Genetic Covariance Among Measures of Information Processing Speed, Working Memory, and IQ

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The genetic relationship between lower (information processing speed), intermediate (working memory), and higher levels (complex cognitive processes as indexed by IQ) of mental ability was studied in a classical twin design comprising 166 monozygotic and 190 dizygotic twin pairs. Processing speed was measured by a choice reaction time (RT) task (2-, 4-, and 8-choice), working memory by a visual-spatial delayed response task, and IQ by the Multidimensional Aptitude Battery. Multivariate analysis, adjusted for test-retest reliability, showed the presence of a genetic factor influencing all variables and a genetic factor influencing 4- and 8-choice RTs, working memory, and IQ. There were also genetic factors specific to 8-choice RT, working memory, and IQ. The results confirmed a strong relationship between choice RT and IQ (phenotypic correlations: -0.31 to -0.53 in females, -0.32 to -0.56 in males; genotypic correlations: -0.45 to -0.70) and a weaker but significant association between working memory and IQ (phenotypic: 0.26 in females, 0.13 in males; genotypic: 0.34). A significant part of the genetic variance (43%) in IQ was not related to either choice RT or delayed response performance, and may represent higher order cognitive processes.

KEY WORDS: Processing speed; working memory; IQ; multivariate analysis; general genetic factor.

INTRODUCTION

Behavioral genetics studies of cognition have increasingly turned to lower level cognitive processes to help understand the genetic structure of human mental ability (Baker *et al.,* 1991; Ho *et al.,* 1988; Rijsdijk *et al.,* 1998; Wright *et al.,* 2000). Such investigations were spurred by findings from the cognitive correlates approach to intelligence, which established modest but consistently significant relationships between various elementary cognitive tasks and IQ (Hunt, 1985; Larson and Saccuzzo, 1989; Neubauer *et al.,* 1997). Correlates of IQ included such measures as choice reaction time (RT),

speed of scanning in short-term memory, visual and auditory discrimination ability, and speed of long-term memory retrieval. In general, the RT measures demonstrated correlations of roughly 0.30 with IQ, whereas measures without a RT component, such as perceptual discrimination speed, reached correlations of 0.50 with IQ (Deary and Stough, 1996; Jensen, 1993). All of these elementary cognitive task measures index forms of information processing speed that have been included in hierarchical models of intelligence (Carroll, 1993).

The process of working memory (WM) is a more complex function that sets limits on the brain's capacity for processing information, especially when attention is required for a novel or complex task that cannot be processed automatically (Baddeley, 1992). WM encompasses short-term memory (the temporary storage system), as well as an executive (or controlled attention) system, which organizes the resources needed in the storage and computation of intermediate information in sequential processing (King and Just, 1991). According

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to the limited capacity hypothesis (Jensen, 1998; Vernon, 1987), a faster speed of information processing would enable better access to the rapidly decaying information in WM relevant to solving problems, whereas a slower processing speed would tax WM capacity to maintain transient information in an accessible form.

Significant associations have been established among processing speed, WM, and IQ measures, with especially high correlations (0.80–0.90) between WM and reasoning ability (Kyllonen and Christal, 1990). However, there have been major inconsistencies regarding the direction of causation in the relationship between processing speed and WM. Miller and Vernon (1992, 1996) attempted to establish whether processing speed determined WM or vice versa. Partial correlations showed that the correlation between the IQ factor and WM factor barely changed ($r = 0.41$) when the RT factor was held constant, but the correlation between the RT factor and IQ factor became nonsignificant when WM was controlled. They suggested that WM was influenced by control processes (e.g., strategy use, resource allocation), which increased the capacity to retain information and hence the potential for faster information processing. Fry and Hale (1996, 2000) also found WM to be a better predictor of IQ than processing speed; they included age in their analysis to investigate a theory proposed by Kail and Salthouse (1994) whereby age affected processing speed, which in turn influenced WM and subsequently IQ. Path analysis subsequently revealed that 71% of the overall effect of age on WM was mediated by age differences in processing speed, thus supporting the prominence of the processing speed function in cognitive ability.

Although genetic studies (Alarcon *et al.,* 1998; Petrill *et al.,* 1998; Thompson *et al.,* 1991) have shown that there are significant genetic correlations between perceptual speed, memory, and verbal/spatial abilities (factors derived from the Cognitive Abilities Test), there have been no studies which directly assess the genetic relationship between processing speed, WM, and IQ. What is needed is a study which measures information processing speed by elementary cognitive tasks, rather than by indices of psychometric perceptual speed, which tap a conceptually distinct process (Kyllonen, 1993). Elementary cognitive tasks have been studied only in relation to IQ (Baker *et al.,* 1991; Ho *et al.,* 1988; Rijsdijk *et al.,* 1998), where the relationship between processing speed and IQ was shown to be substantially genetic, genetic correlations ranged from 0.18 to 1, depending on the task. A recent genetic study of adolescent twins found that the covariation between two-choice RT (i.e., reaction to a single stimulus from a choice of two) and IQ (-0.22) was entirely mediated by a genetic factor (Rijsdijk *et al.,* 1998). Choice RT is a reliable measure which shares at least 10% of variance with IQ (Jensen, 1980), and this made it suitable for indexing processing speed in the present study.

