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## Modality-specific and -independent developmental differences in the neural substrate for lexical processing

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### Abstract

The neuroanatomy of developmental differences in lexical processing was examined with functional magnetic resonance imaging (fMRI) in 15 adults and 15 children. We examined modality specific and modality independent (auditory and visual presentation) patterns of brain activation during spelling, rhyming and meaning judgment tasks. A direct comparison of the modalities revealed that adults showed a large area of activation in the fusiform gyrus for visual word forms and in the superior temporal gyrus for auditory word forms. In contrast, the modality comparison for children revealed no activation in the fusiform gyrus for visual word forms and modest activation in the superior temporal gyrus for auditory word forms. There were also modality independent developmental differences with adults showing more activation than children in the inferior frontal gyrus for the spelling, rhyming and meaning tasks. These results suggest that development is characterized by increasing involvement of the inferior frontal gyrus in lexical processing and by the specialization of unimodal regions for visual and auditory word forms.

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## 1. Introduction

Based on our previous research (Booth & Burman, 2001; Booth et al., 2001a,b, 2002a, b), we have formulated a theoretical model of skilled lexical processing. Our model of skilled processing specifies that written word forms are represented in the unimodal visual association area of the fusiform gyrus and that spoken word forms are represented in the unimodal auditory association area of the superior temporal gyrus. Posterior heteromodal regions including the supramarginal gyrus, angular gyrus and posterior superior temporal gyrus area are involved in the conversion between written word forms and spoken word forms. These heteromodal areas are also responsible for the integration of spoken and written word forms with semantic associations in the middle temporal gyrus. Finally, among other things, the inferior frontal gyrus is responsible for manipulating verbal semantic information represented in posterior components of the language network including the middle temporal gyrus. Functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) research generally support this model of lexical processing (Binder et al., 1994, 1997; Demonet et al., 1992; Flowers, Wood, & Naylor, 1991; Friederici, Opitz, & Cramon, 2000; Fujimaki et al., 1999; Giraud & Price, 2001; Herbster, Mintun, Nebes, & Becker, 1997; Howard et al., 1992; Kapur et al., 1996; Kareken, Lowe, Chen, Lurito, & Mathews, 2000; Lurito, Kareken, Lowe, Chen, & Mathews, 2000; Mummery, Patterson, Hodges, & Price, 1998; Nobre, Allison, & McCarthy, 1994; Petersen, Fox, Snyder, & Raichle, 1990; Poldrack et al., 1999; Price, Moore, Humphreys, & Wise, 1997; Pugh et al., 1996; Tokunaga et al., 1999; Wagner et al., 1998; Xu et al., 2001).

From the event-related potential (ERP) literature, we can also infer a time course associated with each of these components of lexical processing. In visual word processing experiments, Bentin, Mouchetant-Rostaing, Giard, Echallier, and Pernier (1999) provide a convincing demonstration that accessing orthography in the fusiform gyrus occurs at about 200 ms (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Nobre et al., 1994), mapping orthography to phonology in the superior temporal region occurs at about 300 ms and accessing semantics in the temporo-parietal area occurs at about 400 ms (Kutas & Hillyard, 1980, 1984; McCarthy, Nobre, Bentin, & Spencer, 1995). In auditory word processing experiments, Connolly et al. (Connolly & Phillips, 1994; Connolly, Phillips, & Forbes, 1995; Connolly, Phillips, Stewart, & Brake, 1992) also provide a convincing demonstration that accessing phonology in the superior temporal region occurs at about 200 ms and that accessing semantics in the temporo-parietal region occurs at about 400 ms. Earlier ERPs, beginning at about 100 ms are associated with activation in primary cortical regions. Specifically, a negative deflection at about 100 ms in the auditory cortex (BA 41 and 42) has been associated with auditory processing (Sams, Aulanko, Aaltonen, & Naeaetaenen, 1990; Tzourio et al., 1997; Yamamoto, Uemura, & Llinas, 1992) and a positive deflection at about 100 ms in striate and extrastriate cortex (BA 17 and 18) has been associated with early visual processing (Brecelj, Kakigi, Koyama, & Hoshiyama, 1998; Clark, Fan, & Hillyard, 1994; Nakamura et al., 1997; Schacter, Badgaiyan, & Alpert, 1999; Shigeto, Tobimatsu, Yamamoto, Kobayashi, & Kato, 1998).

The formulation of specific predictions regarding developmental differences in brain activation patterns during lexical processing is difficult because of the limited amount

of published work. Most of the ERP research on linguistic processing has been done on infants and young children (Molfese, 2000; Molfese & Molfese, 1979, 1985). Research that has been done on school age children is consistent with the preschool studies and generally suggests that with development there is a reduction in ERP latency (Friedman, Putman, & Sutton, 1990; Taylor, 1988; Taylor & Eals, 1996; Taylor & Keenan, 1999) and amplitude (Juottonen, Revonsuo, & Lang, 1996; Lovrich, Kazmerski, Cheng, & Geisler, 1994). Some have interpreted the developmental decreases of ERP latency in early components as reflecting an increase in efficiency of the perceptual mechanism (Molfese & Molfese, 1997). The ability to rapidly process auditory and visual information is associated with oral language and reading skill (Cornelissen, Hansen, Hutton, Evangelinou, & Stein, 1998; Demb, Boynton, & Heeger, 1998; Denckla & Rudel, 1976; Helenius, Uutela, & Hari, 1999; Livingstone, Rosen, Drislane, & Galaburda, 1991; Lovegrove, Martin, & Slaghuis, 1986; Manis, Seidenberg, & Doi, 1999; Tallal et al., 1996; Wright, Bowen, & Zecker, 2000). The reduction in ERP latency may also correspond to well-established non-linear decreases in processing speed for most cognitive tasks through adolescence (Kail, 1992, 1993; Kail & Hall, 1994; Kail & Park, 1994).

