

Differences in Auditory Processing of Words and Pseudowords: An fMRI Study

Sharlene D. Newman^{1*} and Donald Twieg^{1,2}

¹*Biomedical Engineering Department, University of Alabama at Birmingham, Birmingham, Alabama*

²*Center for Nuclear Imaging Research, University of Alabama at Birmingham, Birmingham, Alabama*

Abstract: Although there has been great interest in the neuroanatomical basis of reading, little attention has been focused on auditory language processing. The purpose of this study was to examine the differential neuroanatomical response to the auditory processing of real words and pseudowords. Eight healthy right-handed participants performed two phoneme monitoring tasks (one with real word stimuli and one with pseudowords) during a functional magnetic resonance imaging (fMRI) scan with a 4.1 T system. Both tasks activated the inferior frontal gyrus (IFG), the posterior superior temporal gyrus (pSTG) and the inferior parietal lobe (IPL). Pseudoword processing elicited significantly more activation within the posterior cortical regions compared with real word processing. Previous reading studies have suggested that this increase is due to an increased demand on the lexical access system. The left inferior frontal gyrus, on the other hand, did not reveal a significant difference in the amount of activation as a function of stimulus type. The lack of a differential response in IFG for auditory processing supports its hypothesized involvement in grapheme to phoneme conversion processes. These results are consistent with those from previous neuroimaging reading studies and emphasize the utility of examining both input modalities (e.g., visual or auditory) to compose a more complete picture of the language network. *Hum. Brain Mapping* 14:39–47, 2001. © 2001 Wiley-Liss, Inc.

Key words: functional magnetic resonance imaging; language; frontal cortex; posterior cortex; cognition

INTRODUCTION

Functional imaging techniques such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have proven to be valu-

able tools in the study of brain function, particularly language. More specifically, functional neuroimaging has afforded a means of providing a neuroanatomical structure to cognitive models of language, which until recently have been based solely on lesion studies. One example of neuroimaging providing such structure is in studies comparing the reading of real words and pseudowords. These studies have provided great insights into the cognitive architecture of word reading [Brunswick et al., 1999; Fiez and Petersen, 1998; Rumsey et al., 1997]. A general finding from these word reading studies is that pseudoword and real word reading tended to activate the same cortical network and that pseudoword reading is more effortful, producing more activation than real word reading. The regions where this differential response to pseudowords

Contract grant sponsor: National Institute of Deafness and Other Communications Disorders; Contract grant number: R03 DC03324; Contract grant sponsors: UAB Comprehensive Minority Faculty Development Program; National Institute of Health/National Center for Research Resources; Contract grant number: P41 RR11811.

*Correspondence to: Sharlene D. Newman, The Center for Cognitive Brain Imaging, Carnegie Mellon University, Baker Hall 327, 5000 Forbes Ave, Pittsburgh, PA 15213.

E-mail: sneman+@andrew.cmu.edu

Received 26 September 2000; Accepted 21 May 2001

is consistently observed is the inferior frontal gyrus, the posterior superior temporal gyrus and the inferior parietal lobe [Brunswick et al., 1999; Fiez and Petersen, 1998; Hagoort et al., 1999; Herbster et al., 1997; Price, 1994; Price et al., 1996]. These results have led to three major conclusions. First, the common neuroanatomical network activated by both real words and pseudowords provides support for single route, connectionist models of word reading opposed to dual route models [Brunswick et al., 1999; Rumsey et al., 1997]. Second, reading pseudowords seems to rely more heavily on grapheme to phoneme conversion processes that appear to be localized to the inferior frontal gyrus [Herbster et al., 1997; Price, 1998; Rumsey et al., 1997]. Finally, lexical access seems to be automatically initiated for both real word and pseudoword processing and these processes seem to be localized to the posterior superior temporal gyrus and inferior parietal region [Brunswick et al., 1999; Fiez et al., 1993; Rumsey et al., 1997].

Although there has been great interest in understanding the neuroanatomical basis of reading, very little attention has been focused on auditory language processing. Using fMRI, the present study examined the neuroanatomy involved in the auditory phonological processing of both real words and pseudowords. The phonological processing task examined was a phoneme monitoring task in which participants judged whether or not the stimulus ended with the /t/ sound. Prior studies examining the neural activity engendered by this type of task found that it tended to involve the inferior frontal gyrus, the left posterior superior temporal gyrus, as well as the inferior parietal lobe [Burton et al., 2000; Demonet et al., 1992, 1994; Zatorre et al., 1992, 1996].

