Ann. of Dyslexia (2009) 59:78–97
DOI 10.1007/s11881-009-0024-y

Phonological awareness predicts activation patterns for print and speech

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Received: 23 October 2008 / Accepted: 20 February 2009 / Published online: 21 March 2009

Abstract Using fMRI, we explored the relationship between phonological awareness (PA), a measure of metaphonological knowledge of the segmental structure of speech, and brain activation patterns during processing of print and speech in young readers from 6 to 10 years of age. Behavioral measures of PA were positively correlated with activation levels for print relative to speech tokens in superior temporal and occipito-temporal regions. Differences between print-elicited activation levels in superior temporal and inferior frontal sites were also correlated with PA measures with the direction of the correlation depending on stimulus type: positive for pronounceable pseudowords and negative for consonant strings. These results support and extend the many indications in the behavioral and neurocognitive literature that PA is a major component of skill in beginning readers and point to a developmental trajectory by which written language engages areas originally shaped by speech for learners on the path toward successful literacy acquisition.

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Keywords Functional MRI · Phonological awareness · Reading development · Superior temporal gyrus

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Functional neuroimaging studies of reading development have shown that during reading and language processing tasks, beginning readers activate a widely distributed set of left hemisphere (LH) regions including occipito-temporal, temporo-parietal, and inferior frontal sites. Studies have further shown that increases in reading skill are most strongly associated with increased engagement of the ventral aspect of the occipito-temporal region (Shaywitz et al. 2002; Turkeltaub et al. 2003). In order to provide insight into the conditions that lead to this neurodevelopmental change, the current study examines the relationship between phonological awareness, a behavioral marker of early reading readiness, and functional activation during both speech and print processing in beginning readers.

According to most models of reading, phonology plays a crucial role in reading acquisition and development, arising from the fact that written language is an arbitrary representation of spoken language. In particular, awareness of the underlying phonological composition of spoken words, termed Phonological Awareness, has been shown to be a major component of reading acquisition and development. Phonological awareness (PA) is defined as the metalinguistic understanding of the segmental nature of speech. That is, that spoken words are composed of segments, including the smallest of these segments, phonemes (understanding at this fine-grained level is referred to as phonemic awareness). Much research has shown that PA predicts later reading achievement (Bradley & Bryant 1983; Stanovich et al. 1984; Torgesen et al. 1999; see Scarborough 1998 for a review) and that deficits in PA reliably separate reading disabled (RD) from non-impaired (NI) children (Stanovich & Siegel 1994). Moreover, instruction in PA promotes the acquisition of reading skills (Ball & Blachman 1991; Foorman et al. 1998; Torgesen et al. 1992; Wise & Olson 1995). Although the exact role of PA is still debated (cf. Castles & Coltheart 2004; Goswami & Bryant 1990), the prominent view has it that PA plays a critical function in connecting reading processes to speech processes that are already well-developed by the time of initial reading acquisition. By examining PA in relation to the functional activation associated with both print and speech processing tasks, the current study attempts to elucidate the role of PA by characterizing, at the level of brain organization, the neural mechanisms by which metaphonological processing abilities might influence reading development.

Whereas several functional imaging studies have confirmed the relationship between reading skill and brain activation in young readers (Hoeft et al. 2007; Shaywitz et al. 2002), relatively few studies have examined the functional regions engaged during metaphonological processing of speech materials. Moreover, studies that have examined metaphonological processing have largely examined non-impaired adult readers and have sought to identify regions involved in these metaphonological processing tasks in general, not to examine the relationship between PA *skill* and cortical activation patterns during early literacy acquisition. For example, researchers have examined functional activation during tasks that involve metaphonological judgments such as syllable counting (Poldrack et al. 1999) and phoneme segmentation (Burton et al. 2000) in attempts to locate the regions that support phonological awareness. In one such study, Katzir et al. (2005) adapted a PA task, sound matching, in which participants indicated whether two pictures began with the same sound. Compared to control conditions in which participants indicated whether two pictures were representations of the same object, sites in the left superior and inferior frontal gyri, insula, and thalamus exhibited greater activation for the PA task. Among the sites identified in this study, the LH inferior frontal gyrus (IFG) is commonly implicated in phonological processing (Fiez & Peterson 1998; Frost et al. 2005; Pugh et al. 1996; Rumsey et al. 1997) and exhibits differences between reading disabled and non-impaired readers (Brunswick et al. 1999; Rumsey et al. 1997; Shaywitz et al. 1998). This suggests that the LH IFG may play a role in developing associations between speech and print and hence early reading development.

Of particular relevance to the current study is a recent examination of the relationship between PA skill, brain activation, and reading in young children. As part of a cross-sectional study examining developmental changes in reading, Turkeltaub et al. (2003) examined correlations between phonological awareness measured behaviorally and functional activation during an implicit reading task. The authors found that PA for children ages 6–18 was significantly correlated with activation of the posterior aspect of the left superior temporal gyrus (STG) and several left IFG sites. In conjunction with their developmental findings demonstrating early engagement of STG in reading acquisition, Turkeltaub et al. suggest that the degree of LH STG activity may serve as an early predictor of reading outcome.

In the current study, we build upon this previous research by examining the relationship between phonological awareness and brain activation in several ways. Specifically, we examine the relationship between PA and functional activation in beginning readers using an explicit language-processing paradigm in which we manipulate level and type of language processing (Fig. 1). In our task, participants are presented with a picture cue and then make match/mismatch identity judgments to spoken and printed tokens. We suggest that this modality contrast is critical for understanding how metaphonological processing abilities influence reading development. Although the previous studies provide important information, both about brain regions engaged during metaphonological processing and the relation between PA and print activation, none of the studies address whether the relation between PA and activation is specific to printed language. Because the prominent view of the role of PA is that it provides an entry for print processing to make contact with areas already engaged by well-instantiated spoken language processes, comparing activation patterns for print and speech allows us to test the intuition that greater PA skill will be associated with increased overlap in the regions activated by print and speech.