Several developmental studies report complex patterns of decreases and increases in ERP amplitude and latency that appear to depend on cognitive task and brain region. In a large study, Holcomb, Coffey, and Neville (1992) presented 130 participants from 5 to 26-years-old with auditory or visual sentences that contained semantically congruous or anomalous words in the final position. Sentence final words that are inconsistent with sentence context have been shown to produce a negative deflection in the ERP at about 400 ms after stimulus onset (Kutas & Hillyard, 1980, 1984). Holcomb et al. (1992) reported an increase in negativity with development at about 400 ms for the occipital region during visual word presentation and for the anterior temporal region during auditory word presentation, whereas there was a decrease in negativity with development in the parietal region during both visual and auditory presentation. Although the spatial resolution of ERPs is limited, these developmental differences could reflect an increasing involvement of unimodal regions for processing written and spoken language with a concomitant decrease in the reliance on posterior heteromodal regions. Similar to the Holcomb et al. (1992) findings, Licht, Bakker, Kok, and Bouma, (1988, 1992) reported age-related decreases (6- to 11-year-olds) in parietal slow-wave (SW) amplitude and increases in temporal SW amplitude during oral reading of single words. The Licht et al. (1988, 1992) findings also suggest a shift in reliance from posterior heteromodal regions to unimodal regions for visual word recognition. The hypothesis that development of lexical processing is characterized by greater reliance on unimodal regions is consistent with cognitive (Ehri, 1992; Perfetti, 1992) and computational (Harm & Seidenberg, 1999; Plaut, McClelland, Seidenberg, & Patterson, 1996; VanOrden, Pennington, & Stone, 1990) models that argue for increasing quality and/or redundancy in orthographic and phonologic representations with development and skill.

Several ERP studies have also demonstrated that brain potentials become more lateralized with development, with robust asymmetries during some linguistic tasks first appearing at about 11–13 years of age (Grossi et al., 2001; Holcomb et al., 1992; Licht et al., 1988; 1992; Taylor and Eals, 1996). Only three fMRI studies, however, have

examined developmental differences in lexical processing. Holland et al. (2001) examined age differences in 7–18-year-old children on a verb generation task to spoken words and found that the degree of lateralization (left > right inferior frontal activation) increased with development. Increasing lateralization during development is consistent with another fMRI study that found less right inferior frontal activation in adults compared to children on a covert word generation task to letters (Gaillard, Hertz-Pannier, Mott, Barnett, & LeBihan, 2000).

The greater involvement of unimodal regions for processing auditory and visual word forms is also supported by a fMRI study in our lab. Booth et al. (2001a) showed that adults had greater activation than children in the unimodal visual areas of fusiform gyrus (BA 37) for processing visual word forms and in the unimodal auditory areas of superior temporal gyrus (BA 22) for processing auditory word forms. Booth et al. (2001a) also reported that children showed primarily overlap of activation in brain regions for the visual and auditory tasks, whereas adults showed selective activation in the fusiform gyrus when processing visual word forms and selective activation in superior temporal gyrus when processing auditory word forms. The primary limitation of the Booth et al. (2001a) study was that we used a relatively small number of participants (4 adults and 5 children) and we used a fixed effects analysis that did not allow for generalization to the population. The purpose of this study was to replicate our past findings of a developmental increase in the reliance on unimodal regions for lexical processing with a different and larger sample of participants (15 adults and 15 children) using random effects statistical analyses that allows for generalization to the population. Based on the ERP and fMRI literature, we also expected to demonstrate developmental differences in activation for the inferior frontal gyrus.

## 2. Materials and methods

### 2.1. Participants

Fifteen adults ( $M$  age = 25.8 years, range = 20.7–35.7 years) and 15 children ( $M$  age = 10.7 years, range = 9.4–11.9 years) participated in this study. There were seven males and eight females in the adult group and there were eight males and seven females in the child group. Both the adults ( $M$  = 87, range = 55–100) and children ( $M$  = 75, range = 20–90) were right-hand dominant (negative scores indicate left-hand dominance) according to a 10-item likert-scale questionnaire. 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.

## 2.2. 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. In the meaning task, participants determined whether a final word was associated with one of two preceding words (Nelson, McEvoy, & Schreiber, 1998). Table 1 presents the stimuli for the spelling, rhyming and meaning 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. For the meaning task, half of the related pairs had a high association and half had a low association. There was no overlap in free association values for the high associates ( $M = 0.59$ ) and the low associates ( $M = 0.27$ ).

For all tasks, 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 non-rhyming 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

Table 1  
Examples of stimuli for the word judgment tasks

	Parametric manipulation	
Spelling	Similar orthography	Dissimilar orthography
1st match	hold–plant–cold	hope–colt–soap
2nd match	built–vote–note	slid–lane–strain
Rhyming	Similar orthography	Dissimilar orthography
1st match	seat–fresh–heat	jazz–last–has
2nd match	wish–fall–wall	myth–home–foam
Meaning	High association	Low association
1st match	found–tank–lost	dish–pill–plate
2nd match	snap–king–queen	swim–call–phone

*Note:* For the spelling and rhyming task, there was a parametric manipulation of orthographic similarity. For the meaning task, the parametric manipulation was association strength.

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. Fourth, none of the words were more than two syllables in length.

*Visual word judgment tasks.* Each word reading task lasted 9 min consisting of 10 blocks of 54 s. This included a 4 s introduction screen to each block: ‘Spelling’ for orthographic task, ‘Rhyming’ for phonologic task and ‘Meaning’ for the semantic 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 ms followed by a 200 ms 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 ms 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 ms 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 female spoke each word in isolation so that there would be no contextual effects. Each word was transferred to the computer for processing at a sample rate of 22,050 Hz and a sample size of 8 bits. Individual files were created for each word and a 1 ms silence was added to the beginning and end of each word. All words longer than 800 ms 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 T 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 set-up 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, *non-linguistic* symbols consisting of straight lines (Table 2).

