

Decoding the Neuroanatomical Basis of Reading Ability: A Multivoxel Morphometric Study

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As a relatively recent cultural invention in human evolution, reading is an important gateway to personal development and socioeconomic success. Despite the well documented individual differences in reading ability, its neuroanatomical correlates have not been well understood, largely due to the fact that reading is a complex skill that consists of multiple components. Using a large sample of 416 college students and 7 reading tasks, the present study successfully identified three uncorrelated components of reading ability: phonological decoding, form-sound association, and naming speed. We then tried to predict individuals' scores in these components from their gray matter volume (GMV) on a subset of participants ($N = 253$) with high-quality structural images, adopting a multivariate support vector regression analysis with tenfold cross-validation. Our results revealed distinct neural regions that supported different aspects of reading ability: whereas phonological decoding was associated with the GMV in the left superior parietal lobe extending to the supramarginal gyrus, form-sound association was predicted by the GMV in the hippocampus and cerebellum. Naming speed was associated with GMV in distributed brain regions in the occipital, temporal, parietal, and frontal cortices. Phonological decoding and form-sound association were uncorrelated with general cognitive abilities. However, naming speed was correlated with intelligence and processing speed, and some of the regions that were predictive of naming speed also predicted these general cognitive abilities. These results provide further insights on the cognitive and neural architecture of reading and the structural basis of individual differences in reading abilities.

Introduction

Reading is an integral part of life in today's information-driven society. Probably due to the lack of a specialized "module" for reading in the relatively short history of evolution, years of formal education and training are generally required to achieve fluent reading, during which existing neural systems are recycled and gradually optimized to process written materials (Schlaggar et al., 2002; McCandliss et al., 2003; Xue et al., 2006a; Dehaene and Cohen, 2007; Schlaggar and McCandliss, 2007; Xue and Pol-drack, 2007; Carreiras et al., 2009; Brem et al., 2010; Dehaene et al., 2010). Probably for the same reason, a wide spectrum of individual differences in learning to read have been well documented, ranging from fast readers to those with reading difficulties (e.g., dyslexia).

Both functional and anatomical imaging techniques have been used to examine the neural architecture of reading and the neural basis of individual differences (Price, 2012). The overlap

in brain regions identified by both methods suggests a link between regional brain morphology and function (Hoeft et al., 2007; Linkersdörfer et al., 2012). Compared with functional imaging, the anatomical approach requires less participant cooperation, and is most cost-effective and less contaminated by performance differences, providing an ideal tool for a large-scale study of participants with various ages and reading abilities. This method has been widely used to examine the neural basis of reading difficulties (Vinckenbosch et al., 2005; Hoeft et al., 2007; Frye et al., 2010; Welcome et al., 2011; Richlan et al., 2013), and also the neural basis of individual differences in reading ability among typical adults (Blackmon et al., 2010, 2011; Zhang et al., 2013).

As most of these studies used a single reading task (or several reading tasks but analyzed them separately) and relatively small sample sizes, a comprehensive and reliable picture might be hard to achieve for two major reasons. First, reading is a complex skill involving different processes. At least three critical components/processes of reading ability, namely, phonological decoding, form-sound association, and naming speed, have been identified in behavioral studies (Hoover and Gough, 1990; Joshi and Aaron, 2000). At the neural level, distributed brain regions are involved in even very simple reading tasks (Fiez and Petersen, 1998; Price, 2012). Because reading ability involves multiple subcomponents and multiple brain regions, it may not be possible to use a single reading task (even a comprehensive one) to dissociate the subsystems that contribute to all aspects of the variances in reading ability. Second, the correlational approach with small sample

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sizes generally over-fits the data and is thus vulnerable to noise (Vul et al., 2009; Cohen et al., 2011).

To address these issues, the present study used several reading tasks and a factor analysis on a large sample ($N = 416$) to identify uncorrelated/orthogonal components of reading ability. A multivariable support vector regression analysis with tenfold cross-validation was then used to provide a predictive decoding of individuals' reading performance from their gray matter volume (GMV).

Materials and Methods

Participants. Four-hundred and sixteen (187 males, 229 females) healthy Han Chinese college students (18–24 years old, mean age = 21.5 years, $SD = 0.98$) were recruited. All of them learned English as a second language for >9 years. They have normal or corrected-to-normal vision and have no history of psychiatric or neurological disease and were strongly right-handed as judged by Snyder and Harris's handedness inventory (Snyder and Harris, 1993). Two-hundred and fifty-three (150 females) of them finished one high-resolution structural MRI scan. An additional 12 participants were tested but excluded from analysis due to missing data in one or more reading tests caused by technical errors. Written consent approved by Institutional Review Board of Beijing Normal University was obtained from each participant after a full explanation of the study purpose and procedure.

Behavioral tasks. Participants were asked to complete seven reading tasks. (1) The *Visual-Auditory Learning* test (in English), adopted from Woodcock Reading Mastery Test-Revised form G (Woodcock, 1997). It assesses the ability to form associations between visual stimuli (nonlanguage symbols) and oral responses. Participants learned 26 symbols and their names, as well as two symbols for word endings (-ing, -s), and then read them in sentence form across seven brief test stories. Participants must respond within 5 s to each symbol. The final score was the number of correct responses of 134 total items. (2) The *Sight Word Efficiency* test (Forms A and B), adopted from the Test of Word Reading Efficiency (TOWRE; Torgesen et al., 1999), which assesses the number of printed words (104 words in each form) that can be accurately read within 45 s. (3) The *Phonetic Decoding Efficiency* test (Forms A and B), adopted from TOWRE (Torgesen et al., 1999) and indexed by the number of pronounceable printed nonwords (i.e., pseudowords, 104 items in each form) that can be accurately decoded within 45 s. (4) The Chinese *Rapid Color Naming* test, and (5) the Chinese *Rapid Object Naming* test. Both were adopted from the Comprehensive Test of Phonology Processing (Wagner et al., 1999). Participants were asked to name colors (black, green, blue, red, brown, and yellow) or objects (boat, star, pencil, chair, fish, and key) in Chinese as fast as they could. For each subtest, 72 items were arranged in two arrays on separate pages, each including four rows of nine items, and the performance was determined by adding the total number of seconds to complete both arrays. (6) The *Chinese Sight Word Efficiency* test, modified from the *English Sight Word Efficiency* test. The 104 high-frequency items in this test were selected from a Chinese character psycholinguistic norm (Liu et al., 2007). (7) The *Chinese Vocabulary test*. Participants were asked to read 40 very low-frequency Chinese characters selected from a Chinese character psycholinguistic norm (Liu et al., 2007). The performance in this test was scored by adding the total number of characters that were correctly read.

