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Reading Differences and Brain: Cortical Integration of Speech and Print in Sentence Processing Varies With Reader Skill

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Functional magnetic resonance imaging (fMRI) was used to investigate the impact of literacy skills in young adults on the distribution of cerebral activity during compre-

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hension of sentences in spoken and printed form. The aim was to discover where speech and print streams merge, and whether their convergence is affected by the level of reading skill. The results from different analyses all point to the conclusion that neural integration of sentence processing across speech and print varies positively with the reader's skill. Further, they identify the inferior frontal region as the principal site of speech–print integration and a major focus of reading comprehension differences. The findings provide new evidence of the role of the inferior frontal region in supporting supramodal systems of linguistic representation.

Written and spoken language abilities are so intertwined in skilled readers that it is often of no consequence for comprehension whether a linguistic message comes by way of speech or print. It is known that accuracy of comprehension on matched reading and listening materials tends to be very strongly correlated (Palmer, MacLeod, Hunt, & Davidson, 1985). This should not blind us to the possibility that the correlation is strongly reflective of the way research participants are chosen. When the influence of input modality on language comprehension is assessed with educated adult readers, as has usually been the case, it is virtually guaranteed that the participants will have had years of literacy instruction and extensive experience with both text and spoken discourse. Clearly, functional equivalence across print–speech modes does not apply to developing readers, nor to the many adults whose literacy skills have remained poorly established.

The question of how reading experience may change functional cerebral organization is an old one. In his seminal paper of 1874 describing receptive aphasia and its anatomic basis in the temporal lobe, Wernicke surmised that lesions at the same site can have differing effects on reading performance in people of high and low literacy. Low literacy people, he claimed, cannot map print to the lexicon automatically, but instead must resort to subvocal articulatory movements to support word recognition. By engaging alternative (motor) regions, the barely literate may evade effects of posterior temporal lesion that undermine reading in the more skilled. If Wernicke's surmise has merit, it would imply more generally that in neurologically intact persons the specific neural networks used in reading will vary with the level of experience and skill. However, many decades later, the status of the question remains unclear. Only in recent years have suitable neuroimaging tools become available that permit an experimental attack. Our approach used neuroimaging tools developed in earlier studies (Braze et al., submitted; Constable et al., 2004; Ni et al., 2000) to investigate the impact of a person's literacy skills on the distribution of cerebral activity during the processing for meaning of connected material in spoken and printed form. We wished to discover where speech and print streams merge, and whether their convergence is affected by skill level.

Some things are known about reading ability that limit the search for sites reflecting skill differences and sites of convergence of speech and print streams. In the first place, because alphabetic writing is essentially a cipher on the phonologic

level of language, phonology is the point of direct contact between the orthography and the spoken language system. Therefore we can expect regions active in nonword decoding and word recognition to be strongly engaged during reading of connected material. Behaviorally, word and nonword reading are strongly correlated with reading comprehension in developing readers (Shankweiler et al., 1999). Skill differences in the distribution of cerebral activity during word-level tasks tend to appear most strongly on those that challenge phonologic processing, such as detection of rhyme (Rumsey et al., 1997b; Sandak, Mencl, Frost, & Pugh, 2004). A primary marker for specific reading disability is underactivation of left hemisphere temporoparietal and occipitotemporal regions, together with a tendency to show heightened activation of right hemisphere homologs of these regions, coupled with high levels of frontal activation bilaterally (Pugh et al., 2000; Shaywitz et al., 2002). These findings give neurobiologic underpinnings to behavioral evidence of the large role that phonologic processes play in reading ability and in distinguishing readers at different skill levels.

These findings raise the possibility that the changes in brain networks associated with gains in skill in mapping orthography to phonology may be reflected in a variety of reading behaviors, certainly in accuracy in word recognition, but also, plausibly, in comprehension of connected material. So we might expect readers who are poorly equipped in basic skills to have difficulty comprehending sentences, especially those that pose vocabulary difficulties or syntactic or pragmatic challenges (Braze, Tabor, Shankweiler, & Mencl, 2007; Shankweiler & Crain, 1986). To the best of our knowledge, only one study in the research literature has examined cortical manifestations of reading connected material in readers at different skill levels: Meyler et al. (2007) report a systematic relationship between reading ability defined by word and nonword measures and local brain activity elicited by a sentence comprehension task (pragmatic acceptability judgments), noting underactivation of three cortical regions (left middle temporal gyrus, the left postcentral gyrus, and the right inferior parietal lobule) during sentence reading by elementary school children (from grades 3 and 5) with poorly developed word-level skills. The underactivated regions overlap in part with earlier findings on dyslexic readers based on phonological and semantic word-level reading tasks (Shaywitz et al., 2002), suggesting that one or more of these regions may contribute to the development of reading comprehension ability at the sentence level.

As for the influence of print versus speech modality on brain activity, a few studies (Constable et al., 2004; Homae, Hashimoto, Nakajima, Miyashita, & Sakai, 2002; Michael, Keller, Carpenter, & Just, 2001; Spitsyna, Warren, Scott, Turkheimer, & Wise, 2006) have investigated brain activity patterns during sentence processing, comparing coordinated spoken and printed sentence materials. In Constable et al. and Michael et al., sentences in each modality activated the inferior frontal region and portions of the temporal lobes, as subjects made pragmatic acceptability judgments (Constable et al., 2004) or responded to true–false com-

prehension questions (Michael et al., 2001). Overlapping sites were found chiefly within the left hemisphere at inferior frontal gyrus, occipito-temporal, middle temporal, and superior temporal regions. In a study by Spitsyna et al. (2006), a search for sites of speech–print convergence was guided by a hypothesis stemming from Mesulam (1998) that convergence should be found in heteromodal regions of the cortex where the circuitry exists for integration of information accessed by auditory and visual input modes. (Definition of unimodal and heteromodal regions of the human cortex is based on extrapolations from physiological studies of nonhuman primates: see Geschwind, 1965; Mesulam, 1998). Spitsyna et al. report evidence of convergence during reading and listening to short narrative passages at anterior and posterior temporal regions, the fusiform gyrus, and the parieto-temporal-occipital junction, all but the first implicated in word-level research on reading differences. We note, however, that subjects in this study were not tested for comprehension of the passages. The findings do not distinguish processes specifically engaged by connected material from word-level reading processes.

A systematic attempt to separate lexical effects from sentence comprehension effects and to identify amodal processing regions in reading and listening was undertaken by Homae et al. (2002). Their subjects had to indicate whether each block of connected sentence material contained a phrase that did not match the context. Spoken and written dialogues, when compared to randomly ordered phrases, each activated portions of inferior frontal and posterior temporal lobes bilaterally. The conjunction of sentence-related activity with modality isolated a ventral portion of the left inferior frontal gyrus. Hence, this region was selectively activated by sentence processing and was modality independent.

So far, modality comparisons have been limited to relatively skilled adult readers. We are aware of no research directed to the possible influence of differences in literacy on the cerebral activity evoked during comprehension of sentence material via reading and speech. In the current study, which samples from a diverse population of young adults who represent a wide range of reading skill levels, we investigate whether the extent of speech–print convergence may vary systematically with the skill of the reader. Our object was to test the hypothesis that a common supramodal language processing system is fully established only among individuals with highly developed reading skills. To obtain relevant evidence, we created sentence materials, in parallel speech and print versions, incorporating a challenge to the language processor that occurred at a consistent location within the sentence. Challenging sentences were presented interspersed among baseline sentences without the challenging feature.

Event-related functional magnetic resonance imaging (fMRI) was used to examine the brain activity of young adults while they read or heard matched sentences that were either well-formed or contained morphosyntactic anomalies (e.g., New shirts have shrink when washed) or anomalies of pragmatic content (New cars might shrink when washed). The participants also received an extensive bat-

tery of analytic reading-related behavioral measures, including online eye-track measures of sentence processing. We expected that for adult readers who range widely in reading abilities, comprehension challenges induced by grammatical and pragmatic sentence anomalies would elicit skill-correlated differences in fMRI BOLD signal within language areas of the left hemisphere. We did, in fact, obtain evidence that variations in reading skills modify the cortical system for both speech and print processing at the sentence level.

