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Genetic Structure of Spatial and Verbal Working Memory

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Working memory (WM) encompasses both short-term memory (storage) and executive functions that play an essential role in all forms of cognition. In this study, the genetic structure of storage and executive functions engaged in both a spatial and verbal WM span task is investigated using a twin sample. The sample consists of 143 monozygotic (MZ) and 93 dizygotic (DZ) Japanese twin pairs, ages 16 to 29 years. In 155 (87 MZ, 62 DZ) of these pairs, cognitive ability scores from the Kyodai Japanese IQ test are also obtained. The phenotypic relationship between WM and cognitive ability is confirmed ($r = 0.26–0.44$). Individual differences in WM storage and executive functions are found to be significantly influenced by genes, with heritability estimates all moderately high (43%–49%), and estimates for cognitive ability comparable to previous studies (65%). A large part of the genetic variance in storage and executive functions in both spatial and verbal modalities is due to a common genetic factor that accounts for 11% to 43% of the variance. In the reduced sample, this common genetic factor accounts for 64% and 26% of the variance in spatial and verbal cognitive ability, respectively. Additional genetic variance in WM (7%–30%) is due to modality specific factors (spatial and verbal) and a storage specific factor that may be particularly important for the verbal modality. None of the variance in cognitive ability is accounted for by the modality and storage genetic factors, suggesting these may be specific to WM.

KEY WORDS: Working memory; general cognitive ability; twin study; genetic structure; spatial ability; verbal ability.

INTRODUCTION

Working memory (WM) is conceptualized as a limited capacity system for the temporary storage and processing of information (Baddeley, 1986; Baddeley and Hitch, 1974), and plays an essential role in all forms of cognition. More recently it is considered to be the central component of higher-order information processing (Engle *et al.,* 1999; Kyllonen, 1996, Miyake and Shah, 1999a). Engle *et al.*, for example, have shown that measures of WM capacity are strong predictors of IQ, particularly fluid ability. Indeed, WM is substantially correlated with reasoning ability (Carpenter *et al.,* 1990), language comprehension (Daneman and Carpenter, 1980; Daneman and Merikle, 1996), mother tongue acquisition (Baddeley *et al.,* 1998), and second language learning (Ando *et al.,* 1992). In contrast, measures of memory storage capacity that do not involve executive functioning are not strongly related to general fluid intelligence (Engle *et al.,* 1999).

One major controversy in WM research is the unitary versus non-unitary nature of WM. Although many now agree that there are multiple subsystems in WM (Miyake and Shah, 1999b), there is some emphasis of its modality-free (e.g., Cowan, 1999) or domain-free (e.g., Engle *et al.,* 1999) nature. In the original conceptualization of WM, Baddeley (1986) postulated two peripheral slave systems—the phonological loop and the visuospatial sketchpad—as well as a central executive controller. His executive function of WM is assumed to be modality free and general. However, Shah and Miyake (1996) and Friedman and Miyake (2000) recently showed that spatial and verbal WM functions are separable from each other. Spatial and verbal in-

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formation processes are a well-established dichotomy of general mental abilities, and separate genetic contributions have frequently been shown (Plomin and DeFries, 1998).

A common methodology to measure individual differences in WM is the dual task paradigm, e.g., reading span or listening span tasks, in which two different kinds of mental processes are manipulated simultaneously. For example, in the reading span task participants recall one to eight digits in addition to verifying whether or not sentences are correct (Baddeley, 1986). Despite the popularity of WM span tasks in the individual differences and cognition literature, there have been no studies that have examined whether there is a significant genetic influence on WM. Most genetic studies have assessed short-term memory using tasks such as the digit span, word recall, and picture memory tasks that require only maintenance of information and do not involve manipulation of information (i.e., transformation, calculation, integration, etc.). Heritability estimates, from twin studies, for short-term memory range from 30% to 60% (Nichols, 1978; McGue and Bouchard, 1989; Pedersen *et al.,* 1992; Finkel and McGue, 1993; 1998; Finkel *et al.*, 1995).

The present study is the first to investigate individual differences in storage and executive functions in WM, in both spatial and verbal modalities, in a genetically informative sample. Using spatial and verbal WM span tasks, we examine the phenotypic correlations and factor structure among four WM components: spatial storage (Ss), spatial executive (Se), verbal storage (Vs), and verbal executive (Ve) function. We then investigate whether there is a significant genetic and environmental contribution to WM, estimating genetic and environmental variance, and examine whether individual differences in storage and executive functions are influenced by a common genetic and/or environmental factor and whether this factor(s) is modality independent. Finally, we examine the extent to which the association between WM and cognitive ability, as measured by a Japanese intelligence test, is due to the same underlying genetic and/or environmental influences.

