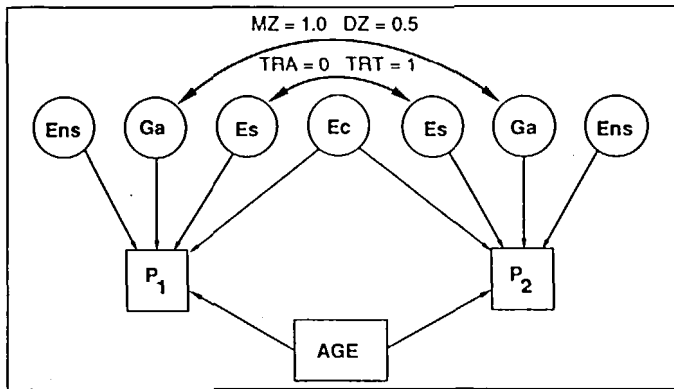


Fig. 1. Path diagram depicting genetic and environmental resemblance for identical and fraternal twins reared apart or reared together. *P1* and *P2* refer to the observed scores for Twin 1 and Twin 2, respectively. Latent factors include additive genetic effects (*Ga*), nonshared environment (*Ens*), shared rearing environment (*Es*), and other forms of correlated environments (*Ec*). TRA = twins reared apart, TRT = twins reared together, MZ = monozygotic twins, DZ = dizygotic twins.

model, and subsequent models entailed a reduction of one or more parameters. If the pattern of intraclass correlations indicated that *Ec* might be of importance, an alternate model with *Ga*, *Ens*, *Es*, and *Ec* was also run.

RESULTS

Intraclass Correlations

The intraclass correlation for MZA pairs is the best single estimate of broad-sense heritability, assuming that selective placement and other types of correlated environments are unimportant. In the SATSA sample, the MZA intraclass correlation (residualized for age and gender) was .78 for the first principal component and ranged from .28 to .65 for the 13 tests (Table 2). The average correlations were .55 for the three verbal-crystallized tests, .39 for the three nonverbal-fluid tests, .61 for the two perceptual speed tests, and .34 for the five memory tests.

Although intraclass correlations for MZA twins may provide the single best estimate of heritability, comparisons between MZ and DZ twins are needed to consider nonadditive versus additive genetic variance, and comparisons between twins reared together and twins reared apart permit investigation of the role of shared rearing environment. The possible importance of nonadditive genetic variance was indicated by DZ correlations less than half the MZ correlations in both rearing groups for the first principal component and the Analogies, Block Design, and Digit Symbol tests. Average reared-together correlations were greater than reared-apart correlations for the Block Design, Card Rotations, and Names and Faces-Immediate tests, indicating the importance of shared rearing

Table 2. Intraclass correlations by zygosity and rearing group for cognitive tests

Measure	Group			
	MZA	MZT	DZA	DZT
First principal component	.78	.80	.32	.22
Verbal-crystallized				
Information	.55	.78	.33	.20
Synonyms	.58	.81	.29	.24
Analogies	.53	.54	.09	.20
Spatial-fluid				
Figure Logic	.28	.36	.34	.06
Kohs Block Design	.57	.71	.14	.33
Card Rotations	.33	.54	.12	.33
Perceptual speed				
Digit Symbol	.65	.56	.21	.30
Figure Identification	.57	.49	.20	.32
Memory				
Digit Span Forward	.29	.37	.33	.07
Digit Span Backward	.40	.47	.19	.14
Names and Faces-Immediate	.15	.31	.18	.24
Names and Faces-Delayed	.42	.39	.15	.25
Thurstone's Picture Memory	.39	.34	.13	.19

Note. Data are residualized for the effects of age and gender. MZA = monozygotic twins reared apart, MZT = monozygotic twins reared together, DZA = dizygotic twins reared apart, DZT = dizygotic twins reared together. The numbers of pairs for the four groups (MZA, MZT, DZA, DZT), respectively, are 45, 63, 88, and 79 for the principal component, and 45-46, 63-67, 95-99, and 83-89 for the specific tests.

