

DEVELOPMENTAL DIFFERENCES IN BRAIN SYSTEMS FOR READING

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Functional magnetic resonance imaging (fMRI) was used to examine the distribution of brain activation during four visual word-processing tasks performed by children (9-12 years) and adults (21-31 years). The four tasks were designed to separately emphasize orthographic, phonological, semantic, and syntactic processes. As expected, the adults performed these tasks more efficiently than the children, who were significantly less accurate in their performance. The patterns of brain activation in the two groups suggest that efficient processing of visual word forms in adults results in part from three trends. (1) A shift in activation from multimodal areas (namely, Wernicke's area in children) to activation of unimodal association areas (fusiform cortex in adults). (2) More restricted interactions between cortical areas in adults as the areas involved in linguistic processes become more specialized and efficient. (3) Overlap of areas associated with high accuracy and quick reaction times in adults as word representations become more directly accessible to areas involved in preparing a behavioral response. These trends reflect plasticity in neural processing during maturation, a process that effectively frees resources for processing unfamiliar stimuli as the ability to respond quickly and accurately to familiar stimuli improves.

Key words: reading, fMRI, developmental differences, visual word processing, neural plasticity

Introduction

Learning to read is a process characterized by increasing efficiency in the ability to recognize written words, pronounce the words, understand the words' meaning, and understand the relationship between words in a sentence. These abilities result from orthographic, phonological, semantic, and syntactic processes. These processes are at least partially separable and likely to be subserved by different brain areas (Dapretto & Bookheimer, 1999; Rumsey et al., 1997a; Vigliocco, 2000). As these processes become more efficient, text can be read quicker and comprehension improves.

Most models of development assume that children initially rely on their semantic knowledge during reading, because graphe-

me (orthography) to phoneme (phonology) decoding processes are inefficient (Perfetti & Lesgold, 1977; Stanovich, 1980). As development proceeds, semantic processes play a lesser role in word identification, whereas phonological processes play a greater role (Booth, Perfetti & MacWhinney, 1999; Plaut & Booth, 2000). Orthographic processes also have an increasing role in word identification as spelling regularities and exception words become more familiar (Gernsbacher, 1984). These developmental changes in single-word processing undoubtedly increase the efficiency of reading. Syntactic processes represent higher-level processes that integrate the appropriate relationship between words. Some knowledge about

syntax precedes reading as a consequence of early exposure to oral language, yet the use of proper syntax typically continues to develop with instruction into late childhood (Landman, 1989). By allowing the reader to identify the writer's intended relationships between words, syntactic processes increase both reading comprehension and reading efficiency.

The goal of this project was to examine whether the neural substrates of word processes used in reading differ in normal children and adults, and to consider whether these differences might account for group differences in reading efficiency. The focus here is not on developmental differences for each component process (i.e., orthographic, phonologic, semantic, and syntactic processes), but rather on more general developmental differences that cross task boundaries. We first briefly review the relevant literature on behavioral development in these domains in order to justify the component tasks used in this study.

Orthographic and phonologic processing

To examine the relative influences of orthographic and phonologic processes in children's visual word recognition, Booth et al (1999) presented three different types of prime-target trials in a priming task. All primes were non-words and shared with a target word (e.g. tomb) either the same phonology (e.g. TUME), a similar orthography (e.g. TAMS), or no letters in common (e.g. USAN). They found that high skill readers (2nd through 6th graders) exhibit more phonologic and orthographic priming than low skill readers. Because these pairs were displayed for a brief duration that prevented complete processing (< 60ms), high skill readers were concluded to activate orthographic and phonologic information more quickly and automatically than low skill readers. They later extended and replicated the results of this study in a population of children and adults with learning disorders (Booth, Perfetti, MacWhinney & Hunt, 2000).

Semantic processing

To examine the effects of semantics on reading, several studies have employed a priming paradigm. Semantics exert a larger priming effect on younger and poor readers than on older and good readers when target words are presented after a single-word or sentential prime (Schwantes, 1985; Schwantes, 1991; Simpson & Lorschach, 1983; Simpson & Lorschach, 1987; West & Stanovich, 1978). Based on their computational model, Plaut and Booth (2000) suggest that older or good readers show small semantic priming effects because their well-developed spelling-sound mapping allows them to decode words rapidly, thereby reducing the effects of semantics on word recognition. Conversely, younger or poor readers show more semantic priming because their underdeveloped grapheme-phoneme connections allow semantic information to influence their slow word recognition processes. Plaut and Booth (2000) suggested that as children learn the statistical regularities between phonology and orthography, they rely less on semantics and more on interactions between orthographic and phonologic processes for efficient, rapid word recognition.

Syntactic processing

Studies on oral-language suggest that normally developing and language impaired children are better at producing and comprehending syntax based on noun-based morphology like possessive and plural forms than on verb-based morphology like past tense forms (Gleason, 1958; Rice, Wexler & Redmond, 1999). Similarly, reading disabled children tend to make more errors when reading auxiliary verbs as compared to nouns (Blank & Bruskin, 1984) and tend to have larger deficits in forming the past tense of verbs than forming the possessive and plural form of nouns (Vogel, 1983; Wiig, Semel & Crouse, 1973). The results of these studies imply that noun- and verb-based morphology may invoke different neural processes.