Table 2  
Examples of stimuli for control tasks in the visual and auditory modality

	Modality	
	Visual	Auditory
1st match	Λ-\\-Λ	300–500–300 Hz
2nd match	//-\\-\\	500–700–700 Hz

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 non-matching trials involved three different stimuli. As with the experimental blocks, 60% of the trials involved a match and 40% involved a non-match. For control blocks in the auditory tasks, the three stimuli were high (700 Hz), medium (500 Hz) and low frequency (300 Hz) *non-linguistic* pure tones (see Table 2). The tones were 600 ms in duration and contained a 100 ms linear fade in and a 100 ms linear fade out. Otherwise, the auditory control task was structured exactly like the visual control. As with the experimental blocks, there was a 4 s introduction screen to each block: ‘Lines’ for visual control and ‘Tones’ for auditory control.

*Counterbalancing.* For the visual and auditory tasks, the presentation of trials in the experimental and control conditions that required ‘yes’ responses and those that required ‘no’ responses were randomized within a block. Randomization was done with the constraint that no more than two ‘no’ responses occurred in a row and no more than two of the similar/dissimilar orthographic items or the high/low association items occurred in a row. This pseudo-randomization was done so that the type of response was distributed equally across each block. The same pseudo-random order of presentation was used for each participant.

### 2.3. Experimental procedure

After informed consent was obtained, participants were administered the informal interview (see earlier) 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 1 h.

All images were acquired using a 1.5 T 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 ms, 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  $3.437 \times 3.437 \times 4 \text{ mm}^3$  voxel size. The acquisition of this volume was repeated every 3 s (TR = 3000 ms) for a total of 9 min per run.

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

*Image data analysis.* Data analysis was performed using SPM-99 (Statistical Parametric Mapping) for motion correction and statistical inference (Friston et al., 1995a,b; 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 participant had more than 3 mm maximum displacement in the *x*-plane, *y*-plane or *z*-plane for any given run (spelling, rhyming or meaning in either the visual or auditory modality).

Images were then segmented and the gray-white matter information was used to co-register the structural and functional images. The co-registered images were normalized to the MNI stereotaxic template (12 linear affine parameters for brain size and position, eight non-linear iterations and  $2 \times 2 \times 2$  non-linear 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 (Talairach & Tournoux, 1988). The major difference between these two atlases is in the inferior portion of the temporal lobes (Calder, Lawrence, & Young, 2001; Duncan et al., 2000). Each normalization procedure was examined to make sure that the participant's brain was not distorted due to the procedure. Muzik, Chugani, Juhasz, Shen, and Chugani (2000) have shown that normalization to a standard template does not result in artifacts in SPM analyses for children between 6 and 14 years of age (Muzik et al., 2000).

Statistical analyses were calculated on the smoothed data (7 mm isotropic Gaussian kernel) using a delayed boxcar design with a 6 s delay from the block onset in order to account for the lag in hemo-dynamic response. A high-pass filter was applied equally to two cycles of the experimental and control conditions (216 s) 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.

Random effect statistics allowed generalization to the population. In the first level analysis, we calculated parameter estimate images for individual subjects across the entire brain. For each individual, we calculated contrasts [experimental-control] in order to analyze the three-word judgment tasks (spelling, rhyming meaning) in the two modalities (visual, auditory). In the second level analysis, these parameter estimate images were entered into statistical analyses. A one-sample *z*-test compared each voxel across all participants to determine whether the activation during a condition was significant (i.e. greater than 0); a two-sample *z*-test was used to determine whether the magnitude of activation across conditions or groups was significantly different. All

reported areas of activation were significant using  $p < 0.001$  uncorrected for the voxel level and contained a cluster size greater or equal to 15 voxels. We concentrate on reporting the results for our regions of interest including unimodal visual regions (fusiform gyrus), unimodal auditory regions (superior temporal gyrus), posterior heteromodal regions (angular, supramarginal and middle temporal gyrus) and inferior frontal gyrus. All areas of significant activation outside of these regions of interest are presented in the tables.

### 3. Results

#### 3.1. Behavioral performance

Means and standard errors for accuracy on the lexical and control tasks are presented in Fig. 1. Only data for the fMRI session is presented because statistical analyses revealed no main effects or interactions involving accuracy on the practice versus fMRI sessions. Fig. 1 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 separately for each of the lexical tasks in each of the modalities. There were main effects of age for all tasks revealing that adults were more accurate than children (visual spelling,  $F(1, 56) = 21.20$ ,  $p < 0.001$ ; visual rhyming,  $F(1, 56) = 17.76$ ,  $p < 0.001$ ; visual meaning,  $F(1, 56) = 25.21$ ,  $p < 0.001$ ; auditory spelling,  $F(1, 56) = 12.89$ ,  $p < 0.01$ ; auditory rhyming,  $F(1, 56) = 9.27$ ,  $p < 0.01$ ; auditory meaning,  $F(1, 56) = 16.12$ ,  $p < .001$ ). There was also a main effect of condition for auditory spelling,  $F(1, 56) = 10.11$ ,  $p < 0.01$ , revealing that word judgment was less accurate than tone judgment for this task. However, these main effects were qualified by interactions between age and condition for visual spelling,  $F(1, 56) = 4.09$ ,  $p < 0.05$ , and auditory spelling,  $F(1, 56) = 4.94$ ,  $p < 0.05$ , indicating that children had especially low accuracy on word judgment for the spelling tasks.

