Development of Brain Mechanisms for Processing Orthographic and Phonologic Representations

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Abstract

Developmental differences in the neurocognitive networks for lexical processing were examined in 15 adults and 15 children (9- to 12-year-olds) using functional magnetic resonance imaging (fMRI). The lexical tasks involved spelling and rhyming judgments in either the visual or auditory modality. These lexical tasks were compared with nonlinguistic control tasks involving judgments of line patterns or tone sequences. The first main finding was that adults showed greater activation than children during the cross-modal lexical tasks in a region proposed to be involved in mapping between orthographic and phonologic representations. The visual rhyming task, which required conversion from orthography to phonology, produced greater activation for adults in the angular gyrus. The auditory spelling task, which required the conversion from phonology to orthography, also produced greater activation for adults in the angular gyrus. The greater activation for adults suggests they may have a more elaborated posterior heteromodal system for mapping between representational systems. The second main finding was that adults showed greater activation than children during the intra-modal lexical tasks in the angular gyrus. The visual spelling and auditory rhyming did not require conversion between orthography and phonology for correct performance but the adults showed greater activation in a system implicated for this mapping. The greater activation for adults suggests that they have more interactive convergence between representational systems during lexical processing.

INTRODUCTION

In a series of studies, Booth et al. (2002a, 2002b) have developed a neurocognitive model of lexical processing using functional magnetic resonance imaging (fMRI). This model suggests that auditory word forms (phonologic representations) involve the superior temporal gyrus, visual word forms (orthographic representations) involve the fusiform gyrus, and meaning forms (amodal semantic representations) involve the middle temporal gyrus (Booth, Burman, Meyer, Zhang, et al., 2003; Booth et al., 2001, 2002a, 2002b). Interactions among these representations are mediated by posterior heteromodal regions including the supramarginal and angular gyrus. In cross-modal tasks that require the conversion of orthography to phonology (rhyming judgments to visually presented words), for example, better performance in adults is associated with greater supramarginal/angular gyrus and superior temporal gyrus activations (Booth, Burman, Meyer, Gitelman, et al., 2003). Similarly, in cross-modal tasks

that require the conversion of phonology to orthography (spelling judgments to auditorily presented words), better performance is associated with greater supramarginal/angular gyrus and fusiform gyrus activations (Booth, Burman, Meyer, Gitelman, et al., 2003). However, developmental differences in the neurocognitive networks involved in cross-modal tasks have not been investigated. Because children are less skilled at lexical processing than adults, we expected that children may show less activation in the supramarginal/angular gyrus for mapping between orthographic and phonologic representations during cross-modal tasks. This greater activation in this posterior heteromodal system may reflect greater elaboration of this system to represent different levels of mapping between orthographic and phonology. Indeed, several behavioral studies have argued for skilled lexical processing involving a mechanism that includes grapheme–phoneme, onset–rime, syllabic and word level mappings for both reading (Ehri, 1995; Marsh, Friedman, Welch, & Desberg, 1981; Gough & Hillinger, 1980) and spelling (Nunes, Bryant, & Bindman, 1997).

Skilled lexical processing may also be characterized by enhanced interactivity between the orthographic and phonologic representational systems. VanOrden, Pennington, and Stone (1990) and VanOrden and Goldinger (1994) have argued that efficient processing is characterized by resonance between representational systems (VanOrden & Goldinger, 1994; VanOrden et al., 1990). Resonance between systems occurs when input to the orthographic system closely matches the information that is fed back from the phonologic system or vice versa. Several lines of research suggest that skilled readers activate phonologic information when reading earlier and more automatically than less skilled readers (Booth, Perfetti, MacWhinney, & Hunt, 2000; Plaut & Booth, 2000; Booth, Perfetti, & MacWhinney, 1999). There is also a 25-year history of behavioral research with adults illustrating the influence of orthographic information on the speed of spoken word recognition (Ziegler & Ferrand, 1998; Dijkstra, Roelofs, & Fieuws, 1995; Jakimik, Cole, & Rudnicky, 1985; Donnenwerth-Nolan, Tanenhaus, & Seidenberg, 1981; Seidenberg & Tanenhaus, 1979). Research shows that the influence of orthography on auditory language tasks is inconsistent in the early elementary grades and becomes reliable in later elementary grades (Zecker, 1991; Perin, 1983; Tunmer & Nesdale, 1982; Ehri & Wilce, 1980). Research on dyslexics has also found evidence for a reduced role of orthographic knowledge on auditory processing in children with reading disabilities compared to control children (Landerl, Frith, & Wimmer, 1996; Zecker, 1991). All of this research suggests that there may be more interactivity between orthographic and phonologic representations in skilled readers. Because adults are more skilled than children, we expected that adults may show more activation in the supramarginal/angular gyrus even during intra-modal tasks that do not require conversion between orthographic and phonologic representations for correct performance.

Our study examined developmental differences between 15 adults and 15 children (9- to 12-year-olds) in the functional neuroanatomy for lexical processing using visual or auditory lexical tasks that required spelling and rhyming judgments (see Table 1). These visual word judgment tasks were compared to a control condition involving line patterns and the auditory word judgment tasks were compared to a control condition involving pure tones (see Table 2). All tasks involved the sequential presentation of three stimuli and required the participants to determine whether the third stimuli matched one of the previous two stimuli based on a predefined criterion. The goal of this study was to examine whether adults would show greater activation in the supramarginal/angular gyrus during cross-modal and intra-modal tasks. Greater activation in this region during cross-modal tasks would indicate a more elaborate system involved in mapping between orthographic and phonologic representations and greater activation in this region for the intra-modal tasks would indicate greater interactivity between the orthographic and phonologic systems.

RESULTS

Behavioral Performance

Means (and standard errors) for accuracy and reaction time on the lexical and control tasks are presented in Table 3. Only data for the fMRI session are presented because statistical analyses revealed no main effects or interactions involving accuracy or reaction time on the practice versus fMRI sessions. This indicates that the environment of the scanner did not adversely affect the behavioral performance of the adults or children. Table 3 shows that both the adults and children could effectively perform the tasks in the fMRI scanner as all mean accuracy levels were above 80%.