Participants also completed several tests that measured their general cognitive capacities, including intelligence, item memory, and reaction time. More details of these tests can be found in our previous publications (He et al., 2010, 2012; Zhu et al., 2010). Briefly, intelligence was measured by the Wechsler Adult Intelligence Scale-Revised Chinese Version with six subscales (three verbal and three performance tests). The verbal section included general knowledge (tapping general information acquired from one's culture), similarities (abstract verbal reasoning), and digit span (attention and concentration). The performance section included picture completion (ability to quickly perceive visual details), symbol digit coding (visual-motor coordination and motor and mental speed), and block design (spatial perception, visual abstract processing, and problem solving). Memory capacity was measured by the Wechsler

Memory Scale using two subscales (recall and recognition). In the recall subscale, participants were asked to study 20 pictures of common objects for 90 s, and then freely recall these items right after learning. In the recognition subscale, eight items of common objects or Chinese characters were simultaneously presented for 30 s. Participants were asked to pick out the eight studied items from a total of 28 items (including eight studied and 20 similar but nonstudied items) right after presentation. The numbers of correctly recalled and recognized items were scored and then entered into a factor analysis to generate a single memory score. Reaction time (RT) was measured by three tests, namely, the simple, choice, and discrimination RT tests. In the simple RT test, participants were instructed to press the button whenever they saw the stimulus (a green or red square) on the computer screen. In the choice RT test, participants were asked to respond to the green square only. In the discrimination RT test, participants were asked to press the left button for the green square and the right button for the red square. The averaged RTs in the three tests were entered into an exploratory factor analysis to generate a single RT score.

Factor analysis of the behavioral data. Using SPSS (version 20.0), two exploratory factor analyses were performed on behavior measures: one on all the 416 participants and one on the 253 participants with high quality structural scans. Principal component analysis was used to extract components. Varimax with Kaiser Normalization was used to rotate the loading matrix, and regression was used to calculate component scores from each task.

MRI protocol. Participants underwent one scan for high-resolution structural images of the whole brain on a 3T Siemens Magnetom Trio system (Siemens) with Total imaging matrix in the Imaging Center for Brain Research, Beijing Normal University. T1-weighted 3D-Magnetization prepared rapid gradient echo (MPRAGE) protocol was acquired using the following parameters: TR/TE = 2530/3.1 ms, flip angle = 10°, FOV = 256, matrix = 256 × 256. Two-hundred and eight sagittal slices were acquired with 1 mm thickness, resulting final resolution to be 1 × 1 × 1 mm.

Structural MRI processing. Structural MRI data were analyzed with The Oxford Centre for Functional MRI of the Brain (FMRIB) Software Library voxel-based morphometry (FSL-VBM), a VBM style analysis toolbox (Good et al., 2001) implemented in FSL. Brains from the structural images were extracted, tissue-type segmented, and then aligned to the gray-matter template in the MNI152 standard space. The spatially normalized images were then averaged to create a study-specific template, to which the native gray matter images were registered again using both linear and nonlinear algorithms. The registered partial volume images were then modulated by dividing them with the Jacobian of the warp field to correct for local expansion or contraction. The modulated segmented images, which represent the GMV, were then smoothed with an isotropic Gaussian kernel with a σ of 3 mm.

Multivariate VBM analysis. The preprocessed imaging data were used to predict individual reading scores using an Epsilon-insensitive support vector regression (SVR; Drucker et al., 1997) with a linear kernel, as implemented in PyMVPA (Multivariate Pattern Analysis in Python; <http://www.pympva.org/>; Hanke et al., 2009). A searchlight procedure with a three-voxel radius (Kriegeskorte et al., 2006) was used to provide a measure of decoding accuracy in the neighborhood of each voxel. Following Jimura and Poldrack (2012), we set the ϵ parameter in the SVR to be 0.01.

A tenfold cross-validation was applied across participants to obtain estimates for each participant. The 253 participants were divided into 10 groups of 25 or 26 participants, with matched gender ratio and reading performance. Different grouping was used for each of the three reading scores. In each iteration, an SVR model was trained based on 226 or 227 participants. Once trained, this SVR model then generated a prediction for the score of the excluded 25 or 26 participants based on their imaging data. Voxelwise accuracy of SVR prediction was then calculated, defined as the Pearson's correlation coefficient between actual and predicted values of the reading scores. The same analysis was done for general cognitive abilities to confirm whether these regions were specifically predictive of reading abilities.

Permutation test of false-positive rate. We used a randomization test to estimate the distribution of classifier accuracy under the null hypothesis of no association between GMV and reading ability. For each analysis, the

Table 1. Descriptive statistics of reading and cognitive tests

	Range	Mean	SD
Visual-auditory learning	81–139	122.6	10.12
Sight word efficiency-Form A	32–95	72.2	9.28
Sight word efficiency-Form B	32–98	73.3	9.53
Phonetic decoding efficiency-Form A	0–62	42.6	8.45
Phonetic decoding efficiency-Form B	0–63	43.9	8.6
Chinese rapid color naming	21–91	49.3	9.69
Chinese rapid object naming	28–81	43.1	6.84
Chinese sight word efficiency	40–103	86.8	11.65
Chinese vocabulary	4–50	31.7	7.74
Wechsler adult intelligence scale-revised	100–147	125.7	7.8
Wechsler memory scale-recall	8–16	14.6	1.42
Wechsler memory scale-recognition	10–20	17.5	1.93
Simple RT (ms)	180.5–357.6	247.9	33.38
Choice RT (ms)	262.1–634.7	393.1	55.86
Discriminate RT (ms)	256.3–677.9	407.2	67.78

individuals' factor scores were randomly shuffled, and then the same SVR was performed. The shuffle was done within each group to make sure it did not change the gender ratio and distribution of reading performance within each group. This procedure was repeated 1000 times to generate a distribution of the association. Because a whole-brain searchlight permutation is extremely computationally intensive (>24,000 processing hours), we thus did the permutation test only on each cluster/sphere with a prediction accuracy >0.15 (approximately corresponding to an uncorrected threshold of $p = 0.01$) and a cluster size >125 voxels. As shown in Tables 4–6, the prediction accuracies in these regions were all above 95th and some were above 99th percentile of the permutation.