#### 3.2. Developmental differences in modality specific activation

Modality specific activation in the adults for the visual tasks is presented in Fig. 2 and for the auditory tasks is presented in Fig. 3 (see Table 3 for the coordinates and significance values). Modality specific activation maps were computed by directly contrasting the auditory and visual modalities each relative to their respective baselines. Adults showed modality specific activation for all visual tasks in the fusiform gyrus with a greater number of voxels in the left than in the right hemisphere. Adults also showed modality specific activation for all auditory tasks in both the left and right superior temporal gyrus. Relatively large clusters of modality specific activation were also produced in the right supramarginal gyrus for the spelling task and right middle temporal gyrus for the spelling and semantic tasks.

Modality specific activation in the children for the auditory tasks is presented in Fig. 4 (see Table 4 for the coordinates and significance values). Children showed

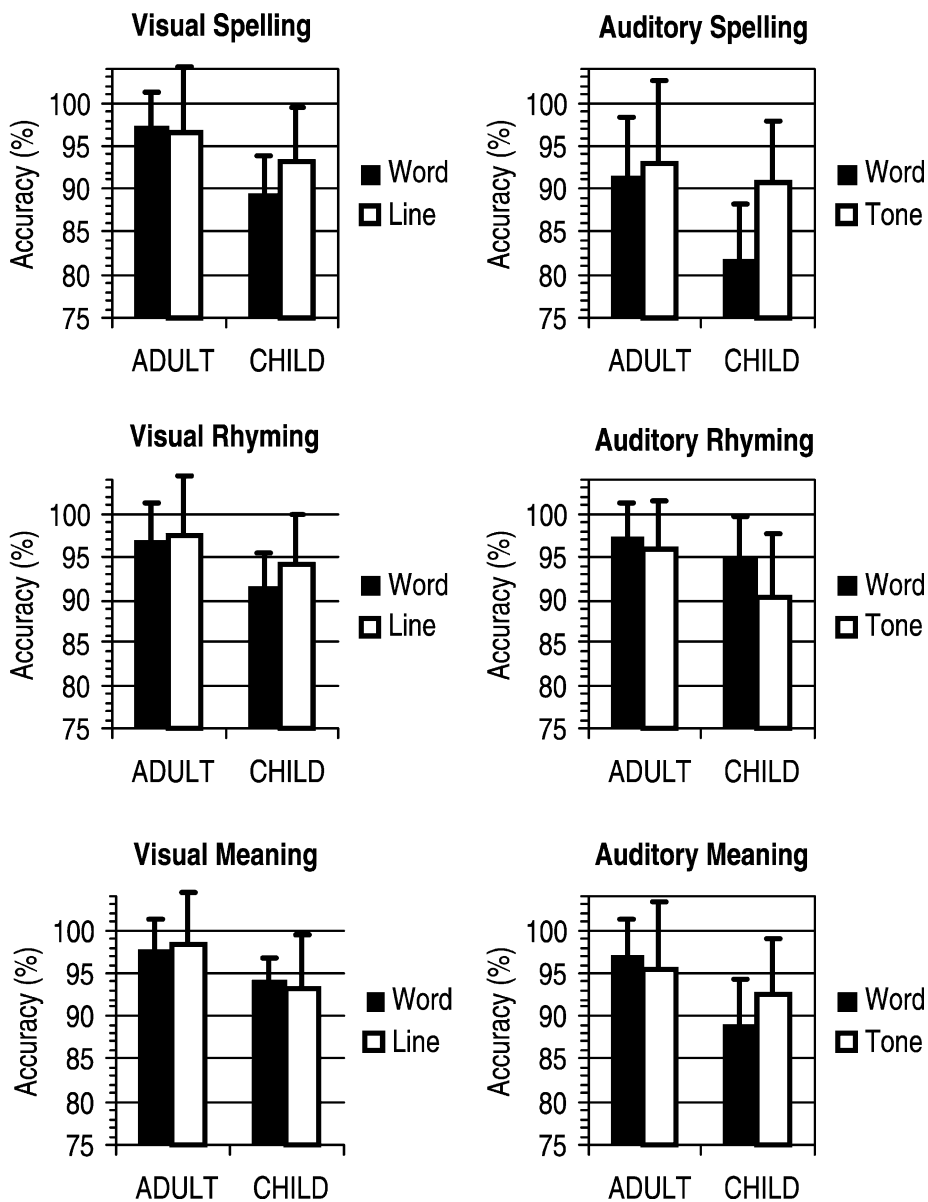


Fig. 1. Means and standard errors for accuracy (%) for the adults and children in the word judgment (spelling, rhyming and meaning) and control (lines versus tones) tasks in the visual and auditory modality.

modality specific activation for the auditory spelling and meaning tasks in bilateral superior temporal gyrus with a greater number of voxels in the left than in the right hemisphere. The children did not show any modality specific activation during the visual tasks in the fusiform gyrus.

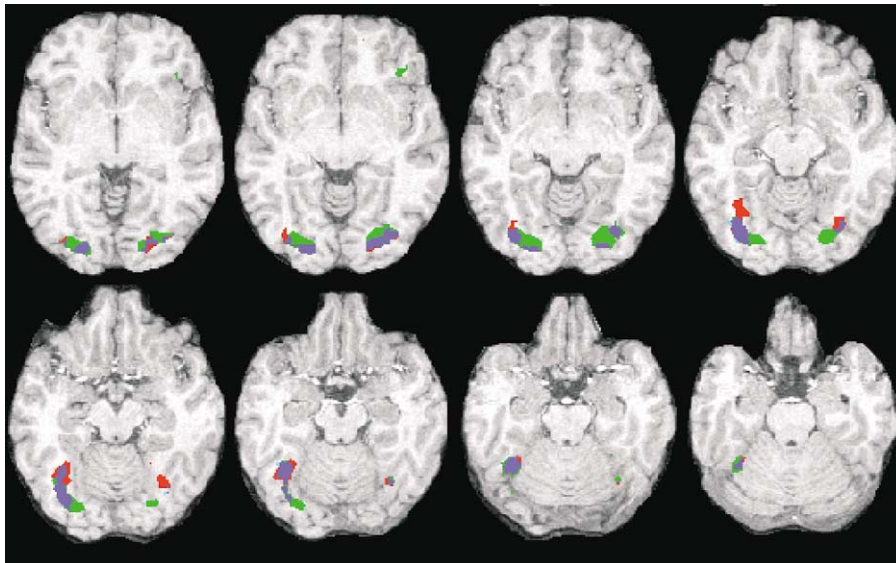


Fig. 2. Modality specific activation for the *adults* in the visual tasks. Purple indicates overlapping activation between the spelling, rhyming and meaning tasks. Red indicates significant activation for the spelling task. Green indicates significant activation for the rhyming task. Cyan indicates significant activation for the meaning task. The figure shows activation in bilateral lingual gyrus and left fusiform gyrus. The left side of the brain is on the left for all figures.