Because the current study was designed to explore developmental differences that generalize across tasks with different processing requirements, syntax based on both noun- and verb-based morphology were included.

Neuro-cognitive model of reading processing

In written language, visual input is transmitted via the lateral geniculate nucleus to striate cortex and then to adjacent extrastriate cortex. From here visual information has a dorsal "where" projection and a ventral "what" projection (Mishkin, Ungerleider & Macko, 1983). The visual association cortices in the ventral pathway, including the fusiform gyrus, contains orthographic representations of words (Fujimaki et al., 1999; Herbster, Mintun, Nebes & Becker, 1997; Nobre, Allison & McCarthy, 1994). The dorsal "where" system, including V5/MT and superior parietal (Brodmann's area 7), is important in the spatial attention aspects of reading. Both the ventral and dorsal visual systems project to Wernicke's area, a heteromodal association area located at the junction of the temporal and parietal lobes (Aboitiz & Garcia, 1997; Mesulam, 1998).

Wernicke's area receives both auditory and visual input, and is interconnected to category specific areas in the inferior temporal lobe containing representations of faces, animals, and tools (Damasio, Grabowski, Tranel, Hichwa & Damasio, 1996; Di Virgilio & Clarke, 1997). Wernicke's area may give rise to semantics by combining auditory and visual word forms with their associated meanings (Mesulam, 1998; Pugh et al., 1996). Wernicke's area has massive connections through the arcuate fasciculus with Broca's area, an area in the inferior frontal gyrus that is activated relatively late in language tasks (Thierry, Boulanouar, Kherif, Ranjeva & Demonet, 1999). Broca's area is involved in both overt (Hagoort et al., 1999) and covert speech production of articulatory word forms (Friedman et al., 1998) as well as syntactic processing (Caplan, Alpert &

Waters, 1998). Broca's area is strongly interconnected with the anterior superior temporal gyrus, which is also implicated in syntactic processing (Mazoyer et al., 1993; Vorob'ev et al., 1998). Finally, the prefrontal cortex is responsible for modulation of processing in posterior heteromodal regions such as Wernicke's area (Frith, Friston, Liddle & Frackowiak, 1991; Raichle et al., 1994), and may be involved in remembering and manipulating verbal information (Gabrieli, Desmond, Demb, Wagner & et al., 1996; Jonides et al., 1997).

Increases in word processing efficiency during childhood are likely to result from underlying developmental processes. For example, myelination occurs throughout childhood until 20 years, whereas cortical gray matter decreases after 4 years (Pfefferbaum et al., 1994; Yakolev & Lecours, 1967). The maturation of fronto-temporal white matter tracks in the left hemisphere may be specifically associated with the development of sophisticated linguistic abilities (Paus et al., 1999). Also, synaptic pruning continues until about 11 years of age (Huttenlocher & de Courten, 1987), consistent with the possibility that cognitive functions involved in speech are represented in more focal neural regions as development proceeds (Casey et al., 1995; Hertz-Pannier et al., 1997). Thus, the normal development of neural systems may involve more efficient transmission of neural signals and increasing differentiation. These trends could help explain why adults process words more efficiently than children, and should produce differences in brain activity that are detectable with functional imaging.

Goal and hypotheses of current study

The goal of this project was to examine developmental changes in the neural substrate of four types of word judgment tasks in the visual modality, tasks that emphasize orthographic, phonologic, semantic, and syntactic processes. As mentioned previously, the focus of this report is

not on developmental differences for each component process, but rather on more general developmental differences that cross task boundaries.

Our general hypothesis was that developmental changes in reading capabilities should be associated with increased efficiency in word processing. First, an increase in word processing efficiency should be manifested both behaviorally (increased accuracy and decreased reaction time) and functionally (less diffuse activation and a shift in activation toward unimodal visual areas such as the fusiform gyrus). Second, we hypothesized that brain regions responsible for efficient processing operate autonomously, displaying activity weakly correlated to that of other regions. Third, brain regions operating efficiently in these tasks must quickly generate clear, accurate linguistic signals. As accurate word representations become quickly available to areas that effect a behavioral response, we hypothesize that brain areas activated by accurate performance will overlap those areas activated by quick responses. These three trends should be evident in the brain activation patterns of normal adult readers compared with normal children.

Method

Subjects

Two groups of subjects were used in this study: children (ages 9 to 12), and adults (ages 21 to 31). All subjects were right-handed with no evidence of intelligence, reading, or oral-language deficits. The children were recruited from schools in the metropolitan Chicago area and the adults were undergraduate or graduate students at Northwestern University. The subjects each provided their informed consent after the experimenter described to the participant the MRI procedure and the risks and benefits of the study.