To test whether a brain region was specifically predictive of a given reading task, we examined whether the prediction accuracy for one reading component was significantly larger than that for another component. To do this, we first transformed the correlation coefficients to Fisher's Z and then performed t tests on the Z -scores.

Univariate analysis. Voxelwise general linear model was used to examine the direction (positive or negative) of the correlation between the GMV and behavior measures. Nonparametric permutation methods (Randomize v2.1 in FSL) were used for inference on statistic maps (Nichols and Holmes, 2002). Null distribution at each voxel was constructed using 10,000 random permutations of the data. False discovery rate (FDR) with a threshold of $p < 0.05$ was used to correct for multiple comparisons across the whole brain. The mean GMV in each significant cluster was then extracted for each individual. To compare the correlation coefficients across components, we again transformed them to Fisher's Z and then performed t tests on the Z -scores.

Results

Behavioral results

Table 1 shows the range, mean, and SD of the 11 measures generated from the seven reading tests, as well as six measures from the cognitive tests. Kaiser–Meyer–Olkin (KMO) test measure of sampling adequacy (KMO = 0.80) and Bartlett's test of sphericity [$\chi^2(36) = 1925.65, p < 0.001$] suggested that our data were suitable for factor analysis. Principal component analysis extracted three components with factor eigenvalues >1, which in total explained 73.22% of the variance.

Table 2 shows the rotated components loading matrix after Varimax rotation for each measure. The first component, with high loadings for *Sight Word Efficiency* (both Form A and Form B) and *Phonetic Decoding Efficiency* (both Form A and Form B), was thus named phonological decoding. The second component, with high loadings for *Visual-Auditory Learning* and *Chinese Vocabulary*, was thus named form-sound association. The third component was named naming speed because it had high loadings for two rapid naming tasks (*Rapid Color Naming* and *Rapid Object Naming*) and the *Chinese Sight Word Efficiency* test.

Table 2. Exploratory factor analysis of all reading tasks revealed three major components

	Phonological decoding	Form-sound association	Naming speed
Phonetic decoding efficiency-Form A	0.887		
Phonetic decoding efficiency-Form B	0.894		
Sight word efficiency-Form A	0.862		
Sight word efficiency-Form B	0.893		
Visual-auditory learning		0.864	
Chinese vocabulary		0.650	
Rapid color naming			0.829
Rapid object naming			0.829
Chinese sight word efficiency			0.540

Loadings smaller than 0.5 are not shown in this table.

Table 3. Correlations between reading components and cognitive abilities

	Phonological decoding	Form-sound association	Naming speed
IQ	−0.01	0.05	0.29**
Memory	0.06	0.09	−0.05
RT	−0.05	−0.08	−0.19**

** $p < 0.01$.

Factor analysis results were highly consistent either using the whole sample or the sample with MPRAGE scans. The factor scores generated from these two analyses were highly correlated ($r_{(253)} = 0.987, p < 0.001$ for phonological decoding; $r_{(253)} = 0.895, p < 0.001$ for form-sound association; and $r_{(253)} = 0.978, p < 0.001$ for naming speed). We used the factor results from the whole sample for subsequent analyses.

Correlation between reading abilities and general cognitive capacities

To examine whether these component scores reflect reading-specific abilities or general cognitive capacities, we computed their correlations with general intelligence, memory, and reaction time scores. As summarized in Table 3, naming speed was significantly correlated with IQ score ($r = 0.29, p < 0.001$) and reaction time ($r = -0.19, p < 0.01$), suggesting it might partially reflect some general cognitive capacities. No other correlations were significant (all $r < 0.09$, all $p > 0.07$), suggesting that phonological decoding and form-sound association might be reading-specific. Of course, the three reading components were independent of each other within the whole sample (all $r = 0$) and within the MPRAGE sample ($r < 0.07, p > 0.15$), allowing us to disentangle their neuroanatomical bases.

Multivariate results

Multivariate pattern analysis (MVPA) results suggested that phonological decoding could be successfully predicted by GMV in the left superior parietal lobe extending to the supramarginal gyrus (SPL/SMG; MNI = −30, −36, 42, prediction accuracy $r = 0.26$), posterior cingulate cortex extending to the precuneus (PCC/PreCu; MNI = −8, −52, 24, $r = 0.25$), right superior frontal gyrus (SFG; MNI = 14, 40, 54, $r = 0.18$), and right lateral occipital cortex (LOC; MNI = 26, −94, 12, $r = 0.18$). ROI analysis suggested that the correlation was positive between phonological decoding and GMV in the left SPL/SMG, right SFG, and right LOC, whereas a negative correlation was found between GMV in the left PCC/PreCu and phonological decoding. In all these four brain regions, prediction accuracy was significantly higher for phonological decoding than for other reading components or general cognitive abilities (Table 4; Fig. 1).