In addition to the principal modality manipulation, we include real words and pseudowords in each modality in order to examine lexicality effects in relation to metaphonological skill. Finally, we also include "non-pronounceable" printed consonant strings, which we can compare to printed pseudowords in order to examine the neurobiological signature of phonological and orthographic well formedness. Previous

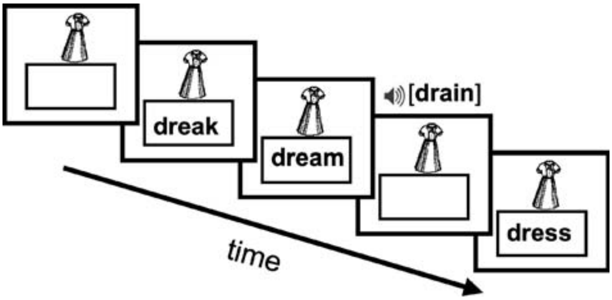

Fig. 1 Schematic of fMRI paradigm in which a picture cue is displayed and participants make identity match/mismatch judgments to print and speech tokens

fMRI studies have shown that pronounceability contrasts yield greater activation for pronounceable words and pseudowords than consonant strings in ventral occipitotemporal cortex, a region that plays a critical role in the acquisition of reading skill (Booth et al. 2001; Shaywitz et al. 2002) and response to reading intervention (Temple et al. 2003; Simos et al. 2002; Shaywitz et al. 2004).

Methods

Participants The data presented here represent an initial report from an ongoing longitudinal study of early reading development, which examines relations among genes, neuroanatomy, neurochemistry, neurocircuitry, and behavior over the course of 2 years in children of varying reading ability from typically developing to children at risk for developing RD. Forty-three native speakers of English (24 males; 19 females) volunteered for the study in the experiment in exchange for payment. All subjects were right-handed native English speakers and had normal or corrected-to-normal vision and normal hearing with no history of neurological impairment and a full-scale IQ of at least 80. Participants ranged in age from 6 to 10 years at time of testing (median 8.04). Informed assent was obtained in compliance with Yale University's human subject protection guidelines.

Behavioral testing Prior to functional imaging, participants completed a behavioral battery at the Yale Reading Center to measure phonological awareness (including both elision and blending subcomponents), as well as to characterize their word reading/decoding, comprehension, vocabulary, and IQ. Measures were obtained from five standardized test batteries: the Woodcock-Johnson III Tests of Achievement (WJ; Woodcock et al. 2001); the Tests of Word Reading Efficiency (TOWRE; Torgesen et al. 1999); the Comprehensive Test of Phonological Processing (CTOPP; Wagner et al. 1999); Peabody Picture Vocabulary Test (PPVT; Dunn & Dunn 1997); and the Wechsler Abbreviated Scale of Intelligence (WASI; The Psychological Corporation 1999). Summary statistics for the sample are provided in Table 1. We report standardized scores for descriptive purposes because they afford comparison to other samples. However, because our interest in the study was to examine how metaphonological skill correlates with brain activation instead of how skill level relative to peers of the same age and/or grade correlates with activation, analyses utilized raw scores or, when necessary, composite scores derived from the component measures by averaging z scores.

fMRI paradigm A cue-target identity task was employed using an event-related protocol that required a match/mismatch judgment on each trial via a button press. Each functional run began with a picture cue of an animal or common object, pretrained to ensure a high degree of familiarity, presented in the upper central portion of the display (e.g., a picture of a DRESS) with a box beneath (see Fig. 1 for a schematic of the design). Each picture remained on the screen through approximately a quarter of the run after which it was replaced by another picture. Picture cues were treated as a trial condition and initially presented on the screen alone, allowing sufficient time to model separately the evoked responses to processing of the picture cues and for participants to encode the picture for comparison to the stimuli on subsequent trials. The majority of trials (80%) were mismatches, and only data from mismatch trials were included in analyses so that brain responses were compared on a common "mismatch" decision. Six types of mismatch trials were presented: (1, 2) spoken and printed high-frequency (HF) monosyllabic real words (e.g.,

Table 1 Descriptive statistics for behavioral measures and age (N=43)

	Mean	SD	Range
Age	8.04	0.49	6.4–10.7
CTOPP phonological awareness	107.77	15.37	67–145
Elision	13.34	5.30	5–17
Blending words	13.25	2.79	4–20
WJ-III letter-word ID	131.14	15.98	87–142
WJ-III word attack	111.83	11.73	88–138
TOWRE sight word efficiency	107.98	15.66	81–139
TOWRE phonemic decoding efficiency	105.37	14.93	84–131
CTOPP phonological memory	102.08	12.29	82–130
PPVT	114.47	11.50	85–142
WASI performance IQ	110.47	17.62	80–145

All measures except age are age-normed standard scores (mean=100; SD=15). Summary statistics are provided in terms of standardized scores for descriptive purposes that afford comparison to other samples. Elision and blending words subscores for CTOPP phonological awareness are raw scores (number correct out of a total of 20)

DREAM); (3, 4) spoken and printed monosyllabic pseudowords (e.g., DREAK); (5) printed HF monosyllabic words that are semantically related to the picture (e.g., SHIRT)[1], and (6) printed consonant strings (e.g., DRLST). Print stimuli were displayed in the box beneath the picture cue for 2,000 ms in 18-point Verdana font and speech stimuli were presented through MR compatible headphones. Stimulus presentation and response collection was controlled by a PC running E-prime 1.2 (Psychology Software Tools, Pittsburgh, PA, USA) and an LCD projector which displayed visual stimuli onto a back-projection screen located at the foot of the MR scanner bed. A mirror placed inside the scanner bore was angled so that participants could view the screen. Participants made responses via button presses with a fiber-optic button box to indicate if the cue and target were the same or if they were different. Prior to functional imaging, a practice session was administered during anatomic scanning. Performance was monitored during the practice to ensure that participants understood the task and corrective feedback was provided if necessary. Participants were also asked whether they were able to hear and see the stimuli clearly and volume and focus adjustments were made as necessary.