MRI practice session

Each subject was acclimated to the scanner environment in a simulator. A simulator reduces anxiety associated with being positioned in the MRI machine when no sedation is used (Rosenberg et al., 1997). The subject slid on a mat into the open tube-like structure of the simulator and grasped a button box in their right hand. The subject was positioned to view a computer monitor about 40cm directly above them. The experimenter played digitized sounds to familiarize the subject with the loud banging noise made by the MRI machine as the subject practiced a full-length version of each word judgment and control task (see below).

Functional activation tasks

Four word judgment tasks and one non-linguistic control condition were used. Subjects rehearsed each task in a practice session, then performed the task with a different set of words in an experimental session. Functional MR images were collected only during the experimental sessions. Each word judgment task lasted 9 minutes, and consisted of 5 experimental blocks of word judgment trials alternating with 5 control blocks of non-linguistic visual judgments. The blocks consisted of one 4-second instruction screen followed by ten 5-second trials.

The order of word judgment tasks was counter-balanced across subjects with the constraint that the orthographic and phonologic tasks could not occur directly after each other, nor could the semantic and syntactic tasks. This constraint was imposed because the orthographic and phonologic tasks were similar in their demand on orthographic-phonologic conversion, whereas the semantic and syntactic tasks required the processing of higher linguistic forms.

Word judgment tasks. In each word judgment trial, 3 consecutive words were presented in lowercase letters during each trial, and the subject was required to make

a judgment about those three words. After the third stimulus was removed, a yellow fixation cross (+) appeared on the screen, indicating that the subject needed to respond during the subsequent 2000 ms if s/he had not already done so. In all tasks, the subject was encouraged to respond as quickly as s/he knew the answer. The orthographic, phonologic, and semantic tasks required the subject to judge whether the last word 'matched' either of the two previous words; they pressed one button if the words 'matched', and a different button if they did not. The criterion used for a 'match' depended on the task. Identical spelling of the 'rime' was a match in the orthographic task, rhyming of the words was a match in the phonologic task, and some form of "relatedness" was a match in the semantic task. The 'rime' included all letters after the first consonant or consonant cluster (Bowey, 1990). The fourth task used a syntactic criterion; the subject had to judge whether all three words together made sense grammatically.

Each of these tasks employed word pairings that emphasized one particular component of word processing. For example, half of the target trials in the orthographic and phonographic tasks contained two words that rhymed and were orthographically similar (i.e. had the same rime), whereas the other half consisted of words that rhymed but were orthographically dissimilar. The orthographic and phonologic tasks required different processing components because the phonologic task required a rhyme judgment based on sound (with the same or different spelling), whereas the orthographic task required a rime judgment based on spelling (with the same or different sound). The matches were easy to identify when the orthography was similar, but more difficult when the orthography of the matching words was dissimilar (see examples in top half of Table 1). Word pairings in the semantic task emphasized semantic processing; half of the 'matches' in the semantic task had a high association, whereas half had a low association (Nelson,

McEvoy & Schreiber, 1994). In all three of these 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 non-matching trials (40%) in these tasks involved three orthographically different words that were non-rhyming and semantically unrelated.

In the syntax task, the word groupings were chosen to emphasize syntactic word judgments based on either noun-based or verb-based morphology. More specifically, subjects determined whether the combination of the second word with the third word was grammatically correct in relation to an animate noun (first word). Half of the animate nouns were plural and half were singular. Both auxiliary verbs (is, are, was, were, has, have, had) and modal auxiliaries (can, could) were included in the second word position. The following verb tense forms were used for the third word: regular past tense -ed, third person singular s, and progressive -ing. In addition, 25% percent of the third words were adjectives. In order for these to be grammatical they must be paired with the copula forms of be. Adjectives were included to make the syntactic task comparable to the other word level tasks, i.e. so they had the same percentage of nouns, verbs, and adjectives. For the 40% ungrammatical trials, one-third of the ungrammatical items involved a noun-based morphology violation that occurred between the animate noun and the second word, and two-thirds involved a verb-based morphology violation between the second and third words.

The presentation of trials in the experimental and control conditions that 'matched' and those that did not 'match' were randomized within a block. The order was constrained so that no more than two non-matches occurred in a row, nor did more than two of each stimulus type (orthographic similarity, semantic association, and morphology). The same pseudo-random order of presentation was used for each subject. Examples of hard and easy word matches from each task are listed in Table 1.

Control conditions. Control blocks were designed to match the experimental blocks in terms of their memory demands and response characteristics. The timing for the control blocks was exactly the same as for the word blocks.

For control blocks, the three stimuli were abstract, *non-linguistic* symbols consisting of straight lines. The first two stimuli in each trial were different; subjects had to judge whether the third stimulus was the same or different from either of the first two stimuli. Half of the correct trials involved a match to the first stimulus (/ /, \ \, / \) and half involved a match to the second stimulus (/ /, \ \, \ \). The non-matching trials (40% of the total trials) involved three different stimuli (/ /, \ \, / \). All possible combinations were included in the matching and non-matching trials.