METHODS

Participants

The participants are 236 twin pairs (101 MZf, 41 MZm, 43 DZf, 22 DZm, 29 DZo), living in Tokyo or in neighboring prefectures of Tokyo, who were recruited through the Keio Twin Project (Ono *et al.*, 2000) for an ongoing behavioral genetics research project at Keio University, Tokyo. All are young adults, ranging from 14 to 29 years of age (mean age = 19.9, *SD* = 3.45) who accepted our invitation by letter to participate in the study. Letters were sent to approximately 2000 pairs of twins in the targeted area.

Participants attend one experimental session lasting approximately 3 h, conducted in either the morning or afternoon. The session consists of both spatial and verbal WM span tasks that take about 1 h, either cognitive ability tasks or problem-solving tasks taking about 20 min, and in addition, a personality questionnaire, a story-telling task, and the collection of a blood sample. Participants are tested in a group of 15 to 25 individuals, and several groups are tested simultaneously, with the order of tasks for each group counterbalanced. Co-twins are tested on the same day but in separate groups. Of the 236 twin pairs tested, 155 pairs (65 MZf, 25 MZm, 30 DZf, 15 DZm, 20 DZo) were administered the cognitive ability tasks, and the rest the computer-administered problem-solving tasks.

Zygosity is determined by questionnaire (Ooki *et al.*, 1991), based on a Japanese translation of Torgersen's questionnaire for zygosity diagnosis (Torgersen, 1979), which consists of three questions about the twins' physical resemblance (i.e., Were you and your twin "as alike as two peas in a pod?" Did people mistake the identity of you and your twin as children? In so, by whom were you mistaken?) with 93.2% accuracy. For twin pairs in whom zygosity is borderline, the genetic polymorphisms of the D4 dopamine receptor gene (DRD4) and the serotonin transporter gene (5-HTT) are examined, providing an accuracy for zygosity diagnosis up to 97.8%.

Working Memory Tasks

The spatial and verbal WM tasks are revised versions of the WM span tasks developed by Shah and Miyake (1996) (original versions are the rotation-arrow task and the verification-word task in their Experiment 2). In both tasks, both storage and executive functions are measured, giving four scores: two modalities by two functions (spatial-storage (Ss), spatial-executive (Se), verbal-storage (Vs), and verbal-executive (Ve). Spatial-storage capacity (Ss) and spatial executive efficacy (Se) are measured by the spatial WM task, whereas verbal-storage capacity (Vs) and verbal executive (Ve) efficacy are measured by the verbal WM task.

Spatial WM Task

The spatial WM task is illustrated in Fig. 1. In this task, the participants are presented with a set of letter-

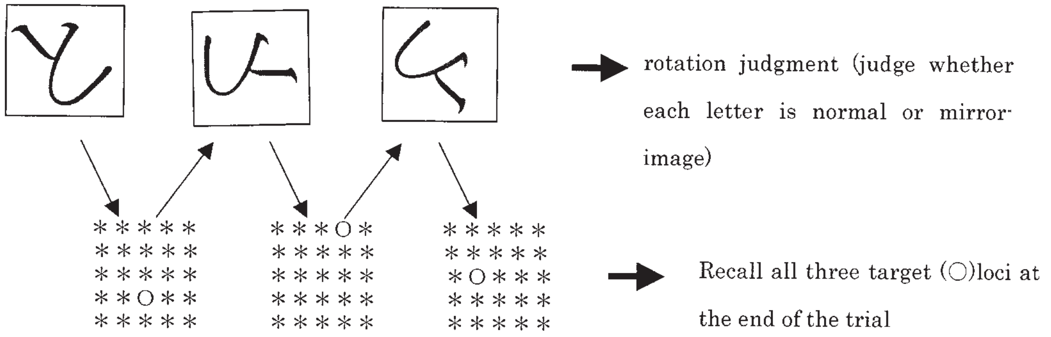

Fig. 1. An example of the Spatial WM task (Set size = 3). Set size goes from two to five items (letter-target pairs), and five trials are presented for each set size.