fMRI acquisition and analysis fMRI data were acquired using a Siemens 1.5 Tesla Sonata scanner at the Yale School of Medicine. Participants' heads were immobilized in a circularly polarized head coil with a neck support, foam wedges, and a restraining band drawn across the forehead. Prior to imaging, 20 axial-oblique anatomic images [TE (echo time), 11 ms; TR (repetition time), 420 ms; FOV (field of view), 20×20 cm; 6 mm slice thickness, no gap; 256×256×1 NEX (number of excitations)] were prescribed parallel to

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[1] Our interest in including the semantic mismatch condition is to address a longitudinal question about the relative influence of semantic and phonological processes over time and is therefore not examined in the context of this report focused on data acquired at entry into the study.

the intercommissural line based on sagittal localizer images (TE, 7.7; TR, 500 ms; FOV, 25.6 cm; 5 mm slice thickness, no gap; 256×256×1 NEX). Activation images were collected using single shot, gradient echo, echo planar acquisitions [FA (flip angle), 80°; TE, 50 ms; TR, 2,000 ms; FOV, 20×20 cm; 6 mm slice thickness, no gap; 64×64×1 NEX] at the same 20 slice locations used for anatomic images. High-resolution anatomical images were gathered for 3D reconstruction (sagittal MPRAGE acquisition, FA, 8°; TE, 3.65 ms; TR, 2,000 ms; FOV, 25.6×25.6 cm; 1 mm slice thickness, no gap; 256×256×1 NEX; 160 slices total). Trials were presented at jittered intertrial intervals (ITIs) of 4, 5, 6, and 7 s durations with occasional longer ITIs (i.e., null trials); visual targets remained onscreen for 2 s. A maximum of ten imaging runs of 3:46 each (3:38 plus 8 s for image stabilization) was obtained for each participant (median=8) with all conditions represented in each run.

Data analysis was performed using software written in MATLAB (Mathworks, Natick, MA, USA). Images were sinc-interpolated to correct for slice acquisition time, motion-corrected with SPM-99 (Friston et al. 1995) and spatially smoothed with a 5.15-mm FWHM Gaussian filter. Images that exceed a tolerance of 2 mm displacement or 2 rotation from the first image in the entire functional series were discarded as well as images that exceeded an image-to-image change of 1 mm displacement or 1 mm rotation. Single-subject event-related analysis used a regression-based method for direct estimation of the hemodynamic response for each trial type, at each voxel separately, without prior specification of a reference function (Miezin et al. 2000). Parameters from this regression model were used to uniquely estimate the mean response for each condition from −3 to +15 s relative to stimulus onset. Subject activation maps were created using the regression estimates to calculate the mean difference in activity for an activation period (3–8 s post-trial onset) relative to a baseline period (0–3 s prior to trial onset) for each condition. Linear contrasts for effects of interest were applied to these regression estimates to obtain contrast images for each participant. Across participants, each voxel in these contrast images was tested versus zero with an F test, implementing a mixed-factors or repeated measures analysis of variance (Kirk 1982). For each participant, a nonlinear transformation to MNI space was obtained using BioImageSuite (www.bioimagesuite.org; Papademetris et al. 2003), mapping between the subject-space high-resolution anatomic and the standard brain space defined by the Montreal Neurological Institute (MNI) “Colin” brain (www.bic.mni.mcgill.ca). Prior to across-subjects analysis, this transformation was applied to the single-subject activation maps, with trilinear interpolation, into 2 mm isotropic MNI space.

Results

fMRI task performance Accuracy levels for the cue-target matching task were routinely high, averaging 85% correct (84% for print trials and 86% for speech trials). Given the 80:20 ratio of mismatch to match responses, nonparametric measures of sensitivity (A') and bias (B''_D) were calculated to assess performance. Mean values of 0.89 (SD=0.09) and 0.11 (SD=.25) were obtained for A' and B''_D, indicating a high level of sensitivity and little bias. In order to ensure that the task was developmentally appropriate and that any correlations between functional activation patterns and PA would be attributable to processing differences and not differences in effort, we conducted analyses examining whether PA modulated task performance. Analyses revealed no significant correlation between PA and bias but a significant positive correlation between PA and sensitivity, $r(43)=0.472$, $p<0.001$. Although increases in PA were associated with higher accuracy, even lower PA participants still produced high levels of A' as indicated by a median split on PA (lower PA=0.87; higher PA=0.92) indicating, in our assessment, that the task was developmentally appropriate for our participants. Examination of latency data also revealed that a significant negative correlation between PA and reaction times, $r(43)=-0.35$, $p<0.05$, such that as PA increased, reaction time decreased. No other interactions with PA were obtained.

fMRI activation As mentioned in the first part of the text, we were interested in a number of comparisons, including modality (print vs. speech), lexicality (words vs. pseudowords), and pronounceability (printed pseudowords vs. consonant strings). However, lexicality did not interact with PA either behaviorally or neurobiologically; therefore, lexicality effects are not discussed further.

Activations to print, speech, and overlap Given that the development of PA may provide the point of entry by which spoken and printed language connect in brain, we were particularly interested in whether correlations between PA and functional activation patterns for speech and print would be observed in areas primarily engaged in speech processing, printed language processing, or both. Figure 2 shows those areas that are more active for print than speech (yellow/red) and areas that are more active for speech than print (blue/purple). Also shown in Fig. 2 are the results of a conjunction analysis (Hadjikhani & Roland 1998), which identifies regions that were significantly active for both tasks (shown in green), regardless of whether they were differentially active for speech or print. Print stimuli produced greater activation than speech stimuli in a swath of striate and extrastriate cortex, including LH occipito-temporal cortex that has been associated with development of reading skill. Speech stimuli produced greater activation than print primarily in the superior temporal gyrus bilaterally. Both print and speech produced activation of sites in IFG, insula, and cerebellum bilaterally, although visual inspection indicates that the extent in the LH was greater than the RH. Moreover, although the LH occipito-temporal region was more active for print than speech tokens, this region was also active for speech as well.