For form-sound association, strong predictive accuracy was found in the bilateral cerebellum (two clusters in left: MNI = −28,

Table 4. Brain regions showing significant correlations between GMV and phonological decoding in MVPA analysis

Brain Regions	L/R	No. Voxels	MNI Coordinates			Prediction Accuracy							
			x	y	z	95%	99%	D	A	S	IQ	M	RT
PCC/PreCu	L	721	−8	−52	24	0.12	0.15	0.26	0.06**	−0.06**	0.12**	0.09**	0.06**
SPL/SMG	L	422	−30	−36	42	0.13	0.17	0.25	0.07**	−0.09**	0.01**	−0.02**	0.09**
SFG	R	201	14	40	54	0.12	0.16	0.18	0.07*	0.06*	0.04*	0.03**	0.09 ^a
LOC	R	174	26	−94	12	0.13	0.17	0.18	0.03**	−0.07**	0.08*	−0.07**	−0.08**

D, Phonological decoding; A, form-sound association; S, naming speed; M, memory ability; RT, reaction time; PCC, posterior cingulate cortex; PreCu, precuneus; SPL, superior parietal lobe; SMG, supramarginal gyrus; SFG, superior frontal gyrus; LOC, lateral occipital cortex.

** $p < 0.01$, * $p < 0.05$, ^a $p < 0.10$. Significance denotes test of prediction accuracy difference between phonological decoding and other two reading components as well as measures of cognitive abilities.

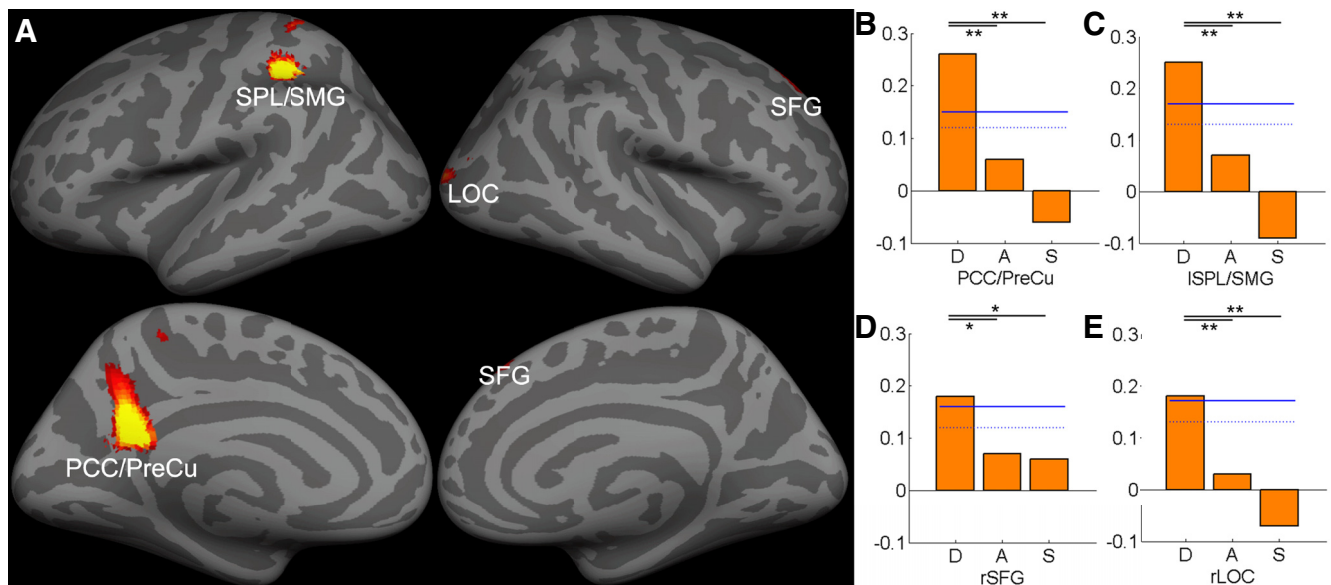


Figure 1. *A*, MVPA revealed significant correlations between GMV and phonological decoding. The multivariate SVR decoding accuracy was mapped onto the inflated gray matter surface using FreeSurfer (<http://surfer.nmr.mgh.harvard.edu/>). The bar graphs show the prediction accuracy in *B*, PCC/PreCu, *C*, left SPL/SMG, *D*, right SFG, and *E*, right LOC. The dotted and solid blue lines represent the 95th and 99th percentile of the distribution of the permutation results, respectively (* $p < 0.05$; ** $p < 0.01$). D, Phonological decoding; A, form-sound association; S, naming speed. See Table 4 for ROI abbreviations.

Table 5. Brain regions showing significant correlations between GMV and form-sound association in MVPA analysis

Brain Regions	L/R	No. Voxels	MNI Coordinates			Prediction Accuracy							
			x	y	Z	95%	99%	D	A	S	IQ	M	RT
Cerebellum	L	1354	−28	−86	−40	0.13	0.17	0.06**	0.23	0.08**	0.04**	0.06**	−0.09**
Hipp	R	486	28	−30	−6	0.13	0.17	0.01**	0.19	−0.02**	−0.01**	0.08*	0.05*
Cerebellum	R	436	36	−60	−44	0.12	0.16	−0.09**	0.22	0.07**	−0.01**	0.04**	0.03**
Hipp	L	332	−24	−30	4	0.12	0.17	−0.03**	0.21	−0.07**	−0.06**	−0.09**	0.05**
SFG	L	295	−4	38	48	0.13	0.17	0.09*	0.22	0.03**	0.08**	0.10*	0.05**
MTG	L	292	−66	−16	−30	0.13	0.16	0.04**	0.18	0.07*	−0.003**	0.10 ^a	−0.06**
STG	R	196	50	−24	2	0.12	0.17	0.01**	0.22	0.06**	0.08**	−0.03**	−0.03**
Cerebellum	L	157	−48	−58	−50	0.12	0.15	−0.03**	0.19	0.09*	−0.04**	0.07*	0.05**
LOC	L	142	−36	−64	2	0.12	0.17	0.08*	0.18	−0.07**	−0.04**	0.06*	0.01**

D, Phonological decoding; A, form-sound association; S, naming speed; M, memory ability; RT, reaction time; Hipp, hippocampus; SFG, superior frontal gyrus; MTG/STG, middle/superior temporal gyrus; LOC, lateral occipital cortex.

** $p < 0.01$, * $p < 0.05$, ^a $p < 0.10$. Significance denotes test of prediction accuracy difference between form-sound association and other two reading components as well as measures of cognitive abilities.