We calculated age (adults, children) by condition (word, control) ANOVAs on accuracy and reaction time separately for each of the lexical tasks in each of the modalities. Adults were more accurate than children on all tasks [visual spelling, $F(1,63) = 21.20$, $p < .001$; visual rhyming, $F(1,63) = 17.76$, $p < .001$; auditory spelling, $F(1,59) = 12.89$, $p < .01$; auditory rhyming, $F(1,63) = 9.27$, $p < .01$]. Adults were also faster than children on all tasks [visual spelling, $F(1,63) = 78.33$, $p < .001$; visual rhyming, $F(1,63) = 69.98$, $p < .001$; auditory spelling, $F(1,59) = 45.11$, $p < .01$; auditory rhyming, $F(1,63) = 65.71$, $p < .01$]. There was a main effect of condition for accuracy on auditory spelling [$F(1,59) = 10.11$, $p < .01$], revealing that word judgment was less accurate than tone judgment for this task. There were main effects of condition for reaction time on all tasks but auditory rhyming, revealing that the word judgment was slower than control judgments [visual spelling, $F(1,63) = 15.88$, $p < .001$; visual rhyming, $F(1,63) = 10.83$, $p < .001$; auditory spelling, $F(1,59) = 20.16$, $p < .01$].

There were no interactions between age and condition for the visual and auditory rhyming tasks for either accuracy or reaction time or for visual and auditory spelling for reaction time. The lack of interactions suggests that any reported fMRI differences may not be attributable to performance differences on these tasks because the exact same analyses (age by condition) were done on the behavioral and fMRI data. However, the main effects for accuracy were qualified by interactions between age and condition for visual spelling [$F(1,63) = 4.09$, $p < .05$] and auditory spelling [$F(1,59) = 4.94$, $p < .05$], indicating that children had especially low accuracy on word judgment for the spelling tasks. This interaction means that part of the developmental effects in the fMRI data may be due to performance differences. In developmental work, it is extremely hard to equate different ages in behavioral performance especially on tasks that tap into explicit judgments of meaningful linguistic contrasts.

Activation for Each Lexical Task

Figure 1 presents significant activation separately for the adults (red) and children (green) in the spelling and rhyming tasks for the visual and auditory modality as compared to the nonlinguistic control tasks (lines or tones). Figure 1 also shows overlap (purple) between the activation maps for the adults and children. Figure 2 presents significantly greater activation for the adults than for children (red) or significantly greater activation for children than for adults (green). The numerical data for Figures 1 and 2 are presented in Tables 4–7. We concentrate our reporting of the results to our regions of interest that included visual association regions (fusiform gyrus, BA 37), auditory association regions (superior temporal gyrus, BA 22), posterior heteromodal regions (angular gyrus, BA 39, and middle temporal gyrus, BA 21), and inferior frontal gyrus (BA 9, 44, 45, 47). All areas of significant activation outside of these regions of interest are presented in the tables and figures.

Visual Spelling Task—Both adults and children showed more activation in the left than right inferior frontal gyrus. However, adults showed significantly greater activation than children in the left (68 voxels) and right (51 voxels) inferior frontal gyrus. Both adults and

children showed activation in the left angular gyrus, but only adults showed activation in the right angular gyrus. Adults showed significantly greater activation in the left (89 voxels) and right angular gyrus (21 voxels). Both adults and children showed more activation in the left than in the right fusiform gyrus and there was no significant developmental difference in this region. Only children showed activation in the left middle temporal gyrus.

Visual Rhyming Task—Both adults and children showed activation in the left inferior frontal gyrus, but only adults showed activation in the right inferior frontal gyrus. Adults showed significantly greater activation than children in the bilateral inferior frontal gyrus (43 voxels for left and 20 voxels for right). Both adults and children showed more activation in the left than in the right fusiform gyrus and there was no significant developmental difference in this region. Both adults and children also showed activation in the left middle temporal gyrus, but only adults showed activation in the left angular gyrus and this activation was significantly greater than for children (34 voxels). Neither the adults nor children showed activation in the left superior temporal gyrus at the $p < .001$ level; however, both the children and the adults showed activation in the left superior temporal gyrus at the $p < .01$ level.

Auditory Spelling Task—Both adults and children showed activation in the left inferior frontal gyrus, but only adults showed activation in the right inferior frontal gyrus. Adults showed significantly greater activation than children in the bilateral inferior frontal gyrus (110 voxels for left and 189 voxels for right). Only adults showed activation in the bilateral angular gyrus and they showed significantly greater activation than children in the left angular gyrus (35 voxels). Both adults and children showed more activation in the left than in the right superior/middle temporal gyrus, but adults showed significantly greater activation in the left superior temporal gyrus (24 voxels) and right middle temporal gyrus (30 voxels). Both adults and children showed activation in the left fusiform gyrus, but children showed significantly greater activation than adults in this region (74 voxels).

Auditory Rhyming Task—Both adults and children showed activation in the left inferior frontal gyrus, but adults showed significantly greater activation in this region (213 voxels). Both adults and children showed more activation in the left than in the right superior/middle temporal gyrus, but adults showed significantly greater activation in the left superior temporal gyrus (23 voxels). Both adults and children showed activation in the left fusiform gyrus and there was no significant developmental difference in this region.

Additional Activation Clusters—The medial frontal gyrus/anterior cingulate was activated for both adults and children for the spelling tasks in both modalities. Only the adults showed activation in the medial frontal gyrus during the visual rhyming task and neither group showed activation in these regions during the auditory rhyming task. In addition, the adults showed activation in the cerebellum for all tasks, but the children only showed activation in the cerebellum in the auditory spelling task.

DISCUSSION

The purpose of this study was to examine developmental differences between adults and 9- to 12-year-old children in the neural substrate for lexical processing using word judgment tasks that required explicit manipulation of orthographic (spelling tasks) and phonologic (rhyming tasks) representations. The left inferior frontal gyrus was activated during all of these tasks for both the adults and children. However, the adults showed significantly greater activation in the left inferior frontal gyrus on the spelling and rhyming tasks in both modalities. This is consistent with previous research that shows developmental increases in the magnitude of activation in the left inferior frontal gyrus during covert verb generation tasks (Holland et al., 2001), overt word generation tasks (Schlaggar et al., 2002), covert verbal fluency tasks (Gaillard et al.,

2003), category judgment tasks (Shaywitz et al., 2002), and implicit reading tasks (Turkeltaub, Garaeu, Flowers, Zefirro, & Eden, 2003). The right inferior frontal gyrus was activated in the adults for all tasks but the auditory rhyming task. The children only activated the right inferior frontal gyrus during the visual spelling task. In a direct statistical comparison, the adults showed significantly greater activation than the children in the right inferior frontal gyrus for the visual spelling, visual rhyming, and auditory spelling tasks. The developmental finding for the spelling task is consistent with a previous study that found greater right inferior frontal gyrus activation in adults than in children (Booth, Burman, Meyer, Zhang, et al., 2003). The finding of bilateral developmental differences during spelling is also consistent with adult research that shows both right and left hemisphere involvement during spelling tasks (Flowers, Wood, & Naylor, 1991).