MRI data acquisition

A research technologist screened the subject for presence of metallic devices, possible health problems, or use of medications. The subject was asked to lie down on the scanner bed and the placement of the head was secured with a specially designed vacuum pillow. During the entire procedure, appropriate measures were taken to ensure that the subject was comfortable before the scanning session began. An optical response button was placed in the subject's right hand and a squish ball was placed in their left hand. This ball was used to signal the operator to terminate the scan if the subject felt that this was necessary for any reason. The head coil was positioned over the subject's head and a mirror system for the visual presentation of stimuli was secured to the head coil. Before leaving the scanning room, the experimenter assured the subject that they would be in continual contact during the scanning procedure. Each imaging session took less than one hour.

All images were acquired using a 1.5 Tesla scanner. Gradient echo localizer images were acquired to determine the placement and angulation of the functional slices. The

orientation of the images was transaxial angled to incorporate the anterior commissure and the posterior commissure.

A susceptibility weighted single shot echo planar method with BOLD (blood oxygenation level-dependent) was used for the functional imaging studies. The scan parameters were as follows: TE= 40, flip angle= 90°, matrix size= 64 X 64, field of view= 22cm, slice thickness= 4mm, number of slices= 32. These scanning parameters resulted in a 3.437 X 3.437 X 4mm voxel size. The acquisition of this volume was repeated throughout the experiment and allowed the whole brain to be imaged every 3 seconds (TR = 3000ms).

At the end of the functional imaging session, a high resolution, T1 weighted 3D image was acquired (3D FLASH, TR= 15ms, TE= 6ms, flip angle= 20°, matrix size= 256 X 256, field of view= 22cm, slice thickness= 1mm). These scanning parameters resulted in a .86 X .86 X 1mm voxel size. The orientation of this 3D volume was identical to the functional slices and was used in conjunction with the functional activation maps to localize brain activation to an anatomic site. The acquisition of the anatomical scan took 10 minutes.

Image data analysis

Data analysis was performed using SPM-96 (Statistical Parametric Mapping) for motion correction and statistical inference (Friston et al., 1995a; Friston et al., 1995b; 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 (or one closest to the T1 anatomical scan) using sinc interpolation. No individual runs had more than 4mm movement (the size of one voxel) in the x, y, or z plane. Images were then segmented (gray matter, white matter, cerebrospinal fluid and scalp) and this information was used to co-register the structural and functional images. The images were then normalized to the SPM template (12 affine parameters, 8 nonlinear

iterations, 2 X 2 X 2 nonlinear basis functions). The normalization process simplifies reporting anatomic locations by using a standardized coordinate system. The normalization of children's brain to an adult template was justified because, in 9 year-old children, the cerebrum is 95% of adult size, the neocortex is 102% of adult size with established sulcal and gyral patterns, and white matter is 85% of adult size (Caviness, Kennedy, Bates & Makris, 1997). The normalized data were then smoothed with a 7 X 7 X 7 Gaussian kernel.

Statistical analyses were calculated on the smoothed data using a delayed boxcar design with a high pass filter equal to 2 cycles of the experimental and control conditions (216 s). Statistics were done through the use of contrasts in a fixed effect analysis. For each subject, we calculated contrasts of experimental minus control for each of the 4 word judgment tasks (orthographic, phonologic, semantic, and syntactic). We examined the activation patterns superimposed on the normalized brain as well as on their own brain without normalization to make sure that the normalization process, particularly in children, did not distort either the statistics or the structural details. All areas of activation reported in the manuscript were significant using the following criteria: $p < .001$ and cluster size > 3 voxels. This significance level adequately controlled for Type I error because we hypothesized a priori regions of interest, including perisylvian structures (Broca's and Wernicke's area), the fusiform gyrus and the superior parietal cortex.

Results

Behavioral performance in visual word processing

Accuracy and reaction time data for adults and children are presented in Table 2. Because there were no significant differences between sessions, we collapsed accuracy and reaction time across the practice and test sessions in order to obtain the most sensitive

measure of each subject's performance. We calculated an age (children, adults) X task (orthographic, phonologic, semantic, syntactic) ANOVA on accuracy and reaction time. Children had significantly lower accuracy levels than adults in the word tasks, $F(1,36) = 23.54$, $p < .001$, whereas reaction times were not significantly different between adults and children. There was no significant effect of task on accuracy or reaction time, nor an interaction between age and task.

There were also no significant age-related differences in accuracy or reaction time for the visual control tasks, nor were there significant differences between the word judgment tasks and the control tasks. The activation patterns described below for the word judgment tasks are therefore not attributable to a general difficulty difference between the experimental and control tasks.

Developmental differences in visual word processing

For each word judgment task, we calculated activation maps for the following three intergroup comparisons. First, [Children [experimental-control] minus adults [experimental-control]] activation maps were generated to show those regions activated significantly more in children than adults. Second, [Adults [experimental-control] minus children [experimental-control]] activation maps were generated to show those regions activated significantly more in adults than in children. Third, a conjunction of activation produced by [children [experimental-control] and adults [experimental-control]] was generated to show overlap in activation between adults and children. This analysis produced a map of areas that were activated significantly and to the same degree in adults and children. These mutually-exclusive conditions were color-coded and plotted on a normalized brain template.