Correlation of PA with modality In the next step, we conducted brain–behavior correlation analyses to examine the relationship between PA and functional activation. Again, we were particularly interested in whether correlations between PA and fMRI modality and pronounceability effects would be observed in areas engaged in speech processing, print processing, or both.

A correlation map of the relation between PA and the modality effect was generated by computing the Pearson correlation coefficient (r) across subjects, between each subject's phonological awareness score, and the regression parameter estimate for the contrast of print minus speech, at each voxel separately (Pugh et al. 1997). For clarity of description, we present the results of correlations of PA to both the simple activations to print and speech separately as well as the more theoretically interesting contrast of activations to print minus speech. Table 2 presents the results of this analysis, which isolates regions at which differences in activation levels for speech and print are related to PA. A significant correlation between PA and the magnitude of the modality effect was observed in two left hemisphere regions previously implicated in language processing; (1) the occipito-temporal region (OT; $r(43)=0.538$, $p<0.001$) and (2) the superior temporal gyrus (STG). Two distinct loci were observed in the STG, one close to the planum temporale in primary auditory cortex (BA 41/42, MNI Z-coordinate$=-2$; $r(43)=.484$, $p<0.001$) and a more superior posterior site (BA 22, $Z=16$; $r(43)=0.444$, $p<0.005$) close to the superior temporal sulcus (Fig. 3a). In order to illustrate the form of the interaction, we extracted activation values for each subject at voxels that showed a significant modality effect in the composite

Fig. 2 Areas of activation for speech and print and overlap. Areas more active for print than speech are shown in *yellow/red*, and areas more active for speech than print are shown in *blue/purple*. *Green areas* were significantly active in both tasks. Images are presented in radiological convention with the left hemisphere on the right side of the images at a univariate threshold of $p<0.0001$, corrected for mapwise false discovery rate (FDR; Genovese et al. 2002) with a cluster threshold of ten contiguous significant voxels. *Numbers on the left side of the image* correspond to the position along the *Z*-axis in MNI space

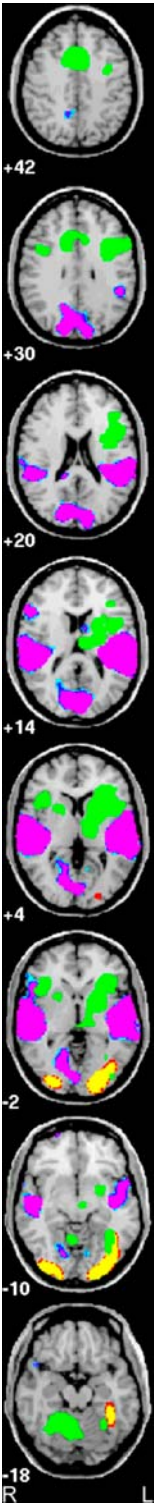

Table 2 Regions showing a correlation of phonological awareness with modality (print–speech)

Region	Volume	MNI coordinates (peak voxel)					
	(mm^3)	*X*	*Y*	*Z*	Peak *r*	*r* Print	*r* Speech
L. occipito-temporal/fusiform	2,984	−34	−56	−18	0.538	0.510	−0.130
R. superior parietal lobule	1,168	36	−74	51	0.547	0.322	−0.321
L. posterior thalamus	776	−28	−22	−2	0.517	0.438	−0.130
R. supramarginal	768	36	−44	30	0.498	0.310	−0.228
L. superior temporal	624	−58	−22	2	0.484	0.356	−0.205
L. parahippocampus	560	−30	−14	−14	0.467	0.005	−0.206
R. lingual	528	8	−54	4	0.439	0.372	−0.066
R. cuneus	376	10	−64	12	0.451	0.325	−0.146
R. lateral occipital	368	38	−84	26	0.450	0.412	−0.080
L. anterior thalamus	320	−10	−2	0	0.493	0.380	−0.116
L. superior temporal	320	−54	−36	14	0.444	0.354	−0.078
L. medial frontal/orbital	816	2	50	−20	−0.586	−0.09	0.432

Also shown are the simple correlations with print and corresponding speech tokens. *r* values greater than ±0.484 significant at $p<0.001$. *r* values greater than ±0.30 significant at $p<0.05$

map and generated scatterplots of the correlations of PA with speech and PA with print for the OT and the superior STG region[2] (Fig. 4**a**, **b**).

Correlation of PA with pronounceability Table 3 presents the regions showing a correlation between PA and pronounceability, i.e., the contrast of printed pseudoword minus consonant strings. Because these two stimulus types should be equally unfamiliar to participants, this comparison isolates regions for which the relationship between PA and activation for print is a function of whether the stimuli are phonologically well formed or not. Figure 5 shows that significant correlations between PA and pronounceability were observed in several language-related regions, including a left STG site near planum temporale ($Z=-2$; $r(43)=0.516$, $p<0.001$) and a left posterior superior STG site near the superior temporal sulcus ($Z=16$; $r(43)=0.571$, $p<0.0001$), both of which overlap with the areas observed in the analysis of PA by modality. A site in the left IFG also expressed a correlation between PA and pronounceability ($r(43)=0.587$, $p<0.0001$). We illustrate these relationships by showing scatterplots of the correlations of PA with pseudowords and PA with consonant strings for the superior STG and IFG regions (Fig. 6**a**, **b**). Given the importance of the occipito-temporal region in previous studies of decoding and word reading skill (Shaywitz et al. 2002; Temple et al. 2003; Turkeltaub et al. 2003), it is worth noting that the pronounceability effect was also correlated with PA in this region as well ($r(43)=0.415$, $p<0.01$; Fig. 5**a**), although the spatial extent of this activation (128 mm^3) did not meet our threshold for inclusion in Table 3.