Several lines of research suggest that the left fusiform gyrus is important for processing orthographic information (Fujimaki et al., 1999; Herbster, Mintun, Nebes, & Becker, 1997; Nobre, Allison, & McCarthy, 1994; Petersen, Fox, Snyder, & Raichle, 1990) and that the superior temporal gyrus is important for processing phonologic information (Giraud & Price, 2001; Binder et al., 1994; Howard et al., 1992). Consistent with this, both adults and children in our study showed greater activation in the left than in the right fusiform gyrus for the visual tasks and showed greater activation in the left than in the right superior temporal gyrus for the auditory tasks. Our study included cross-modal tasks that required the mapping between orthographic and phonologic representations. Both adults and children showed activation in the left fusiform gyrus during the auditory spelling task that required access to orthographic representations and both also showed activation in the left superior temporal gyrus during the visual rhyming task that required the access to phonologic representations. However, the adults showed significantly greater activation in the angular gyrus for both of the cross-modal tasks, suggesting that they may have a more elaborated system that allows for more efficient mapping between representations (Booth et al., 1999, 2000). The developmental differences in our study are similar to a previous study that has reported a positive correlation between skill and brain activation during cross-modal tasks within a group of adults (Booth, Burman, Meyer, Gitelman, et al., 2003). These differences are also consistent with behavioral studies which suggest that acquisition is marked by the elaboration of a single mechanism for mapping between orthography and phonology that includes grapheme–phoneme, onset–rime, syllabic, and word level mappings (Nunes et al., 1997; Ehri, 1995; Marsh et al., 1981; Gough & Hillinger, 1980).

Some models of skilled reading suggest that there are two separate mechanisms for mapping between orthography and phonology—one system directly maps between whole word representations and the other involves a grapheme–phoneme correspondence rule system (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Coltheart, Curtis, Atkins, & Haller, 1993). Some developmental models argue that reading and spelling acquisition is marked by a shift from reliance on the grapheme–phoneme (alphabetical) system to the direct mapping between whole word representations (Frith, 1985). Our neurocognitive model of lexical processing argues that the supramarginal/angular gyrus is involved in extracting statistical regularities (or probabilistic rules) between orthography and phonology, so dual mechanism models predict a developmental decrease of activation in this region due to an increasing reliance on direct mapping between whole word representations. Because we show a developmental increase of activation in the angular gyrus, this suggests that acquisition may be marked by the greater role of a system for abstracting regularities between orthography and phonology. Therefore, our results seem to be more consistent with models of reading which argue for one mechanism that maps between orthography and phonology (Harm & Seidenberg, 1999; Plaut, McClelland, Seidenberg, & Patterson, 1996; Seidenberg & McClelland, 1989).

There was also evidence for access of orthographic information during auditory processing as both adults and children also showed activation in the left fusiform for the auditory rhyming task. This is consistent with previous literature which has shown the influence of orthographic information on spoken word recognition (Ziegler & Ferrand, 1998; Dijkstra et al., 1995; Jakimik et al., 1985; Donnenwerth-Nolan et al., 1981; Seidenberg & Tanenhaus, 1979). We also found that the adults showed greater activation than children in the angular gyrus/superior parietal lobule during the auditory rhyming task, suggesting that the adults showed greater interactivity between orthography and phonology during spoken word processing. This is consistent with research which shows that the influence of orthography on auditory language tasks is weak in the early elementary grades and becomes reliable in later elementary grades (Zecker, 1991; Perin, 1983; Tunmer & Nesdale, 1982; Ehri & Wilce, 1980).

Skilled lexical processing seems to involve increasing resonance between the orthographic and phonologic systems (VanOrden & Goldinger, 1994; VanOrden et al., 1990). This would explain the greater activation for the adults in the angular gyrus during the auditory rhyming task (as discussed above) and also during the visual rhyming task. Previous research clearly shows that older and more skilled readers have faster and more automatic access of phonologic information when reading (Booth et al., 1999, 2000). Although both adults and children showed reliable activation in the angular gyrus during the visual spelling task, the greater activation for the adults in this region may be related to their more automatic access of phonology. Further research should confirm this finding by manipulating the orthographic and phonologic consistency between word pairs. Research clearly shows that orthographically (e.g., *grade, laid*) and phonologically (e.g., *pint, mint*) inconsistent pairs are more difficult during spelling and rhyming judgments (McPherson, Ackerman, & Dykman, 1997; Levinthal & Hornung, 1992; Kramer & Donchin, 1987; Rugg & Barrett, 1987; Johnston & McDermott, 1986; Rack, 1985; Polich, McCarthy, Wang, & Donchin, 1983; Seidenberg & Tanenhaus, 1979). If there is more automatic access of orthography for the adults during auditory rhyming tasks then one may expect greater interference (more activation in the angular and fusiform gyrus) for the orthographically inconsistent pairs. Similarly, if there is more automatic access of phonology for the adults during visual spelling tasks, then one may expect greater interference (more activation in the angular and superior temporal gyrus) for the phonologically inconsistent pairs. We are currently investigating these orthographically and phonologically inconsistent word pairs during intra-modal and cross-modal tasks using an event-related fMRI design.