Multivariate studies of IQ or specific cognitive abilities have indicated that memory subtests (or factor) are influenced by a general genetic factor, but even more so by a specific genetic factor (Cardon *et al.,* 1992; Finkel *et al.,* 1995b; Luo *et al.,* 1994). One study has further reported a genetic relationship between processing speed and various short-term memory tests, including word recall, immediate and delayed text recall, and figure memory (Finkel and McGue, 1993). These studies, however, used either short-term memory tasks (predominantly to tap memory storage) or a conglomerate measure of different memory types (e.g., short- and long-term) rather than a specific test of WM. To measure WM, we use a visual-spatial delayed response (DR) task, which involves both short-term storage and executive function. This task requires the participant to retain information over the course of a short time delay during which they are required to withhold responses. It is more complex than the choice RT task because of the requirement of inhibition, timing the motor response, and remembering the target position while ignoring distractors. Prefrontal cortex areas are one anatomic region implicated in executive function and are activated during task performance, indicating that the DR task does tap some process in the multidimensional WM system (Geffen *et al.,* 1997; Goldman-Rakic, 1992).

The question we wish to address in the present study is whether measures of information processing speed, WM, and intelligence share the same underlying genetic factor or whether they relate to each other through a number of different genetic factors. Here, we use a classical twin design to examine the covariation among choice RT, delayed response, and IQ, which represent the increasingly complex information processes of processing speed, WM, and intelligence.

METHOD

Participants

This is an ongoing study of cognition in 16-year-old twins and their non-twin siblings (Wright *et al.,* 2001). We have analyzed data from the first 390 twin pairs who participated (90 MZ female, 76 MZ male, 49 DZ female, 46 DZ male, 95 opposite sex). Zygosity

was determined by ABO, MN, and Rh blood groups and by nine independent polymorphic DNA markers. Twin pairs were excluded if either one had a history of significant head injury, neurological or psychiatric illness, substance dependence, or if they were currently taking long-term medications with central nervous system (CNS) effects. Participants had normal or corrected-to-normal vision (better than 6/12 Snellen equivalent). The twins were mostly in their penultimate year of secondary school and were between 15 and 18 years of age (16.17 years; $SD = 0.34$). To increase motivation, they received a monetary reward based on their performance on the DR task. Written informed consent was obtained from the participants, as well as their parent/guardian, prior to testing.

A sub-sample of twins (49 pairs) returned for retesting approximately 3 months (1–5 months) after their initial test session so that the test-retest reliability of the measures could be estimated. All participants who were approached for retesting agreed. This sample comprised 23 MZ and 26 DZ pairs (57 females, 41 males).

Experimental Protocol

The CRT task and IQ test were part of a psychometric battery, which also included an inspection time task and two reading tests. The DR task was administered in a parallel testing session and involved recording both performance measures and event-related potentials. Each session approximated 1.5 h in length. Tests were computer administered in the presence of a research assistant. One twin completed the psychometric session while the other completed the WM session. The order of session testing was counterbalanced between twin pairs based on the birth order of the twins. In the retest sample an identical battery of tests was administered on both occasions and to minimise confounding effects the participants performed the sessions in the same order on retest. A full description of the protocol is given in Wright *et al.* (2001).

Tests

Multidimensional Aptitude Battery (MAB)

A shortened version of the MAB was used, including three verbal subtests, (Information, Arithmetic, Vocabulary) and two performance subtests (Spatial and Object Assembly). The MAB is based on the WAIS-R and the subtests that we chose are reported to correlate with corresponding WAIS-R subtests in the range of 0.80 to 0.88 (based on the average from five studies; Jack-

son, 1998). All subtests had a multiple-choice format and were timed at 7 min each. The timed nature of the IQ test should not upwardly bias the correlation between IQ and RT, as Vernon and Kantor (1986), using a between-subjects design demonstrated that timed and untimed measures of the MAB correlated equally with RT.

Participants were not penalized for guessing and were encouraged to answer every item within the time period. Administration and scoring were computerized. IQ scores derived from computerized versus paper-and-pencil administration of the verbal subtests have been shown to be equivalent by Harrell *et al.* (1987) and MacLennan *et al.* (1988).

Three composite IQ scores were calculated (verbal, performance, full scale), but only the full-scale IQ score was used in this analysis. All participants were normed on a 16- to 17-year-old group, except for one 18-year-old pair who were normed on an 18- to 19-year-old group. Of the 35 pairs of 15-year-olds, almost all were within 3 months of their 16th birthday, and furthermore only 9 of these pairs were in the school grade below that typical for 16-year-olds. Twins were tested as closely as possible to their 16th birthday; a consequence of this was that there was differential completion of months of schooling between pairs. Because the MAB was primarily tapping crystallized ability, the effects of months of schooling completed at the time of study participation was tested. Partial regressions showed that months of schooling completed since the beginning of grade 10 was significantly correlated with IQ after controlling for age ($p < 0.01$), whereas age was not significantly correlated with IQ when the effects of education were partialled out. Months of schooling was thus included as a regression coefficient in the means model of the genetic analyses.