target pairs and are asked to judge whether a letter that has been rotated is normal or a mirror image, and subsequently to remember the location of a target (circle) which is presented in a 5 × 5 dot matrix. Five kana letters (“to”, “mo”, “u”, “yo”, and “no”) are used which are a symmetrical and cannot be confused with other similar letters when rotated. Letters are rotated either 45°, 90°, 135°, 180°, 225°, 270°, or 315°, with half normally oriented and half mirror-imaged (i.e., 5 letters × 7 rotations × 2 orientations). They are projected on a screen in front of the room and presented in a random order, which is fixed for all participants in all groups. Following presentation of a letter, participants are given approximately 1 s to mark on the answer sheet whether the letter is normally oriented (indicated by a O) or mirror-imaged (indicated by a X). The target, in a 5 × 5 matrix, is then presented on the screen for 1 s and participants are required to remember its location in the matrix. Following the presentation of either 2-, 3-,4-, or 5-letter target pairs (i.e., set size of 2 to 5 items), the locations of which target are marked on an answer sheet, for which 5 (set size of 2) to 10 (set size of 5) seconds is given. Trials are presented with increasing difficulty, with five trials presented at each level for a total of 20 trials. Prior to data collection, practice consisting of three trials at set-size 2 is given.

The total number of target locations correctly answered in the right order is designated as the spatial storage (Ss) score. Although the spatial storage score was originally defined as the highest set size for which all of the target locations are correctly recalled in at least three of five trials (Shah and Miyake, 1996), our preliminary analysis found that both scores are highly correlated ($r = 0.97$). The spatial executive (Se) efficacy score is defined as the total number of letters correctly answered. The maximum score for both Ss and Se is 70. Although it is likely that judging the orientation of a letter and the ability to recall the locations of a target requires both storage and executive functions, it is plausible that recalling the locations of a target places a greater load on storage processes than being able to recall the location of a target requires manipulation of the information stored in STM. Similarly, it is plausible that judgment of letter orientation loads more on executive functions because it requires manipulation and comparison of relevant information in-WM. Therefore, in this study, spatial storage (Ss) capacity is measured as the number of target locations remembered correctly, and the number of letters judged correctly is taken as a measure of spatial executive (Se) efficiency.

Verbal WM Task

The verbal WM task is illustrated in Fig. 2. In this task, participants listen to a set of sentence-word pairs, spoken in Japanese, and recorded and played on audio tape. The sentences (e.g., “Sugar is sweet.” “An elephant is a flower.”) are all simple sentences and the participants’ task is to judge whether a sentence, which has an equal probability of making sense or not, is correct or incorrect. Sentences are presented randomly and in a fixed order for all participants. After each sentence, 1 s is given for participants to indicate on their answer sheet whether the sentence is correct or incorrect. A single word (noun) is then presented, such as desk, umbrella etc., which participants are instructed to remember and later recall. Trials vary in difficulty from three to six sentence-word pairs and are presented with increasing difficulty, with five trials presented per level. For example, for a trial with five sentence-word pairs, after the presentation of each sentence the par-

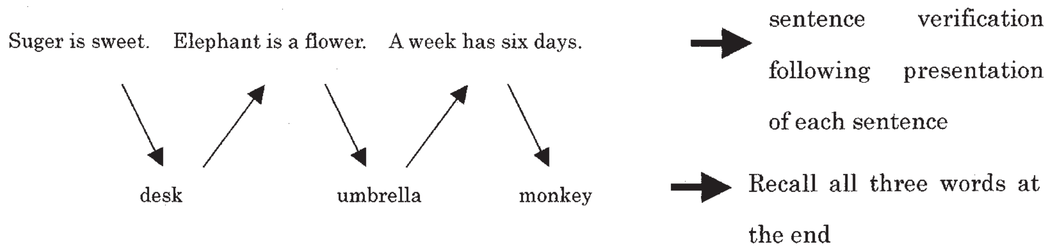

Fig. 2. An example of the Verbal WM task (Set size = 3). Set size goes from three to six items (sentence-word pairs), and five trials are presented for each set size.

ticipants indicate whether the sentence is correct or incorrect, and then, at the end of the trial, recall the five nouns and write them down on the answer sheet in the order presented. Prior to data collection, three trials with three sentence-word pairs are given as practice. The total number of words correctly answered in the right order is defined as a measure of verbal storage (Vs). Verbal executive (Ve) efficacy is defined as the total number of sentences judged correctly. The maximum score for both Vs and Ve is 90.

Cognitive Abilities

Two composite scores, a spatial cognitive ability score (SC) and verbal cognitive ability score (VC) from the Kyodai NX15 intelligence scale (a standardized intelligence test which is widely used in Japan), are used as a measure of higher order cognitive ability. The Kyodai NX15 is a paper-and-pencil task consisting of 12 sub-tests (6 verbal, 6 nonverbal) (Osaka and Umemoto, 1973) and can be administered in a group setting. The SC score consists of the sum of two nonverbal subtests: the two-dimensional mental rotation task and the paper folding task. In the two-dimensional mental rotation task, participants identify the location of the target on a square after it is rotated 90° or 180° (3 mins for 12 sub-items). In the paper folding task, the location of holes in a folded sheet of squared paper are to be identified when it is unfolded (1 min for 12 subitems). The VC score consists of the sum of two verbal sub-tests: the sentence making task, which requires words to be put in the correct order (2 mins for 12 subitems), and the verbal reasoning task, in which two blanks in a sentence have to be filled with the correct word (1.5 mins for 25 sub-items).