Activation associated with pseudoword processing versus real word processing should match that observed in previous reading studies. Both tasks are expected to activate the same brain regions, again providing support for the connectionist model of language perception. Although the same cortical network is expected to activate for both conditions they are not expected to activate at the same level. One region where differential activation is expected is the temporal-parietal region. As stated above, this region has been shown in previous neuroimaging studies to show a differential response to stimulus type due to differential lexical access processing elicited by real words and pseudowords. The inferior frontal gyrus, on the other hand, is not expected to reveal a differential response to stimulus type due to its hypothesized involvement in grapheme to phoneme conversion processes, which are not necessary in auditory processing.

MATERIALS AND METHODS

Participants

Participants were eight right-handed volunteers between the ages of 21 and 35 years (three men, five women), with no history of neurological or auditory symptoms. Each participant gave informed written consent approved by the University of Alabama at Birmingham Institutional Review Board.

fMRI Data Acquisition

Scanning was performed at 4.1 Tesla on a system with a Bruker magnetic resonance spectrometer and console and Philips magnet and gradients, located at the Center for Nuclear Imaging Research at the University of Alabama at Birmingham. Participants were placed in the scanner with custom-made earmolds, two push buttons (one in each hand), and padding behind the neck and between the head and inner surface of the head coil as needed. The stimuli were presented binaurally via air conduction. Two imaging protocols were used because of a system upgrade mid-way through data collection. The first had the following parameters: eight 128×128 gradient echo axial scout images and six 6 interleave spiral functional images; 120 sequential images of each slice using a TR = 4200 msec and a TE = 25 msec (six participants). The second protocol had the following parameters: 20 256×256 gradient echo anatomical scout images and 18–20 64×64 EPI functional images; 120 sequential images of each slice using a TR = 2500 msec and a TE = 38.5 msec. The slice thickness was 5 mm with a 5 mm slice gap for both protocol and the voxel size was $3.44 \times 3.44 \times 5$ mm. *t*-Tests revealed that there was no significant difference in the amount of activation observed in the ROIs as a result of protocol used ($P > 0.1$ for each ROI).

Two separate imaging series were collected, one for each stimulus type. A series of 14 successively presented words of the same type (e.g., pseudowords or real words) constituted an epoch. There were five epochs in each image series and 12 images were acquired during each epoch. The baseline used was the 30 sec rest periods between experimental epochs.

Experimental Design and Procedures

Before the fMRI experiment, participants were familiarized with the task and stimuli. During the practice session earmolds were made and a handedness inventory [modified from Annett, 1967; source: Briggs

and Nebes, 1975] was completed. The range of the handedness score is from -24 (extremely left-handed) to +24 (extremely right handed). All participants scored as right handed with a mean of 21 ± 2.7 .

During both phoneme monitoring tasks, participants were given the following instructions: "You will hear a series of pseudowords (words) and your task it to respond "yes" with the left push button if the stimuli ended in the /t/ sound and "no" with the right button if it did not. Blocks of pseudowords will be alternated with periods of rest in which you are to relax and refrain from thinking about anything." The presentation of the word and pseudoword task was counterbalanced across sessions to reduce order effects.

Stimuli were 16-bit digital recordings of a male voice. These samples included 50 consonant vowel consonant (CVC) pseudowords and 50 CVC high frequency words with the following consonant and vowel sounds: ch, k, t, z, m, n, d, j, p, l, g, r, w, s, a, u, i, and o (i.e., wat, suit). All syllables were edited to so that their duration was 500 msec. The amplitude of the initial and final consonants was boosted to compensate for the losses due to transmission. Half of the stimuli contained the /t/ sound and of that half, half ended in the /t/ and half began with the /t/ sound.

Image Analysis and Task Comparisons

Data analysis was performed with the STIMULATE [Strupp, 1996] image analysis package. A cine loop of the 120 frames was used to detect gross subject motion, and to eliminate data sets with observable subject

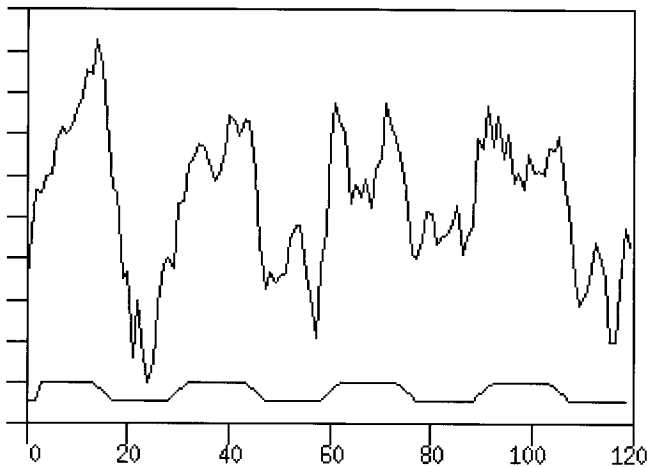


Figure 1.