In many respects, the four word judgment tasks produced a similar overall pattern of results. Adults and children activated a similar network involving extrastriate

and fusiform areas bilaterally, and Wernicke's and Broca's areas in the left hemisphere (see Figure 1). However, adults showed statistically more activation bilaterally in the fusiform gyrus, whereas children showed statistically more activation in Wernicke's area, superior parietal cortex and cerebellum. These developmental differences are consistent with the hypothesis that adults processed visual word forms efficiently and automatically in the fusiform gyrus, whereas children utilized additional resources in the superior parietal cortex, cerebellum and Wernicke's area to integrate visual and linguistic forms. The children produced activation in bilateral superior parietal cortex during all tasks, suggesting a greater role of spatial attention in less skilled reading (Mesulam, 1990).

Functional connectivity in visual word processing

Functional connectivity refers to the temporal correlation between activity in spatially distinct brain regions. Eigen image analysis is a principal component procedure that uses singular value decomposition to examine functional connectivity in fMRI. The first Eigen image is the spatial mode that accounts for the most variance-covariance in the whole brain data set over time; the second component is orthogonal (independent) and accounts for the next most amount of variance-covariance. Voxels that share a high correlation with either component demonstrate strong functional connectivity. We calculated Eigen image analysis separately on the orthographic, phonologic, semantic, and syntactic tasks for adults and also for children.

Figure 2 presents the functional connectivity of adults and children from the semantic task only, but the pattern of results from the semantic task was similar to the results from the orthographic, phonologic, and syntactic tasks. Generally, adults had focal connectivity whereas children had widespread connectivity. In adults, activation associated with the first component was

centered on the fusiform gyrus, whereas activation associated with the second component was centered on Broca's and prefrontal areas. Because input during the visual word judgment task first entered into the occipital lobe, we assume that activation of the fusiform gyrus (first component) preceded the activation of Broca's area (second component). These findings suggest that quick and efficient recognition of visual word forms by adults occurred in the fusiform gyrus, whereas a slower, independent process involved Broca's area and other frontal regions. By contrast, activation in children's fusiform gyrus, angular gyrus, superior parietal cortex, Wernicke's area, Broca's area, and prefrontal cortex was associated with both the first and second components. These patterns of functional connectivity suggest that the brains of children were less specialized in processing words than adults.

Relationship of accuracy to reaction time

Accuracy and reaction time were negatively correlated for adults on these word judgment tasks [$r(16) = -.57, p < .05$ for experimental; $r(16) = -.93, p < .001$ for control], but positively correlated for children [$r(20) = .09, ns$ for experimental; $r(20) = .70, p < .01$ for control]. Because of significant differences in performance, the relationship between behavioral performance and brain activation was examined separately for adults and children.

The relationship between performance and brain activation was examined by statistically comparing the behavioral scores of individuals with the level of activation in the brain. The behavioral measures for each subject were collapsed across tasks. This procedure was justifiable because essentially the same brain areas were activated during each task and there were no significant task effects on accuracy or reaction time. In this procedure, the behavioral measure for each individual was subtracted from the mean for that age group. Thus, the most accurate

adults (or children) were assigned positive values proportional to the elevation of their scores above the mean, and the least accurate adults (or children) were assigned negative values proportional to the drop of their scores from the mean. A statistical analysis was then performed within SPM to identify those brain regions whose activity across subjects was significantly correlated with behavioral accuracy. This same procedure was used to examine brain regions associated with fast and slow reaction time, both in adults and children. We then created overlap maps for the adults and children to determine if areas associated with high accuracy overlapped areas associated with either fast or slow reaction time.

Among adults, there was considerable overlap in activation associated with high accuracy and fast reaction time. Indeed, every focus of activity associated with high accuracy overlapped a focus associated with fast reaction times. The situation was very different for children, however, which showed no overlap of high accuracy with fast reaction time. Among children, overlapping activation was only observed for high accuracy and slow reaction time, and most areas associated with high accuracy were unrelated to either fast or slow reaction time.

Discussion

Overview of results

Our hypothesis that adults are more efficient than children at processing language was supported by observed developmental differences in behavior and brain activation. First, adults were significantly more accurate in task performance. Second, adults showed less functional connectivity between brain regions than children in the visual word judgment tasks. Widespread correlated activity in children suggests that they have not developed independent systems for efficiently processing word forms. Third, overlapping activation was associated with high accuracy and fast reaction time in adults, suggesting that accurate performan-

ce was associated with fast, efficient processing. In contrast, overlapping activation was associated with high accuracy and slow reaction time in children, indicating that accurate performance in children was associated with slow, inefficient processing. Indeed, most areas associated with high accuracy in children showed no relationship to reaction time. In contrast for adults, the areas associated with high accuracy almost entirely overlapped areas associated with quick reaction times.