Previous studies have shown significant correlations between a measure of printed pseudoword decoding skill, Woodcock Johnson Word Attack (WA), and activation during printed word recognition tasks (Hoeft et al. 2007; Shaywitz et al. 2002). Given these previous findings and because behavioral scores on PA and WA were strongly correlated for

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[2] As shown in Tables 2 and 3, sites in STG show the same pattern of correlations. In the interest of brevity and simplicity, we selected just one of the sites for illustrating the pattern and for use in the multiple regression analyses described below.

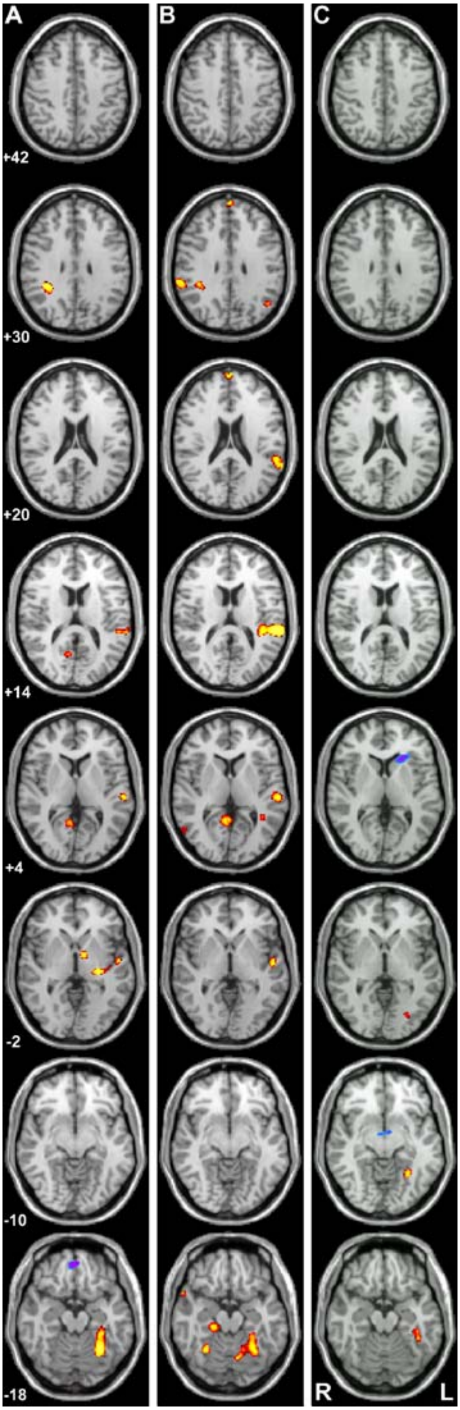

Fig. 3 Correlations of print–speech modality effect with phonological awareness composite (**a**) and elision (**b**) and blending (**c**) subcomponents, $p<0.01$, FDR corrected (Genovese et al. 2002) with a cluster threshold of ten contiguous significant voxels

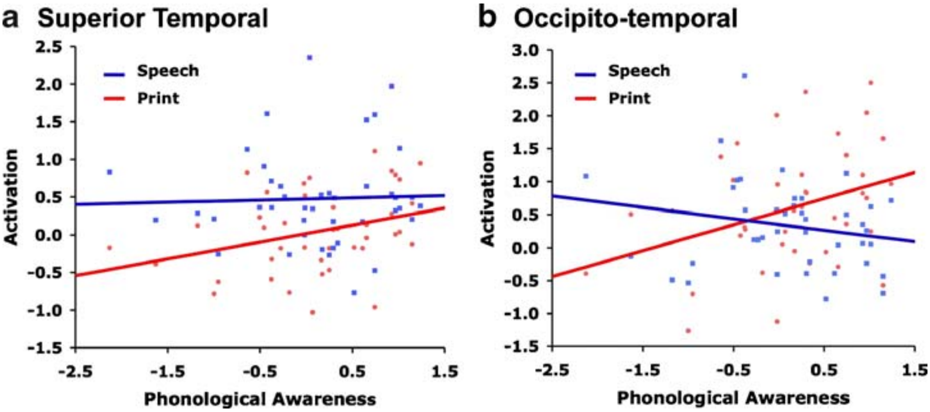

Fig. 4 Scatterplots of correlations of PA with speech and PA with print for the superior STG (**a**) and OT (**b**) regions

our participants, $r(42)=0.656$, $p<0.0001$, we conducted analyses to determine where the correlations between PA and activation were mediated by printed word reading/decoding ability. We extracted activation values for each subject at voxels in each region that showed either a significant correlation between PA and modality or a significant correlation between PA and pronounceability and subjected the values to a multiple regression with the derived PA composite scores and WA *z* scores as predictors of activation level at each region.[3] As shown in Tables 4 and 5, when entering both PA and WA into the regression model, only PA was a significant predictor of activation levels in each region, except for the model examining pronounceability in the occipito-temporal region. WA was not a significant predictor of activation for the STG or IFG regions (all $F<1$), suggesting that the modality and pronounceability effects in these regions were driven uniquely by individual differences in PA, not by correlated early reading indices. In the occipito-temporal region, both PA and WA were significant in simple regression models; however, when both were entered into the model simultaneously, only WA continued to be a significant predictor.