A completed study that addressed the imaging data on sentence comprehension only for the more-skilled readers forms the background to the present study that focuses on individual differences (Braze et al., submitted). When the total participant group was split at the median on a composite measure of reading comprehension, the distribution of these skill measures for the upper half proved to be within expected limits for a university student sample, permitting comparisons with other findings in the research literature. The purpose of Braze et al. (submitted) was to identify the networks at which abstract linguistic processing cuts across speech and print sentence presentations, resulting in overlapping activity. To this end, a scheme was developed for identifying functionally defined regions of interest that proved useful for our present purposes. The results showed considerable overlap for matched printed and spoken sentences containing anomalies, especially in inferior prefrontal regions.

The present study extended this mode of analysis to investigate the effects of differences in reader skill. A major purpose was to test the idea that the speech and print systems become better integrated with increasing skill. The sentences presented in the scanner, as described earlier, contained instances of syntactic and pragmatic anomalies, but in view of the large measure of overlap in the cortical responses to these anomaly types, we did not attempt to distinguish their effects (see also Kuperberg et al., 2000; Ni et al., 2000; and a review by Kaan & Swaab, 2002, for additional evidence of overlap, especially at the inferior frontal gyrus (IFG)). Anomaly is exploited as a means of sensitizing sentence materials to individual differences.

In this study, we asked whether the nodes of the language system are more completely integrated across modality with increases in reading skills, and, if so, to identify the specific regions where integration takes place. A plausible way that integration might be instantiated is for relevant heteromodal regions to come on line as skill increases. We tested this idea by measuring the proportion of voxels active in both speech and print sentence conditions for each of several regions of interest, correlating these proportions with external reading skill measures to determine whether the regions that show greatest convergence across modality are also the regions that are most strongly correlated with reading skills. From the results based on the more skilled readers in our sample, we supposed that IFG and its surround is a prime candidate for integration. Moreover, this region could be expected to be a focus for reading skill differences based on the symptom pattern from lesions located there (Benson, 1977) and the imaging findings mentioned earlier.

METHOD

Participants

Coordinated neuroimaging and behavioral data are based on 36 young adults who represent a wide range of reading experience and skill. They are a subset of a group of 44 individuals, each of whom received an extensive battery of cognitive and educational tests aimed at assessing the relative strengths of the factors governing reading skill differences. Criteria for inclusion were: age from 16–24 years; native speakers of English, Full-Scale IQ of at least 80, ability to read well enough to comprehend simple material (based on The Fast Reading subtest of the Stanford Diagnostic Reading Test [Karlson & Gardner, 1995]; we required an accuracy of at least 70% on the items attempted). The protocols were approved by the Yale University Human Investigation Committee. Participants gave informed consent and were paid for completing the behavioral testing and fMRI session. Eight individuals were excluded because their fMRI data showed excessive motion artifact.

Reading Skill–Related Measures

A large group of cognitive measures was obtained on all the participants (see Braze et al., 2007 for full details). A subset of these is relevant here: (a) for listening comprehension, even numbered items from the Peabody Individual Achievement Test–Revised (PIAT–R) Reading Comprehension subtest were tape recorded for auditory presentation; (b) Reading comprehension composite: derived from the Peabody Individual Achievement Tests–Revised (PIAT–R) Reading Comprehension subtest (odd-numbered items) for comprehension of individual sentences, plus a portion of the Gray Oral Reading Test (GORT) for comprehension of short passages; (c) Nonword reading: The Woodcock-Johnson III Tests of Achievement (WJ–III), Word Attack subtest, Form A; (d) Word reading: WJ–III, Word Identification subtest, Form A; (e) Vocabulary composite, derived from Peabody Picture Vocabulary Test–Revised (PPVT–R) and the Weschler Abbreviated Scales of Intelligence (WASI) Vocabulary subtest; (f) Verbal working memory: an auditory version of the Daneman and Carpenter (1980) Sentence Span task; (g) Visual memory: a computerized version of the Corsi Blocks task, based on Corkin (1974); (h) Estimated print experience composite, derived from title and author checklists based on Cunningham and Stanovich (1990). Details of the tasks can be found in Braze et al. (2007); participants in the present study are a subset of those detailed in that report.

Materials and fMRI Task

The in-magnet stimuli consisted of short, syntactically simple sentences made up of words from the common vocabulary (mean length 6 words). Eighty percent were syntactically well formed and expressed a conventional meaning. The re-

maining 20% were anomalous, containing either morphosyntactic or pragmatic anomalies. Those sentences with morphosyntactic anomaly were meaningful but contained violations related to the verb morphology. Sentences with pragmatic anomaly were grammatical but expressed meanings that were odd or inconsistent with common knowledge. An example of each sentence type is given in Table 1. In all the anomalous sentences, the anomaly becomes apparent at the main verb. Each anomalous sentence was generated from a nonanomalous parent sentence by substitution of the subject noun (in cases of pragmatic anomaly) or the auxiliary verb (in morphosyntactic anomaly). Parent sentences, like the bracketed examples in Table 1, were not incorporated in the test sequence. The nonanomalous sentences the subjects read or heard were similar to the anomalous pairs in length, syntactic structure, and word frequency.

The test sequence consisted of 560 sentences, half presented in print and half in speech. There were 28 occurrences of each anomaly type in each modality yielding a total of 112 anomalous sentences and 448 unrelated nonanomalous ones. Counterbalancing ensured that participants read or heard one example from each anomaly pair. Additionally, 25% of the sentences included mention of a specific semantic category, a plant or plant product. These sentences were evenly distributed across anomaly and modality.

Task. Participants were instructed to monitor sentences they read or heard for mention of a plant or plant product, and at the end of the sentence to press a button indicating whether or not the target category was mentioned. Button presses were made with the first and second fingers of the right hand, corresponding to YES and NO, respectively. Expected Yes and No responses were evenly distributed across anomaly and modality conditions. Test sentences that contained mention of the target semantic category were structured to ensure that participants actually processed the entire sentence, and did not selectively attend only to the semantic target words. In these sentences the plant-relevant words were placed in the latter part of the sentence *after* the main verb. Hence, *the point at which a sentence becomes anomalous always precedes the cue words for semantic categorization.* Therefore, a reader reading an anomalous sentence cannot perform the semantic judgment

TABLE 1
Example Sentences

A	New cars might shrink when washed.	Pragmatic Anomaly
	New shirts have shrink when washed.	Syntactic Anomaly
	[New shirts might shrink when washed.]	Non-anomalous
B	Paint can attack wooden fences.	Pragmatic Anomaly
	Termites are attack wooden fences.	Syntactic Anomaly
	[Termites can attack wooden fences.]	Non-anomalous

task without first encountering the anomaly. Participants received practice with both print and speech conditions before entering the scanner.

Organization of the fMRI Protocol

The 560-item sequence was divided into 14 blocks, 7 each in speech and print modalities. Each block contained 40 sentence items, 32 nonanomalous sentences, and 4 items each of syntactically anomalous and pragmatically anomalous sentences. Thus, anomalous sentences were relatively infrequent occurrences in the test sequence. Each block constituted a single functional activation imaging run.

For all participants, odd numbered runs contained speech blocks and even numbered runs contained print blocks. Block order was random within each modality. Inter-trial interval was 5 seconds. A minimum of 15 seconds (two trials) intervened between successive occurrences of anomalous verbs, allowing the associated hemodynamic response to return to baseline between anomaly trials. Print stimuli were presented word by word at a rate of two per second. Spoken sentences were presented at a natural speaking rate. Sentence duration for speech trials was only slightly shorter than for print trials.

Stimulus presentation and recording of responses was controlled by computer using Psyscope (Cohen, MacWhinney, Flatt, & Provost, 1993). Speech stimuli were presented through MR compatible headphones and print stimuli were displayed through an LCD projector onto a back-projection screen located at the foot of the MR scanner table. Participants viewed the screen through a mirror situated inside the scanner tube. A fiber optic button box was used to collect the responses.