Choice Reaction Time (CRT) Task

This task was presented to the participants in the visual form of dripping taps. The participant was instructed to quickly press the appropriate computer key to stop a tap from dripping. They aligned and rested their fingers on the keys Z, X, C, and V (left hand, index finger on V) and the keys M, comma (,), period (.), and slash (/) (right hand, index finger on M) of a standard QWERTY keyboard. Different coloured taps corresponded to the same fingers on both hands to aid tap and finger alliance, for example, the taps matching the index fingers were both red. Although the home key CRT task has been employed in most previous research, the keyboard variant has been found to be highly correlated

(0.75) with the home key task in a four-choice condition, and it also demonstrated similar correlations with measures of intelligence (Small *et al.,* 1987). In studies (e.g., Neubauer *et al.,* 1997; Small *et al.,* 1987) using the keyboard variants, the stimuli that have been used—for example, dots appearing beneath boxes, addition signs appearing in squares—are comparable to our own in that the reaction stimulus (i.e., the water) is related to stationary orienting stimuli (i.e., the taps). Welford (1971) demonstrated that the RT difference noticed across differing choice conditions is not an artifact of variation in motor speed across fingers (e.g., ring and little fingers used for 8-choice RT show slower response speeds) but is dependent on perceptual factors.

To familiarize the participants with the response keys, they were initially presented with the eight taps and were required to respond to each tap in a left-to-right sequence. To minimize between-subject practice and order effects, the sequence of choice conditions was fixed in the order of four, two, then eight (Smith and Stanley, 1983). The number of trials presented in each of the two-, four-, and eight-choice conditions was 96, 48, and 96, respectively. For all conditions, eight taps appeared on the monitor; those taps in use for the two- and four-choice conditions were made salient by brightening their colour. The output measure was the mean RT (in ms) of correct responses only in each choice condition. RT trials less than 150 ms or greater than 2000 ms were excluded from the calculation of the mean. Correlations between mean RT and accuracy showed evidence of a speed-accuracy trade-off effect in all choice conditions, although this effect was small for two-choice ($r = 0.10$) and four-choice ($r = 0.08$), but large for eight-choice ($r = 0.45$). Mean RT was thus adjusted for percentage of correct responses in the means model of the genetic analysis.

Delayed Response (DR) Task

The apparatus and conditions of the DR task were similar to those used by Geffen and colleagues (Geffen *et al.,* 1997). The computer featured a touch-sensitive screen, which radiated a constant brightness and displayed a grey background so that afterimage effects of the target were minimized. It was covered with a black hood which had a 205-mm diameter circle removed so that the center was concordant with the center of the screen. The cover was designed to preclude participants from using the sides of the computer to reference spatial locations. The screen was activated by a rubber-tipped (5 mm in diameter) pointer. When not

responding, participants rested their hand with the pointer on a touch sensitive response pad situated approximately 10 cm outward from the base of the monitor.

Each trial began with the appearance of a filled black circle in the center of the screen. This fixation point measured 0.5° visual angle in diameter and was presented for 250 ms plus the delay period of 1 s or 4 s. The target (checkered circle) measured 1.5° visual angle in diameter and appeared at pseudo-random positions 250 ms from the trial commencement. On control trials, the target remained on the screen for the delay period, whereas on memory trials the target appeared for 150 ms. The disappearance of the fixation point was the signal for the participant to make a response: touching the target on control trials or the memorized position of the target on memory trials. A distractor that looked like the target was randomly presented on half of the trials. It appeared for 150 ms at a random delay period ranging from 300 to 700 ms following target onset. Participants were instructed to ignore the distractor. Following a response, an intertrial interval randomly varied between 750 ms and 1000 ms. During this time, participants received feedback on the screen. Correct responses were rewarded with 2, 4, 8, or 10 cents, depending on how close the response was to the center of the target. Fast responses (<200 ms), slow responses (>1500 ms) and incorrect position responses incurred a 5-cent penalty.

Practice trials were given until approximately 80% accuracy was achieved. The experimental task comprised six blocks, each containing 72 trials (32 control, 32 memory and 8 catch trials). It followed a 2 (control/memory) $\times$ 2 (1 s delay/4 s delay) $\times$ 2 (distractor present, distractor absent) within subjects design. All conditions contained an equal number of trials.

During the task EOG measurements were recorded to detect eye movement because participants who shifted their gaze to the target instead of the fixation point gained an advantage over those who viewed the target in their peripheral vision. Tin cup electrodes (6 mm) were placed on the upper orbital ridge and the outer canthus of the left eye to monitor EOG activity. EOG was amplified via Grass preamplifiers (Model P511K) with a bandpass of 0.01 to 100 Hz. Signals were subsequently sampled every 2 ms from 100 ms before fixation point onset to 200 ms post-fixation point offset. Trials were rejected offline if the root mean square amplitude of any EOG channel exceeded ± 50 μV.