Statistical Analysis

Descriptive statistics such as means, *SD*, and intraclass correlation coefficients of the phenotypic scores are calculated by SPSS Ver. 10. Structural equation modeling using the statistical programs EQS (Bentler, 1995) and MX (Neale *et al.*, 1999), which use the maximum likelihood estimation technique to estimate the specified latent variable loading based on the covariance matrix, are used to estimate the genetic and environmental contributions to WM and depict its underlying structure. The fit of each model is evaluated by examining the difference in chi-squared between the full and nested model, and where models are not nested, the Akaike's Information Criterion (AIC) is used as an index of fit.

In the univariate genetic analysis, four sub-models, ACE, ADE, AE, and CE (A: additive genetic, D: dominance, C: shared environment, E: non-shared environment), are considered. If the intraclass correlation of the DZs is more than half that of the MZ pairs, shared environmental components are considered (i.e., ACE and CE model), and when the DZ correlation is less than half the MZs, dominance components are considered (ADE model).

In order to do multivariate genetic modeling, we first examine the phenotypic relationships among the WM variables. Models are fitted to MZ and DZ matrices separately, but with equal constraints on parameters. The Cholesky model is used as the base model because it assumes no underlying systematic structure. Several models based on current theories of working memory are tested: (1) a common factor model with specific test components, (2) a two-factor model comprising a spatial modality factor and a verbal modality factor plus specifics, (3) a common, two modality (spatial and verbal), and two specifics factor model, (4) a common, two modality, and a storage-specific factor model, and (5) a common, two modality, and an executive specific factor model. The phenotypic modeling of WM is then extended to include the cognitive ability variables that are available for a reduced sample (155 pairs).

The multivariate genetic models are based on the best phenotypic model, with sources of additive genetic and non-shared environmental variance parameterized. Genetic models including only the WM scores are examined first, followed by an analysis including both WM and cognitive ability scores with the smaller sample.

RESULTS

Preliminary Data Analysis

Three individuals did not take the WM tasks and data from 5 to 13 individuals who did not follow instructions correctly are excluded. The final number of individuals and matched pairs are reported in Table I. The Spatial and Verbal executive scores (Se and Ve) are negatively skewed (Se = −1.66, Ve = −2.82). Therefore, the data reported here are based on a log (base 10) transformation. Following a log transformation the skewness is .09 (Se) and .05 (Ve). All other scores (Ss, Vs, SC, and VC) are normally distributed.

No significant sex or zygosity differences in the means and *SD* for Se, Vs, SC, and VC are evident and intraclass correlations for males, females, and opposite sex pairs for the DZ groups are similar. For Ss, a significant mean difference is found between males (36.2) and females (43.5) of opposite sex twins ($t(25) = 2.24$, $p = .034$). Differences in the intraclass correlation among the three types of DZ twins for Ss (DZf = 0.06, DZm = 0.54m, DZo = −0.30) are also evident and, in addition, for Ve (DZf = 0.11, DZm = 0.46, DZo = 0.17). However, in the larger MZ groups there are no significant male-female differences in the mean, *SD,* or intraclass correlation for both Ss and Ve. Because the sample size of each zygosity group is small and the confidence intervals (CI) of the correlations are wide, male and female twin samples are combined for both zygosities in all of the following analyses.

Descriptive Statistics and Univariate Genetic Analysis

Table I shows the means, *SD,* and intraclass correlations with their 95% CI for all scores for both zygosities. There are no significant mean differences between MZ and DZ pairs. For all scores, the MZ correlation exceeds those of DZ, indicating substantial genetic contributions. For Ss, Se, and VC, the possibility of a non-additive genetic contribution is indicated because the DZ correlation is less than half the MZ correlation.

Table II shows the fitness statistics (chi-squared tests and AICs) for the univariate model fitting. For the spatial cognitive ability score, SC, dropping C from the ACE model results in a nonsignificant change in chi-squared, whereas dropping A from the model results in a significantly worse fit, confirming a significant genetic influence. For the verbal WM scores, Vs and Ve, dropping A or C from the ACE model results in a nonsignificant change in chi-squared, indicating that either or both could be the cause of the familial correlation. For Ss, Se, and VC, an ADE model is fitted; dropping D from the model results in a nonsignificant change in chi-squared, indicating the importance of additive over non-additive genetic factors. The last three columns of Table II show the heritability estimates under an AE model are moderate (43%–49%) for the four WM scores and high (65%) for the two cognitive ability measures.