A typical time course from an active voxel within Broca's area and the trapezoidal reference function. As shown the on/off trend can still be observed even through the noise from various sources (e.g., noise due to respiration, and the cardiac cycle).

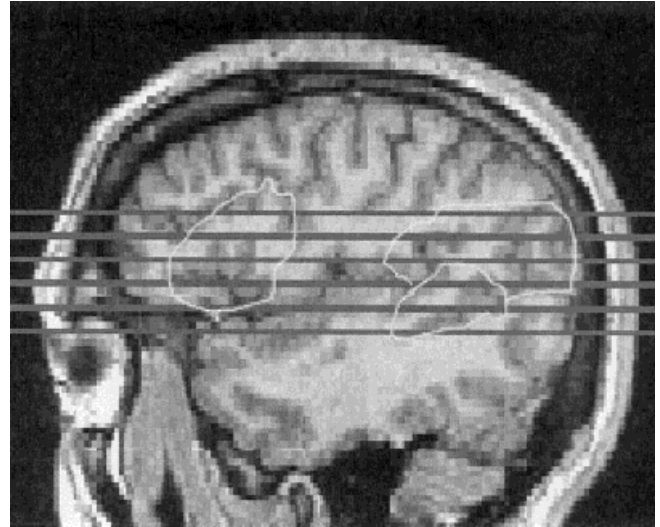


Figure 2.

A typical slice prescription with the ROIs overlaid that captures the inferior frontal gyrus, the superior temporal gyrus and the inferior parietal lobe.

motion from further analysis. Activation maps were obtained using correlational analysis with a trapezoidal reference function (see Fig. 1). The r threshold ($r > 0.3$) was calculated using an F-statistic with $\alpha = 0.005$. The determination of activation also had to meet the requirement of three contiguous activated voxels as well as having a signal increase that did not exceed 10% to reduce noise.

The ROIs were defined by using the parcellation method originally described by Rademacher et al. [1992]. This approach uses anatomical landmarks on the coronal plane and limiting sulci to segment cortical regions. For each participant, the limiting sulci and cerebral landmarks were identified by viewing the structural images in the three orthogonal planes of a 3D rendering of the axial slices. The major analysis focused on three ROIs: IFG, the inferior parietal region (supramarginal/angular gyrus), and the left posterior superior temporal gyrus (lpSTG). In the Rademacher et al. [1992] nomenclature, the IFG ROI corresponded to F3t and F3o. The inferior parietal ROI corresponded to SGa, SGp and AG. The lpSTG corresponded to T1p, primary auditory cortex was excluded from this ROI. Figure 2 depicts the ROIs overlaid on a single participant along with the slice orientation. As shown, the six slices covers the majority of IFG and pSTG as well as a significant portion of the inferior parietal region.

The data analysis focuses on quantifying the volume of fMRI-measured activation using the average number of voxels that have an activation level that is significantly above the baseline. The voxel counts