Image Acquisition and Analysis

Imaging for 33 subjects was performed on a Siemens 1.5T Sonata MR system and imaging for 3 subjects was performed on a 1.5 T GE, Signa LX system. In either case, sagittal localizer images (TE, 14 msec; TR, 500 msec; FOV, 24 × 24 cm; matrix, 256 × 192; 5-mm slice thickness, no skip; 1 NEX) were acquired to identify the inter-commissural line. Subsequently, 20 axial-oblique anatomic images, parallel to the AC-PC line, were acquired (TE, 11 msec; TR, 420 msec; FOV, 20 × 20 cm; matrix, 256 × 256; 6-mm slice thickness, no skip; 1 NEX). Functional activation images were collected at the same slice locations using single shot, gradient echo-planar sequencing (flip angle, 80 degrees; TE, 50 msec; TR, 2000 msec; FOV, 20 × 20 cm; matrix 64 × 64; 6-mm slice thickness, no skip; 1 NEX). Fourteen runs of functional activation images were acquired. Each run provided 103 full volume images, for a total of 1,442 per participant.

Functional images for each participant were corrected for slice acquisition time, motion-corrected (Friston et al., 1995), and, finally, spatially smoothed using a gaussian filter of 3.125-mm full-width at half-maximum. An affine transforma-

tion to Montreal Neurologic Institute (MNI) standard space was obtained for each set of single-subject images using the intensity-only module of the algorithm described in Papademetris, Jackowski, Schultz, Staib, and Duncan (2004), mapping between the subject-space anatomic image and the MNI-space “Colin” brain (available at <http://www.bic.mni.mcgill.ca>). Transformation to 2 mm isotropic MNI space, with trilinear interpolation, is applied to single-subject maps before across-subjects analysis.

Map-based data analysis was performed using in-house software within MATLAB (Matlab, 2001). Region of interest (ROI) data (Anomaly Contrast and Convergence Index) were exported from MATLAB and analyzed in the R statistical environment (R Development Core Team, 2004). Multiple regression was used for single-subject, event-related analyses. At each voxel, signal intensity over time was modeled with a set of synthetic hemodynamic response functions (HRF) created from a gamma variate (τ : .9, n : 5, onset delay: 1.4, time to peak: 5 sec). The specific time-to-peak was chosen based previous work from our lab using similar materials and protocols (Ni et al., 2000). The peak of the synthetic HRF was temporally aligned to the onset of the critical word (the verb) in each stimulus sentence. Individual regressors were employed for each of 12 sentence conditions (3 anomaly [non-, syntactic, pragmatic] \times 2 modality [print, speech] \times 2 semantic-category responses [yes, no]). A simultaneous multiple regression was employed with these 12 predictors of interest, and additional regressors to account for run-to-run mean offsets in signal intensity. The resulting regression parameters (B -weights) were then converted to standardized activation scores by scaling them against the square root of the error mean-square for the model (Frost et al., 2005). Standardized activation maps were transformed into MNI space for subsequent across-subjects analysis. Across-subjects, at each voxel, an ANOVA was employed with stimulus condition as a within-subjects variable, implementing a mixed-model or repeated measures ANOVA (Holmes & Friston, 1998; Kirk, 1982). Planned comparisons were applied within this model to address hypotheses of interest. Cross-subject contrast maps were used to create images showing both the logical intersection and the union of activations for two contributing contrasts (Hadjikhani & Roland, 1998; Ledberg, O’Sullivan, Kinomura, & Roland, 1995). Statistical tests involving whole-brain comparisons were corrected for multiple comparisons using the false discovery rate (FDR) procedure (Genovese, Lazar, & Nichols, 2002).

Two approaches were taken to definition of regions of interest for analysis of the relations between task-elicited BOLD activity and behavioral skill measures:

1. *Functionally defined ROIs.* Within general cortical areas found by earlier research to be sensitive to sentence characteristics of sentence anomaly and grammatical complexity (Caplan, 2004; Indefrey, in press), six ROIs were identified with reference to our data. Probes within these regions determined the peak response to a contrast between our anomalous and non-

anomalous sentence types. The procedure was developed and described in an earlier article from our laboratory (Braze et al., submitted).

2. *Anatomically defined ROIs.* Masks for anatomic regions of interest were created based on an electronic atlas (Wake Forest University "Pickatlas"; Maldjian, Laurenti, Kraft, & Burdette, 2003; Lancaster, Summerlin, Rainey, Freitas, & Fox, 1997; Lancaster et al., 2000) yielding approximations of areas based on the Talairach and Tournoux atlas (Talairach & Tournoux, 1988). Details are given in Table 2.

The rationale for (a) the motor face area and (f) auditory cortex (transverse temporal gyri, or TTG), is to test Wernicke's hypothesis that unskilled readers must call on speech processes (articulatory and/or auditory-phonetic) to support the mapping from print to the lexicon. IFG, a heteromodal zone (b, and c) is represented by separate dorsal and ventral ROIs in view of the indications that this region is heterogeneous anatomically (Amunts et al., 1999) and is multifunctional

TABLE 2
Atlas-Based Definitions (Maldjian et al., 2003) of Left-Hemisphere Anatomic ROIs

	<i>Label</i>	<i>Atlas-Based Definition</i>	<i>Note</i>
a)	Motor Face Area	BA 4 + BA 6 inferior to MNI $z < 28$ and dilated by 1 voxel	Approximately the inferior third of the precentral gyrus
b)	Dorsal Inferior Frontal Gyrus	IFG with MNI $z \geq 6$	Includes BA 44 in pars opercularis, and most of BA 45 in pars triangularis
c)	Ventral Inferior Frontal Gyrus	IFG with ($-20 < \text{MNI } z < 6$)	Includes most of BA 47 in pars orbitalis and the most inferior portion of BA 45 in pars triangularis
d)	Superior Temporal Gyrus	STG with MNI $y \geq -20$ and MNI $z > 4$	Includes portions posterior to the TTG at its most lateral extent and superior to the most inferior reaches of BA 41 and 42
e)	Middle Temporal Gyrus	MTG with MNI $y \geq -20$ and MNI $z > -4$	Approximately the posterior third
f)	Transverse Temporal Gyrus	TTG	Includes most of BA 41 and 42
g)	Fusiform Gyrus	FG with MNI $z > -24$	Superior portion
h)	Angular Gyrus	AG	
i)	Supramarginal Gyrus	SMG	
j)	Calcarine Sulcus	BA 17 dilated by 1 voxel	Includes most of the calcarine sulcus

ROI: Region of interest; BA: Brodmann's area; MNI: Montreal Neurologic Institute; IFG: inferior frontal gyrus; STG: superior temporal gyrus; MTG: middle temporal gyrus; TTG: transverse temporal gyri; FG: fusiform gyrus; AG: angular gyrus; SMG: supramarginal gyrus.

(e.g., Cooke et al., 2006). For the superior temporal gyrus (STG) (d) and the middle temporal gyrus (MTG) (e) we chose the posterior third, corresponding roughly to Wernicke's region and its surround, regions that are largely heteromodal. The fusiform gyrus in the inferior occipito-temporal region (g) is a secondary visual region that shows skill effects in word reading. Our ROI includes coordinates that mark the center of a zone that fulfills Cohen et al. (2002) criteria for a "visual word-form area." The inferior parietal region, a heteromodal zone, is represented by the angular gyrus (h) and the supramarginal gyrus (i), each repeatedly active in studies of word reading. The calcarine sulcus (j), the primary visual region, is included because of the possibility that it is influenced by skill-based, top-down feedback from other regions. Calcarine cortex, is, in fact, one of the posterior cortical zones that has been found to be poorly activated in dyslexic readers by basic, decoding tasks (Shaywitz et al., 2002). Within these regions, for each subject, we computed a "Convergence Index." This index is the proportion of voxels within an ROI with a standardized activation score for the anomaly contrast of at least .05 for both speech and print trials.

RESULTS

Overview

This section is organized as follows: first, behavioral results of reading skills tests and the in-scanner task; second, whole brain survey: (1) conjunction maps showing BOLD activity for Baseline and Anomaly Contrast measures with demonstration of print–speech differences and overlap and (2) correlations of BOLD signal with reading skill measures for spoken and printed sentences; third, regression-based analysis testing for effects of modality and skill and their interactions at functionally defined ROIs; and fourth and fifth, measuring integration of speech and print at anatomically defined ROIs in relation to reading skill.

Results of Reading Skills Tests and In-Scanner Task Behavior

Summary statistics for the skill measures are reported in Table 3. Composite scores used in some analyses are derived from the component measures by averaging *z*-scores.