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environments for these tests. When MZ correlations are not greater than DZ correlations, twin similarity may reflect correlated environments rather than genetic similarity. This appears to be the case for the Figure Logic, Digit Span Forward, and Names and Faces-Immediate tests. These impressions from the patterns of twin correlations are tested more rigorously in the following section.

Model-Fitting Results

In the first series of analyses, a model with *Ga*, *Gd*, *Es*, and *Ec* was applied to the data. A satisfactory fit of the model, indicated by a chi-square with $p \geq .05$, was obtained for all of the measures; however, several of the parameters were estimated as zero or had nonsignificant *t* values (i.e., parameter estimate divided by standard error was less than 1.96). These parameters were fixed at zero in the next series of analyses. Inspection of the intraclass correlations indicated that, in some cases, *Gd* might be more appropriate than *Ga*, or that *Ec* might be an important source of twin similarity. Exclusion of parameters from subsequent models reflected these considerations. (A summary of model-fitting results, including parameter estimates and goodness-of-fit values, is reported in the appendix.)

Genetic parameters (either additive or nonadditive) were significant for the principal component and all tests. As suggested by the twin correlations, a model with nonadditive genetic variance fits the data best for the principal component and five of

the tests. This result should not be overinterpreted to mean that all of the genetic variance is nonadditive, as the twin design has only modest power to discriminate the relative importance of *Ga* and *Gd*. Additional model-fitting analyses that adjusted the *Ga* expectation for DZ groups for an assortative mating coefficient of .35, using the approach described by Chipuer et al. (1990) and Loehlin (1989), were also conducted. An even greater portion of the genetic variance was found to be nonadditive in these models.

Shared rearing environment was significant for four of the tests, and the effect of correlated environments was significant for three of the tests for which exclusively environmental models could be fitted to the data.

For present purposes of interpretation, the most relevant information pertains to the amount of variation which can be accounted for by each of the genetic and environmental effects. The estimates from the most parsimonious "reduced model" for each of the measures are summarized in Table 3. Heritability estimates from model-fitting analyses are in most cases very similar to estimates based on the MZA correlations. Estimates of heritability are lower for the specific tests than for the principal component. The heritabilities for all five of the memory tests are among the lowest in Table 3.

The environmental results are also interesting. Shared rearing environment is significant for two verbal and two nonverbal tests, and accounts for less than 15% of the variance in these tests. Effects of correlated environments are significant for

Table 3. Percentages of variance explained by genetic and environmental sources

Measure	Genetic sources	Environmental sources		
		Nonshared	Shared rearing	Correlated
First principle component	81*	19	—	—
Verbal-crystallized				
Information	60*	26	14	—
Synonyms	63*	23	14	—
Analogies	52*	48	—	—
Spatial-fluid				
Figure Logic ^a	40	60	—	—
Figure Logic ^b	0	73	—	27
Kohs Block Design	58*	30	11	—
Card Rotations	40	49	11	—
Perceptual speed				
Digit Symbol	64*	36	—	—
Figure Identification	51	49	—	—
Memory				
Digit Span Forward ^a	37	63	—	—
Digit Span Forward ^b	0	73	—	27
Digit Span Backward	44	56	—	—
Names and Faces-Immediate ^a	32	68	—	—
Names and Faces-Immediate ^b	0	76	—	24
Names and Faces-Delayed	42	58	—	—
Thurstone's Picture Memory	37	63	—	—

^a Model excludes *Ec*.
^b Model excludes *Ga* and *Gd*, but includes *Ec*.
 * Evidence for nonadditive genetic effects.

three measures when genetic parameters are excluded from the model. In these cases, *Ec* subsumes most twin resemblance. Relative to the other parameters, it accounts for about a quarter of the total variance. In the main, however, environmental influences relevant to these cognitive tests later in life operate as nonshared factors.

Hierarchical Multiple Regressions

Effects of separation on twin similarity

In the SATSA sample, there is sufficient variation among the TRA pairs in the age at separation, degree of separation, and number of years separated to assess the importance of these measures for twin similarity. A hierarchical multiple regression (HMR) procedure, described by Ho, Foch, & Plomin (1980) and previously applied to the SATSA personality and alcohol measures (Pedersen, McClearn, Plomin, & Nesselroade, in press), was used to test whether twin similarity for the cognitive measures varied as a function of separation. Two-way interactions between twin resemblance and the separation measures and three-way interaction terms which assess whether the effect of separation on twin resemblance differs in MZ and DZ twins reared apart are of particular interest. Only 1 out of 84 terms of interest was significant: Resemblance of SATSA twins reared apart for cognitive abilities is independent of age at separation, degree of separation, and the number of years separated.