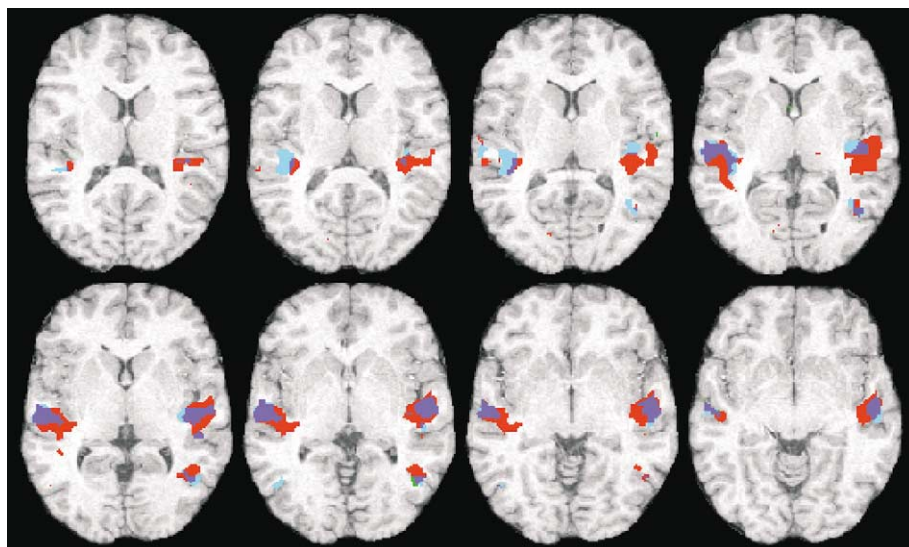


Fig. 3. Modality specific activation for the *adults* in the auditory tasks. Purple indicates overlapping activation between the spelling, rhyming and meaning tasks. Red indicates significant activation for the spelling task. Green indicates significant activation for the rhyming task. Cyan indicates significant activation for the meaning task. The figure shows extensive activation in bilateral superior temporal gyrus.

Table 3  
Modality specific activation for *adults* on the spelling, rhyming and meaning tasks

	Location			Significance		Coordinate		
	Area	H	BA	z-test	Voxels	X	Y	Z
<i>Visual</i>								
Spelling	Middle cingulate gyrus	B	31	3.78	19	3	-33	42
	Lingual/fusiform gyrus	L	18/19/37	5.41	225	-21	-90	-6
	Lingual/fusiform gyrus	R	18/19/37	5.1	127	27	-84	-6
Rhyming	Inferior frontal gyrus	R	47	4.24	17	42	33	-6
	Lingual/fusiform gyrus	R	18/19/37	5.47	169	24	-81	-12
	Lingual/fusiform gyrus	L	18/19/37	5.49	269	-39	-57	-21
Meaning	Lingual/fusiform gyrus	L	18/19/37	4.24	151	-36	-78	-15
	Fusiform gyrus	R	37	4.26	15	36	-72	-15
<i>Auditory</i>								
Spelling	Superior parietal lobule/ supramarginal gyrus	R	7/40	4.24	58	27	-45	63
	Middle temporal gyrus	R	37	4.15	91	48	-60	6
	Cuneus	L	17	3.81	15	-12	-78	6
	Superior temporal gyrus	R	22	5.27	484	60	-18	3
Rhyming	Superior temporal gyrus	L	22	4.79	367	-48	-18	-3
	Postcentral gyrus	R	2	4.16	21	60	-12	39
	Middle temporal gyrus	R	37	3.89	20	51	-63	0
	Superior temporal gyrus	R	22	4.48	125	63	-15	-3
Meaning	Superior temporal gyrus	L	22	4.51	88	-51	-15	-6
	Superior parietal lobule	R	7	4	35	18	-54	69
	Superior parietal lobule	L	7	3.44	18	-24	-45	60
	Supramarginal gyrus	L	40	4.04	30	-39	-33	45
	Superior temporal gyrus	L	22	4.84	264	-42	-27	9
	Middle temporal gyrus	R	37	4.52	62	42	-54	6
	Superior temporal gyrus	R	22	5.53	215	48	-15	3
	Middle temporal gyrus	L	37	3.87	23	-45	-63	-3

Note: H: left (L), right (R) or bilateral (B) hemispheres. BA: Brodmann's area of peak activation as determined by z-test ( $p < 0.001$  uncorrected at the voxel level). Voxels: number of voxels in cluster including this peak, only clusters 15 or greater are presented. Coordinates: -X left hemisphere, +X right hemisphere, -Y behind anterior commissure, +Y in front of anterior commissure, -Z below anterior-posterior commissure plane, +Z above anterior-posterior commissure plane. Regions are sorted by Z coordinate within a group.

A comparison of modality specific activation between the adults and children in the auditory tasks is presented in Fig. 5. This figure shows that adults showed a greater number of activated voxels than children in bilateral superior temporal gyrus.