Phenotypic Structure of WM

Table III provides the phenotypic correlation matrix across WM and cognitive ability scores. All four

Table I. Descriptive Statistics for Working Memory and Cognitive Scores

	MZ			DZ		
	Mean (*SD*)	N^a	*r* (95% CI)	Mean (*SD*)	N^a	*r* (95% CI)
Ss	39.2 (10.7)	277 (137)	0.50 (0.36–0.61)	39.7 (10.3)	178 (87)	0.04 (−0.17–0.25)
Se	63.4 (6.7)	278 (138)	0.50 (0.36–0.62)[b]	62.4 (7.2)	177 (87)	0.22 (0.02–0.41)[b]
Vs	60.7 (12.1)	285 (142)	0.45 (0.31–0.57)	59.0 (12.3)	179 (87)	0.34 (0.14–0.51)
Ve	85.9 (4.2)	283 (141)	0.44 (0.30–0.56)[b]	85.3 (4.9)	179 (86)	0.23 (0.02–0.42)[b]
SC	10.2 (3.0)	178 (87)	0.68 (0.55–0.78)	10.3 (2.7)	128 (62)	0.34 (0.11–0.55)
VC	16.2 (4.8)	176 (85)	0.66 (0.52–0.76)	15.8 (4.9)	126 (60)	0.22 (−.03–0.45)

[a] Numbers of participants (matched pairs).

[b] Correlations calculated after a log transformation.

Ss: spatial storage score of WM, Se: spatial executive score of WM, Vs: verbal storage score of WM Ve: verbal executive score of WM, SC: spatial cognitive ability score, VC: verbal cognitive ability score.

Table II. Univariate Genetic Analysis: Fit Statistics and Additive Genetic and Non-Shared Environmental Estimates (±SE)*

	ACE (*df* = 3)			ADE (*df* = 3)			AE (*df* = 4)			CE (*df* = 4)			Contributions (±SE)	
	χ^2	*p*	AIC	χ^2	*p*	AIC	χ	*p*	AIC	χ	*p*	AIC	a^2	e^2
Ss				3.26	0.35	−2.74	6.71	0.15	−1.29				0.45 (±0.08)	0.55 (±0.06)
Se				0.12	0.99	−5.88	0.15	0.99	−7.85				0.49 (±0.08)	0.51 (±0.06)
Vs	0.78	0.85	−5.22				2.06	0.73	−5.94	2.13	0.71	−5.87	0.48 (±0.08)	0.52 (±0.06)
Ve	1.93	0.59	−4.07				1.94	0.75	−6.06	5.03	0.29	−2.97	0.43 (±0.08)	0.57 (±0.07)
SC	6.90	0.08	0.90				7.25	0.13	−0.76	15.95	0.00	7.95	0.65 (±0.08)	0.35 (±0.04)
VC				1.13	0.77	−4.87	2.65	0.62	−5.35				0.65 (±0.08)	0.35 (±0.04)

*See Table I for abbreviations.

WM scores are positively correlated with each other. The spatial processes tapped by Ss, Se, and SC correlate more highly with each other than with verbal processes (*r* (Ss, Se) = .41, *r* (Ss, SC) = .44, *r* (Se, SC) = .42), and verbal processes tapped by Vs, Ve, and VC correlate more highly with each other than cross-modality correlations (*r* (Vs, Ve) = .41, *r* (Vs, VC) = .37, *r* (Ve, VC) = .35). Also indicated is a function-specific resource for storage processing, because the two storage scores (Ss and Vs) are moderately correlated (*r* (Ss, Vs) = .40). Phenotypic correlations among WM scores and higher-order cognitive ability scores are also moderately high.

Model fitting is conducted at the phenotypic level to explore the relationship among the four WM variables. The Cholesky decomposition model (Model 0 in Table IVa), which assumes no systematic underlying structure, yields a reasonably good fit to the data (AIC = 7.85). Next, a common factor model (Model 1) that assumes one common factor mediates all WM scores and a unique factor specific to each WM score is fitted (AIC = 17.89), but it has a worse fit than the Cholesky model. Model 2, which includes two independent modality-specific factors (spatial and verbal), also did not fit well (AIC = 79.25). In the next model (Model 3), the fitness worsens when both a common factor and two modality factors are included (AIC = 194.28), suggesting that there are both two modality-specific and one common factor mediating the four WM scores. Finally, in Models 4 and 5, a storage-specific factor and executive factor are added, respectively, both of which provide an identical fit to the data as the Cholesky model (Table IVa).