The greater activation in the angular gyrus during the intra-modal and cross-modal tasks is likely not due to developmental differences in the involvement of semantics. Research shows that older and more skilled readers rely less on semantics than younger and less skilled readers during rapid word recognition (Schwantes, 1981, 1985; Briggs, Austin, & Underwood, 1984; Simpson & Lorsbach, 1983; Simpson, Lorsbach, & Whitehouse, 1983; West, Stanovich, Freeman, & Cunningham, 1983; Stanovich, West, & Freeman, 1981; West & Stanovich, 1978). Studies have generally shown that the middle temporal gyrus is involved in a variety of semantic tasks including action, abstract or concrete, living or nonliving, and category judgments (Phillips, Noppeney, Humphreys, & Price, 2002; Devlin et al., 2002; Friederici, Opitz, & von Cramon, 2000; Price, Moore, Humphreys, & Wise, 1997; Pugh et al., 1996). Another way to examine the neural representation of semantics is to compare activation patterns between words and pseudowords, because the latter do not have meaning representations. Most studies have found that the left inferior frontal gyrus, the left posterior superior temporal gyrus, the left inferior parietal lobule, and the left fusiform gyrus show greater activation for pseudowords than for words (Mechelli, Gorno-Tempini, & Price, 2003; Fiebach, Friederici, Mueller, & von Cramon, 2002; Simos et al., 2002; Xu et al., 2001; Mechelli, 2000; Fiez, Balota, Raichle, & Petersen, 1999; Hagoort et al., 1999; Herbster et al., 1997). The only brain region that seems to consistently show greater activation for words than for pseudowords is the left posterior middle temporal gyrus (Fiebach et al., 2002; Simos et al.,

2002; Hagoort et al., 1999). Taken together, these behavioral and neuroimaging results seem to predict a developmental decrease in the involvement of the left middle temporal gyrus during our spelling and rhyming tasks. In contrast, we found developmental increases in activation in the angular gyrus, so this region is probably not associated with age-related differences in semantic involvement but rather with extracting statistical regularities between orthography and phonology. Although some studies have suggested that the angular or supramarginal gyrus are involved in semantic processing (Devlin, Matthews, & Rushworth, 2003; Rossell, Price, & Nobre, 2003), if the developmental differences reported for the angular gyrus in our study were due to semantic effects, we would have expected to find developmental decreases in activation for this region. Further research will have to be done to confirm our prediction that development should be marked by developmental decreases in the involvement of the middle temporal gyrus in nonsemantic lexical processing.

The central finding of this study is an age-related increase in activation in the angular gyrus during both cross-modal and intra-modal tasks. Previous reports on adults have shown greater activation in the angular gyrus during cross-modal than intra-modal lexical tasks suggesting that cross-modal tasks require mapping between orthography and phonology, whereas intra-modal tasks do not (Booth et al., 2002a). These previous results, together with the present results, show that there is more robust activation in the angular gyrus during cross-modal tasks than intra-modal tasks, but that reading skill may be associated with a more elaborated system for mapping and increasing interactivity between orthographic and phonologic representations.

METHODS

Participants

Sixteen adults (*M* age = 25.2 years, range = 20.7–35.7 years) and 16 children (*M* age = 10.7 years, range = 9.4–11.9 years) participated in this study. There were 6 men and 10 women in the adult group and there were 8 boys and 8 girls in the child group. One child was removed from the auditory spelling task due to low accuracy performance. One adult had missing behavioral data on the auditory spelling task due to computer malfunction. All adults were undergraduate or graduate students at Northwestern University. All children were recruited from private and public schools in the Evanston, Illinois, area.

All participants were given an interview to ensure that they did not have a history of intelligence, reading, or oral-language deficits. All participants were native English speakers and had normal hearing and normal or corrected-to-normal vision. All participants were free of neurological diseases or psychiatric disorders and were not taking medication affecting the central nervous system. The Institutional Review Board at Northwestern University and Evanston Northwestern Healthcare Research Institute approved the informed consent procedures.

Functional Activation Tasks

Word Judgment Tasks—In the word judgment tasks, three words were presented sequentially and the participant had to determine whether the final word matched either of the two previous words according to a predefined rule. In the spelling task, participants determined whether the final word had the same "rime" spelling as either of the first two words. The rime included all letters after the first consonant or consonant cluster (Bowey, 1990). In the rhyming task, participants determined whether the final word "rhymed" with either of the first two words. Table 1 presents the stimuli for the spelling and rhyming tasks.

For both the spelling and rhyming tasks, half of the target trials contained a target word that rhymed and was orthographically similar to one of the two preceding words (i.e., had the same

rime). The other half contained a target word that rhymed but was orthographically dissimilar to one of the two preceding words. In addition, half of the correct trials involved a match to the first stimulus (first match) and half involved a match to the second stimulus (second match). The unrelated trials (40%) involved three orthographically different words that were nonrhyming and semantically unrelated. If there was a match according to the criterion, the participant pressed a button with the index finger; if there was no match, the participant pressed a different button with the middle finger.

Stimulus Characteristics—All tasks were structured in a similar way so patterns of brain activation could be directly compared across tasks (Crosson et al., 1999). First, the tasks consisted of words with similar written word frequency for children and adults (The Educator's Word Frequency Guide, 1996) and similar adult word frequency for written and spoken language (Baayen, Piepenbrock, & Gulikers, 1995). Second, no homophones were included in the experimental lists. Third, the tasks contained about the same number of nouns (55–65%), verbs (25–35%), and adjectives (10–20%) based on their most frequent usage in the *Oxford English Dictionary.*

Visual Word Judgment Tasks—Each word reading task lasted 9 min consisting of 10 blocks of 54 sec. This included a 4-sec introduction screen to each block: "Spelling" for orthographic task and "Rhyming" for phonologic task. The five experimental blocks alternated with the five control blocks. In each trial for the experimental blocks, three consecutive words were presented in lowercase letters with each word presented for 800 msec followed by a 200-msec blank interval. A yellow fixation cross (+) appeared on the screen after the third stimulus was removed, indicating the need to make a response during the subsequent 2000-msec interval. Participants were told that they could respond before the yellow cross (+) appeared on the screen. Participants were encouraged to respond as quickly as possible without making errors. Each trial lasted a total of 5000 msec and there were 10 trials in each block.

Auditory Word Judgment Tasks—The timing for the auditory tasks was the same as for the visual tasks, but the auditory tasks employed a different list of stimuli. All stimuli for this task were recorded in a soundproof booth using a digital recorder and a high-quality stereo microphone. A native Chicagoan woman spoke each word in isolation so that there would be no contextual effects. All words longer than 800 msec were shortened to this duration (less than 1% of the words). All words were then normalized so that they were of equal amplitude. The stimuli were easily heard through the headphones in the 1.5 Tesla scanner.