Effects of age on twin similarity

Although the majority of the SATSA twins were over age 50 at the time of testing, differences in twin similarity across the age range were possible. However, HMR results indicate no significant effects of age on twin resemblance or on the interaction of twin resemblance with zygosity. This finding suggests that estimates of heritability are stable across the age range of the SATSA sample.

DISCUSSION

Heritability is estimated to be about 80% for the first principal component, which can be viewed as a measure of general cognitive ability. This finding suggests that genetic influence on general cognitive ability in adults is greater than the estimates of 50% typically found earlier in life. Although it is possible that this high heritability estimate is specific to our sample of Swedish twins, the finding is bolstered by the results of two other twin studies of IQ in the middle adult years which yield heritability estimates of 75% and 80% (Bouchard et al., 1990; Tamba et al., 1984). The lack of differences in twin similarity as a function of age in the present study suggests that heritability does not differ across the age range of the SATSA sample, from 50 to 84 years. Finding genetic influence for general cognitive ability is greater in midlife and late life than in earlier years is particularly interesting for two reasons. First, this finding is contrary to assumptions that environmental influences become proportionally more important for individual differences during the life course. Second, it fits with a general prediction made in developmental behavioral genetics: When heritability changes during development, it increases (Plomin, 1986). In the case of

cognitive abilities, this increase appears to reach a plateau in midlife.

Our predictions concerning the genetics of specific cognitive abilities were also largely supported. First, heritability estimates for the individual tests were considerably lower than for the principal component. Although the individual tests are reasonably reliable, this difference might in part be due to lower reliability for the individual tests than for the principal component score. However, the plausibility of the hypothesis that general cognitive ability is more heritable than specific cognitive abilities is strengthened by an additional analysis in which factor loadings of cognitive tests on the first principal component were correlated with the heritabilities of the tests (Jensen, 1987). In our sample, we found that the correlation between *g* loadings and heritabilities was .77 after differential reliabilities of the tests were controlled, which is comparable to results of other studies (Jensen, 1987). In other words, the more a test taps general cognitive ability, the more heritable the test score is.

Although specific cognitive abilities appear less heritable than general cognitive ability, the heritabilities of the specific tests were substantial, especially for the verbal and perceptual speed tests. Heritability estimates for these latter tests ranged from 51% to 64%, exceeding the typical heritability estimate of about 40% for specific cognitive abilities (Plomin, 1988). This finding may be an indication that specific cognitive abilities as well as general cognitive ability show greater genetic influence and less environmental influence later in life.

Our other genetic prediction was that memory tests would show less genetic influence than tests of other cognitive abilities, and this prediction also received some support. Heritabilities for the five memory tests ranged from 32% to 44%. Moreover, two of the five memory measures (Digit Span Forward and Names and Faces-Immediate) fit a model with no genetic influence, whereas the nonmemory tests (with the single exception of Figure Logic) required a genetic parameter in order to obtain a model that was not rejected.

Also of interest is the finding of nonadditive genetic variance. Although genetic influence on cognitive abilities has been assumed to be additive, evidence for nonadditive genetic variance on IQ has recently been reported (Chipuer et al., 1990). Finding significant nonadditive genetic variance has theoretical implications in terms of suggesting the possibility of directional selection during evolution. It is a maxim of population and evolutionary genetics that additive genetic variance is related to reproductive fitness in human evolution. Thus, a preponderance of nonadditive variance suggests that the phenotype may have been subjected to natural selection. The practical importance of this finding is that studies of first-degree relatives will not detect such nonadditive genetic variance because only identical twins share all genetic variance, whether additive or nonadditive. The finding of nonadditive variance may also account for lesser heritability estimates for IQ based on comparisons of parents and offspring or sibling correlations, and in part explain the relatively greater heritabilities found in twin studies.