Table III. Phenotypic Correlations Among Working Memory [spatial storage (Ss), spatial executive (Se), verbal storage (Vs), verbal excecutive (Ve)] and Spatial and Verbal Cognitive Ability Scores (SC and VC)

	Ss	Se	Vs	Ve	SC
Se	0.41				
Vs	0.40	0.24			
Ve	0.23	0.24	0.41		
SC	0.44	0.42	0.34	0.40	
VC	0.26	0.29	0.37	0.35	0.41

All correlation coefficients are significant at 0.001 level.

To investigate whether a storage or an executive function factor is necessary, the modeling is extended to include the spatial and verbal cognitive ability scores (SC, VC) that are available for two-thirds of the sample. Table IVb shows that neither the fit of the Cholesky model nor the models that include an executive function factor fit the data well. The best-fitting model includes a common factor, two modality specific factors (i.e., spatial and verbal), plus a storage-specific factor, and six specific factors mediating test specific variance. The standardized path coefficients of this model are presented in Table V.

Genetic Structure of WM

Because the univariate results indicate the contributions of additive genetic and non-shared environmental effects are substantial, and because the sample size is small and therefore may not provide an accurate estimate of any shared environmental variance, only AE models are considered in the multivariate genetic analysis.

A genetic model based on the same underlying structure as the best phenotypic model (i.e. one com-

Table IV. Model Fitting Results of Phenotypic Factor Models Applied (A) WM (Ss, Se, Vs, Ve), and (B) WM and Cognitive Ability (SC, VC)

Model		χ^2	*df*	AIC	*p*
A	Ss, Se, Vs, Ve				
0	Cholesky decomposition (base)	12.15	10	−7.85	0.28
1	One common, 4 specifics	41.88	12	17.89	$p < .001$
2	Two modality (spatial, verbal), 4 specifics	107.25	14	79.25	$p < .001$
3	One common, 2 modality, 2 specifics	218.25	12	194.28	$p < .001$
4	One common, 2 modality, 1 storage (Ss, Vs)	12.15	10	−7.85	0.28
5	One common, 2 modality, 1 executive (Se, Ve)	12.15	10	−7.85	0.28
B	Ss, Se, Vs, Ve, SC, VC				
0	Cholesky decomposition	17.32	21	−24.68	0.69
1	One common, 2 modality, 1 storage (Ss, Vs), 1 executive (Se, Ve), 6 sp.	17.85	22	−26.15	0.72
2	One common, 2 modality, 1 executive (Se, Ve), 6 specifics	32.81	23	−13.19	0.08
3	One common, 2 modality, 1 storage (Ss, Vs), 6 specifics	17.85	23	−28.15	0.77

mon, two modality-specific and one storage-specific factor) is a saturated model and provides an identical fit to the data as the Cholesky ($\chi^2(df) = 40.21$ (52), AIC $= -63.79$). Dropping of nonsignificant paths modeling the non-shared environmental variance further improves the fit of the model ($\chi^2(df) = 42.98$ (55), AIC $= -67.02$). Fig. 3 shows the common genetic factor (Gcom) accounts for 36% and 43% of the variance in spatial WM in storage and executive functions, respectively, and in verbal WM, 11% and 13% of the variance in storage and executive function, respectively. A spatial modality genetic factor (Gs) accounts for a further 7% of the variance in both spatial storage and executive processes, with a verbal modality specific genetic factor (Gv) accounting for 9% of the variance in verbal storage and 30% in verbal executive function. The storage specific genetic factor (Gst) accounts for a further 3% of the variance in spatial storage and 28% in verbal storage. Although non-shared environmental influences are mostly component specific, some non-shared environmental mediation within modalities (Se and Se, Vs and Ve) and between storage components (Ss and Vs) are indicated.