### 3.3. Developmental differences in modality independent activation

Greater modality independent activation for the adults than for children is presented in Fig. 6 (see Table 5 for the coordinates and significance values). Developmental differences in modality independent activation maps were computed by directly contrasting the adults and children collapsing across both modalities. This analysis revealed that adults showed

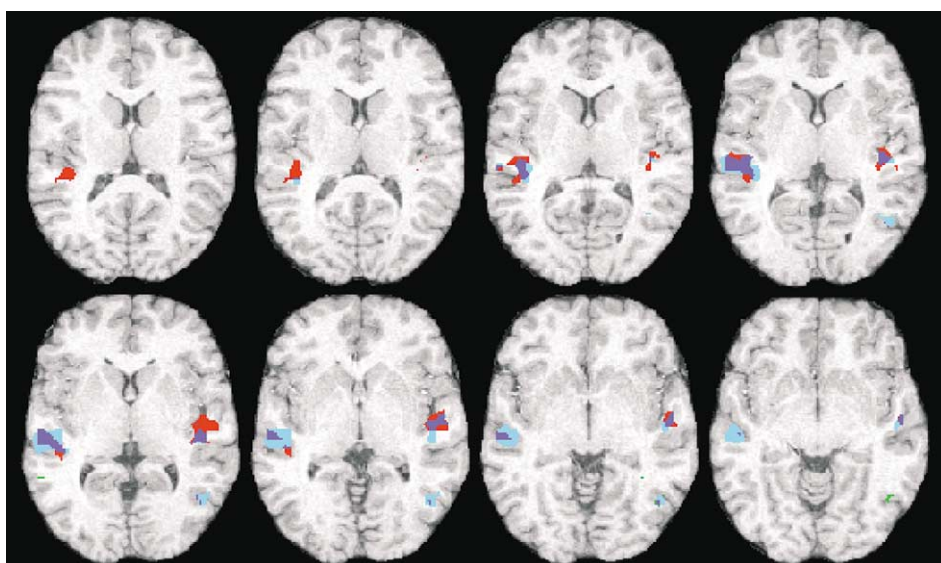


Fig. 4. Modality specific activation for the *children* in the auditory tasks. Purple indicates overlapping activation between the spelling, rhyming and meaning tasks. Red indicates significant activation for the spelling task. Green indicates significant activation for the rhyming task. Cyan indicates significant activation for the meaning task. The figure shows activation in bilateral superior temporal gyrus.

Table 4  
Modality specific activation for *children* on the spelling, rhyming and meaning tasks

	Location			Significance		Coordinate		
	Area	H	BA	$z$ -test	Voxels	X	Y	Z
<i>Visual</i>								
Spelling	*	*	*	*	*	*	*	*
Rhyming	*	*	*	*	*	*	*	*
Meaning	Middle occipital gyrus	L	18	4.42	25	-27	-84	-15
<i>Auditory</i>								
Spelling	Superior temporal gyrus	L	22	4.77	207	-42	-30	12
	Superior temporal gyrus	R	22	4.81	139	60	-6	-3
Rhyming	Middle occipital gyrus	R	19	4.03	33	51	-63	-9
Meaning	Middle occipital gyrus	R	37	4.46	58	54	-66	0
	Superior temporal gyrus	L	22	5.41	232	-51	-21	-6
	Superior temporal gyrus	R	22	4.26	99	60	-6	-6

Note: H: left (L), right (R) or bilateral (B) hemispheres. BA: Brodmann's area of peak activation as determined by  $z$ -test ( $p < 0.001$  uncorrected at the voxel level). Voxels: number of voxels in cluster including this peak, only clusters 15 or greater are presented. Coordinates:  $-X$  left hemisphere,  $+X$  right hemisphere,  $-Y$  behind anterior commissure,  $+Y$  in front of anterior commissure,  $-Z$  below anterior-posterior commissure plane,  $+Z$  above anterior-posterior commissure plane. Regions are sorted by Z coordinate within a group.