It is noteworthy that environmental influences relevant to cognitive abilities are largely nonshared, which is consistent with other analyses of postadolescent samples (Plomin, Chipuer, & Neiderhiser, in press). Nonetheless, some evidence was

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found for the effect of shared rearing environment using the direct test of the adoption/twin design, which compares twins reared together and twins reared apart. For two verbal tests and two spatial tests, shared rearing environment was significant and accounted for 11% to 14% of the variance. Shared postrearing environment (*Ec*) showed little effect on general cognitive ability, although it accounted for substantial variance for three of the tests of specific cognitive ability.

These quantitative genetic results for general cognitive ability support the view that heredity continues to be a powerful influence on individual differences in cognitive functioning in older human beings. Much is yet to be learned about the genetic architecture of individual differences in aging. For example, to what extent are genetic effects important for late-life phenomena such as terminal decline in cognitive abilities? Longitudinal follow-up of the SATSA sample will provide new insights into the importance of genetic differences during this largely unstudied developmental period.

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APPENDIX

Table A1. Model-fitting results for model based on data from twins reared apart and twins reared together:
Reduced models

Measure	Parameter estimates \pm standard error					Goodness of fit		
	<i>Ga</i>	<i>Gd</i>	<i>Ens</i>	<i>Es</i>	Age	χ^2	<i>df</i>	<i>p</i>
First principle component	0	0.80 \pm 0.03	-0.38 \pm 0.03	0	-0.44 \pm 0.05	17.82	20	.599
Information	0	6.05 \pm 0.44	3.99 \pm 0.32	2.98 \pm 0.76	-1.68 \pm 0.38	21.81	19	.294
Synonyms	0	4.47 \pm 0.30	2.67 \pm 0.22	2.10 \pm 0.52	-1.20 \pm 0.27	25.70	19	.139
Analogies	0	2.67 \pm 0.20	2.55 \pm 0.16	0	-1.40 \pm 0.18	15.88	20	.720
Figure Logic ^a	2.34 \pm 0.23	0	2.84 \pm 0.16	0	-1.27 \pm 0.18	23.58	20	.260
Figure Logic ^b	0	0	-3.14 \pm 0.13	-1.91 ^c \pm 0.21	-1.27 \pm 0.18	25.73	20	.175
Kohs Block Design	0	5.40 \pm 0.41	3.88 \pm 0.30	2.37 \pm 0.80	-2.88 \pm 0.36	17.32	19	.568
Card Rotations	-10.61 \pm 1.38	0	-11.87 \pm 0.81	5.60 \pm 2.48	-6.26 \pm 0.86	19.35	19	.435
Digit Symbol	0	8.27 \pm 0.48	6.22 \pm 0.41	0	-6.46 \pm 0.56	26.50	20	.150
Figure Identification	4.90 \pm 0.37	0	4.83 \pm 0.23	0	-3.57 \pm 0.36	26.23	20	.158
Digit Span Forward ^a	0.70 \pm 0.07	0	0.91 \pm 0.05	0	-0.20 \pm 0.05	9.48	20	.970
Digit Span Forward ^b	0	0	0.98 \pm 0.04	0.59 ^c \pm 0.07	-0.20 \pm 0.05	10.82	20	.951
Digit Span Backward	0.77 \pm 0.07	0	0.86 \pm 0.05	0	-0.20 \pm 0.06	21.34	20	.370
Names and Faces-Immediate ^a	0.99 \pm 0.12	0	1.44 \pm 0.08	0	-0.59 \pm 0.08	25.81	20	.170
Names and Faces-Immediate ^b	0	0	1.53 \pm 0.06	0.85 ^c \pm 0.11	-0.59 \pm 0.08	25.60	20	.180
Names and Faces-Delayed	1.03 \pm 0.10	0	1.23 \pm 0.07	0	-0.52 \pm 0.08	23.43	20	.260
Thurstone's Picture Memory	2.76 \pm 0.78	0	3.57 \pm 0.23	0	-0.93 \pm 0.21	13.04	19	.836

^a Model excludes *Ec*.

^b Model excludes *Ga* and *Gd*, but includes *Ec*.

^c Parameter estimated was *Ec*.