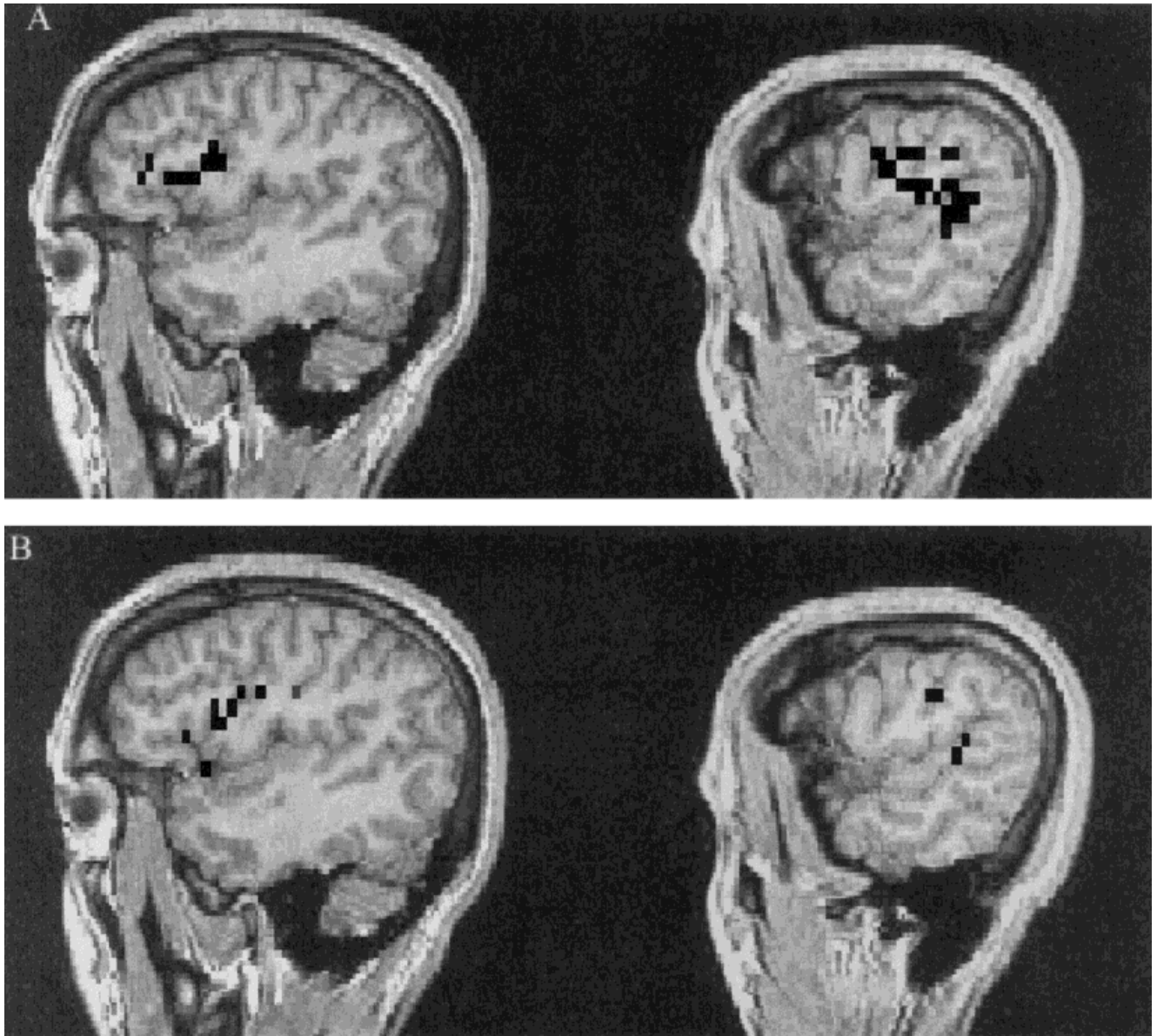


Figure 3.

Functional activation results from a single participant, overlaid on the corresponding structural slices. The top row (**A**) depict activation during the pseudoword condition and the bottom row (**B**) the real word condition.

were obtained by counting the number of active voxels within each of the anatomically defined ROIs for each participant. Because our main prediction concerned the interaction between stimulus type and cortical region, the activation was examined using analysis of variance (ANOVA) with ROI (inferior frontal gyrus vs. inferior parietal lobe vs. posterior superior temporal gyrus), laterality (left vs. right), and stimulus type (pseudoword vs. real word) as within-subject factors. In addition, ANOVA were calculated for each

ROI with stimulus type and laterality as within-subject factors. Because the general level of activation can vary across participants, a within-subject analysis was performed to determine whether the condition effects observed were consistent across participants.

RESULTS AND DISCUSSION

Figure 3 illustrates the general results by showing the pattern of thresholded fMRI-measured activation