Accuracy levels for the in-scanner semantic judgment task were high, averaging 91% correct for print trials and 89% for speech trials. In the development of the test materials and choice of the semantic judgment task, our aim was to create a task that would be successfully negotiated by readers at all skill levels. To assess whether the performance pattern is independent of reading skill, we divided the total group at the median on the Reading Comprehension Composite and computed

TABLE 3
Means and Standard Deviations for Education and Experience Measures
and Age ($N = 36$)

<i>Measure</i>	<i>M</i>	<i>SD</i>	<i>Max. Possible</i>
WJ-III Word-ID	68.44	5.58	76
grade equiv.	14.09	4.90	—
WJ-III Word Attack	27.56	2.86	32
grade equiv.	11.14	4.50	—
PIAT-R (print) sent. comp.	34.50	6.19	41
GORT comprehension	12.22	2.24	15
WASI vocabulary	58.14	8.79	84
PPVT vocabulary	175.17	17.98	204
age equiv.	20.02	4.47	—
PIAT-R (speech) sent. comp.	35.42	4.66	41
Sentence Span	32.64	5.50	42
Corsi Blocks	5.19	1.42	9
Title recognition	11.53	5.95	40
Author recognition	8.28	6.60	40
Age	20.74	2.33	—

WJ-III: Woodcock-Johnson III Tests of Achievement; PIAT-R: Peabody Individual Achievement Tests-Revised; GORT: Gray Oral Reading Test; WASI: Weschler Abbreviated Scales of Intelligence; PPVT: Peabody Picture Vocabulary Test-Revised (PPVT-R).

accuracy level for more- and less-skilled subgroups separately. Table 4 gives the breakdown by sentence type, modality, and skill group.

ANOVA shows significant main effects of modality, $F(1, 34) = 7.50, p < .0098$ (subjects are more accurate on print trials) and sentence condition, $F(2, 68) = 4.85; p < .011$ (subjects were less accurate on anomaly trials), and skill group, $F(1, 34) = 8.83; p < .005$ (the more-skilled readers averaged about 7% greater accuracy on the semantic judgment task). There were no interactions of reading skill group with sentence type or modality. The import is that the in-magnet task was managed well across the whole range of subject reading levels, and the independent variables of modality and anomaly did not differentially affect task performance of more- and less-skilled readers.

Results of Whole Brain Survey

Conjunction of fMRI responses to speech and print conditions. Figure 1A shows the evoked response to nonanomalous baseline sentences for the conjunction of speech and print at representative slices. Six axial-oblique slices are displayed (MNI z : -32, -20, -2, 4, 22, 34). These simple sentences, in the context of the semantic judgment task, evoked widespread activity in perisylvian and extrasyylvian cortex in frontal, insular, temporal, parietal, and occipital areas bilat-

TABLE 4
 Accuracy Scores (Percent Correct) by Anomaly and Modality and Skill Group.
 Groups are Defined by Median Split on Reading Comprehension Composite

Modality	Sentence Type		
	Nonanomalous	Pragmatic	Syntactic
<i>High-Skilled Readers (N = 18)</i>			
Print	95.31	94.64	94.84
Speech	93.65	91.27	90.48
<i>Low-Skilled Readers (N = 18)</i>			
Print	87.65	87.60	86.20
Speech	87.45	84.40	85.00
<i>All Participants (N = 36)</i>			
Print	91.50	91.14	90.54
Speech	90.56	87.85	87.75

erally and in cerebellum. In each of these regions there are zones of overlapping activity (yellow) interspersed among zones where the response to speech (green) or print trials (red) predominates.

Figure 1B shows maps of the conjunction of speech and print conditions for the contrast between anomalous sentences (averaged over anomaly type) and the nonanomalous baseline sentences. This measure isolates sentence processing effects from other task-related influences by subtracting the baseline. Accordingly, we use the anomaly contrast in subsequent analyses as the preferred measure. Print trials gave rise to larger anomaly effects in portions of the inferior frontal gyrus, precentral gyrus, superior temporal gyrus, parahippocampal, fusiform and lingual gyri, and subcortically at cerebellum. Speech trials yielded greater anomaly contrast at closely abutting sites in inferior and middle frontal regions, as well as posteriorly in temporal and occipital regions. Responses that overlap in speech and print can be seen chiefly at inferior and middle frontal regions, but also at fusiform and cerebellum. In cortical areas, modality overlap is visible only on the left.

Correlations of anomaly contrast BOLD signal with reading skill. Table 5 gives results of a whole brain survey that identified clusters of voxels at which the BOLD signal for the anomaly contrast was correlated with a measure of reading skill, our reading comprehension composite measure. Table 5A and 5B gives details for reading trials and speech trials, respectively. Most of the correlations were positive in direction. Print sites are concentrated in inferior and middle frontal gyri with smaller clusters in the posterior region. Except for the single cerebellar site, all are within the cerebrum. Twelve of the 20 cortical sites are in the left hemisphere, but total volume is nearly equal on the right. Speech sites, in contrast, implicate posterior portions of the hemispheres, mainly inferior and middle temporal

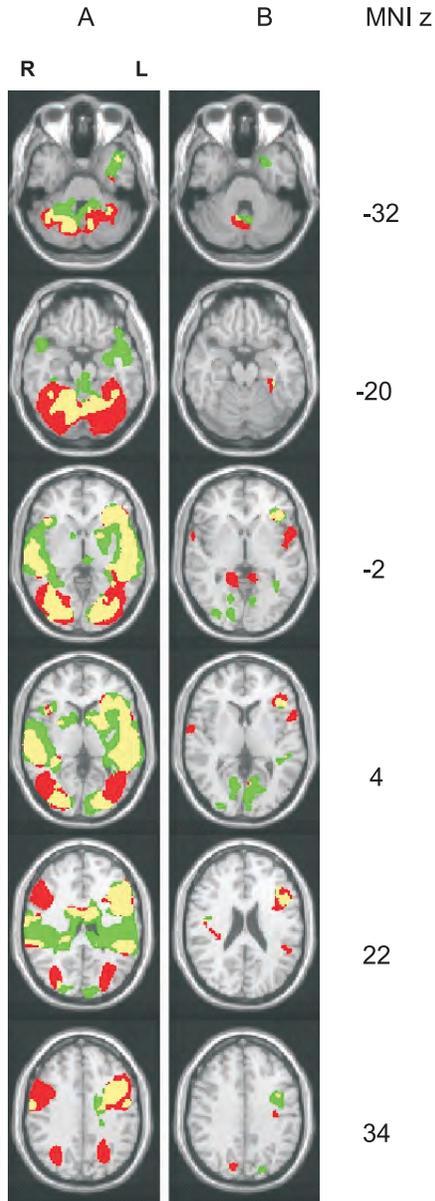


FIGURE 1 A: print–speech conjunction for non-anomalous sentences (threshold $p < .00000001$). B: print–speech conjunction for the anomaly minus nonanomaly contrast (threshold $p < .01$). Green = speech only; red = print only; yellow = overlap. Left and right hemispheres are reversed, as shown.