−86, −40, $r = 0.23$, MNI = −48, −58, −50, $r = 0.19$; right: MNI = 36, −60, −44, $r = 0.22$), bilateral hippocampus (Hipp; left: MNI = −24, −30, 4, $r = 0.21$; right: MNI = 28, −30, −6, $r = 0.19$), left SFG (MNI = −4, 38, 48, $r = 0.22$), left MTG (MNI = −66, −16, −30, $r = 0.18$), right STG (MNI = 50, −24, 2, $r = 0.22$), and left LOC (MNI = −36, −64, 2, $r = 0.18$). All correlations were positive. Prediction accuracy was significantly higher for form-sound association than for other reading components and general cognitive abilities (Table 5; Fig. 2).

In contrast, naming speed could be predicted by the GMV in a distributed occipital-temporal-parietal-frontal regions, includ-

ing the bilateral LOC/PreCu (MNI = −12, −70, 34, $r = 0.23$), right inferior/middle temporal gyrus (ITG/MTG; MNI = 56, −62, 24, $r = 0.23$), left superior temporal gyrus/angular gyrus (STG/AG; MNI = −62, −30, 12, $r = 0.21$), right insular cortex (Ins; MNI = 44, 12, −4, $r = 0.23$), right temporal-parietal junction (TPJ; MNI = 56, −38, 18, $r = 0.22$), right superior/middle frontal gyrus (SFG/MFG; MNI = 16, 16, 68, $r = 0.18$), left STG (MNI = −60, −8, 0, $r = 0.20$), left PCC (MNI = −12, −40, 4, $r = 0.20$), right MFG (MNI = 36, 4, 40, $r = 0.23$), left ACC (MNI = −12, 38, 30, $r = 0.24$), and left ventromedial prefrontal cortex (VMPFC; MNI = −4, 56, −12, $r = 0.17$). Correlational

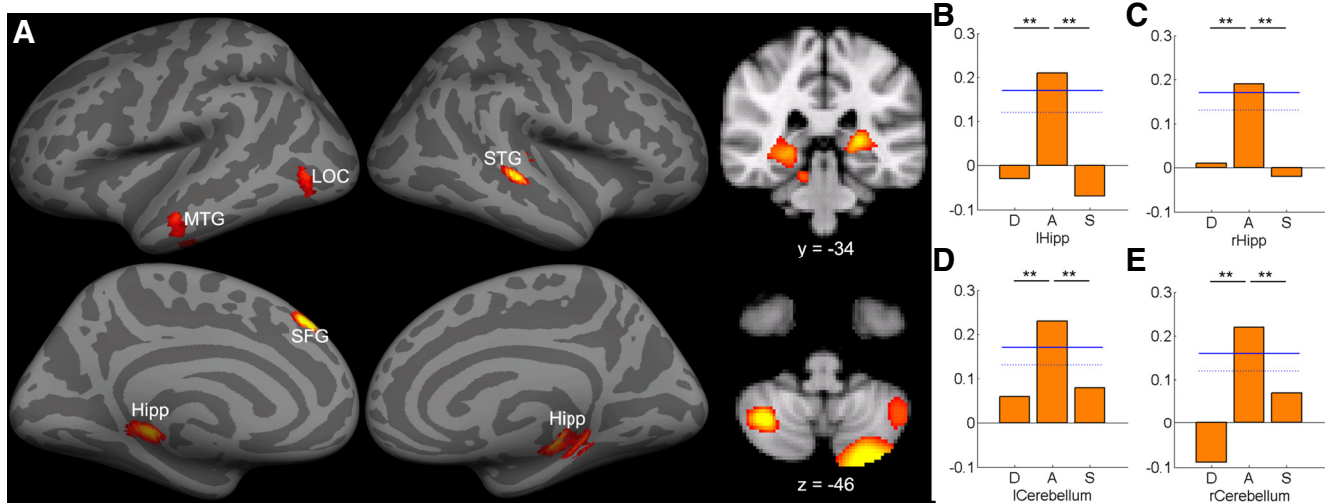


Figure 2. A, MVPA revealed significant correlations between GMV and form-sound association mapped onto the inflated gray matter surface as well as in coronal and axial slice. The bar graphs show the prediction accuracy in four example ROIs, including (B) left hippocampus, (C) right hippocampus, (D) left cerebellum, and (E) right cerebellum. Permutation-based 95th percentile (dotted blue line) and 99th percentile (solid blue line) prediction accuracies are also shown (***p* < 0.01). Images are reversed left to right to follow radiologic convention. See Table 5 for ROI abbreviations.

Table 6. Brain regions showing significant correlations between GMV and naming speed in MVPA analysis

Brain Regions	L/R	No. Voxels	MNI Coordinates			95%		99%		Prediction Accuracy				
			<i>x</i>	<i>y</i>	<i>z</i>	D	A	S	IQ	M	RT			
LOC/PreCu	L/R	1276	-12	-70	34	0.12	0.17	0.02**	0.01**	0.23	0.11*	-0.02**	-0.01**	
ITG/MTG	R	999	56	-62	-24	0.13	0.17	0.02**	-0.05**	0.23	0.11*	0.08**	-0.06**	
STG/AG	L	875	-62	-30	12	0.13	0.17	-0.03**	0.03**	0.21	0.06**	0.01**	0.06**	
Ins	R	626	44	12	-4	0.13	0.17	-0.02**	0.02**	0.23	0.03**	0.06**	-0.03**	
TPJ	R	352	56	-38	18	0.12	0.16	0.04**	0.03**	0.22	0.07**	-0.07**	0.08**	
SFG/MFG	R	340	16	16	68	0.12	0.16	-0.04**	-0.08**	0.18	0.11 ^{ns}	0.09 ^a	0.08*	
STG	L	303	-60	-8	0	0.13	0.16	-0.07**	-0.01**	0.20	0.09*	0.04**	-0.03**	
PCC	L	263	-12	-40	4	0.14	0.18	0.002**	-0.01**	0.20	0.02**	-0.05**	0.12 ^a	
MFG	R	199	36	4	40	0.12	0.17	0.03**	0.06**	0.22	0.01**	0.07**	0.13 ^a	
ACC	L	176	-12	38	30	0.12	0.16	-0.04**	-0.08**	0.24	0.10*	0.02**	0.005**	
VMPFC	L	176	-4	56	-12	0.13	0.16	-0.001**	0.04*	0.17	0.15 ^{ns}	-0.09**	0.13 ^{ns}	

D, Phonological decoding; A, form-sound association; S, naming speed; M, memory ability; RT, reaction time; LOC, lateral occipital cortex; PreCu, precuneus; ITG/MTG/STG, inferior/middle/superior temporal gyrus; AG, angular gyrus; Ins, insula; TPJ, temporal-parietal junction; SFG/MFG, superior/middle frontal gyrus; PCC, posterior cingulate cortex; ACC, anterior cingulate cortex; VMPFC, ventromedial prefrontal cortex.