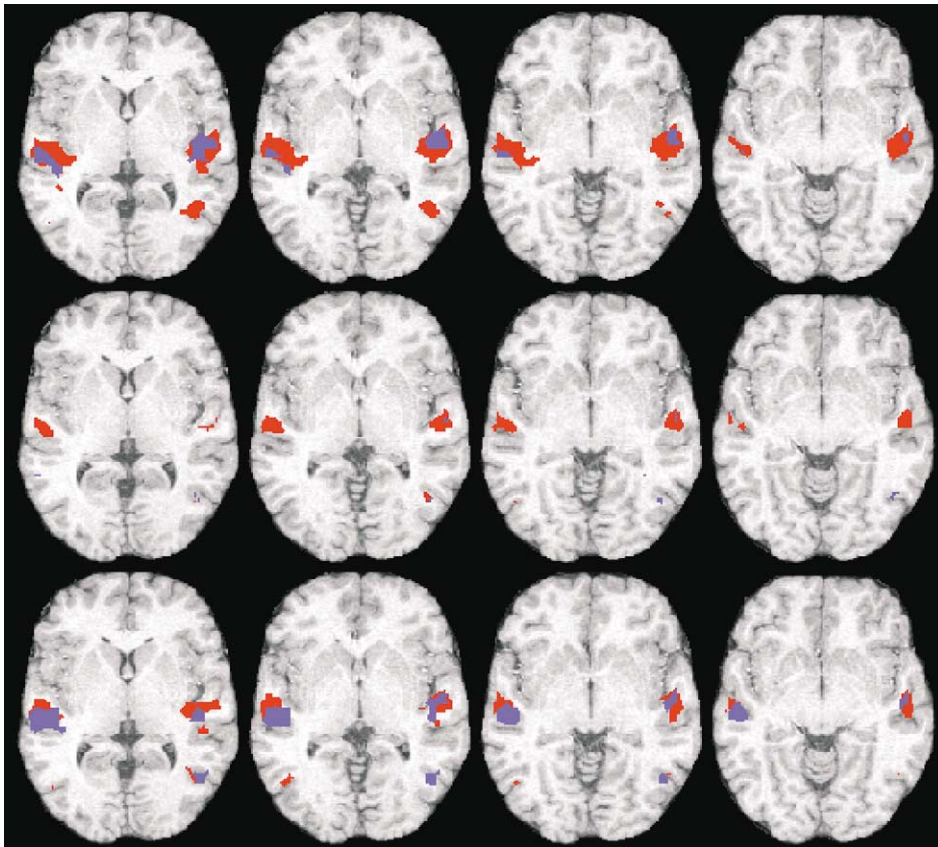


Fig. 5. Modality specific activation for the *adults* versus *children* in the auditory tasks for the spelling (top panel), rhyming (middle panel) and meaning (bottom panel) tasks. Purple indicates overlapping activation between the adults and children. Red indicates significant activation for the adults. Green indicates significant activation for the children. The figure shows greater activation in bilateral superior temporal gyrus for the adults than for the children.

greater activation than children in the inferior frontal gyrus for all tasks. However, these developmental differences were primarily right hemisphere for the spelling and rhyming tasks, and primarily left hemisphere for the rhyming tasks. The children showed a relatively small cluster of activation in the fusiform gyrus for the meaning task.

#### 4. Discussion

##### 4.1. Summary of results

Our finding of developmental increases in the amount of activation in fusiform gyrus for visual word processing and in superior temporal gyrus for auditory word processing is consistent with past behavioral and neuroimaging research. Our finding of more activation for adults in unimodal regions is consistent with ERP studies showing greater occipital and

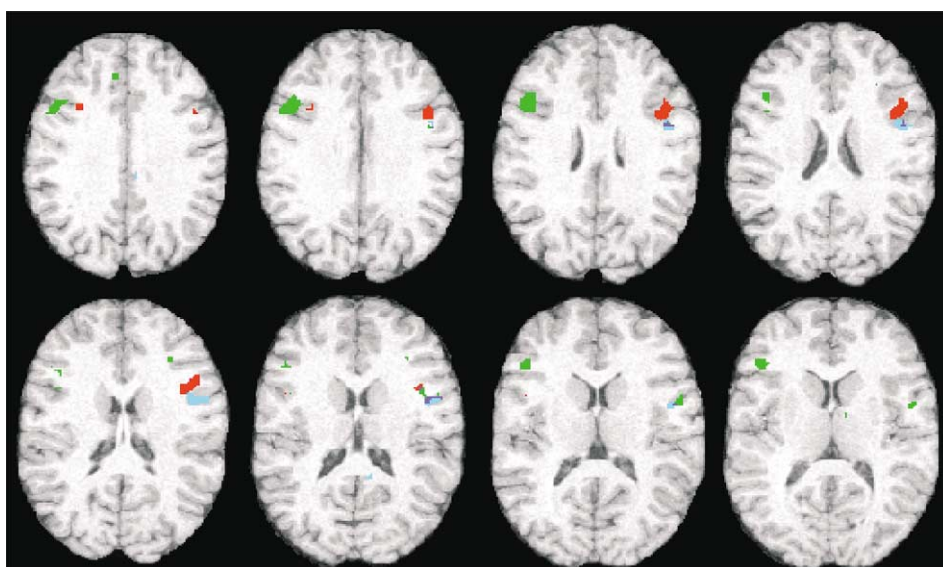


Fig. 6. Significantly greater modality independent activation for the *adults* than for the *children*. Purple indicates overlapping activation between the spelling, rhyming and meaning tasks. Red indicates significant activation for the spelling task. Green indicates significant activation for the rhyming task. Cyan indicates significant activation for the meaning task. The figure shows primarily left inferior frontal gyrus activation for the rhyming task and right inferior frontal gyrus activation for the spelling and meaning tasks.

anterior temporal activation in reading and oral-language tasks, respectively, in older as compared to younger participants (Holcomb et al., 1992) and with fMRI studies showing greater activation in regions associated with the modality of input for skilled processing in adults (Dong et al., 2000; Grill-Spector, Kushnir, Hendler, & Malach, 2000; Pantev et al., 1998; Poldrack, Desmond, Glover, & Gabrieli, 1998; Poldrack & Gabrieli, 2001). Our finding of less activation for children in unimodal regions is consistent with behavioral research showing children are slower at processing orthographic and phonologic information (Booth, Perfetti, & MacWhinney, 1999; Booth, Perfetti, MacWhinney, & Hunt, 2000), with ERP research showing longer latencies to lexical stimuli in younger children (Friedman et al., 1990; Taylor, 1988; Taylor & Eals, 1996; Taylor & Keenan, 1999) and with fMRI research showing reading disorders are associated with less activation in unimodal areas (Brunswick, McCrory, Price, Frith, & Frith, 1999; Helenius, Tarkianinen, Cornelissen, Hansen, & Salmelin, 1999; Nagarajan et al., 1999; Shaywitz et al., 1998).

As reviewed in the introduction, previous research has suggested that development is marked by increasing left lateralization of linguistic processing in the inferior frontal gyrus (Gaillard et al., 2000; Holland et al., 2001). Our study revealed developmental increases in activation in the inferior frontal gyrus, but the laterality of these differences depended on the task. The most pronounced developmental differences were for the right inferior frontal gyrus for the spelling and meaning task and for the left inferior frontal gyrus for

Table 5

Developmental differences (adults–children or children–adults) in modality independent activation on the spelling, rhyming and meaning tasks