During the auditory tasks, a white fixation cross (+) was presented during the presentation of the auditory stimuli. As in the visual word tasks, a yellow fixation cross (+) appeared on the screen after the third stimulus was presented, indicating the need to make a response. Participants were asked to fixate on the cross during the entire trial.

Control Conditions—The control blocks for the visual and auditory tasks were designed to equate the experimental and control blocks in terms of their memory demands and response characteristics. The experimental setup and timing for the control blocks was exactly the same as for the word blocks. For control blocks in the visual tasks, the three stimuli were abstract, "nonlinguistic" symbols consisting of straight lines (see Table 2). Participants determined whether the third stimulus was the same as one of the first two stimuli. Half of the correct trials involved a match to the first stimulus (first match) and half involved a match to the second stimulus (second match). The nonmatching trials involved three different stimuli. As with the experimental blocks, 60% of the trials involved a match and 40% involved a nonmatch. For control blocks in the auditory tasks, the three stimuli were high (700 Hz), medium (500 Hz), and low frequency (300 Hz) "nonlinguistic" pure tones (see Table 2). The tones were 600 msec

in duration and contained a 100-msec linear fade in and a 100-msec linear fade out. Otherwise, the auditory control task was structured exactly like the visual control.

Experimental Procedure

After informed consent was obtained, participants were administered the informal interview (see above) and the first practice session in a simulator in order to acclimate the participant to the scanner environment (Rosenberg et al., 1997). The participant practiced a full-length version of each experimental task in the simulator. Different stimuli (matched in their stimulus characteristics) were used in the practice and fMRI sessions. Within 3 days, the participant was administered the first MRI session. Within 2 months, the participant was administered the second practice and MRI session. The auditory and visual tasks were run on separate days with an approximately equal number of participants receiving the visual and auditory modality first.

MRI Data Acquisition—After screening, the participant was asked to lie down on the scanner bed. The head position was secured with a specially designed vacuum pillow (Bionix, Toledo, OH) that allowed for the insertion of two earphones (for the auditory sessions). An optical response box (Lightwave Medical, Burnaby, Canada) was placed in the participant's right hand and a compression alarm ball was placed in the left hand. The head coil was positioned over the participant's head and a goggle system for the visual presentation of stimuli (Avotec, Jensen Beach, FL) was secured to the head coil. Each imaging session took less than one hour.

All images were acquired using a 1.5 Tesla GE scanner. Gradient-echo localizer images were acquired to determine the placement of the functional slices. For the functional imaging studies, a susceptibility weighted single-shot EPI (echo-planar imaging) method with BOLD (blood oxygenation level dependent) was used. The following scan parameters were used: TE = 40 msec, flip angle = 90°, matrix size = 64 × 64, field of view = 22 cm, slice thickness = 4 mm, number of slices = 32. These scanning parameters resulted in a 3.437 × 3.437 × 4 mm voxel size. The acquisition of this volume was repeated every 3 sec (TR = 3000 msec) for a total of 9 min per run.

At the end of the functional imaging session, a high-resolution, T1-weighted 3-D image was acquired (SPGR, TR = 21 msec, TE = 8 msec, flip angle = 20°, matrix size = 256 × 256, field of view = 22 cm, slice thickness = 1 mm). These scanning parameters resulted in a 0.86 × 0.86 × 1 mm voxel size. The orientation of this 3-D volume was identical to the functional slices.

Image Analysis—Analysis was performed using SPM-99 (Statistical Parametric Mapping) for motion correction and statistical inference (Friston, Ashburner, et al., 1995; Friston, Holmes, et al., 1995; Friston, Jezzard, & Turner, 1994). Application Visualization System (AVS) software with customized modules was used for visualization.

The functional images were realigned to the last functional volume in the scanning session using affine transformations. All statistical analyses were conducted on these movement-corrected images. No individual runs had more than 3 mm of movement. We calculated 2 Age (children, adults) × 2 Mode (visual, auditory) × 2 Task (spelling, rhyming) ANOVAs separately on the x-plane, y-plane, and z-plane motion estimates. This analyses revealed no significant main effects or interactions involving age indicating that movement was not reliably different between the adults and children for the x-plane ($M = 0.18$; range = 0.02 to 0.70 vs. $M = 0.21$; range = 0.02 to 1.60), y-plane ($M = 0.31$; range = 0.06 to 1.66 vs. $M = 0.30$; range = 0.05 to 1.41), or z-plane ($M = 0.54$; range = 0.10 to 2.48 vs. $M = .66$; range = 0.12 to 2.64).

Images were then segmented and the gray–white matter information was used to coregister the structural and functional images. The coregistered images were normalized to the MNI

stereotaxic template (12 linear affine parameters for brain size and position, 8 nonlinear iterations and $2 \times 2 \times 2$ nonlinear basis functions for subtle morphological differences). The MNI template used for normalization by SPM-99 is similar to the Talairach and Tournoux (1988) stereotaxic atlas. The major difference between these two atlases is in the inferior portion of the temporal lobes (Calder, Lawrence, & Young, 2001; Duncan et al., 2000). Considering the age of our participants and our voxel size, it is reasonable to normalize all participants into the standard MNI template (Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003; Burgund et al., 2002; Wilke, Schmithorst, & Holland, 2002; Muzik, Chugani, Juhasz, Shen, & Chugani, 2000).

Statistical analyses were calculated on the smoothed data (7 mm isotropic gaussian kernel) using a delayed boxcar design with a 6-sec delay from onset of block in order to account for the lag in hemodynamic response. A high pass filter was applied equal to two cycles of the experimental and control conditions (216 sec) in order to remove low-frequency effects such as signal drift, cardiac and respiratory pulsations. We used global normalization to scale the mean of each scan to a common value in order to correct for whole brain differences over time.

We calculated contrasts (word-control) in order to analyze the two word judgment tasks (spelling, rhyming) in the two modalities (visual, auditory). A one-sample *t* test compared each voxel across all participants within a group (children or adults) to determine whether the activation during a condition was significant (i.e., greater than 0). A two-sample *t* test was used to determine whether the magnitude of activation across groups was significantly different. Reported areas of activation were significant using $p < .001$ corrected at the voxel level for the one-sample tests and $p < .01$ corrected at the voxel level for the two-sample tests. All clusters were greater or equal to 15 voxels.