The accuracy of a response was measured by (1) percent correct—the percentage of correct trials without EOG artifact; (2) position displacement—the distance

(in millimeters) between the target center and response position on correct trials; and (3) winnings—amount of money awarded across all trial types. RT was measured by (1) initiation time—interval from fixation point offset to removal of the hand from the response pad; and (2) movement time—interval from removal of the hand from the response pad to the screen response. DR percent correct (accuracy) collapsed across all memory conditions was used as the WM index in the present analysis because it was more internally reliable than the individual conditions and it took into account correctness of the response rather than the precision of a correct response (position error). The median estimate across each individual's trials was used in preference to the mean, because it is generally less sensitive to outliers.

Analysis

All hypotheses concerning means, variances, correlations, and components of variation and covariation were tested within the framework of maximum likelihood (ML) analysis of raw data using Mx 1.50 (Neale, 2000). Models were fitted to the data, progressing from the most saturated to more restricted models. Means and variances were tested for equality across birth order, zygosity, and sex. Other mean effects tested for were order of session testing, months of schooling completed at time tested (IQ only), and accuracy (CRT variables only). Once a means model was decided on, hypotheses concerning homogeneity of correlations between sexes within zygosity groups were tested. Because this was the first analysis of the DR task variables, we chose to initially apply a multivariate triangular decomposition to the data to gain a preliminary understanding of the pattern of genetic effects across DR task performance, CRT, and IQ. Because test-retest reliability data were available, they were also included in the multivariate model. Modelling thus began from the approach of Cholesky decomposition of additive genetic (A), common environment (C), and unique environment (E) covariance between the measures. This specifies as many factors as there are variables for each source of variance, with each factor having one loading less than the previous one. However, this arrangement was modified so that pathways leading to the same variable at test and retest were equal. Further, an additional source of variance, U (unreliability), was specified that was unique to each variable (but constrained to equality across test and retest). Fig. 1 depicts the path structure of this model (incorporating test and retest)
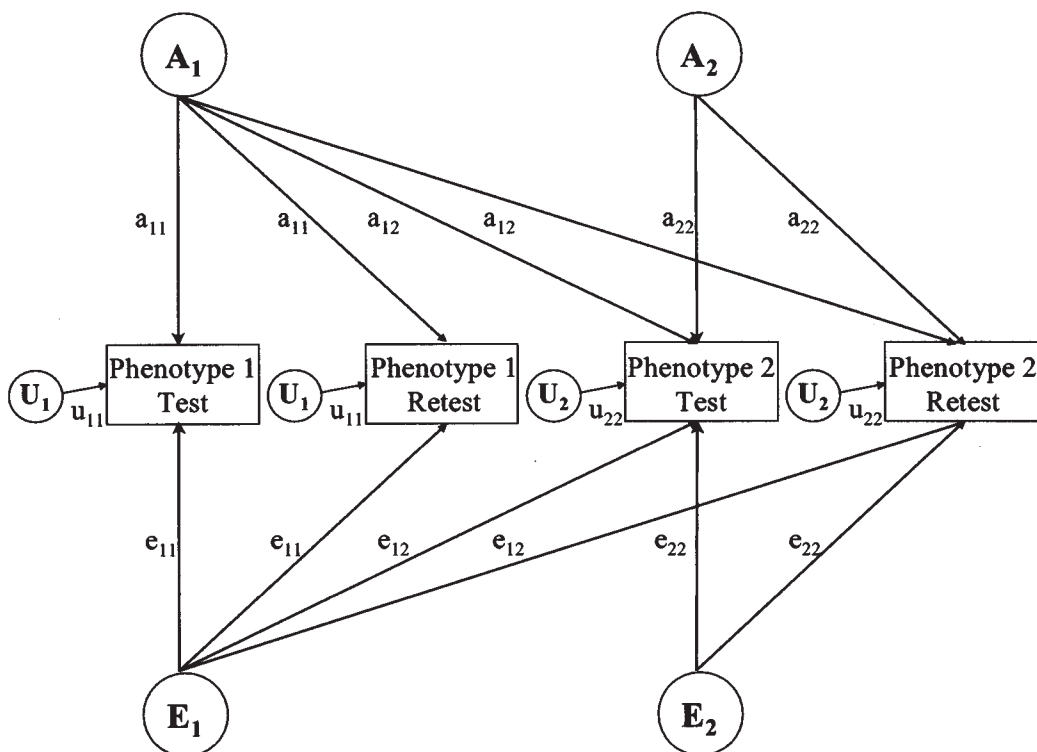

Fig. 1. Example of an AE Cholesky decomposition modified to include test-retest reliability data and applied to two variables.

but using an example of an AE model with two phenotypes only. A practice effect (which was significant in all variables) was modelled for the means across test and retest in addition to the other mean adjustments.

Reduced models are favored if the likelihood ratio chi-square comparing the models is less than the critical value (alpha = .05) of the chi-squared distribution, indicating that there is no significant difference between the saturated model and the reduced model. The most parsimonious Cholesky model (i.e., the one with the fewest sources [A, C, E] of variation) was used as a baseline against which to compare submodels with fewer factors or loadings using the chi-squared difference test (Neale and Cardon, 1992).