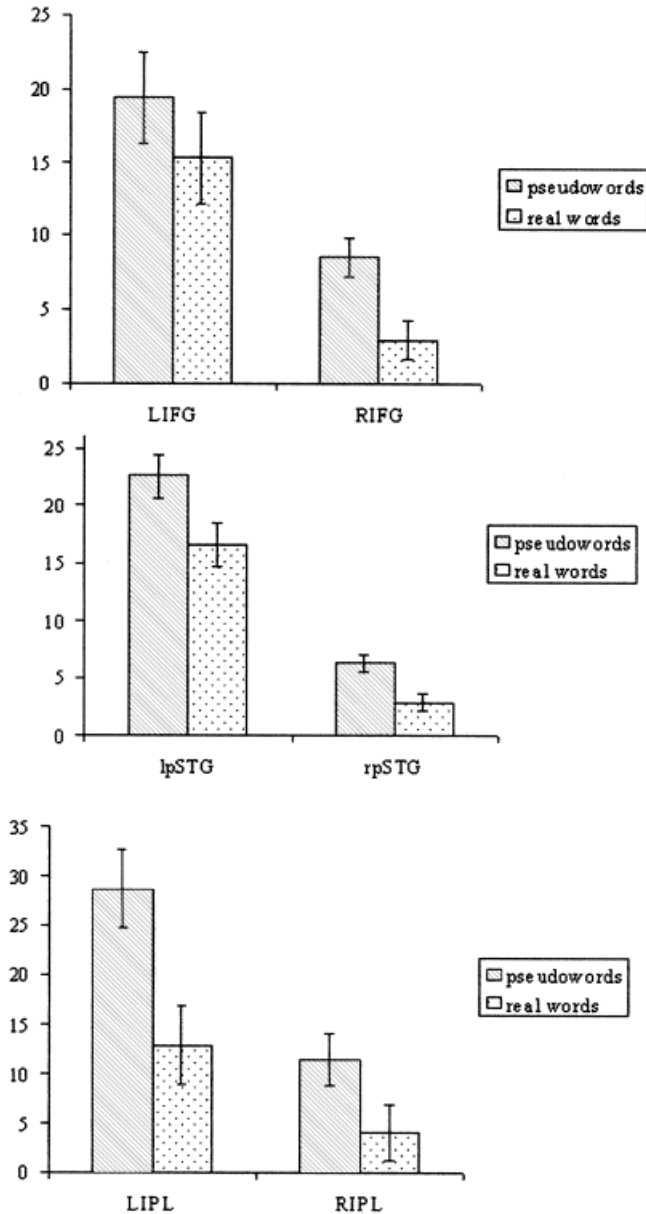


Figure 4.

Multi-subject averaged voxel counts for each of the ROIs. Error bars represent 95% confidence intervals based on the pooled *Mse* from the corresponding ANOVA [Loftus and Mason, 1994].

superimposed on structural images for a set of slices for a typical participant. As Figure 3 shows, both pseudowords and real words activated the same cortical network. Activation was observed in the inferior frontal gyrus, the temporal region, the parietal region, the posterior cingulate and prefrontal regions.

As shown in Figure 4, both conditions activated the three regions of interest: inferior frontal gyrus, the posterior superior temporal gyrus and the inferior

parietal region. As in previous reading studies, the multisubject averaged results revealed that the amount of cortical activation varied as a function of stimulus type with pseudowords, generally producing significantly more activation than real words, $F(1,6) = 39.66, P < 0.0007$. In addition, Figure 3 suggests that the left hemisphere ($M = 19.24$) was more active than the right hemisphere ($M = 6$), $F(1, 6) = 15.02, P < 0.008$. Although there was a slight trend of an interaction between stimulus type and ROI, it failed to reach significance, $F(2,12) = 2.25, P < 0.15$.

Frontal ROI.

The left inferior frontal gyrus, which includes Broca's area, is one of the major language processing regions and has been implicated in both phonological processing as well as working memory functions. As predicted, this region did not reveal significant effects of stimulus type and the activation was left lateralized [$F(1,6) = 4.38, P > 0.08$; $F(1,6) = 9.22, P < 0.03$]. As predicted, the left IFG did not reveal effects of stimulus type, $F < 1$.

When the location of activation within the left IFG was examined, the activation appeared to be concentrated around two regions, one at the inferior frontal/precentral sulcal junction and one in and around the ascending ramus/anterior insula. Previous studies have associated these two regions with different processes. For example, in a study examining phonetic processing, activation was observed near the junction of the inferior frontal sulcus and precentral sulcus [Burton et al., 2000]. In addition, in studies examining working memory functions activation near the ascending ramus was observed [Owen et al., 1999; Postle et al., 1999]. Both phonetic and working memory processes are used to perform the phonological processing task and they appear to not be significantly affected by stimulus type.

Posterior ROIs.

The left posterior superior temporal region is another major language region and is the site of Wernicke's area. As predicted, the pSTG, as in previous reading studies, revealed a significant effect of both stimulus type and laterality, $F(1,6) = 11.46, P < 0.02$ and $F(1,6) = 6.65, P < 0.04$, respectively. Further analysis revealed a marginally significant increase in activation for pseudoword processing in left pSTG, $F(1, 6) = 4.88, P < 0.07$.

The left inferior parietal region has been associated with several language functions (e.g., lexical access,

phonological processing, and orthographic to phonological conversion) as well as mnemonic functions [Demonet et al., 1996; Jonides et al., 1998; Paulesu et al., 1993]. As predicted, the IPL, like the pSTG, revealed a significant effect of stimulus type as well as laterality, $F(1,6) = 13.58, P < 0.01$; $F(1,6) = 8.9, P < 0.03$ respectively. Further analysis revealed a reliable increase in the amount of activation in left IPL for pseudoword processing, $F(1,6) = 7.72, P < 0.04$.

Like the left IFG, both the left pSTG and the left IPL are also involved in the current phonetic processing task. Although the lpSTG is thought to be the site of Wernike's area, it is also an auditory association region, which has been shown to be active in various auditory processing tasks. The IPL, as stated above is thought to be involved in working memory functions. In fact, IPL, along with the IFG are hypothesized to make up the phonological working memory system. Unlike the left IFG, however, both the lpSTG and left IPL also seem to be significantly effected by stimulus type.

Right hemisphere.

Activation was observed in the right hemisphere for both the real word and pseudoword condition. Both the right IFG and the right pSTG revealed that pseudoword processing elicited significantly more activation than real word processing [$F(1,6) = 9.61, P < 0.02$ and $F(1,6) = 10.35, P < 0.02$]. Conversely, the right IPL did not revealed a significant difference in the amount of activation for pseudowords compared with real words, $F < 3.5, P > 0.1$.