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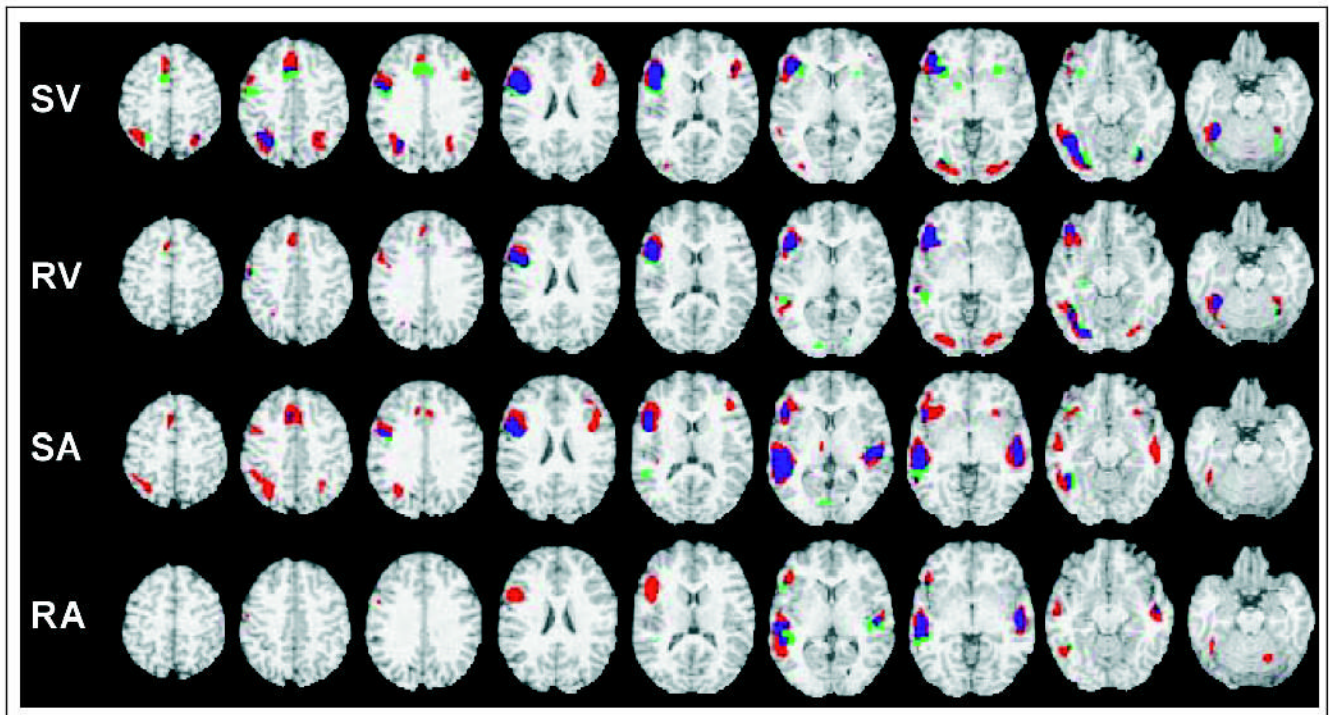
Figure 1.
Significant activation for the adults and children on the spelling (S) and rhyming (R) tasks in the visual (V) and auditory (A) modalities. These slices show activation for the adults (red), for the children (green), and for both adults and children (purple).
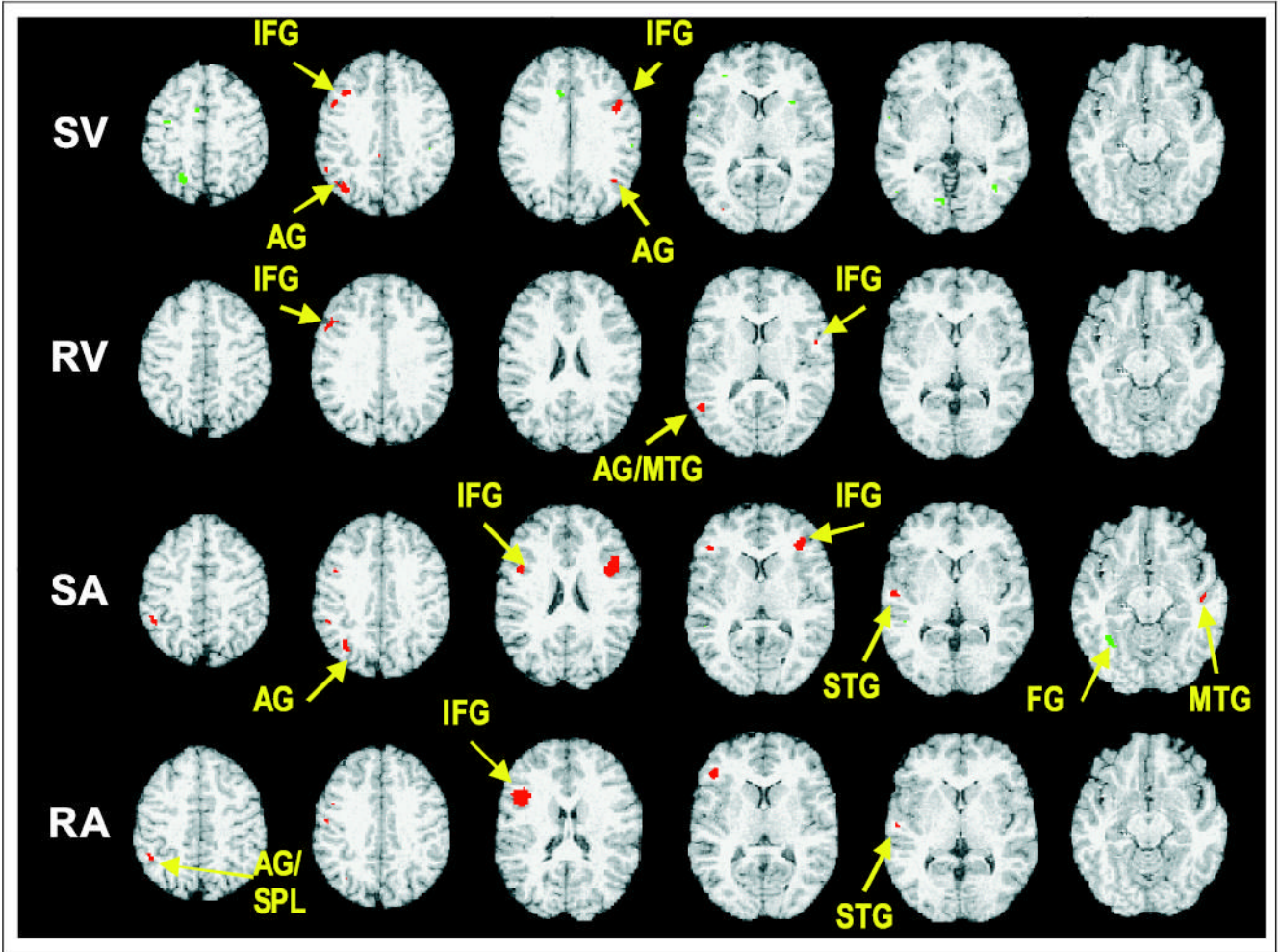
Figure 2.
Significant differences between the adults and children activation on the spelling (S) and rhyming (R) tasks in the visual (V) and auditory (A) modalities. These slices show significantly greater activation for the adults (red) or for the children (green). Only clusters in our regions of interest are labeled (see Tables 4, 5, 6, and 7 for all significant regions). Slices were chosen to maximize visualization of clusters while selecting similar *z*-coordinates across tasks (AG = angular gyrus; FG = fusiform gyrus; IFG = inferior frontal gyrus; MTG = middle temporal gyrus; STG = superior temporal gyrus).