PA: A multicomponent construct

A number of metaphonological tasks have been used to measure PA, including blending strings of orally presented segments such as syllables or phonemes into smoothly articulated words or pseudowords and eliding segments from a spoken word to form a new word. Although there appears to be general agreement that these tasks tap the same underlying construct, there are indications from the literature that various PA tasks differ in their difficulty and/or sensitivity at points in the developmental continuum (Anthony et al. 2007; Schatschneider et al. 1999; Vloedgraven & Verhoeven 2007). Moreover, it is an open question whether these PA tasks may emphasize differential aspects of PA and thus have different neurobiological signatures. We explored this issue by conducting separate correlations of the elision and blending subtest scores of the CTOPP with functional

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[3] Word Attack scores (mean raw score=17.78; SD=6.97; range 3–30) were not obtained for one of the participants; therefore these analyses only include data from 42 of the 43 participants.

Table 3 Regions showing a correlation of phonological awareness with pronounceability (pseudowords-consonant strings)

Region	Volume	MNI coordinates (peak voxel)					
	(mm^3)	X	Y	Z	Peak r	r Pseudoword	r Consonant
R. superior frontal	5,960	8	62	20	0.558	0.297	−0.445
R. lingual	3,672	8	−58	2	0.494	0.406	−0.056
L. cuneus	2,456	−10	−92	18	0.544	0.429	−0.076
L. parahippocampus	1,816	−28	−40	−4	0.469	0.349	−0.172
R. fusiform	1,608	26	−46	−21	0.488	0.208	−0.210
R. posterior middle temporal	1,448	62	−62	−8	0.599	0.556	−0.238
L. precuneus	1,416	−12	−62	19	0.456	0.405	−0.116
R. lateral occipital/middle temporal	1,408	40	−78	20	0.483	0.204	−0.397
L. inferior frontal	1,216	−56	34	6	0.587	0.327	−0.326
L. cerebellum	1,160	−20	−80	−20	0.530	0.339	−0.206
L. superior frontal	1,072	−10	52	36	0.482	0.462	−0.100
L. Superior Temporal	960	−52	−2	−2	0.516	0.286	−0.318
R. Fusiform	928	32	−66	−12	0.539	0.348	−0.169
R. Thalamus	768	22	−18	−6	0.482	0.231	−0.446
L. Superior Temporal	456	−44	−40	16	0.571	0.439	−0.183
L. Superior Parietal Lobule	400	−24	−82	40	0.480	0.271	−0.224
L. Thalamus	392	−24	−24	−3	0.451	0.360	−0.142
L. Lateral Occipital/Middle Temporal	384	−42	−76	20	0.497	0.224	−0.307
R. Cuneus	336	16	−90	12	0.452	0.423	0.034

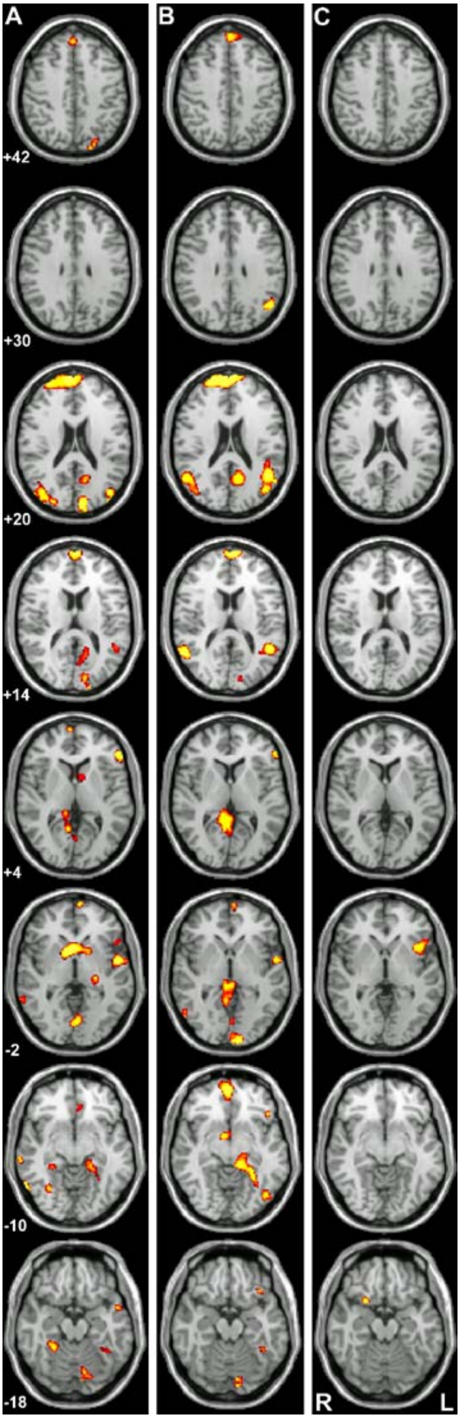
Also shown are the simple correlations with pseudowords and consonant strings. r values greater than ±0.484 significant at $p<0.001$; values greater than ±0.30 significant at $p<0.05$

activation levels for the regions of interest described above from both the modality contrast and the pronounceability contrasts.

Modality Figure 3**b** and **c** shows the correlations with modality for elision and blending, respectively. As the figure shows, whereas the correlation in LH STG is driven by elision, the correlation in LH OT is seen both for elision and blending with the region of significant correlation being larger for elision relative to blending. In order to test these observations, we extracted activation values for these regions of interest as described above and performed multiple regression analyses with elision and blending scores as predictors (Table 6). Results of the multiple regression confirmed the observations from the individual correlation maps for the LH STG regions; however, in LH OT, a marginal effect was observed for each of the predictors, suggesting that the effect observed in the individual correlation maps was driver by common variance shared by the two PA tasks.