DISCUSSION

Although several studies have demonstrated that the stimulus type can significantly affect the resulting activation [Brunswick et al., 1999; Fiez et al., 1993; Herbster et al., 1997; Price et al., 1996; Rumsey et al., 1997], to our knowledge, this is the only neuroimaging study to compare the auditory processing of words and pseudowords. Overall, the results of the current study confirm what has been observed in previous reading studies, that although pseudoword processing engages the same cortical network as real word processing, the level at which pseudowords engage the network is greater. Greater activation for pseudoword processing was observed in both the posterior superior temporal gyrus as well as the inferior parietal region.

Broca's area.

The inferior frontal region, however, did not reveal an effect of word type that is typically seen in reading studies. Normal subjects have been found to show a lexical effect during phonetic categorization tasks [Ganong, 1980] and Broca's aphasics have been shown to reveal a larger than normal lexical effect, placing a greater reliance on the lexical status of the stimulus in making their phonetic decisions than on the perceptual information in the stimulus [Blumstein, 1994]. This would suggest that Broca's area should have revealed some differential response in left IFG. In addition, IFG has been associated with semantic functions [Fiez, 1997; Gabrieli et al., 1998; Petersen et al., 1988, 1989]. In fact, even in the absence of a semantic task, greater activation has been found in the prefrontal cortex for words than for meaningless stimuli such as pronounceable nonwords, unpronounceable letter strings, or false-font strings [Gabrieli et al., 1998; Petersen et al., 1990; Price et al., 1994]. This would seem to suggest that the these two effects, the lexical and semantic effects, may have canceled each other out resulting in a lack of a significant difference in the left IFG activation.

If this is true, what explains the significant difference observed in previous reading studies? Certainly both effects would be observed in reading as well as in auditory language processing. Previous reading studies have suggested a role for IFG in orthographic processing, namely orthographic to phonological conversion. Specifically Broca's region has been thought to be involved in phonological retrieval. This suggests that the activation differences observed in previous reading studies may be attributed to the increased demands placed on phonological retrieval for pseudowords [Price, 1998]. Therefore, the failure to observe the same differential effect of stimulus type in left IFG in the current auditory task lends support for the theory that the difference observed in reading studies is due to the orthographic to phonological conversion because the auditory phonetic task examined here may not have relied heavily upon phonological retrieval processes.

Posterior regions.

Whereas the current study did not reveal significant effects of stimulus type in the frontal region, the posterior language regions, as in previous reading studies, did reveal a significant increase in activation for pseudoword processing compared with real word processing. In previous neuropsychological and neu-

roimaging studies the temporal-parietal region has been implicated as being the site of the visual word form center [Chertkow and Murtha, 1997; Howard et al., 1992], which is responsible for determining orthographic regularity and triggering the retrieval of a word's meaning, grammatical features, pronunciation, etc. [Cohen et al., 2000; Hillis and Caramazza, 1995; Warrington and Shallice, 1980]. The temporal-parietal region, however, has been shown to be active in several auditory linguistic tasks [Binder, 1997; Demonet et al., 1994; Price et al., 1996; Zatorre et al., 1996]. In addition, a strong correlation between this area and the fusiform gyrus during reading [Horwitz et al., 1998] suggests an important role for the temporal-parietal area in a phonological/semantic functions, but not specifically to a visual function.

As stated previously, the lpSTG, along with the inferior parietal region has been linked to a network that is responsible for lexical access [Luders, 1991; Luders et al., 1986]. There have been several researchers to hypothesize that lexical access is automatic. For example, Petrides [1998] hypothesized that "...automatic [lexical] retrieval is a by-product of the triggering of stored representations in posterior cortical association regions either by incoming sensory input that matches pre-existing representations or by recalled events that trigger stored representations of related information..." Therefore the increase in the amount of activation engendered by pseudowords in this region may be a function of word frequency, with high frequency real words having a greater advantage and requiring less work to process than pseudowords. These frequency effects have been previously observed in temporal cortex [Fiez et al., 1993; Keller et al., 2001]. For example, a direct comparison of the affect of word frequency on sentence processing found that the STG was significantly affected by word frequency, producing more activation when sentences contained low-frequency nouns compared with those containing high frequency nouns [Keller et al., 2001].