Table 1

Examples of Stimuli for the Word Judgment Tasks

	Parametric Manipulation	
	Similar Orthography	*Dissimilar Orthography*
Spelling		
First match	hold–plant–cold	Hope–colt–soap
Second match	built–vote–note	slid–lane–strain
Rhyming		
First match	seat–fresh–heat	Jazz–last–has
Second match	wish–fall–wall	myth–home–foam

For the spelling and rhyming task, there was a parametric manipulation of orthographic similarity.

Table 2

Examples of Stimuli for Control Tasks in the Visual and Auditory Modality

	Modality	
	Visual	**Auditory**
First match	/ \–\\–/ \	300–500–300 Hz
Second match	//–\\–\\	500–700–700 Hz

Table 3

Means (*M*) and Standard Errors (*SE*) for Accuracy (%) and Reaction (RT) for the Word Judgment and Control Tasks

	Word						Control					
	%		RT				%		RT			
	M	*SE*	*M*	*SE*			*M*	*SE*	*M*	*SE*		
ADULT—VIS												
Spelling	97.3	4.1	931	80			96.5	4.6	797	69		
Rhyming	96.9	4.4	947	79			97.5	3.9	804	70		
CHILD—VIS												
Spelling	89.3	7.7	1545	105			93.4	6.2	1214	93		
Rhyming	91.6	6.9	1444	89			94.2	5.8	1229	82		
ADULT—AUD												
Spelling	91.4	7.0	1265	107			93.0	6.4	1003	73		
Rhyming	97.4	4.0	993	68			95.9	5.0	977	68		
CHILD—AUD												
Spelling	81.8	9.6	1660	123			90.7	7.3	1391	94		
Rhyming	94.8	5.6	1350	84			90.5	7.3	1376	92		

Data are presented separately for the adults and children for each task (spelling, rhyming, and meaning) in each modality (visual and auditory).

Table 4

Significant Activation Separately for the Adults and Children and Significant Differences between Adults and Children for the *Visual Spelling Task*

Location			Significance		Coordinate		
Area	H	BA	z-test	Voxels	x	y	z
Adult							
Angular gyrus/Precuneus/Superior parietal lobule	L	39/19/7	15.13	372	−30	−66	42
Angular gyrus/Precuneus/Superior parietal lobule	R	39/19/7	12.61	236	30	−54	42
Medial frontal gyrus/Anterior cingulate	B	6/8/32	12.44	257	−3	33	42
Inferior frontal gyrus	R	9/44/45	11.78	302	51	30	21
Inferior frontal gyrus	L	9/44/45/47	21.22	1073	−48	36	6
Middle occipital gyrus/Fusiform gyrus	R	18/19/37	17.61	199	24	−90	−6
Middle occipital gyrus/Fusiform gyrus	L	18/19/37	22.51	639	−36	−51	−21
Cerebellum	L	*	8.85	20	−9	−81	−30
Cerebellum	R	*	8.63	37	12	−78	−33
Child							
Medial frontal gyrus/Anterior cingulate	L	6/32	10.09	283	−6	15	45
Angular gyrus/Precuneus/Superior parietal lobule	L	39/19/7	12.59	205	−24	−57	39
Inferior frontal gyrus	L	9/44/45/47	18.20	1140	−42	9	24
Inferior frontal gyrus	R	44/45	7.11	37	51	33	18
Middle temporal gyrus	L	21	8.83	41	−51	−36	0
Inferior frontal gyrus/Insula	R	47/13	8.35	83	30	27	−3
Putamen	L	*	7.62	51	−15	6	−3
Middle occipital gyrus/Fusiform gyrus	L	18/19/37	14.52	392	−36	−72	−12
Middle occipital gyrus/Fusiform gyrus	R	19/37	10.39	131	39	−69	−18
AD–CH							
Angular gyrus/Superior parietal lobule	L	39/7	8.09	89	−30	−69	45
Inferior frontal gyrus	L	9	7.34	68	−48	15	39
Middle cingulate	L	31	6.44	18	−6	−36	36
Medial frontal gyrus	L	9	6.09	18	−3	42	33
Inferior frontal gyrus	R	9/44	8.38	51	51	18	30
Angular gyrus	R	39	6.26	21	45	−54	30
CH–AD							
Medial frontal gyrus	L	6	6.40	40	−6	3	54
Precuneus	L	7	8.43	54	−21	−57	51
Postcentral gyrus	R	2	5.85	30	48	−24	45
Precentral gyrus	L	6	6.48	49	−42	−3	42
Anterior cingulate	L	32	6.41	25	−6	27	30
Insula	R	13	7.01	25	33	21	6
Lingual gyrus	L	18	6.60	35	−6	−75	0
Inferior temporal gyrus	R	37	6.52	15	57	−54	−3

H = left (L), right (R), or bilateral (B) hemispheres; BA = Brodmann's area of activation; voxels = number of voxels in cluster, only clusters 15 or greater are presented; coordinates = −X left hemisphere, +X right hemisphere, −Y behind anterior commisure, +Y in front of anterior commisure, −Z below anterior–posterior commisure plane, +Z above anterior–posterior commisure plane. Regions are sorted by z-coordinate within a group.