Pronounceability Figure 5**b** and **c** shows the correlations with pronounceability for elision and blending, respectively. Here, we show that while the correlations in LH STG and LH OT are driven by elision ability, the correlation in LH IFG is accounted for by both elision and blending. Multiple regression analyses on these regions confirmed these observations (Table 7) with only elision accounting for unique variance in the pronounceability effect in

Fig. 5 Correlations of pseudoword—consonant string pronounceability effect with phonological awareness composite (**a**) and elision (**b**) and blending (**c**) subcomponents, $p<0.01$, FDR corrected (Genovese et al 2002) with a cluster threshold of ten contiguous significant voxels



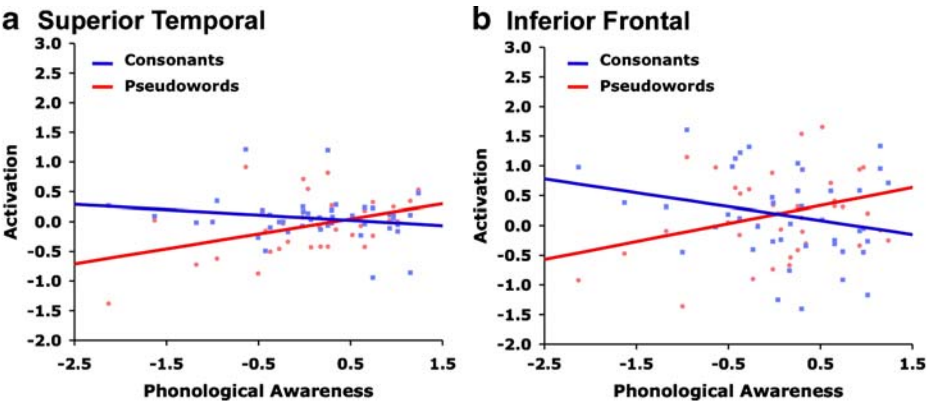


Fig. 6 Scatterplots of the correlations of PA with pronounceability and PA with print for the superior STG (**a**) and IFG (**b**) regions

LH STG and LH OT. In LH IFG, although the regression model was significant, both predictors yielded marginal effects, indicating that variance shared by elision and blending accounted for the effects observed in the individual correlation maps.

Taken together, these findings show that elision and blending measure are overlapping but are partially distinct constructs with respect to functional activation. Moreover, the findings show that elision accounts for the largest portion of the variance in our findings with the composite of these PA tasks, consistent with the results from previous behavioral studies mentioned above suggesting that elision is a more sensitive measure of important individual differences in metaphonological skill than blending.

Discussion

The present study examined the neurobiological underpinning of phonological awareness, a variable long known to successfully predict development of early reading skills and reliably distinguish reading disabled from non-impaired readers. The findings provide additional insight into how these variables operate at the early stages of reading development across varying levels of ability, showing that PA modulates the functional neuroanatomy associated with modality and pronounceability in beginning readers.

For our modality comparison, individual differences in PA were associated with significant changes in the relative activation levels for print and speech in the LH superior temporal and occipito-temporal gyri. More specifically, increases in PA were associated with increases in activation for print tokens such that the activation level for print approached the level obtained for speech in LH STG, the primary region activated for speech. For print, the response in posterior STG was further selective such that only phonologically well-structured stimuli (i.e., pseudowords but not consonant strings) activated this region with increases in PA. In LH OT, a region also engaged by spoken tokens, increases in PA were associated with a relative decrease in activation for speech and a relative increase in activation for print tokens. From these data, it appears that LH OT becomes increasingly more dedicated to processing of print relative to speech as individuals acquire greater literacy skills.

As described in the first part of the text, many studies attest to the importance of PA as a precondition for reading acquisition. However, studies have demonstrated that the

Table 4 Multiple regressions examining the contribution of phonological awareness and decoding (Word Attack) in activation of the LH STG and OT for modality

Region	Variable	β	t value	p value
Superior temporal				
	Word attack	−0.167	−0.866	0.3920
	Phonological Awareness	0.509	2.641	0.0118
Multiple R^2 0.175				
Occipito-temporal				
	Word attack	−0.351	−1.815	0.0772
	Phonological awareness	0.545	2.819	0.0075
Multiple R^2 0.169				

relationship between PA and reading skill is reciprocal; PA begets reading achievement (decoding), which begets further development of PA (e.g., Perfetti et al. 1987; Wagner et al. 1994). Given the reciprocal relationship between reading skill and PA, we wanted to determine whether our findings were specific to PA or reflected an indirect measure of facility with reading. We therefore conducted multiple regression analyses to assess whether the observed PA effects in LH STG, LH OT, and LH IFG were qualified by print decoding (as indexed by Word Attack). LH OT was the only region where PA effects were qualified by decoding skill such that WA was the only significant predictor of the pronounceability effect in OT (even though PA had a strong zero order correlation with pronounceability in this region). However, WA did not qualify the relation between PA and modality in this region, indicating a complex dynamic between speech and reading processes in this region, perhaps reflecting the reciprocal relationship between PA and reading skill and findings suggesting that the representation of spoken language is influenced by learning to read (Castro-Caldas et al. 1998; Morais 1993; Petersson et al. 2007; Ziegler & Goswami 2005). This possibility that spoken language shapes the developing specialization of the LH OT for written language is also consistent with data from the current study and previous work showing that this region is also activated during spoken language processing (Chee et al.

Table 5 Multiple regressions examining the contribution of phonological awareness and decoding (Word attack) in activation of the LH STG, OT, and IFG for pronounceability

Region	Variable	β	t Value	p Value
Superior temporal				
	Word attack	−0.013	−0.068	0.9461
	Phonological awareness	0.403	2.065	0.0456
Multiple R^2 0.155				
Occipito-temporal				
	Word attack	0.395	2.042	0.0480
	Phonological awareness	0.023	0.120	0.9053
Multiple R^2 0.168				
Inferior frontal				
	Word attack	−0.230	−0.1219	0.2302
	Phonological awareness	0.573	3.033	0.0043
Multiple R^2 0.208				

Table 6 Multiple regressions examining the contribution of elision and blending to activation of the LH STG and OT for modality

Region	Variable	*β*	*t* Value	*p* Value
Superior temporal				
	Blending words	0.034	0.254	0.8005
	Elision	0.575	4.296	0.0001
Multiple R^2 0.344				
Occipito-temporal				
	Blending words	0.254	1.711	0.0947
	Elision	0.280	1.884	0.0666
Multiple R^2 0.189				

1999) as well as research suggesting that the LH OT may be involved in both modality-dependent and modality-independent linguistic processes (Hillis et al. 2005).