RESULTS

Descriptive Statistics

Computer or experimenter error resulted in the loss of IQ data from 6 participants (0.76%) and DR task data from 8 (1%) participants. All variables were normally distributed with the exception of DR accuracy. DR accuracy was transformed by a reflected (maximum value + 1) square root function. Scores were considered univariate outliers (single distribution of twin 1 and twin 2 scores) if they exceeded ± 3.5 *SD* from the mean. In the two-, four-, and eight-choice conditions of the CRT task the number of outliers were eight, seven, and five, respectively. There were no outliers in DR accuracy or IQ. No multivariate outliers (screened using Mx 1.50 through the %P function) were identified.

Contrasts of means and variances across birth order and zygosity showed only differences between groups for eight-choice RT and IQ. For eight-choice RT, birth order differences were apparent in MZ male and DZ female groups. First-born twins of the MZ male group had faster RTs than second-born twins, and first-born twins of the DZ female group had slower RTs than second-born twins. There were also differences in variance between twin 1 and twin 2 which mimicked the mean differences found in the MZ male group, so that variance was larger in the second-born twin. These differences in birth order were inconsistent across zygosity group, so equal means and variances were assumed. Birth order effects were detected in IQ. These effects were of borderline significance and were only in the direction of the first born having an advantage in the MZ groups, it was decided not to model this minor effect. Also, the female and male means in the DZ opposite sex female first born and DZ opposite sex male first-born groups could not be equated with each other, although they could be equated with the female and male mean of the rest of the sample. There was no rational reason why this inconsistency should arise, so it was attributed to the presence of sampling error and equal means were assumed.

The ML estimates of means, *SD,* and effect size of regression coefficients of the variables on first testing occasion are shown in Table I. IQ scores were normally distributed ranging from 79 to 145. The mean percentages correct in the two-, four-, and eight-choice conditions were 91.6, 81.7, and 78.6, respectively. As expected, mean RT increased with larger number of choices, in

Table I. Maximum Likelihood Estimates (MLE) of Means, Standard Deviations (SD) and Regression Deviations for the CRT and DR Task Variables and Full Scale IQ on First Testing Occasion

Measure	Mean (SD)	Sex effect[a]	Education effect[b]	RT accuracy effect[c]	Session order effect[d]
2-choice RT (ms)	288 (30)	ns	—	0.53	15
4-choice RT (ms)	486 (110)	ns	—	1.95	23
8-choice RT (ms)	578 (90)	ns	—	3.63	25
DR accuracy*	78.82 (15.9)	ns	—	—	ns
Full scale IQ	105 (13)	5	0.19	—	ns

*Mean value was back-transformed; SD was not obtained by MLE.

ns, no significant

[a] Deviation of male participants from female mean.

[b] Regression coefficient on months of schooling beyond beginning of grade 10.

[c] Regression coefficient on % of correct responses for each RT condition (i.e., more accurate responses all have slower RTs).

[d] Deviation for those performing in the 2nd session from the 1st session mean (i.e., 2nd session RT responses slower due to fatigue).

Table II. MLE of Twin Correlations (with 95% Confidence Intervals) Across Zygosity Group (and Pooled MZ and DZ Groups) for the CRT, DR Task, and IQ Variables (all correlations are corrected for mean effects shown in Table I)

Measure	Twin correlations							
	MZF	MZM	DZF	DZM	DZFM	DZMF	MZ	DZ
2-choice RT	0.39	0.42	0.26	0.35	0.25	0.35	0.51	0.38
	(0.19–0.54)	(0.25–0.56)	(−0.08–0.50)	(0.66–0.55)	(−0.02–0.46)	(0.06–0.56)	(0.40–0.60)	(0.24–0.49)
4-choice RT	0.61	0.43	0.30	0.25	0.37	0.46	0.54	0.36
	(0.46–0.71)	(0.24–0.58)	(0.03–0.51)	(−0.03–0.47)	(0.11–0.56)	(0.22–0.63)	(0.43–0.63)	(0.23–0.47)
8-choice RT	0.77	0.67	0.48	0.60	0.32	0.23	0.72	0.39
	(0.69–0.83)	(0.55–0.75)	(0.22–0.65)	(0.37–0.73)	(0.06–0.52)	(−0.03–0.45)	(0.64–0.77)	(0.26–0.50)
DR Accuracy	0.36	0.49	0.31	0.31	0.39	0.37	0.42	0.35
	(0.18–0.51)	(0.33–0.62)	(0–0.53)	(0.01–0.52)	(0.15–0.57)	(0.12–0.55)	(0.30–0.53)	(0.22–0.46)
Full Scale IQ	0.84	0.79	0.53	0.52	0.62	0.35	0.82	0.50
	(0.78–0.88)	(0.71–0.85)	(0.30–0.68)	(0.32–0.66)	(0.44–0.74)	(0.10–0.53)	(0.77–0.85)	(0.40–0.59)

accordance with Hick's Law (1952). Twin correlations for all variables in each zygosity group (and pooled MZ and DZ groups) estimated by ML and adjusted for any significant effects of sex, education, CRT accuracy, and session order are shown in Table II. Note that the CRT variables appeared to show a trend of increasing twin correlations from conditions of low to high choice.

The size of the difference between MZ and DZ twin correlations was more consistent with common environment effects or assortative mating rather than dominance effects. Thus, we tested only for the presence of additive genetic, common environment, and individual environmental effects.