TABLE 5
 Correlation Sites of Anomaly Minus Nonanomaly Contrast for (A) Print
 Trials and (B) Speech Trials with Reading Comprehension Composite,
 Sorted in Order of Cluster Size with a Minimum Cluster of 10 Voxels

A: Printed Sentences

Hemisphere	Name	volume (mm ³)	MNI coord (peak voxel)			peak r
			x	y	z	
Left	Inferior Frontal Gyrus	1952	-46	24	14	.63
Right	Middle Frontal Gyrus	1448	51	20	30	.57
Right	Inferior Frontal Gyrus	1160	42	27	8	.58
Right	Middle Frontal Gyrus	968	32	6	51	.68
Left	Middle Frontal Gyrus	872	-34	36	-12	.61
Right	Tuber, Cerebellum	760	38	-67	-38	.61
Right	Precentral Gyrus	720	14	-22	76	-.61
Right	Superior Frontal Gyrus	488	10	14	58	.66
Left	Medial Frontal Gyrus	480	-4	14	-18	-.56
Left	Middle Occipital Gyrus / ITG	472	-48	-50	-10	.58
Left	Inferior Parietal Lobule	440	-48	-34	32	-.57
Left	Precentral Gyrus	368	-38	-4	32	.60
Left	Middle Occipital Gyrus	352	-40	-84	4	.59
Right	Superior Frontal Gyrus	312	24	28	54	.53
Left	Superior Frontal Gyrus	232	-24	40	31	.54
Left	Middle Frontal Gyrus	216	-16	2	68	-.56
Right	Middle Frontal Gyrus	200	48	28	40	.56
Right	Fusiform Gyrus	184	44	-54	-10	.51
Left	Precentral Gyrus	88	-10	-18	78	-.51
Left	Precuneus	88	-10	-66	62	-.48
Left	Middle Frontal Gyrus	80	-40	14	52	.49

B: Spoken Sentences

Hemisphere	Name	volume (mm ³)	MNI coord (peak voxel)			peak r
			x	y	z	
Left	Inf. Semi-Lunar Lob., Cerebellum	4368	-24	-82	-48	.82
Left	Middle Temporal Gyrus	1056	-54	-42	-2	.55
Left	Culmen, Cerebellum	760	-4	-51	-26	.58
Left	Middle Frontal Gyrus	384	-34	29	30	.58
Right	Culmen, Cerebellum	328	12	-40	-30	.51
Right	Inferior Temporal Gyrus	288	51	-40	-24	.54
Left	Insula	256	-34	26	16	.51
Left	Middle Temporal Gyrus	248	-56	-12	-11	.62
Left	Culmen, Cerebellum	232	2	-30	-38	.53
Left	Insula	136	-36	-6	9	.50
Right	Inferior Temporal Gyrus	128	60	-52	-18	.50
Left	Culmen, Cerebellum	128	-26	-56	-34	.54
Right	Pre-central Gyrus	104	46	-8	22	.49
Right	Uncus, Cerebellum	96	20	-4	-30	-.50
Left	Middle Frontal Gyrus	80	-36	2	62	-.49

Threshold $p < .01$, false discovery rate (FDR) corrected. MNI: Montreal Neurologic Institute

lobes, and five are subcortical (cerebellum). Six of the 10 sites within the cerebrum are in the left hemisphere, occupying a total volume of 2,256 mm³ compared with 616 mm³ for the remaining four right hemisphere sites.

Other reading skill measures yielded numerous sites of correlation with BOLD anomaly contrast. These measures included Woodcock Johnson III Word Attack, WJ-III Word Identification, Listening Comprehension, a Spoken Vocabulary composite, Sentence Span, and estimated print experience. They yielded moderate to high intercorrelations with each other in the behavioral testing that was carried out with the same participants (Braze et al., 2007). These skill measures yielded mainly positive correlations with the anomaly contrast.

To sum up, reading skill influences on BOLD activity elicited by printed and spoken sentences were readily detectable using our anomaly contrast measure. For reading comprehension as the skill measure, location of sites of correlation was chiefly anterior (i.e., inferior and middle frontal) for printed sentences, posterior and subcortical for spoken sentences, but each modality elicited one or more sites in prefrontal heteromodal cortex.

Effects of Modality and Skill on Anomaly Contrast at Functional ROIs

The whole brain approach to identifying correlations between the anomaly contrast in print and speech and reading-related skill measures yielded many sites of correlation including some outside the limits of what is usually considered language brain. We now turn our focus to regions within the putative language brain, that is, the perisylvian and extrasylvian cortex where previous imaging studies of sentence processing show effects of sentence anomaly or grammatical complexity. Accordingly, seven left hemisphere ROIs were identified, two in the inferior frontal region (IFG2 is superior to IFG1), two in the temporal lobe (superior temporal gyrus and inferior temporal gyrus), and, posteriorly in the lingual gyrus, fusiform gyrus, and the inferior parietal lobule. Each of the general regions in which these ROIs are located has independently been found to contain zones of sensitivity to reader skill differences on word and nonword tasks (Shaywitz, Shaywitz, Pugh, Fulbright, et al., 1998; Pugh et al., 2000). Within these areas, we used the anomaly contrast to specify ROIs that reflect sentence-related activity. The center of each spherical ROI corresponds to the maximally active voxel for the anomaly contrast. MNI coordinates for these ROIs are given in Table 6A. Table 6B lists clusters which showed a reliable anomaly contrast (at $p < .05$, FDR corrected).

Spearman rank-order correlations of the behavioral measures with the anomaly contrast on print trials yielded one significant correlation in these ROIs, involving the Sentence Span Measure at IFG1: $r = .52$, ($p < .001$). In addition, there was a borderline correlation with Vocabulary Composite ($r = .30$, $p < .09$) at that ROI, and two further borderline correlations, one in the adjoining ROI, IFG2, with Vo-

TABLE 6
 (A) Anomaly-Defined Spherical Regions of Interest (radius 6 mm), MNI Coordinates. (B) Maxima for Anomaly Minus Nonanomaly Contrast, Collapsed Across Modality, in Order of Cluster Size (Minimum 10 Voxels)

A: Spherical ROIs

	Name	Volume (mm ³)	MNI Coordinates (Centers)			p values	Polarity
			x	y	z		
1	Left Fusiform Gyrus	984	-32	-36	-18	.00533	A>NA
2	Left Inferior Temporal Gyrus	984	-64	-12	-22	.00258	A>NA
3	Left Inferior Parietal Lobule	984	-44	-62	40	.00331	A<NA
4	Left Lingual Gyrus	984	-6	-78	4	.00765	A>NA
5	Left Inferior Frontal Gyrus (1)	984	-40	28	4	.00021	A>NA
6	Left Inferior Frontal Gyrus (2)	984	-46	13	20	.00002	A>NA
7	Left Superior Temporal Gyrus	984	-51	-36	8	.01018	A>NA

B: Maxima for Anomaly Minus Nonanomaly Contrast. Corresponding Spherical ROIs are Indicated in Parentheses

Hemisphere	Name	Volume (mm ³)	MNI Coordinates (Peaks)			p value	Polarity
			x	y	z		
Left	Inferior Frontal Gyrus	16296	-46	13	20	<.0001	A>NA (5&6)
Right	Cingulate Gyrus	5640	4	-28	40	.0012	A<NA
Right	Medial Frontal Gyrus	4208	4	54	8	.0028	A<NA
Left	Inferior Parietal Lobule	2304	-44	-62	40	.0033	A<NA (3)
Left	Lingual Gyrus	1872	-6	-78	4	.0076	A>NA (4)
Right	Fastigium (Cerebellum)	1856	10	-60	-30	.0015	A>NA
Left	Superior Frontal Gyrus	1768	0	14	58	.0020	A>NA
Left	Inferior Temporal Gyrus	1656	-64	-12	-22	.0026	A<NA (2)
Right	Superior Temporal Gyrus	832	60	-44	6	.0180	A<NA

(continued)

TABLE 6 (Continued)

B: Maxima for Anomaly Minus Nonanomaly Contrast. Corresponding Spherical ROIs are Indicated in Parentheses

Hemisphere	Name	Volume (mm ³)	MNI Coordinates (Peaks)			p value	Polarity
			x	y	z		
Right	Lingual Gyrus	720	12	-68	4	.0128	A>NA
Left	Fusiform Gyrus	672	-32	-36	-18	.0053	A>NA (1)
Right	Thalamus	656	12	-12	16	.0132	A<NA
Right	Supramarginal Gyrus	616	62	-46	36	.0138	A<NA
Left	Superior Temporal Gyrus	616	-51	-36	8	.0102	A>NA (7)
Left	Cuneus	528	-16	-94	24	.0113	A>NA
Left	Anterior Cingulate	472	-8	36	20	.0112	A<NA
Left	Thalamus	424	-14	-10	6	.0089	A<NA
Right	Caudate	400	28	-42	8	.0108	A>NA
Left	Precentral Gyrus	384	-42	-20	64	.0102	A<NA
Left	Tonsil (Cerebellum)	352	-12	-50	-46	.0045	A>NA
Left	Posterior Cingulate	304	-16	-58	6	.0258	A>NA
Left	Cuneus	288	-2	-84	28	.0176	A>NA
Right	Middle Frontal Gyrus	192	44	14	24	.0205	A>NA
Right	Precuneus	192	18	-82	40	.0210	A>NA
Left	Precentral Gyrus	184	-36	-20	32	.0113	A>NA
Left	Precuneus	168	-2	-86	40	.0140	A>NA
Right	Lingual Gyrus	168	18	-46	-1	.0298	A>NA
blLeft	Precuneus	112	-14	-84	48	.0053	A>NA
Right	Precuneus	104	14	-82	48	.0210	A>NA
Left	Middle Occipital Gyrus	88	-20	-86	-10	.0237	A>NA
Right	Postcentral Gyrus	88	48	-10	22	.0146	A>NA
Right	Tonsil (Cerebellum)	88	24	-60	-42	.0161	A>NA
Right	Clastrum	88	34	0	0	.0217	A<NA
Left	Superior Temporal Gyrus	88	-58	8	-4	.0240	A>NA
Left	Middle Occipital Gyrus	80	-26	-82	20	.0284	A>NA
Left	Superior Parietal Lobule	80	-36	-67	52	.0285	A<NA

Threshold $p < .05$, false discovery rate (FDR) corrected. ROI number from A corresponds to maxima indicated by corresponding numbers in B (final column). MNI: Montreal Neurologic Institute.

cabulary ($r = .30, p < .08$, and the other at STG with Listening Comprehension ($r = .30, p < .08$).