Our results also suggest that visual association cortices — especially areas within the fusiform gyrus — are increasingly important for processing visual word forms during development. Significant activation within the fusiform gyrus was more widespread in adults than in children, despite less activation in other regions of the adult brain, such as in Wernicke's area, the superior parietal cortex, and the cerebellum. Furthermore, the fusiform gyrus in adults was activated independently of other brain areas active during our word tasks. By contrast, activation in the fusiform gyrus of children was more limited, although its functional connections were widespread. We interpret these findings to mean that processing of orthographic word forms occurs within visual association cortices in adults, even though these areas have fewer interactions with other brain regions.

Activation of unimodal visual association areas by our word tasks suggests that reading words may activate different areas than hearing words. This interpretation is consistent with other studies that suggest a different neural focus for the auditory and visual lexicons (Demonet & Frackowiak, 1993; Howard et al., 1992; Petersen & Fiez, 1993; Zurif & Swinney, 1994). The heavier reliance on these unimodal processing areas suggests that adults could be more efficient at visual word recognition, an interpretation confirmed by cognitive developmental research that shows increased efficiency in processing orthographic as well as phonological forms (Booth et al., 1999).

Our results also showed that children exhibited more activation in posterior heteromodal Wernicke's area during the processing of visual word forms. Posterior Wernicke's area is involved in integrating different sources of information (e.g. auditory and visual sources), and our assumption is that integrating different sources of information is less efficient. Wernicke's area may be responsible for the integration of auditory and visual word forms with arbitrary associations that give rise to meaning or semantics (Mesulam, 1998). The greater activation in Wernicke's area is consistent with behavioral findings and computational models that show greater reliance on semantics in younger children (Plaut & Booth, 2000).

Implications for research on reading disorders

Our developmental data provide some interesting contrasts with the results of previous research on linguistic processing in adults with reading disorders. A robust and consistent finding in the literature is that reading disability in adults is associated with decreased activity in the temporo-parietal area, a finding which has been interpreted to reflect an underdeveloped or inefficient posterior reading network (Rumsey et al., 1992; Rumsey et al., 1997b). One might therefore predict that children, who are less skilled readers, should show less activation than normal adults in the temporo-parietal area. However, we found that children activate posterior Wernicke's area more than normal adults in the visual word judgment tasks.

Others have suggested that the dysfunction of temporo-parietal areas in adults with reading disorders result from a disconnection of posterior reading areas (namely the angular gyrus) from other brain regions involved in reading, such the inferior frontal gyrus (Horwitz, Rumsey & Donohue, 1998; Paulesu, Frith & Frackowiak, 1993). However, current evidence for disconnection appears to be limited to visual tasks that

require orthographic to phonological conversion (Pugh et al., 2000). Based on these results, one might predict that children, who are less skilled readers, should show less functional connectivity in reading tasks. We did not find evidence for this in our comparison of children and adults without reading disorders — in fact, we found evidence for a greater degree of functional connectivity in children than in adults. As noted previously, this widespread functional connectivity suggests that the brains of children were less specialized and less efficient than adults. We suggest that children require this widespread functional connectivity, plus integrative processes within Wernicke's area and the angular gyrus, in order to develop efficient orthographic word-processing mechanisms within visual association cortices. Functional connectivity decreases during normal development once visual association cortices have become efficient, independent processors of visual word forms. According to this interpretation, adults with reading disorders have failed to properly develop this efficient processing system because they lack the requisite integrative processes within posterior reading areas, due either to limited connectivity or to improper function. Because adults with reading disorders do not share the activation patterns we observed for normal children, the brain activation and functional connectivity results of our study imply that adult reading disorders do not simply reflect an arrested state of early development.

Conclusion

The goal of this study was to examine the general hypothesis that the development of reading is characterized by increased efficiency in word processing within the brain's linguistic areas. This hypothesis is supported by observed developmental changes in the intensity of activation, the functional connectivity among different brain regions, and the relation of accuracy and reaction time to activation patterns.

Processing of linguistic information appears to be most efficient when processes within the fusiform gyrus are activated extensively and largely independent of other brain areas.

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Table 1 Examples of hard and easy stimuli for the four word judgment tasks.

	<u>HARD</u>	<u>EASY</u>
<u>Orthographic</u>	<u>Dissimilar Orthography</u>	<u>Similar Orthography</u>
First match	hope – colt – soap	hold – plant – cold
Second match	boil – nest – blessed	built – vote – note
<u>Phonologic</u>	<u>Dissimilar Orthography</u>	<u>Similar Orthography</u>
First match	jazz – last – has	seat – fresh – heat
Second match	myth – home – foam	wish – fall – wall
<u>Semantic</u>	<u>Low Association</u>	<u>High Association</u>
First match	hate – wire – like	frame – gain – picture
Second match	input – boots – cowboy	got – left – right
<u>Syntactic</u>	<u>Verb-based Morphology</u>	<u>Noun-based Morphology</u>
	boys – could – running mother – had – clever	girls – was – swimming student – have – jumped

Table 2 Means (M) and standard errors (SE) for adults and children in the four word judgment tasks and control task.