Phenotypic correlations (estimated by ML) amongst the variables from the CRT and DR tasks, and IQ are presented in Table III; there were no significant differences between estimates for female and male participants. Note that for correlations with DR accuracy the direction of the correlation has been reversed to be commensurate with the untransformed variable. As would be expected, within-task correlations for CRT were high. The CRT measures were more highly correlated with IQ than the DR measure, whereas DR accuracy was more highly correlated with CRT variables than IQ.

Genetic Analysis

Results of the Cholesky analysis are shown in the upper part of Table IV. An additive genetic (A) and unique environment (E) model best fitted the data, as evidenced by the nonsignificant change in chi-square of the nested model ($\Delta\chi^2 = 12.55$, $\Delta df = 15$, $p < 0.05$). A common and unique environment model resulted in a significant change in chi-square and was not investigated further. Simplified theoretical models which involved remodelling of A parameters were tested by a comparison with the AE Cholesky model (see Table IV). We also fitted a submodel with a single genetic common factor and specific genetic factors, as would be predicted by a general factor theory of intelligence (e.g., Spearman, 1904). Because three RT variables were included in the analysis, we also fitted a submodel which included a genetic RT factor in addition to a general genetic factor and specific genetic factors. Neither submodel fitted the data, indicating that a more complicated pattern of genetic covariance existed among the variables. Thus, an approach was taken which involved dropping nonsignificant pathways in the AE Cholesky model to arrive at a more parsimonious solution.

Table III. MLE of Phenotypic Correlations Among CRT, DR Task, and IQ Variables on First Testing Occasion, Separately for Female (lower diagonal) and Male (upper diagonal) Participants

	2-choice	4-choice	8-choice	DR Accuracy	IQ
2-choice	—	0.54	0.66	−0.31	−0.32
4-choice	0.51	—	0.68	−0.27	−0.56
8-choice	0.62	0.65	—	−0.36	−0.50
DR Accuracy	−0.17	−0.26	−0.19	—	0.13
IQ	−0.31	−0.53	−0.46	0.26	—

Note: These separate estimates for the male and females samples fall within overlapping confidence intervals.

Table IV. Results of Fitting Multivariate Models to the Covariances of CRT, DR, and IQ Measures: Difference in -2 Log Likelihood ($-2LL$) Ratio and Degrees of Freedom (df) of the Nested Models and their Probability (P) Level of Significance (all models also estimate unreliability of measurement for each variable)

Model	$-2LL$	df	Δ_{-2LL}	Δ_{df}	P
i. ACE Cholesky Decomposition	4819.04	4189			
ii. CE Cholesky Decomposition	4889.67	4204	70.63	15^a	$< .001$
iii. AE Cholesky Decomposition	4831.59	4204	12.55	15^a	$> .50$
iv. A General factor + A Specifics	4917.58	4209	85.99	5^b	$< .001$
v. A General factor + A RT Factor + A Specifics	4849.29	4206	17.70	2^b	$< .001$
vi. Reduced AE Cholesky Decomposition	4843.74	4216	12.15	12^b	$> .25$

[a] Compared to model i.

[b] Compared to model iii.

A reduced AE Cholesky model, in which non-significant loadings were fixed to zero, showed the presence of five genetic factors. The standardized parameter loadings of this factor model are displayed in Fig. 2; corrected parameters loadings (shown in brackets) were standardized by constraining the sum of the A, C, and E variance components equal to one, whereas the uncorrected loadings were estimated by constraining the sum of A, C, E, and U variance components to one. The first genetic factor loaded on all