For speech trials, the one ROI that yielded brain-behavior correlations was IFG2. Correlations with our anomaly-contrast measure at that site were obtained for the Reading Comprehension Composite ($r = .39, p = .02$) and WJ-III Word Attack ($r = .49, p = .003$). Marginal correlations were obtained with WJ-III Word Identification and age (each $r = .30$). An initial multiple regression model, including Reading Comprehension Composite, Word Attack, and age indicates that only Word Attack captures unique variance. However, removing two excessively influential observations (identified through iterative examination of Cook's distance statistic) and refitting the model results in R^2 of .37 with both Word Attack and age capturing unique variance in BOLD activity. The regression model is shown in Table 7.

In sum, the anomaly defined ROIs yielded rather few significant correlations between the skill measures and our BOLD indicator of sentence-related brain activity, the anomaly contrast. Moreover, peak correlations with the anomaly contrast in the whole brain survey tended to be situated at somewhat different locations than peak magnitude of the contrast.

We made further use of the anomaly contrast-defined ROIs to examine the effects of modality and reading skills and their interactions. Separately for each skill measure, we predicted the evoked BOLD response to sentences with a mixed-model AnCoVa for generalization to subjects that included modality, a skill measure and their interaction. Across all models, we found robust main effects of modality at two posterior temporal locations: dorsally at STG, which showed a greater effect of speech trials ($p < .001$), and ventrally in the fusiform gyrus ($p < .01$), which showed a greater effect of print trials.

Six interactions involving modality and reading skills proved significant, or nearly so. Five of these involved a portion of IFG. Word reading skill (WJ-III Word Identification) interacted with modality at IFG1 ($p = .036$). Decoding skill (WJ-III Word Attack) interacted with modality at IFG2 ($p = .014$). Verbal working memory (Sentence Span) yielded a reliable interaction with modality at IFG1 ($p = .016$), and marginal ones in IFG2 ($p = .053$) and angular gyrus ($p = .079$). In behav-

TABLE 7
Multiple Regression Model Targeting Anomaly Minus Nonanomaly Contrast for Speech Trials in IFG2

Variable	β	<i>t</i> value	<i>p</i> value	Unique R^2
Reading comprehension composite	-.16936	-.873	.3897	.015
Word attack	.34731	2.058	.0483	.089
Age	.51318	2.905	.0068	.177

Multiple R^2 : 0.37. IFG: IFG: inferior frontal gyrus.

ioral testing with these participants, WJ–III Word Identification and Sentence Span were substantially correlated, $r = .59$ (Braze et al., 2007). A further interaction involving the Reading Comprehension Composite as the skill measure approached significance at IFG1 ($p = .08$).

All of the interactions with skill measures had the same form, showing convergence by high-skilled readers. Figure 2 shows plots of the interaction at IFG1 of modality with the Reading Comprehension Composite, and modality with WJ–III Word Identification. It is apparent that in low-skilled readers the two modalities have different effects on BOLD signal level in this region. For each of the two skill measures, the net result of these interactions is convergence of activity for print and speech in more skilled readers, who responded at nearly equivalent levels of BOLD to printed and spoken sentences at this region. For high-skilled, but not for low-skilled readers, the sentence processing system seems to have become integrated at this inferior frontal ROI. This result further substantiates IFG as a skill region, and in addition identifies it as a focus for print-speech integration.

Measuring Speech–Print Convergence at Anatomic ROIs

As shown in Figure 1, the distribution of cerebral activity evoked by spoken and printed sentence materials includes major areas of overlap. These overlapping areas are seen as good candidates for functional integration of the speech stream and the print stream. We wished to make a more rigorous test of the hypothesis that speech–print convergence (on the anomaly contrast measure) occurs primarily in heteromodal portions of the cerebral cortex. As explained in Method, we defined 10 anatomic regions of interest within the left hemisphere, selected to include both auditory and visual unimodal regions and heteromodal regions. These include regions within the perisylvian and extrasyylvian cortex where previous work has shown reading skill differences.

To investigate the site/s of convergence of speech and print streams, we created a Convergence Index. This index was computed for each participant as the proportion of voxels within an ROI with a standardized activation score for the anomaly contrast of at least .05 for both speech and print trials. Average values of the Convergence Index at each ROI are given in Table 8. Values range from .33 (dorsal IFG) to .08 (angular gyrus).

Convergence as a Function of Skill Level

We used the Convergence Index at the anatomically defined ROIs to investigate whether speech–print convergence is related to reading skill, and, if so, at which regions and for which skill measures. Our *a priori* predictions were for linear relationships between the convergence index and skill measures, particularly in frontal regions. First, we note a high correlation of the index with the Reading

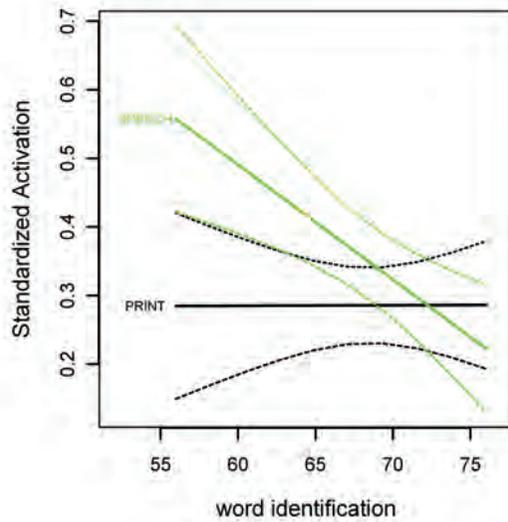
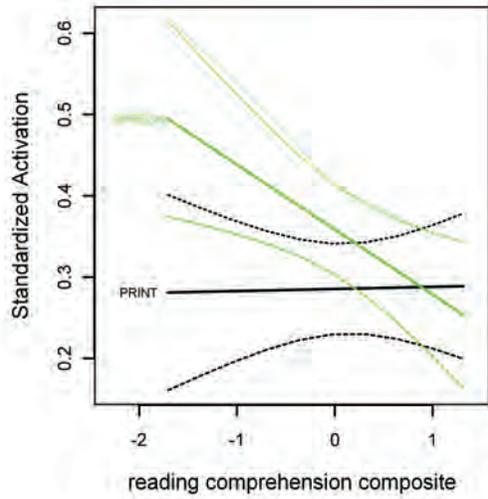


FIGURE 2 Interaction plots of evoked response to print and speech trials at the more ventral anomaly-defined IFG region, IFG1, with (A) Reading Comprehension Composite scores, (B) Woodcock-Johnson III Tests of Achievement Word Identification scores. Confidence bands indicate point-wise 95% confidence intervals.

TABLE 8
Average ($N = 36$) Effect-Size–Based
Convergence Index at Each Anatomically
Defined Region of Interest

<i>Region</i>	<i>Mean</i>	<i>SD</i>
dIFG	.332	.215
vIFG	.305	.190
pSTG	.244	.167
AG	.080	.141
Calcarine sulcus	.231	.173
SMG	.166	.153
FG	.253	.165
TTG	.182	.180
motor (face)	.243	.157
pMTG	.229	.135

dIFG: dorsal inferior frontal gyrus; vIFG: ventral inferior frontal gyrus; STG: superior temporal gyrus; AG: angular gyrus; SMG: supra-marginal gyrus; FG: fusiform gyrus.