	<u>ADULTS</u>				<u>CHILDREN</u>			
	<u>RT</u>		<u>Accuracy</u>		<u>RT</u>		<u>Accuracy</u>	
	<u>M</u>	<u>SE</u>	<u>M</u>	<u>SE</u>	<u>M</u>	<u>SE</u>	<u>M</u>	<u>SE</u>
Orthographic	1440	108	92.7	3.3	1683	103	82.8	3.8
Phonologic	1451	147	95.2	1.0	1625	135	90.3	3.3
Semantic	1666	126	90.9	3.3	1727	87	89.9	2.7
Syntactic	1429	150	95.9	1.5	1609	89	89.4	3.1
Control	1450	159	89.1	5.4	1356	113	88.3	2.3

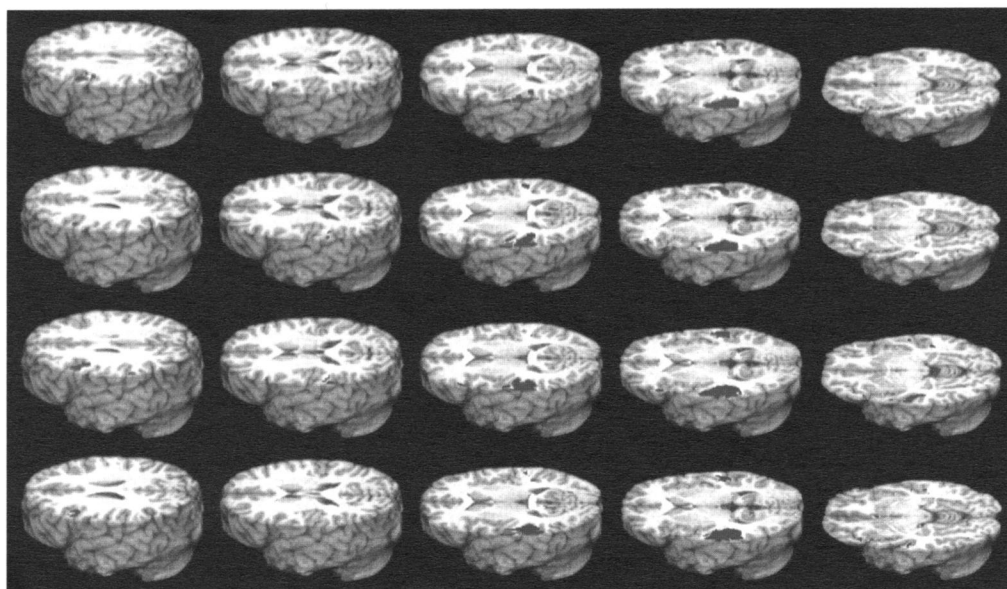


Figure 1. Activation maps for the visual orthographic (1st row), phonologic (2nd row), semantic (3rd row), and syntactic tasks (4th row). Green indicates significantly more activation in children, red indicates significantly more activation in adults and purple indicates equal activation in children and adults.