	Location			Significance		Coordinate		
	Area	H	BA	z-test	Voxels	X	Y	Z
<i>Adults</i>								
Spelling	Medial frontal gyrus	L	9	4.26	23	–9	39	36
	Inferior frontal gyrus	L	9	3.48	19	–30	18	27
	Inferior frontal gyrus	R	44/9	4.56	90	45	12	24
Rhyming	Medial frontal gyrus	L	9	4.49	36	0	36	39
	Inferior frontal gyrus	L	44/45/9	4.96	129	–45	21	30
	Inferior frontal gyrus	R	44	4.1	59	57	6	12
Meaning	Caudate body	R	*	3.75	28	9	3	6
	Middle cingulate gyrus	R	23	3.95	25	9	–30	33
	Inferior frontal gyrus	R	44	3.95	73	51	6	15
	Inferior frontal gyrus	R	47	4.21	18	45	42	0
	Cerebellum	B	*	4.48	24	0	–60	–36
<i>Children</i>								
Spelling	Anterior cingulate	L	24	4.09	31	0	24	27
	Insula	R	13	3.93	18	48	–21	18
	Lingual gyrus	R	18	3.64	23	18	–69	–9
Rhyming	Lingual gyrus	L	19	3.91	18	–15	–60	–3
Meaning	Fusiform gyrus	L	37	4.63	26	–33	–39	–15

*Note:* H: left (L), right (R) or bilateral (B) hemispheres. BA: Brodmann's area of peak activation as determined by z-test ( $p < 0.001$  uncorrected at the voxel level). Voxels: number of voxels in cluster including this peak, only clusters 15 or greater are presented. Coordinates: –X left hemisphere, +X right hemisphere, –Y behind anterior commissure, +Y in front of anterior commissure, –Z below anterior–posterior commissure plane, +Z above anterior–posterior commissure plane. Regions are sorted by Z coordinate within a group.

the rhyming task. Our finding of the task dependency of developmental differences in the left inferior frontal gyrus is consistent with adult studies that show primarily left hemisphere activation during rhyming tasks (Xu et al., 2001) and more involvement of the right hemisphere in spelling (Flowers et al., 1991) and meaning tasks (Booth et al., 2002b; Buckner, Koutstaal, Schacter, & Rosen, 2000).

#### 4.2. Issues in the neuroimaging of development

This study used a cross-sectional approach to demonstrate differences in lexical processing between pre-teenagers and adults. To map the time course of these developmental changes, studies are needed that compare children of different ages, preferably using a longitudinal design. No published fMRI studies have examined developmental processes using a longitudinal design, although there are a limited number of longitudinal ERP studies examining lexical processing (Licht et al., 1988, 1992). Longitudinal designs are ideal for examining developmental processes because they allow the investigator to examine age differences using a within-subject design. This is important because of the large variability within an age range in behavior and

activation patterns (Licht et al., 1988, 1992). Longitudinal designs also allow for the detection of subtle developmental differences in children who differ by 1 or 2 years of age (Friedman, Putnam, Hamberger, & Berman, 1992; Friedman et al., 1990) and avoid the potential cohort effects in cross-sectional designs (Baltes, Cornelius, & Nesselroade, 1979; Schaie, 1977).

Much of neuroimaging research has focused on identifying the brain regions involved in a particular cognitive operation. Although our study is the first to examine overlapping brain regions for children in different tasks, many studies in adults show that brain areas involved in different cognitive processes overlap (Chee et al., 2000; Kim et al., 1999; LaBar, Gitelman, Parrish, & Mesulam, 1999; Nobre, Gitelman, Dias, & Mesulam, 2000). Indeed, Mesulam (Mesulam, 1990, 1998) has argued that cognitive processing is mapped at the level of multifocal neural systems rather than specific anatomical sites. This multifocal organization gives rise to brain-behavior relationships that are both localized and distributed. Thus, developmental differences may be reflected both in differences in focal processing and in the degree of overlap between cognitive processes.

Parametric manipulations in visual-spatial and language paradigms often show that 'harder' cognitive tasks produce more activation than 'easier' tasks (Caplan, Alpert, & Waters, 1998; Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Just, Carpenter, Keller, Eddy, & Thulborn, 1996). Developmental studies have shown differences between younger and older adults in the neural networks associated with several cognitive processes (Cabeza, 2001; Iidaka et al., 2001; Rypma & D'Esposito, 2000). However, some have argued that observed differences in activation between groups may result from differences in the nature of the hemo-dynamic response in certain brain regions (D'Esposito, Zarahn, Aguirre, & Rypma, 1999; Hesselmann et al., 2001; Huettel, Singerman, & McCarthy, 2001). In order to deal with this issue, Buckner, Snyder, Sanders, Raichle, and Morris (2000) proposed examining group differences with designs that rely on group interactions with parametric manipulations, task conditions or brain regions. For example, developmental changes are inferred if the difference between 'easier' and 'harder' conditions is larger for both behavior and brain activation in younger compared with older participants. Buckner et al. (2000) argued that this approach is valid because the summation of the hemo-dynamic response over all trials was similar across age groups. This approach may also be appropriate for developmental comparisons with children of different ages.

To our knowledge, Licht et al. (1988, 1992) is the only developmental study that has examined the relation between individual differences in skill and brain activation during lexical processing. In addition to demonstrating increasing lateralization to the left hemisphere, they reported two important findings. First, individual differences in skill explained less variance in ERPs in younger than in older children, despite the fact that younger age groups tended to be more variable in skill levels than older age groups. Second, they reported that reading skill was more strongly correlated with ERP (N360) amplitudes over the right temporal area in younger children, whereas reading skill was more strongly correlated with ERP amplitudes over the left temporal area in older children. This finding is consistent with the hypothesis that skill differences should be related to the brain regions that the groups are recruiting to perform the task and argues for the importance of examining the relation of skill within a developmental level.

## 5. Conclusion

In conclusion, this study suggests that development is characterized by increasing involvement of the inferior frontal gyrus in lexical processing and by the specialization of unimodal regions for visual and auditory word forms. Future developmental research should use longitudinal design, multiple task, parametric manipulation and skill correlation approaches to more accurately characterize age-related trajectories.

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