Comprehension Composite measure, $r = .55$, $p = .0005$, at dorsal IFG. Figure 3 shows a scatterplot of this relationship. This correlation confirms indications from the interaction analysis in the third section that a relation exists between reading skill and the degree of print–speech convergence. However, it is also quite clear that the relationship is not strictly linear. A post-hoc regression analysis that includes both linear and quadratic terms for reading comprehension shows an overall fit of $r = .73$, $p < .0001$ (omitting the apparent outlier in the upper left-hand quadrant of Figure 3 yields similar results for both simple linear and curvilinear fits).

In addition there are lesser but significant correlations of the Convergence Index with other reading-related skills at this ROI: Listening Comprehension $r = .38$, $p = .022$, WJ–III Word Attack $r = .47$, $p = .004$, WJ–III Word Identification, $r = .43$, $p = .008$, Vocabulary, $r = .43$, $p = .009$, print experience, $r = .41$, $p = .01$. A multiple regression model including these skill measures and reading comprehension, with age as a covariate, indicated that only the Reading Comprehension Composite captured unique variance. Including a quadratic term for each skill measure yields substantially the same pattern.

The next highest value obtained for the mean Convergence Index was at ventral IFG, but this region showed no correlations with skill measures. Few correlations of the Convergence Index with skills occurred at posterior regions: Angular gyrus showed borderline correlations with Sentence Span, and WJ–III Word Attack. Interestingly, auditory cortex (TTG) shows a negative correlation of the Convergence Index with the Reading Comprehension Composite, $r = -.35$, $p = .037$ (see Discussion).

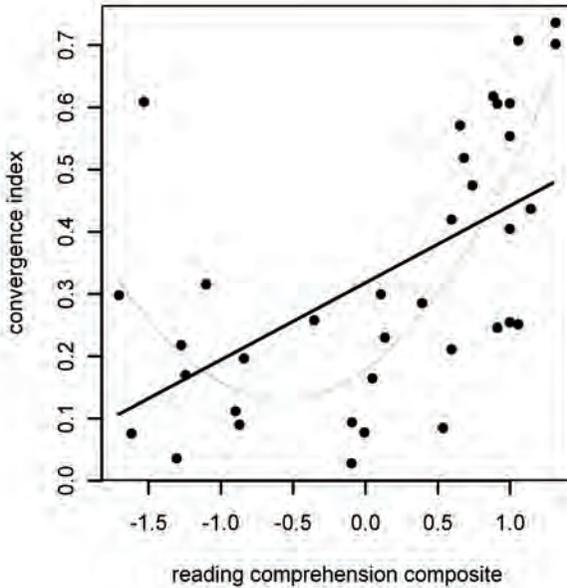


FIGURE 3 Reading Comprehension Composite scores plotted against the Convergence Index in dorsal IFG, with linear and curvilinear fits.

Overall, the data yield consistent evidence that neural convergence of speech and print versions during sentence processing can be detected and is positively related to reading comprehension and reading subskills. Skilled readers tend to converge more than unskilled readers within the inferior frontal region. The dorsal IFG region showed the highest value of the Convergence Index, the strongest relation of convergence with skill in reading comprehension, and the most consistent relations across the range of reading subskill measures.

DISCUSSION

In totality the results point to the conclusion that supramodal integration of speech and print processing varies with the reader's skill, and they identify the inferior frontal region as the principal focal site of convergence. Sentence processing in speech and print engages partly separate and partly overlapping brain regions. Whereas earlier studies identified modality-overlapping sites of sentence-elicited cortical activity, this study newly asked whether the extent of overlap during sentence processing varies concomitantly with reading skill among young adults who differ in amount and quality of schooling and reading experience.

Recruiting readers of widely varying skill levels, we examined the influence of sentence type and modality on the cortical response. Simple, nonanomalous sentences provided the baseline which was compared with similarly constructed sentences containing syntactic and pragmatic anomalies, with the subject's task (is there a plant or plant product mentioned?) held constant. The task required comprehension, but it was expected to be neutral with respect to the sentence-type contrast. In fact, accuracy of in-scanner semantic judgments did not interact with sentence type. Nor did they interact with modality. Hence, we maintain that differences in performance on the behavioral task cannot explain differences in implicit BOLD response to anomalous sentences in either modality. The anomaly contrast enabled us to unequivocally distinguish sentence-specific activity from general activity associated with the stimulus materials and the task (Braze et al., submitted, Ni et al., 2000). Because information for semantic judgment was placed near sentence end, always after the occurrence of an anomaly (in sentences where one was present), we can surmise that words bearing the anomaly were generally processed as sentential elements, although the participant's attention was directed elsewhere (in search of a plant-related word).

The findings link the behavioral data from the in-scanner task, the out-of-scanner measures of reading skill, and the imaging data from spoken and printed sentences. BOLD responses to sentences in each modality were assessed in multiple ways. These included conjunction maps of the distribution of sentence-elicited activity in each modality and their overlap, a whole-brain survey showing magnitude of correlations of the anomaly contrast with skill measures, regression-based probes for interactions involving modality and skill based on anomaly defined ROIs, and probes for supramodal convergence of the anomaly contrast based on anatomically defined ROIs. Each mode of analysis complements the others.

As shown in Figure 1, the anomaly contrast yielded residual activity in some cortical regions over and above the activity elicited by nonanomalous baseline sentences, as has repeatedly been reported in other studies (for reviews see Caplan, 2004; Indefrey, in press). For spoken sentences, these regions included left inferior and middle frontal areas, and posterior temporo-parietal and occipital areas, in line with findings of Ni et al. (2000, Exp. 2), who used an oblique task similar to the task we adopted here. For print, inferior frontal sites are also prominent; also implicated is precentral gyrus, superior temporal, fusiform, and lingual gyri. Overlapping sites were confined to the left hemisphere, most prominently in inferior and middle frontal regions, consistent with findings of Constable et al. (2004), Homae et al. (2002), and Michael et al. (2001).

The anomaly contrast, our probe for sentence-processing activity, proved very sensitive to skill differences. As we saw (Table 5), the magnitude of the effect for print sentences co-varied with reading comprehension at a number of sites, but most robustly at inferior and middle frontal regions. The near absence of sites of correlation within temporal regions is noteworthy. In processing the spoken ver-

sions of the test sentences, however, temporal regions and cerebellum assume greater prominence, but prefrontal involvement was a common factor. We leave it to future research to probe the role of subcortical structures, especially the cerebellum, in building literacy skills. There is evidence that the cerebellum has reciprocal connections to cortical areas including inferior frontal cortex (Middleton & Strick, 1994), and that portions of this structure are engaged in component processes of printed word recognition (Fulbright et al., 1999).

The question most relevant to our chief concern is whether overlapping activity in the networks supporting print and speech comprehension increases as a function of reading skill. We addressed this question in two ways. First, we probed for interactions with skill measures of local cortical activity arising from speech and print at selected regions of interest to ask whether the form of the interaction is consistent across regions and whether convergence is a characteristic of skilled but not unskilled readers. Specific locations of ROIs within each portion of language cortex were defined by responsiveness to the anomaly contrast. As we noted, modality made a significant difference in total sentence-evoked BOLD level at each of the posterior ROIs, but not at either of the two inferior frontal ROIs. The inferior frontal region, which also showed the greatest modality overlap in the conjunction map (Figure 1b) appeared indifferent to modality in the region-based analysis. In fact, collapsing across sentence type we found interactions of BOLD total evoked signal level with modality at IFG that were significant or borderline for each of three skill measures, Reading Comprehension Composite, WJ-III Word Identification, and Sentence Span. It is telling that the form of the interaction is the same in each case. In each we observed convergence of BOLD signal level for print and speech sentences for higher-skilled and separation for lower-skilled readers.