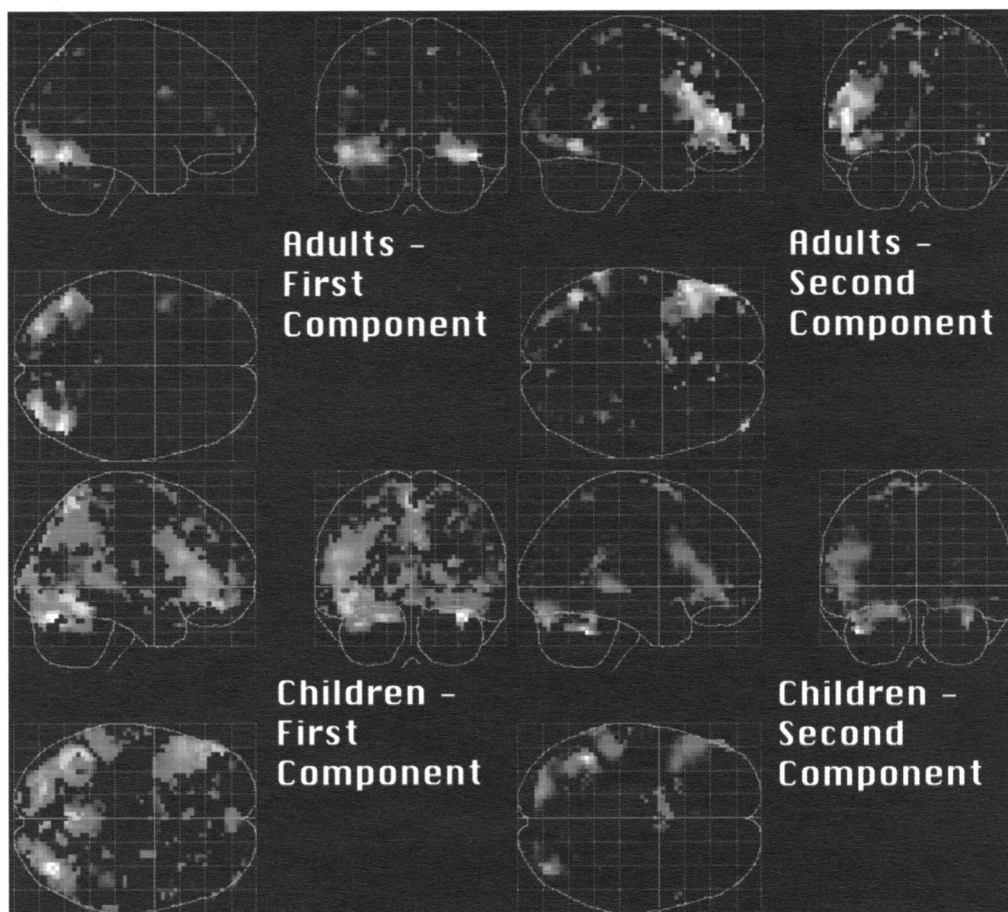


Figure 2. Activation associated with first and second components in the Eigen image analysis for adults and children for the semantic task.

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RAZVOJNE RAZLIKE U MOŽDANIM STRUKTURAMA ZA ČITANJE

SAŽETAK

Učenje čitanja proces je pri kojem se povećava uspješnost prepoznavanja pisanih riječi, izgovora riječi, razumijevanja značenja riječi te razumijevanja odnosa između riječi u rečenici. Te sposobnosti rezultat su ortografskih, fonoloških, semantičkih i sintaktičkih procesa. Ti su procesi barem djelomično odvojeni te postoji vjerojatnost da njima upravljaju različiti dijelovi mozga (Dapretto i Bookheimer, 1999; Rumsey i suradnici, 1997a, Vigliocco, 2000). Kako oni postaju djelotvorniji, tekst se čita brže te se povećava razumijevanje.

Većina razvojnih modela polazi od toga da se djeca u početku prilikom čitanja oslanjaju na svoje poznavanje semantike, jer su procesi pretvaranja grafiema (ortografija) u foneme (fonologija) nedjelotvorni (Perfetti i Lesgold, 1977; Stanovich, 1980). Kako se razvoj nastavlja, semantički procesi igraju manju ulogu u prepoznavanju riječi, dok fonološki procesi igraju veću (Booth, Perfetti i MacWhinney, 1999; Plaut i Booth, 2000). S boljim poznavanjem pravopisnih pravila i iznimaka povećava se i uloga ortografskih procesa u prepoznavanju riječi (Gernsbacher, 1984). Te razvojne promjene u obradi pojedinačnih riječi nesumnjivo povećavaju uspješnost čitanja. Sintaktički procesi predstavljaju procese višeg reda kojima se povezuju odgovarajući odnosi među riječima. Iako se zbog rane izloženosti govornom jeziku određeno znanje o sintaksi usvaja prije čitanja, primjena sintakse u užem smislu uglavnom se nastavlja razvijati podukom koja traje do kasnog djetinjstva (Landman, 1989). Omogućujući čitatelju da prepozna odnose između riječi koje je pisac namjeravao izraziti, sintaktički procesi povećavaju i razumijevanje i uspješnost čitanja.

Cilj ovog projekta bio je ispitati razlikuju li se neuralni substrati obrade riječi koji se koriste kod normalne djece i odraslih te razmotriti mogu li ove razlike objasniti skupne razlike u uspješnosti čitanja. Ovdje težište ne leži u razvojnim razlikama kod svakog pojedinačnog procesa (tj. ortografskog, fonološkog, semantičkog i sintaktičkog procesa), nego u općenitijim razvojnim razlikama koje nadilaze granice između zadaća. Kako bismo opravdali upotrebu sastavnih zadataka u ovoj studiji, prvo ćemo dati kratak pregled relevantne literature o razvoju ponašanja u tim područjima.

Funkcionalni imidžing magnetskom rezonancijom (fMRI) korišten je kako bi se ispitala raspodjela moždane aktivnosti tijekom četiri vizualna zadatka obrade riječi kod djece (9-12 godina) i odraslih (24-31 godina). Svrha tih četiriju zadataka bila je odvojeno naglasiti ortografske, fonološke, semantičke i sintaktičke procese. U skladu s očekivanjima, odrasli su te zadatke izveli uspješnije od djece, koja su ih izvela sa značajno manjom točnošću. Obrasci moždane aktivnosti u te dvije skupine pokazuju da je uspješnost obrade vizualnih oblika riječi kod odraslih djelomično posljedica triju trendova. (1) premještanje aktivnosti iz multimodalnih područja (tj. Wernickeova područja kod djece) na jednomodalna asocijativna područja. (2) veća restriktivnost interakcija između kortikalnih područja kod odraslih jer područja uključena u lingvističke procese postaju specijaliziranija i učinkovitija. (3) Preklapanje područja povezanih s većom preciznošću i većom brzinom reagiranja odraslih zbog toga što predodžbe o riječima postaju dostupnije područjima koja su uključena u pripremu ponašajnog odgovora. Ovi trendovi odražavaju plastičnost neuralne obrade tijekom sazrijevanja, procesa kojim se djelotvorno oslobađaju resursi za obradu nepoznatih podražaja zahvaljujući povećanju sposobnosti brzog i točnog odgovora na poznate podražaje.