***p* < 0.01, **p* < 0.05, ^a*p* < 0.10, ^{ns}*p* > 0.10. Significance denotes test of prediction accuracy difference between naming speed and other two reading components as well as measures of cognitive abilities.

analysis suggested that all correlations were positive. In all these regions, prediction accuracy was significantly higher for naming speed than for phonological decoding or form-sound association (Table 6; Fig. 3).

Consistent with the results that naming speed was significantly correlated with IQ and reaction time, some of these regions that could predict naming speed could also (marginally) significantly predict general IQ (right SFG/MFG and left VMPFC) and reaction time (left PCC, right MFG and left VMPFC; Table 6).

Univariate results

Table 7 summarizes findings on brain regions that showed positive or negative correlations between GMV and the three components of reading abilities in univariate VBM analysis. In particular, phonological decoding was positively correlated with GMV in the left SPL/SMG (Fig. 4A; Table 7; MNI = -30, -38, 42, *Z* = 4.35), but negatively correlated with GMV in the left PCC/PreCu (MNI = -6, -52, 24, *Z* = 4.43). The GMV in these two regions was more highly correlated with phonological decoding than with naming speed (both *Z* > 2.90, *p* < 0.01) or form-sound association (both *Z* > 2.21, *p* < 0.05).

Form-sound association was positively correlated with GMV in the bilateral hippocampus (Fig. 4B; Table 7; left: MNI = -28, -32, -6, *Z* = 3.98; right: MNI = 24, -36, 4, *Z* = 4.39), right SFG

(MNI = 4, 36, 48, *Z* = 4.20), and left AG (MNI = -56, -50, 20, *Z* = 3.94). No negative correlation was found between GMV and form-sound association. The GMV in these regions was more highly correlated with form-sound association than with phonological decoding (all *Z* > 1.72, *p* < 0.05) or naming speed (all *Z* > 1.83, *p* < 0.05).

Naming speed was positively correlated with GMV in several brain regions (Fig. 4C; Table 7), including the right insular cortex (MNI = 44, 12, -6, *Z* = 4.12), right TPJ (MNI = 56, -38, 16, *Z* = 3.73), right MFG (MNI = 36, 6, 38, *Z* = 3.60), left ACC (MNI = -8, 40, 28, *Z* = 4.36), and left PCC/PreCu (MNI = -10, -66, 34, *Z* = 3.80), whereas no brain regions showed negative correlation between GMV and naming speed. The GMV in these regions was more highly correlated with naming speed than with phonological decoding (all *Z* > 2.05, *p* < 0.05) or form-sound association (all *Z* > 1.72, *p* < 0.05).

Discussion

Although a multicomponential view of reading ability has been widely accepted in cognitive research of reading and reading difficulties (e.g., dyslexia, Norton and Wolf, 2012), few studies have examined the neuroanatomic basis of these components. To fill this gap, the present study administered several reading tasks to a

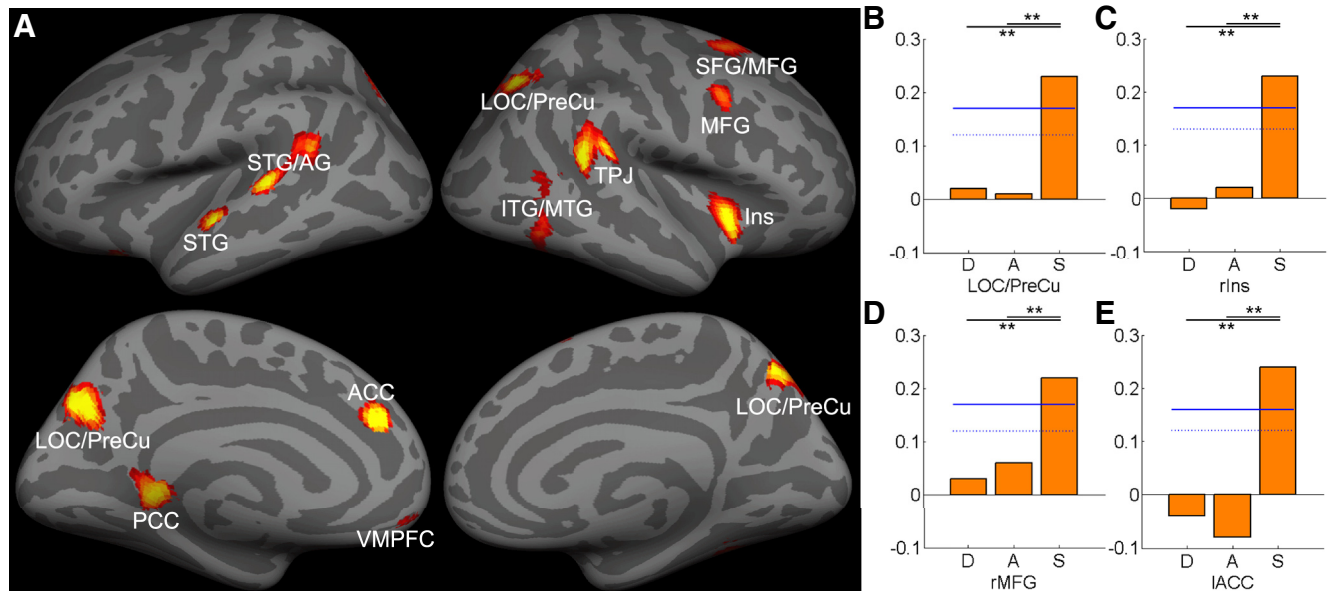


Figure 3. *A*, MVPA revealed significant correlations between GMV and naming speed mapped onto the inflated gray matter surface. The bar graphs show the prediction accuracy in four ROIs, including (*B*) LOC/PreCu, (*C*) right insula, (*D*) right MFG, and (*E*) left ACC. Permutation-based 95th percentile (dotted blue line) and 99th percentile (solid blue line) prediction accuracies are also shown (** $p < 0.01$). See Table 6 for ROI abbreviations.