measures but it was most clearly defined by the CRT variables. The second factor also loaded on all variables except two-choice RT, although its loading on DR accuracy was comparatively low. The remaining genetic factors were each specific to eight-choice RT, DR accuracy, and IQ. Uncorrected (and corrected for unreliability) heritability estimates were 0.81 (0.89) for IQ, 0.70 (0.85) for eight-choice RT, 0.59 (0.90) for four-choice RT, 0.52 (0.79) for two-choice RT, and 0.48 (0.93) for DR accuracy. Correlated unique environment
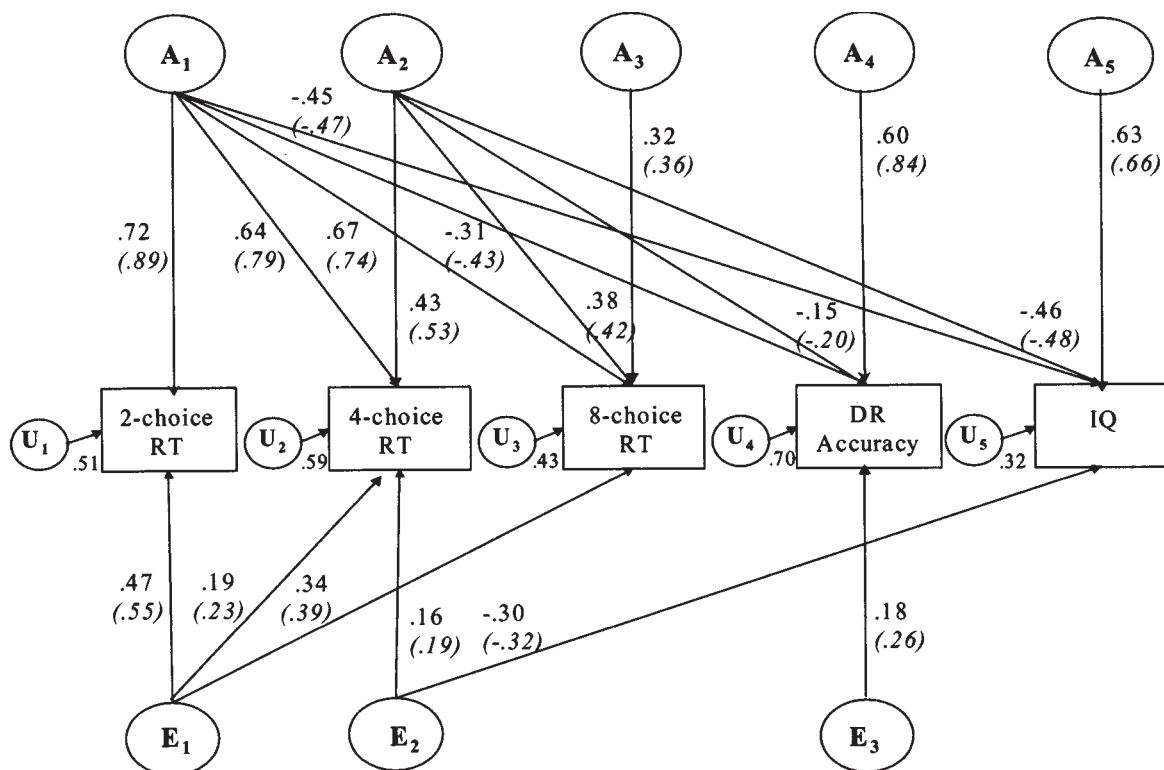
Fig. 2. Standardized path coefficients for the reduced Cholesky model, where A represents additive genetic factors and E represents unique environmental factors. The path coefficients adjusted for test unreliability are shown in brackets.

factors existed among those variables from the CRT task, and additionally between four-choice RT and IQ.

Genetic and environmental correlations estimated from the full AE Cholesky model are displayed in Table V. The genetic correlations of the experimental cognitive measures with IQ were highest for four-choice RT and lowest for DR accuracy.

DISCUSSION

The prediction of significant genetic covariance among processing speed, working memory, and IQ was supported. The decomposition of genetic covariance showed that two genetic factors could explain the relationship among all the variables, although the first factor best captured the variance in DR accuracy. The differential influence of the first two factors on choice RT and DR performance was consistent with the finding of a stronger phenotypic relationship between choice RT and IQ than with DR performance. Other genetic factors emerged which reflected those genes influencing functions specific to choice response at increased choice (eight-choice RT), DR accuracy, and IQ. Estimates of heritability (unadjusted for reliability) agreed with previous findings of IQ and CRT (Baker *et al.,* 1991; Boomsma and Somsen, 1991) and the heritability of DR performance was consistent with studies of short-term memory (Finkel *et al.,* 1995a; Thapar *et al.,* 1994). For tasks with poor test-retest reliability, the adjusted estimates of heritability were considerably higher. These were perhaps overestimates of the heritability, because in variables like DR accuracy and four-choice RT, the MZ twin correlation was almost as high as the test-retest correlation.

Two factors were necessary to explain the relationship among CRT, DR accuracy, and IQ. However, the first factor had higher loadings on four- and eight-choice RT and DR accuracy than did the second factor. Because two-choice RT is the most simple of the CRT task measures, theoretically it should be the purer measure of mental speed, which indicates that the first factor might reflect mental processing speed, whereas the second factor reflects common information processes involved in choice RT, DR, and IQ performance. The first two Cholesky genetic factors accounted, respectively, for 22% and 23% of variance in IQ. Forty-three percent of the genetic variance in IQ was actually independent of that determining the lower level processes sampled by the choice RT and DR task, suggesting that although processing speed and working memory processes may be necessary for higher order functioning, they may not be sufficient to explain a large component of the individual variation in IQ. The independent genetic variance in IQ may be reflective of information processing abilities not tapped by the current tasks (e.g., access to long-term memory), or even personality factors such as conscientiousness. Without an increased number of informative variables in this analysis, such interpretation can only be speculative.

Because DR accuracy did not demonstrate a genetic relationship with IQ independent from CRT variables, this supports theories of intelligence encompassing an interdependence of processing speed and WM in predicting IQ (Fry and Hale, 2000; Kail and Salthouse, 1994; Miller and Vernon, 1996), but the direction of causation between processing speed and WM cannot be established from our data. Likewise, the question of whether processing speed influences IQ (limited capacity theory), rather than the reverse, (more intelligent people optimising their information processes) cannot be resolved.

Although the phenotypic correlation between CRT and IQ was consistent with previous studies (perhaps slightly higher for four- and eight-choice RT), the correlation between DR accuracy and IQ was lower than other WM tasks, thus limiting the comparison of our study with others using speed and WM constructs. It may be that the amount of executive functioning required by the DR task is less than that demanded by dual tasks, which have predominantly been used to measure WM. It may also be that our measure of IQ—composed of three verbal and two performance subtests—was primarily tapping crystallized (acculturalized) intelligence.