It is noteworthy that reading skill differences appear to influence the neural response to spoken sentences, not just printed ones, as shown in the modality \times skill interaction plots depicted in Figure 2. In this connection, we mention related findings by Castro-Caldas, Petersson, Reis, Stone-Elander, and Ingvar (1998), which showed that illiterate adults were inaccurate in repeating *spoken* pseudowords, differing sharply from matched controls with only basic literacy. Moreover, their repetition task failed to activate left-hemisphere perisylvian regions ordinarily engaged by phonologically driven behavior, regions that were strongly active in the subjects who could read, suggesting that the basic auditory-verbal language network is restructured as a consequence of acquiring reading skills. Our findings suggest further that restructuring induced by literacy affects additional levels of language processing beyond the phonologic level.

The findings to this point prompted us to examine more closely the properties of those brain regions that respond similarly to sentence characteristics in both print and speech, and also are sensitive to skill differences. As a second approach to modality integration, we conducted a direct quantitative test of the hypothesis that speech-print convergence in sentence processing should occur in heteromodal

cortical regions. For the new set of anatomically defined ROIs, we computed a voxel-based Convergence Index based on the proportion of voxels activated in common within the region.

The ROIs for this analysis were defined anatomically, representing heteromodal and unimodal portions of cortex anteriorly and posteriorly. As we saw, there were variations in size of the index from one ROI to another; dorsal IFG yielded the highest value. Thus, the Convergence Index yielded additional confirmation that the inferior frontal region contains zones of speech–print convergence during sentence processing, consistent with the hypothesis. Moreover, as we saw, research carried out previous to and in parallel with this study, identified the inferior frontal region of the left hemisphere as a major site of overlapping activity from spoken and printed versions of challenging sentences (Braze et al., submitted; see also Constable et al., 2004; Indefrey, in press, Michael et al., 2001). The present results, which directly measure the extent of speech–print convergence, confirm and extend those results.

Dorsal IFG which showed the strongest convergence also showed the strongest and most consistent skill correlations. This region is unique among our ROIs in showing positive correlations with every skill measure we tested. As shown in Table 8, both ROIs within IFG showed higher values of the Convergence Index than other regions. Moreover, unimodal regions, visual cortex and auditory cortex, also showed values greater than zero. These values apparently reflect secondary, top-down influences. Notably, TTG, containing primary auditory cortex, yielded a significant correlation with skill in reading comprehension, but in the negative direction (negative correlations at TTG with the other skill measures also occurred, though none reached significance). Presumably the source of this convergence is top-down activation. Conceivably, this could result from a need by unskilled readers to subvocalize (as Wernicke long ago proposed), giving rise to auditory reafference. Tracking such influences by inter-regional correlation analyses would be worthwhile, but beyond the scope of this article.

Our results with regard to convergence and skill are in one respect surprising. Given the well-attested importance of temporoparietal and occipitotemporal structures for reading differences, we expected to find more evidence of convergence-related skill differences at posterior sites in addition to the prefrontal sites we found. In this respect, our findings are on their face at variance with those of Spitsyna et al. (2006) who also reported convergence in heteromodal regions, but, as we noted, at posterior cortical regions. Differences in task and baselines employed in our study and Spitsyna et al. make it difficult to directly compare the results of the two studies. It is perhaps worth noting that Spitsyna et al. mention that whereas they chose to focus exclusively on posterior regions, their data also implicated other regions, one being the prefrontal area. Hence, it is possible that the results have some commonality. Moreover, our findings with the anomaly contrast measure are in accord with the findings of Homae et al. (2002). As we noted, that

study incorporated baselines that isolated pragmatic comprehension at the sentence level. In both Homae et al. and the present study, IFG emerged as the sole region that was selective both for sentence processing and modality independence. But, as we showed, modality independence at IFG applies only to skilled readers.

Having reviewed complementary results from two analyses indicating that skilled readers showed evidence of greater integration across speech and print than unskilled ones, each broadly implicating IFG we must now consider why this should be true. These findings raise two further questions: first, what does it say about the nature of reading that convergence is a good thing? Secondly, why should IFG be the primary site of print–speech integration and reading skill correlation, eclipsing temporal and parietal regions that are also heavily implicated in studies of reading differences?

As to the first question, we suppose that as a person's literacy advances, the foundation of reading skill becomes increasingly integrated with the biologically endowed speech system, such that the neurobiology of speech and print become richly interconnected at each level of linguistic processing from the grapho-phonologic subword level (Atteveldt, Formisano, Goebel, & Blomert, 2004) to the syntactic-pragmatic sentence and discourse levels. Because integration of print and speech must be forged by explicit learning and staged instruction, full convergence is achieved only in the educated, mature reader. To frame speech–print convergence in neurobiological terms, we maintain that an essential feature of skilled reading is reaching a state in which the two modalities evoke the same response within the language brain.

As to the second question, why convergence might selectively involve IFG, we can only offer speculation. The heteromodal hypothesis poses a constraint on possible sites of convergence. A candidate region is limited to zones that receive inputs from each relevant modality. IFG meets that test (Poremba et al., 2003). But of course, IFG is only one of a number of heteromodal regions. Moreover, IFG is far removed from the polysensory region at the intersection of parietal, temporal and occipital lobes that Geschwind (1965) regarded as a critical site for development of printed language functions. An upshot is that the heteromodal hypothesis is too general to explain why IFG yielded the strongest evidence of convergence.

It is possible, of course, that our stimulus materials and anomaly contrast response measure pushed the results toward IFG. In his meta-analysis of 70 imaging studies of sentence processing, Indefrey (in press) finds that IFG or its surround is a common factor when sentence materials included syntactic or pragmatic anomalies. A review by Kaan and Swaab (2002) concurs. More generally, in both spoken language and reading, IFG tends to surface whenever the stimuli or task are especially resource demanding (Caplan, 2004; Gabrielli, Poldrack, & Desmond, 1998). Although we cannot dismiss the possibility that our results are circumscribed by anomaly, possibly reflecting processes not involved in ordinary language process-

ing, we point out that our task was not an anomaly detection task; our participants made semantic judgments that were irrelevant to the anomalies; hence, we maintain that the effect of anomaly on the BOLD signal was an implicit effect, perhaps occurring at a preattentive level. Recall, in this connection, that sentence type (anomaly/nonanomaly) did not interact with either modality or skill in the behavioral responses. Moreover, in research we reviewed earlier, nonanomalous sentences that present comprehension challenges have also been shown to strongly activate portions of inferior frontal cortex (Constable et al., 2004; Michael et al., 2001).

We consider that when the brain learns to read it is constrained to exploit neural systems already in place for spoken language. Therefore, we could expect movement toward speech–print integration to be expressed as overlapping activity within systems already exploited for primary language learning, both within posterior and anterior regions. Certainly there is considerable agreement that phonological and lexical processes in both spoken language and reading depend heavily on structures in temporal and inferior parietal regions. But, in addition, the evidence is compelling of involvement of the inferior frontal region in reading ability, both at the level of the word and its parts (Booth et al., 2002; Pugh et al., 2000; Rumsey et al., 1997a, Shaywitz et al., 2002) and also at the phrase and sentence level (Constable et al., 2004; Homae et al., 2002; Kang, Constable, Gore, & Avrutin, 1999; Michael et al., 2001). Complementing the findings from imaging studies of neurologically intact people, there is evidence that lesions of left IFG disrupt reading and writing skills as well as spoken language abilities both at the word-subword level (Fiez, Tranel, Seager-Frerichs, & Damasio, 2006) and the sentence level. Thus, Benson (1977) finds that reading problems associated with lesions of this region, like the difficulties in production and perception of spoken language, regularly include problems in comprehending morphosyntactic structures (function words and clitics) and in maintaining sequences (sequences of letters and sequences of words).

There is, in short, a variety of evidence that the IFG region is the nexus of interrelated processes that bind sequences of linguistic units (Hagoort, 2005) and function independently of input modality. IFG emerges from this study as the primary region of speech–print convergence for sentence processing, supporting the hypothesis advanced by Braze et al. (submitted) that a major function of this region is to bind speech and print representations into a common currency. IFG also emerges as the primary site of reading skill correlation, consistently more active in skilled than in unskilled readers. It is the coalescence of speech–print convergence and skill sensitivity that makes IFG so arresting and possibly unique. Our findings add to the ever-growing list of functions of IFG. Most important, these findings lend neurobiological substance to the idea that reading skill can be interpreted as the graded convergence and unification of print representations with those of spoken language.

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