Table 7. Brain regions showing significant correlations between GMV and reading abilities in univariate VBM analysis

	Brain Regions	L/R	No. Voxels	MNI Coordinates			Z	Person's <i>r</i>		
				<i>x</i>	<i>y</i>	<i>z</i>		D	A	S
Phonological decoding										
Positive	SPL/SMG	L	45	−30	−38	42	4.35	0.24	−0.10	−0.01
Negative	PCC/PreCu	L	193	−6	−52	24	4.43	−0.28	−0.09	−0.02
Form-sound association										
Positive	Hipp	R	40	24	−36	4	4.39	−0.02	0.25	−0.06
	SFG	R	75	4	36	48	4.20	0.08	0.23	0.06
	Hipp	L	104	−28	−32	−6	3.98	0.07	0.23	0.003
	AG	L	34	−56	−50	20	3.94	−0.08	0.23	0.07
Negative	NONE									
Naming speed										
Positive	Ins	R	69	44	12	−6	4.12	0.03	0.04	0.24
	TPJ	R	33	56	−38	16	3.73	−0.04	0.02	0.22
	MFG	R	33	36	6	38	3.60	0.04	0.02	0.22
	ACC	L	54	−8	40	28	4.36	−0.01	−0.01	0.26
	PCC/PreCu	L	52	−10	−66	34	3.80	−0.03	0.01	0.23
Negative	NONE									

SPL, Superior parietal lobe; SMG, supramarginal gyrus; PCC, posterior cingulate cortex; PreCu, precuneus; Hipp, hippocampus; M/SFG, middle/superior frontal gyrus; AG, angular gyrus; Ins, insula; TPJ, temporal-parietal junction; ACC, anterior cingulate cortex.

large sample of participants and identified three uncorrelated components of reading ability: phonological decoding, form-sound association, and naming speed. Using a multivariate predictive decoding method, we found that the GMV in distinct neural regions were correlated with the three components of reading ability.

Phonological decoding refers to the procedure of extracting phonology from printed words, which is a critical component in early reading development (Hamada and Koda, 2008) and a reliable predictor of reading success (Wagner et al., 1994). Growing literature has posited the left SMG in phonological decoding. For example, neuroimaging studies have consistently revealed SMG activation during phonological processing of written words, especially pseudowords, when the application of grapheme-to-phoneme correspondence is required (Tan et al., 2005; Richlan et al., 2009). Transcranial magnetic stimulation applied over the SMG could selectively disrupt phonological decoding (Hartwig-

sen et al., 2010). Not only were subjects with dyslexia found to show functional and structural impairment in this region (Richlan et al., 2009), the functional (Welcome and Joanisse, 2012) and anatomical (Lee et al., 2007; Goldman and Manis, 2013) variations in this region could also account for individual differences in reading performance among typical readers.

The brain region whose GMV was correlated with phonological decoding in the present study was located in the SPL that extended to the SMG. As participants in the current study were native Chinese speakers who were learning English as a second language, our result might reflect cultural differences in reading and the role of native language experiences in shaping the neural substrates of second language reading (Tan et al., 2003; Chen et al., 2009). Chinese and English, based on two different writing systems, rely on partially distinct neural substrates (Tan et al., 2005; Chen et al., 2009). Specifically, Chinese is a logographic writing system in which each character maps on a morpheme,

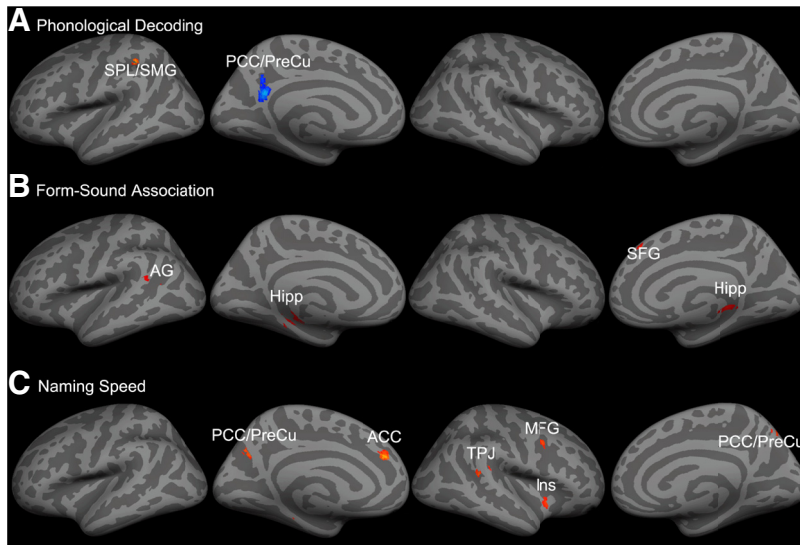


Figure 4. *A*, Univariate VBM results showed significant correlations between GMV and phonological decoding mapped onto gray matter surface. GMV in left SPL/SMG (in red) was positively correlated with phonological decoding, whereas GMV in left PCC/PreCu (in blue) was negatively correlated with phonological decoding. *B*, Univariate VBM results showed significant correlations between GMV and form-sound association mapped onto gray matter surface. GMV in bilateral hippocampus, left AG and right SFG were positively correlated with form-sound association. *C*, Univariate VBM results showed significant correlations between GMV and naming speed mapped onto gray matter surface. GMV in the PCC/PreCu, left ACC, right TPJ, right MFG and right insula were positively correlated with naming speed. See Table 7 for abbreviations.

and the sublexical reading or grapheme-phoneme correspondence rule is impossible. As a result, Chinese reading relies more on the SPL than the SMG (Tan et al., 2005). Furthermore, native language experience may shape the neural strategy of second language learning such that the SPL showed strong activation when Chinese readers were reading English (Tan et al., 2003). Our structure–function correlation results are consistent with this observation.