*
No Brodmann's area for this brain region.

Table 5

Significant Activation Separately for the Adults and Children and Significant Differences between Adults and Children for the *Visual Rhyming Task*

Location			Significance		Coordinate		
Area	H	BA	z-test	Voxels	x	y	z
Adult							
Medial frontal gyrus	L	6/8	9.84	161	−6	33	42
Precuneus	L	7	7.55	27	−24	−54	39
Inferior frontal gyrus	R	44	7.26	19	54	33	12
Inferior frontal gyrus	L	9/44/45/47	19.69	1070	−48	33	6
Middle temporal gyrus/Angular gyrus	L	21	8.01	74	−48	−42	6
Middle temporal gyrus	L	21	8.93	58	−63	−33	3
Middle occipital gyrus/Fusiform gyrus	R	18/37	13.69	224	24	−90	−6
Middle occipital gyrus/Fusiform gyrus	L	18/19/37	21.31	485	−39	−54	−21
Cerebellum	R	*	9.57	87	12	−75	−30
Child							
Inferior frontal gyrus	L	9	8.57	33	−51	−3	42
Inferior frontal gyrus	L	44/45/47	14.30	707	−51	30	9
Cuneus	R	17	7.36	16	21	−81	3
Middle temporal gyrus	L	21	11.49	128	−51	−36	0
Parahippocampus	L	35	7.21	47	−24	−27	−12
Middle occipital gyrus/Fusiform gyrus	L	18/19/37	14.99	355	−39	−48	−21
Fusiform gyrus	R	37	8.27	58	36	−63	−21
AD–CH							
Inferior frontal gyrus	L	9	7.73	43	−48	21	33
Angular gyrus/Middle temporal gyrus	L	39/37	7.47	34	−51	−57	12
Inferior frontal gyrus	R	44	7.04	20	57	6	12
CH–AD							
No significant differences							

See Table 4 note.

Table 6

Significant Activation Separately for the Adults and Children and Significant Differences between Adults and Children for the *Auditory Spelling Task*

Location			Significance		Coordinate		
Area	*H*	*BA*	*z-test*	*Voxels*	*x*	*y*	*z*
Adult							
Medial frontal gyrus/Anterior cingulate	L	6/8/32	14.72	296	−6	24	42
Angular gyrus/Superior parietal lobule	R	39/7	7.23	38	33	−51	42
Angular gyrus/Precuneus/ Superior parietal lobule	L	39/19/7	13.05	343	−30	−63	36
Inferior frontal gyrus	L	9/44/45/47	22.4	1101	−45	12	21
Inferior frontal gyrus/Middle frontal gyrus	R	45/46	9.58	253	54	33	18
Putamen	L	*	7.43	68	−12	0	9
Superior temporal gyrus/Middle temporal gyrus/Fusiform gyrus	L	22/21/37	25.89	948	−60	−12	−3
Superior temporal gyrus/Middle temporal gyrus	R	22/21	21.5	539	60	−12	−6
Inferior frontal gyrus/Insula	R	47/13	9.84	79	33	27	−9
Cerebellum	R	*	7.16	29	30	−66	−30
Cerebellum	R	*	11.56	72	12	−81	−33
Child							
Medial frontal gyrus	L	6	7.28	48	−6	27	39
Inferior frontal gyrus	L	9/44/45/47	12.25	516	−48	12	21
Posterior cingulate	L	30	6.90	61	−6	−78	6
Superior temporal gyrus/Middle temporal gyrus/Fusiform gyrus	L	22/21/37	18.91	765	−60	−18	−3
Superior temporal gyrus/Middle temporal gyrus	R	22/21	13.6	317	60	−12	−3
Inferior frontal gyrus	L	47	6.93	15	−30	21	−9
Cerebellum	R	*	7.50	20	12	−75	−27
AD–CH							
Superior parietal lobule	L	7	7.46	40	−45	−42	48
Inferior frontal gyrus	L	9	6.25	15	−45	12	42
Angular gyrus	L	39	7.50	35	−30	−63	36
Inferior frontal gyrus	R	9/44	8.12	138	48	12	27
Inferior frontal gyrus	L	9/44	7.06	70	−42	36	9
Inferior frontal gyrus	L	45	6.95	25	−45	36	9
Inferior frontal gyrus	R	45	7.58	51	42	36	6
Superior temporal gyrus	L	22	7.35	24	−60	−9	0
Middle temporal gyrus	R	21	6.53	30	54	−15	−12
CH–AD							
Fusiform gyrus	L	37	7.55	74	−33	−54	−15

See Table 4 note.

Table 7

Significant Activation Separately for the Adults and Children and Significant Differences between Adults and Children for the *Auditory Rhyming Task*

Location			Significance		Coordinate		
Area	H	BA	z-test	Voxels	x	y	z
Adult							
Precentral gyrus	L	6	8.00	27	−54	−6	42
Inferior frontal gyrus	L	9/44/45/47	13.51	489	−48	36	6
Superior temporal gyrus/Middle temporal gyrus/Fusiform gyrus	L	22/21/37	24.69	660	−63	−12	−3
Superior temporal gyrus/Middle temporal gyrus	R	22/21	20.48	309	63	−9	−6
Cerebellum	R	*	9.40	58	24	−63	−24
Child							
Inferior frontal gyrus	L	44/45/47	10.11	61	−54	27	3
Superior temporal gyrus/Middle temporal gyrus	L	22/21	17.74	442	−60	−18	−3
Superior temporal gyrus/Middle temporal gyrus	R	22/21	15.81	270	60	−9	−6
Fusiform gyrus	L	37	7.43	21	−42	−51	−15
AD–CH							
Angular gyrus/Superior parietal lobule	L	39/7	6.51	27	−42	−45	48
Precentral gyrus	L	6	6.57	17	−48	−9	39
Inferior frontal gyrus	L	9/44/45	8.37	213	−45	36	9
Superior temporal gyrus	L	22	7.74	23	−60	−9	−3
CH–AD							
No significant differences							

See Table 4 note.