Table V. Genetic and *Unique Environmental* (with Measurement Error Removed) Correlations Amongst Measures of CRT, DR, and IQ Estimated From the Full AE Cholesky Model

	2-choice	4-choice	8-choice	DR accuracy	IQ
2-choice		0.73	*0.99*	−*0.30*	−*0.28*
4-choice	0.82		*0.82*	−*0.48*	−*0.68*
8-choice	0.80	0.91		−*0.38*	−*0.35*
DR Accuracy	−0.40	−0.44	−0.43		*0.21*
IQ	−0.45	−0.70	−0.59	0.34	

In other studies of WM and higher cognition, reasoning (or fluid intelligence) tests of ability have primarily been used.

The strong genetic relationship between CRT and IQ was in accord with findings of Rijsdijk and colleagues (1998), who used a two-choice RT task in a similar aged sample. They obtained a genetic correlation with the Raven Progressive Matrices of −0.36, we report correlations of −0.45, −0.59, and −0.70. In our study, we found that a specific genetic factor influenced eight-choice RT. Instead of being speed related, this factor may represent visual attention because in the eight-choice condition visual focus must extend across a larger area than in the two- and four-choice conditions. If this is so, it provides support against the criticism that the RT-IQ correlation is confounded by the sensory phenomenon of visual attention (Longstreth, 1984). Alternatively, this specific factor may reflect sustained performance or motivation because the eight-choice condition was preceded by the two- and four-choice conditions plus the IQ subtests.

The genetic correlations between CRT variables and DR accuracy were similar to those reported (0.44 and 0.50) by Finkel and McGue (1993), who used a speed factor and a host of short-term memory tasks, but the genetic correlations between DR accuracy and IQ were lower than those observed in studies where a general memory factor was used (e.g., Cardon and Fulker, 1994), due in part to their low phenotypic correlation.

The WM variable was mostly influenced by specific genes. Genes related to processing speed and IQ affected visual-spatial WM, but there were other more prominent genes determining the efficiency of this system, and these genes did not directly affect IQ. Others have also reported that specific genes have more influence on memory than do common genes (Cardon *et al.,* 1992; Finkel *et al.,* 1995b; Luo *et al.,* 1994). Engle and colleagues (1999) demonstrated via path analysis that the relationship between short term memory (the storage component of WM) and fluid intelligence was mediated entirely by the central executive (as measured by dual tasks). Given this finding one might speculate that those genes common to processing speed, WM, and IQ might actually affect the central executive component of WM, whereas those genes specific to WM relate to the storage component.

Genetic studies of memory have made little attempt to differentiate between different memory systems (e.g., short term versus long term) and subsystems (e.g., storage versus processing). In our own study, the central executive was not explicitly captured. Hence,

studies are required where a battery of WM tasks, which separate executive and storage functions of WM, are administered alongside tests of intelligence. A current study (Ando *et al.*, 2001) tests the association between spatial and verbal dual tasks and higher-order spatial and verbal cognitive ability. Results show phenotypic correlations ranging from 0.20 to 0.41 between the WM and IQ measures. Modality (spatial, verbal) specific genetic components for the storage function of WM were found, as well as genetic overlap between modalities and function (storage, executive).

A substantial part of the covariance in the CRT variables was accounted for by unique environment, which could include effects of one's physiological state which is known to influence CRT (Jensen, 1982). Nonshared environmental effects also showed a small common influence on four-choice RT and IQ. The four-choice condition was somewhat confounded because it was unpracticed and hence may have contained variation due to speed of learning, a unique environment factor influencing speed of learning (e.g., strategy use) is possible. DR accuracy was the only variable exhibiting specific unique environmental variance, and this might be associated with differences between individuals in strategies adopted. Although our point estimates indicated the presence of small common environmental (or assortative mating) effects for the cognitive measures, there was insufficient power to detect them simultaneously with additive genetic effects. The MZ and DZ twin correlation difference suggests that DR accuracy and two-choice RT (also the least reliable measures) have larger influences from common environment than the other measures. Petrill and colleagues (1996) found that common environment did affect lower order and higher order cognitive processes and its effect was general rather than specialized. However, in their study the sample ranged in age from 6 to 13 years; because the behavior genetics literature (McCartney *et al.,* 1990; McClearn *et al.,* 1997; Wilson, 1986) shows an increase in the heritability of cognition with age (and a decrease of shared environment influences), this may explain the discrepancy between our results.

In summary, the present study demonstrated that genetic factors influenced the relationship between processing speed, visual-spatial WM, and intelligence variables, with further genetic factors unique to eight-choice RT, DR accuracy, and IQ. Because this was a preliminary analysis of the pattern of genetic variation across these measures, future analyses will be directed toward a theoretical model, including IQ subtests, choice RT, inspection time, and DR task variables. It

will be interesting to test whether verbal and performance intelligence factors emerge and whether these factors (or even the IQ subtests) show differing relationships with the processing speed and WM measures. Hierarchical modeling can address the presence of genes for group factors of intelligence and their relationship to the experimental cognitive measures of choice reaction time and delayed response.

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