Form-sound association refers to the ability to make connections between a new morpheme and sound, thus is critical to both learning and reading (Manis et al., 1987). Not surprisingly, the regions that are predictive of this ability, particularly the hippocampus, have been consistently implicated in language learning and general memory tasks. For example, the hippocampus has also been implicated in learning new lexicons (Breitenstein et al., 2005; Davis et al., 2009), and the integrity of the hippocampus and surrounding white matter is correlated with language training success in aphasia (Meinzer et al., 2010). On the other hand, studies on patients with hippocampal lesions (e.g., patient HM Corkin, 2002) and neuroimaging studies on healthy participants (Schacter and Wagner, 1999; Eldridge et al., 2000; Greicius et al., 2002; Zeineh et al., 2003) have all emphasized the role of the hippocampus in memory encoding and retrieval. These observations are quite consistent with the idea that the declarative memory system supported by the medial temporal cortex plays an important role in lexicons (Ullman, 2004). The low prediction accuracy between the hippocampus GMV and item memory is also consistent with the finding that the hippocampus is particularly important for associative memory rather than for item memory (Eichenbaum, 2004; Giovanello et al., 2004; Mayes et al., 2007).

Although rapid automatized naming (RAN) has been found to predict reading across a large life span, its neural correlates have been poorly understood (Norton and Wolf, 2012). The only published study found a distributed brain region, including the

inferior frontal cortex, temporoparietal junction, and the ventral visual stream, for rapid naming of letters and objects (Misra et al., 2004). RAN performance was correlated with activation in several frontal and temporal regions during an implicit reading task (Turkeltaub et al., 2003) and the brain volume in the cerebellum and pars triangularis (Eckert et al., 2003). Our results are in general agreement with these observations by revealing that the GMV in a distributed neural network could predict naming speed.

More interestingly, our results suggest that naming speed is associated with general intelligence and reaction time, which is consistent with the tight relationship between reaction time and intelligence (Jensen and Munro, 1979; Fry and Hale, 2000). Although a close examination of the anatomical basis of processing speed and intelligence is beyond the scope of this study, we did find that some of the regions that were predictive of naming speed also predicted intelligence and processing speed. Consistently, functional MRI studies have suggested that a distributed brain network subserves processing speed, including the prefrontal, occipital, temporal, and parietal cortices (for review, see Deary et al., 2010). Both white matter volume and GMV in those regions were also associated with processing speed (Kochunov et al., 2010); age-related processing speed decline was associated with decreased gray matter density in the prefrontal regions, temporal lobe, and posterior parietal cortex (Tisserand et al., 2004).

Our results provide solid evidence for multiple components of reading ability that are supported by distinct cognitive and neural mechanisms. Furthermore, these abilities are at least partially independent from general processing abilities, such as episodic memory and processing speed. This is not to say that these processes and the supporting neural structures are exclusive for reading, as there is no doubt that reading must be built upon some general cognitive functions. For example, our observation that RAN is moderately correlated with general intelligence and processing speed, and they are supported by partially overlapping neural mechanisms is consistent with many previous studies (Kail and Hall, 1994; Catts et al., 2002; Powell et al., 2007). Nevertheless, RAN made additional contribution to reading after controlling for general processing speed (Cutting and Denckla, 2001; Powell et al., 2007), suggesting that RAN builds on the existing architecture for more general speeded processing to support automatic form-sound associations (Wolf and Bowers, 1999). Similarly, the SPL/SMG and the hippocampus play many functions in addition to reading. The lack of correlation, for example, between form-sound association and memory certainly can be due to the specific memory task we chose. However, many years' experience of reading might have finely tuned these systems to meet the special requirement of reading, like applying grapheme-phoneme correspondence rule and building the word form and sound association, and thus form a special microanatomical pattern for reading (Dehaene and Cohen, 2007). By dissociating or associating reading with other general cognitive abilities, our method could potentially contribute to a deeper understanding of the nature of reading ability and reading diffi-

culties, especially when combined with methods that can identify finer functional segregations within a brain region (Fedorenko et al., 2010).

VBM is relatively fast and automated, yet sensitive to the morphological change in gray matter (Good et al., 2001). These advantages make it suitable for studies with large samples. However, as suggested by Mechelli et al. (2005), the GMV measured by VBM could be contributed by changes in neuronal size, dendritic or axonal arborization, cortical folding, or cortical thickness. How these micro anatomical changes affect behavior is barely understood. In addition, our results could not pinpoint whether the observed correlations were caused by preexisting individual differences (Xue et al., 2006b; Wong et al., 2011) or brain plasticity during language learning (Mechelli et al., 2004; Carreiras et al., 2009). Future longitudinal studies might help to address this issue (Hoeft et al., 2011).

Recently, multivariate pattern analysis has gained increasing attention in the neuroimaging field (Norman et al., 2006). Beyond categorizing objective processing and mental states, emerging studies have used this method to decode continuous variables (Dosenbach et al., 2010; Cohen et al., 2011). Direct comparison between univariate and multivariate analyses suggests that although both methods identify similar regions and the MVPA method was in general more sensitive than the univariate methods, these two methods did also capture different aspects of the data (Jimura and Poldrack, 2012). The searchlight method used in the current study aimed to provide finer structure–function associations, but did not answer the question as to how accurately one can read out an individual’s reading ability when all the anatomical data are aggregated. Our results could provide important prior knowledge to facilitate feature selection and to improve accuracy in future research.

In summary, our results suggest that reading ability consists of multiple components that are related to the anatomical structure in distinct brain regions. These results shed light on the important relationship between brain structure and function, and can be leveraged to understand individual differences among populations with typical and atypical reading development.

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