Recently, it has been suggested that the inferior parietal lobe contains an interface system mediating between auditory and articulatory representations [Hickok and Poeppel, 2000] and therefore, would work closely with both the IFG and temporal regions. In the current study, it seems as though the differential response to stimulus type by this region is a function of its interaction with the temporal cortex in the "automatic" lexical retrieval processes. As stated earlier, the IPL has also been implicated in the storage of verbal material by several neuroimaging studies of working memory as well as lesion studies [Milberg et al., 1988; Milota et al., 1997; Swick et al., 1998]. In fact,

in a study in which encoding and retrieving real words were compared with pseudowords, it was found that pseudoword processing elicited significantly more activation within the IPL [Jonides et al., 1998]. It was hypothesized that because of the semantic associations, real words may not require a phonological storage strategy. Instead, semantic codes may play a greater role causing pseudowords to rely more on short-term storage than real words. Therefore, pseudowords may be expected to activate the inferior parietal region to a greater degree than real words. This theory fits with the current results as well as with Petrides [1998] theory. In addition, Petrides [1998] suggests that the IFG only becomes involved when lexical access is deliberate, explaining the absence of a differential response in IFG when there is an increase in phonological "storage."

Another possible explanation for the results observed in the current study is differences in demands on attention. Because pseudowords are more difficult to understand than real words greater attentional demands are placed on the language network when processing pseudowords. This is true not only during auditory processing but also reading. Numerous studies have shown a direct influence of attention on the extent and magnitude of cortical activation [Corbetta et al., 1995; Friston and Buchel, 2000]. In addition to task difficulty, there is also a possibility that participants recognized the real words before they processed the entire word. This, too, would decrease the task difficulty of the real word task. If we assume that these attentional effects have influenced the results presented here there remains no significant difference in the amount of activation within left IFG, the only region that failed to show a significant effect of stimulus type. In addition, although the results of the current study suggest a dissociation between stimulus type and modality we can not rule out the possibility of a type II error. This is further complicated by the lack of a significant interaction between ROI and stimulus type, which would have provided further support for our hypothesis. Further imaging studies are needed to clarify these issues as well as to advance our understanding of how modality (auditory vs. visual) modulates the activation within prefrontal cortex during the processing of words and pseudowords.

Right hemisphere.

The right hemisphere revealed a significant effect of stimulus type in both the IFG and temporal ROIs. In fact, right hemisphere regions have been found in previous studies to show more activation during lan-

guage related functions relative to a nonlinguistic baseline [Price, 1998]. Also, in a study comparing auditory and visual language processing it was found that the total amount of activation in both left and right IFG and temporal cortex was significantly greater in the auditory conditions than in the visual conditions and both of these right hemisphere regions revealed sentence complexity effects [Michael et al., in press]. Although the specific functions of the right hemisphere are not well understood, it seems obvious that even though these regions are not necessary for language processing, they are involved.

Auditory phonetic processing is subserved by a large-scale neural network, which includes the inferior frontal gyrus, the posterior superior temporal gyrus, and the inferior parietal lobe. The lack of a differential response in IFG for auditory processing supports its hypothesized involvement in grapheme to phoneme conversion processes. As in previous reading studies, the posterior cortical regions revealed a significant increase in activation for pseudoword processing supposedly due to an increased demand on the lexical access system. In the current study, examining auditory processing of real words and pseudowords have provided information that is both complementary and congruent to that obtained from reading studies.

ACKNOWLEDGMENTS

We would like to thank the UAB Speech Hearing Science Department for their assistance in stimuli preparation and providing hearing tests for participants. We would also like to thank Todd Harshbarger and Edward Conture for their helpful insights.