Genetic Relationship Between WM and Higher-Order Cognitive Abilities

The genetic relationship between WM and cognitive ability factors is examined by including in the model the spatial and verbal cognitive ability scores (SC and VC). The genetic variance is based on the phenotypic model (one common genetic factor (Gcom), two modality-specific genetic factors (Gs, Gv) plus a storage-specific genetic factor (Gst), and in addition, includes two independent genetic factors specific to the cognitive ability factors (Gsc and Gvc). Non-shared environmental variance is modeled as for the AE model for WM above. The fitness ($\chi^2(df) = 102.85$ (122), AIC $= -141.15$) of the model is improved by dropping the nonsignificant loading from the genetic verbal modality factor (Gv) to VC ($\chi^2(df) = 103.52$ (123), AIC $= -142.49$). Similarly, the loading from the spatial modality genetic factor (Gs) to SC ($\chi^2(df) = 103.68$ (124), AIC $= -144.32$), and the nonsignificant path from the specific factor (Gsc) to SC ($\chi^2(df) = 104.07$ (125), AIC $= -145.92$). Finally, nonsignificant, non-shared environmental paths are dropped ($\chi^2(df) =$

Table V. Factor Loadings for the Phenotypic Factor Model of WM and Cognitive Ability

	Common	Spatial	Verbal	Storage	Specifics
WM Spatial storage (Ss)	0.39	0.58	—	0.43	0.58
WM Spatial executive (Se)	0.41	0.43	—	—	0.80
WM Verbal storage (Vs)	0.56	—	0.10	0.43	0.70
WM Verbal executive (Ve)	0.62	—	0.63	—	0.47
Spatial cognitive ability (SC)	0.62	0.37	—	—	0.69
Verbal cognitive ability (VC)	0.67	—	0.12	—	0.73

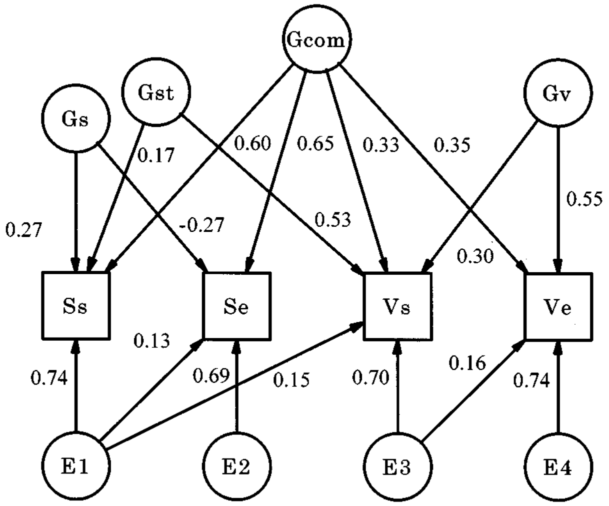

Fig. 3. Path diagram showing the reduced common (Gcom) and group (Gs, Gv, Gst) genetic and unique environmental (E1-E4) factor loadings on WM (Ss, Se, Vs, Ve).

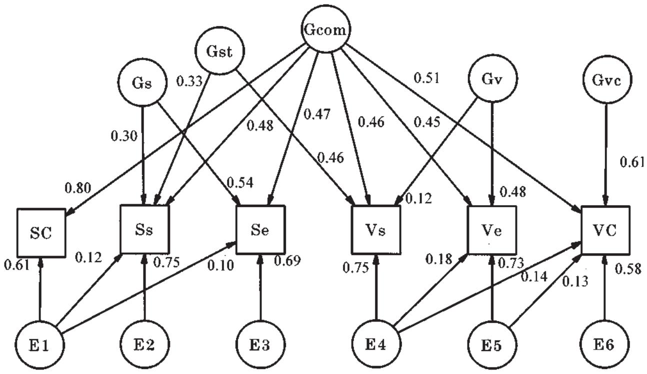

Fig. 4. Path diagram showing the reduced common (Gcom), group (Gs, Gv, Gst) and specific (Gvc) genetic factor loadings, and the unique environmental (E1-E6) factor loadings on WM (Ss, Se, Vs, Ve) and cognitive ability (SC, VC).

115.82 (132), AIC = −148.18). This model is depicted in Fig. 4. It shows the higher-order spatial and verbal cognitive abilities are mediated by a common genetic factor (Gcom) that accounts for 20% to 22% of the variance in WM, and which accounts for 64% of the variance in spatial ability and 26% in verbal ability. There is a genetic factor specific to verbal cognitive ability (Gvc), but there is no overlap with modality-specific WM factors (Gs-SC and Gv-VC). Non-shared environmental factors are modality specific and there are no significant cross-modality overlaps in environmental paths between spatial and verbal scores.

DISCUSSION

In the present study, using spatial and verbal WM tasks that are commonly used in cognitive psychology to engage both storage and executive functions, the genetic influence on WM in a Japanese twin sample is investigated. This is the first study to examine the heritability of WM using a WM span task and to investigate whether the relationship between WM and cognitive ability found in previous studies (Turner and Engle, 1989; Shah and Miyake, 1996) is due to a common genetic factor(s). It is also the first to examine the heritability of the Japanese cognitive ability tests.