Whereas analyses revealed a complex relationship between phonological awareness and print decoding skill in the LH OT skill zone, only PA predicted the relation between activation for print and speech in the superior temporal gyrus. Whereas previous work by Turkeltaub et al. (2003) showed that activation in LH STG for printed word relative to false font strings was correlated with PA, the current study extends this finding by showing PA predicts the overlap in activation for print and speech in LH STG such that increases in PA were associated with greater overlap in activation levels for print and speech in this region. We suggest that the LH STG is important in bridging between print and speech, and more directly reflects on the unique contribution that PA contributes to early literacy development, making the neuronal networks dedicated by nature and early language experience to speech available for print processing.

Additionally, exploratory analyses examining the contributions of elision and blending subcomponents to our PA findings revealed independent and overlapping areas of activation, indicating that PA is a multifaceted construct with dissociable neural representation. Specifically, the modality effect in STG was significant for elision only;

Table 7 Multiple regressions examining the contribution of elision and blending to activation of the STG, OT, and IFG for pronounceability

Region	Variable	*β*	*t* Value	*p* Value
Superior temporal				
	Blending words	0.097	0.669	0.5071
	Elision	0.432	2.969	0.0050
Multiple R^2 0.223				
Occipito-temporal				
	Blending words	0.020	0.130	0.8975
	Elision	0.358	2.327	0.0250
Multiple R^2 0.133				
Inferior frontal				
	Blending words	0.239	1.593	0.1088
	Elision	0.270	1.795	0.0801
Multiple R^2 0.172				

the effect for blending was not even marginal. Whereas the simple correlations of elision and blending with the modality effect in the LH OT were significant for both subcomponents, multiple regression analysis suggested that the effects in this region were accounted for largely by variance shared by the two tasks. A pattern of higher peak values and greater spatial extent for elision was also observed in the comparison of printed pseudowords versus consonant strings and supported by results of multiple regression. One possibility is that these PA subcomponents are differentially sensitive, at least in the age and skill range that we examined in the current study.[4] Some findings from a recent study by Vloedgraven and Verhoeven (2007) examining PA in kindergarten and first graders support this possibility, showing that items measuring phoneme segmentation were the most discriminating between high- and low-ability individuals relative to blending, rhyming, or identification. Moreover, the mean and range of the raw scores for elision and blending are quite similar, making the findings unlikely to be related in any simple manner to difficulty of these tasks (see Table 1).

The fact that the relation between PA skill level and print-speech modulation is expressed in a well-documented speech region, STG fits with two common observations: (1) that writing in an alphabetic orthography is essentially a cipher on the phonological level of language and (2) that it is phonological awareness, in conjunction with the understanding that the letters of a printed word map to phonemes, allows readers to connect printed words to the corresponding words in his or her speech lexicon. Moreover, functional neuroimaging studies have demonstrated extensively the importance of STG in printed language processing (Simos et al. 2002). For example, a recent study showed that reading-disabled children exhibited little or no activation of posterior LH STG prior to a reading intervention (Simos et al. 2002; see Temple et al. 2003 for similar findings). Post-intervention scans revealed that increase in posterior LH STG was significantly correlated with improvement on pseudoword rhyming, a task that requires mapping from the printed form to phonology. We suggest that the correlation in STG between the modality effect and PA observed in the current study elucidates the nature of this mapping, such that more skilled beginning readers engage their already well-developed spoken language regions for processing written language.

Our findings in the LH occipito-temporal region, that is, a relatively increasing activation associated with print and corresponding decreasing activation associated with speech processing as PA increased, converge with previous work in suggesting that as literacy skills develop, this region becomes increasingly tuned to print (e.g., Shaywitz et al. 2002 Paulesu et al. 2001; Rumsey et al. 1997; Salmelin et al. 1996; Shaywitz et al. 2002; Shaywitz et al. 1998).

By using an explicit language processing task which allowed us to examine the relationship between PA skill and modality and PA skill and pronounceability, the current study yields a fuller understanding of the neurobiological signature associated with the development of phonological awareness and the means by which this skill might exert an influence on subsequent reading development. Our results suggest that the degree to which

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[4] Our approach was to examine the correlation between raw PA skill and functional activation. However, we did conduct multiple regression analyses with age as a predictor in order to ensure that the effects in the regions of interest we report were not accounted for or qualified by individual differences in age. We felt that this was particularly important for the analyses involving elision and blending given that studies have suggested that blending more accurately discriminates metaphonological skill in younger children, whereas and elision is a better discriminator in older children. Results of the analyses revealed no effect of age, and all of the effects for each region discussed remained significant.

activation for print increases, relative to activation for speech in LH STG and LH OT may be an early predictor of successful reading acquisition. Although the findings from the current study are provocative, we point out that magnitude of the correlations reported here are modest in size and leave much variance for which future work will need to account. Our continuing research in the context of this longitudinal study will provide a means to assess the specificity of this biomarker and its subcomponents (elision and blending) by examining the degree to which these modulations are sensitive predictors of later reading skill and diagnosis reading disability.

Acknowledgments This study is supported by National Institute of Child Health and Human Development grant HD 01994 to Carol Fowler (Haskins Laboratories) and NICHD grant HD 048830 to Kenneth R. Pugh (Yale University). We thank Gina DellaPorta, Kelley Delaney, and Ashley Zennis, for behavioral assessment and Hedy Serofin and Teri Hickey for help with imaging participants.

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