Results from the univariate genetic analyses indicate that for both WM and cognitive ability, the contributions of additive genetic and non-shared environmental effects are substantial. A possible non-additive genetic contribution on Ss, Se, and VC, and shared environmental contribution on Vs and Ve is indicated, but this is probably to be due to the relatively small sample size. Heritability estimates for each of the four WM scores are moderate (43%–49%) and are comparable to those previously reported for measures of short-term memory (Nichols, 1978; McGue and Bouchard, 1989; Pedersen *et al.,* 1992; Finkel and McGue, 1993, 1998; Finkel *et al.,* 1995). The heritability estimates for both spatial and verbal cognitive ability are high (65%) and similar to those previously reported in the literature (Bouchard and McGue, 1981; Loehlin, 1989; Chipuer *et al.,* 1990; Plomin *et al.,* 2000).

Multivariate analysis to examine the relationships between the four WM variables (Ss, Se, Vs, Ve) at the phenotypic level shows the WM structure comprises one common factor, two modality factors (spatial and verbal), and a storage specific factor. Although it was not possible to differentiate between the Cholesky and a common and two modality-specific factor model with either a storage or executive specific factor, when spatial and verbal cognitive ability are included the best-fitting model is one that includes a common and two-modality factors plus a storage specific factor. This suggests that there may be a modality-specific WM resource underlying spatial and verbal processing and supports the multi-source view of WM (Shah and Miyake, 1996; Freidman and Miyake, 2000), which separates WM into verbal and spatial sources, in addition to an overlap between them.

Extending this model to the genetic level, we found a similar WM factor structure comprising four genetic factors: one common, two modality-specific (spatial and verbal), and a storage-specific factor. The common genetic factor not only explains a large proportion (11%–43%) of the variance in WM, but also that modality-specific and storage-specific genetic factors also explain a substantial amount (7%–30%) of the variance. This suggests that multiple genetic factors influence spatial and verbal WM processes. This may be similar to the hierarchical model of cognitive ability in which genes influence top-down as well as bottom-up processes (Alarcon *et al.*, 1998; Cardon and Fulker, 1993; Plomin *et al.*, 2000). Moreover, recent findings in neuroimaging studies indicate that although the prefrontal cortex plays an important role in WM, there are also modality-specific regions in the brain that dynamically work together as a whole (e.g., spatial processing may be dominant in the right parietal lobe; Courtney *et al.*, 1996), verbal processing may be dominant in the left temporal or Wernicke's region (Rep *et al.*, 1996). Thus, it is reasonable to hypothesize that in different parts of the brain different information processes may be mediated by separate genetic influences.

When the higher-order cognitive ability scores are included in the analysis, we find that the common genetic factor explains a substantial amount of overlap between the cognitive ability scores and WM parameters and accounts for 64% of the genetic variance in SC and 26% of the variance in VC. There are also nonshared environmental overlaps among the cognitive and WM variables, although the covariances explained are less ($<13\%$), indicating that it is the genetic influence rather than the environmental influence that contributes to the high phenotypic correlation between WM and higher order cognitive abilities reported in the literature (Turner and Engle, 1989; Carpenter *et al.*, 1990; Shah and Miyake, 1996; Engle *et al.*, 1999). The finding of no influence of modality specific genetic factors on the cognitive ability scores suggests that these genetic factors may be specific to WM.

What is this common genetic component? It is well known that the more complex a cognitive task becomes, the more performance is *g*-loaded. Therefore, one possible interpretation of the common genetic factor influencing WM and cognitive ability is that it corresponds to a core function of *g*, or more specifically, the central executive function free from modality constraints. Miyake and colleagues suggested that maintenance of information might be an essential function for appropriate execution and that the central executive includes various functions like switching attention, active inhibition, monitoring and updating of the content, etc. (Miyake and Shah, 1999b; Miyake *et al.*, 2000). The finding that a storage-specific genetic component is identified, whereas no executive-specific factor is found may also support this view. The executive functions of both spatial and verbal WM are explained only by a common genetic factor that might tap the executive function of general cognitive ability.

In the present study, executive efficacy is operationally defined as the scores of rotation/sentence judgement tasks and maintenance capacity is defined as the span score of location/word memory tasks. However, our measures of storage and executive function in this study are limited because both tasks in each modality involve to some extent both storage and executive processing. The separation of these two functions is still unresolved and has recently been raised (Miyake and Shah, 1999b). In future studies, it may be necessary to focus on executive processes such as active inhibition or controlled attention (Engle *et al.*, 1999), which is hypothesized to be domain-free, to shed further light on the genetic relationship between *g* and WM.

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