REFERENCES

- Annett M (1967): The binomial distribution of right, mixed and left handedness. *Quart J Exp Psych* 19:327–333.
- Binder JR (1997): Neuroanatomy of language processing studied with functional MRI. *Clin Neurosci* 4:87–94.
- Blumstein SE (1994): Impairments of speech production and speech perception in aphasia. *Philos Trans R Soc Lond* 346:29–36.
- Briggs GG, Nebes RD (1975): Patterns of hand preference in a student population. *Cortex* 11:230–238.
- Brunswick N, McCrory E, Price CJ, Frith CD, Frith U (1999): Explicit and implicit processing of words and pseudowords by adult developmental dyslexics: a search for Wernicke's Wortschatz? *Brain* 122:1901–1917.
- Burton MW, Small SL, Blumstein SE (2000): The role of segmentation in phonological processing: an fMRI investigation. *J Cogni Neurosci* 12:679–690.
- Chertkow H, Murtha S (1997): PET activation and language. *Clin Neurosci* 4:78–86.
- Cohen L, Dehaene S, Naccache L, Lehericy S, Dehaene-Lambertz G, Henaff M, Michel F (2000): The visual word form area spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain* 123:291–307.
- Corbetta M, Shulman GL, Miexin FM, Petersen SE (1995): Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* 270:802–805.
- Demonet J, Chollet F, Ramsay S, Cardebat D, Nespoulous J, Wise R, Rascol A, Frackowiak R (1992): The anatomy of phonological and semantic processing in normal subjects. *Brain* 115:1753–1768.
- Demonet J-F, Fiez JA, Paulesu E, Petersen SE, Zatorre RJ (1996): PET studies of phonological processing: a critical reply to Poeppel. *Brain Lang* 55:352–379.
- Demonet J-F, Price C, Wise R, Frackowiak RSJ (1994): A PET study of cognitive strategies in normal subjects during language tasks. *Brain* 117:671–682.
- Fiez JA, Petersen SE (1998): Neuroimaging studies of word reading. *Proc Natl Acad Sci USA* 95:914–921.
- Fiez JA (1997): Phonology, semantics, and the role of the left inferior prefrontal cortex. *Hum Brain Mapping* 5:79–83.
- Fiez JA, Balota DA, Raichle ME, Petersen SE (1993): The effects of word frequency and spelling-to-sound regularity on the functional anatomy of reading [abstract]. *Soc Neurosci Abstr* 19:1808.
- Friston KJ, Büchel C (2000): Attentional modulation of effective connectivity from V2 to V5/MT in humans. *Proc Natl Acad Sci USA* 97:7591–7596.
- Gabrieli HDE, Poldrack RA, Desmond JE (1998): The role of the left prefrontal cortex in language and memory. *Proc Natl Acad Sci USA* 95:906–913.
- Ganong WF (1980): Phonetic categorization in auditory word perception. *J Exp Psychol Hum Percept Perform* 6:110–125.
- Hagoort P, Brown C, Indefrey P, Herzog H, Steinmetz H, Seitz RJ (1999): The neural circuitry involved in the reading of German words and pseudowords: a PET study. *J Cogni Neurosci* 11:383–398.
- Herbster AN, Mintun MA, Nebes RD, Becker JT (1997): Regional Cerebral blood flow during word and nonword reading. *Hum Brain Mapping* 5:84–92.
- Hickok G, Poeppel D (2000): Toward a functional neuroanatomy of speech perception. *Trends Cogn Sci* 4:131–138.
- Hillis AE, Caramazza AA (1995): A framework for interpreting distinct patterns of hemispatial neglect. *Neurocase* 1:189–207.
- Horwitz B, Rumsey JM, Donohue BC (1998): Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proc Natl Acad Sci USA* 95:8939–8944.
- Howard D, Patterson K, Wise R, Brown WD, Friston K, Weiller D, Frackowiak R (1992): The cortical localization of the lexicons. Positron emission tomography evidence. *Brain* 115:1769–1782.
- Jonides J, Schumacher EH, Smith EE, Koeppel RA, Awh E, Reuter-Lorenz PA, Marshuetz C, Willis CR (1998): The role of parietal cortex in verbal working memory. *J Neurosci* 18:5026–5034.
- Keller TA, Carpenter PA, Just MA (2001): The neural bases of sentence comprehension: an fMRI examination of syntactic and lexical processing. *Cereb Cortex* 11:223–237.
- Loftus GR, Mason MEJ (1994): Using confidence intervals in within-subject designs. *Psychol Bull Rev* 1:476–490.
- Luders H (1991): Basal temporal language area. *Brain* 114:743–754.
- Luders H, Lesser RP, Hahn J, Dinner DS, Morreis H, Resor S, Harrison M (1986): Basal temporal language area demonstrated by electrical stimulation. *Neurology* 36:505–510.

- Michael EB, Keller TA, Carpenter PA, Just MA (2001): An fMRI investigation of sentence comprehension by eye and by ear: modality fingerprints on cognitive processes. *Hum Brain Mapping* 13:239–252.
- Milberg W, Blumstein S, Dworetzky B (1988): Phonological processing and lexical access in aphasia. *Brain Lang* 34:279–293.
- Milota VC, Widau AA, McMickell MR, Juola JR, Simpson GB (1997): Strategic reliance on phonological mediation in lexical access. *Mem Cognit* 25:333–344.
- Owen AM, Herrod NJ, Menon DK, Clark JC, Downey SPMJ, Carpenter A, Minhas PS, Turkheimer FE, Williams EJ, Robbins TW, Sahakian BJ, Petrides M, Pickard JD (1999): Redefining the functional organization of working memory processes within human lateral prefrontal cortex. *Eur J Neurosci* 11:567–574.
- Paulesu E, Frith CD, Frackowiak RSJ (1993): The neural correlates of the verbal component of working memory. *Nature* 362:342–345.
- Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1988): Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature* 331:585–588.
- Petersen SE, Fox PT, Posner MI, Mintun M, Raichle ME (1989): Positron emission tomographic studies of the processing of single words. *J Cogn Neurosci* 1:153–170.
- Petersen SE, Fox PT, Snyder AZ, Raichle ME (1990): Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli. *Science* 249:1041–1044.
- Petrides M (1998): Specialized systems for the processing of mnemonic information within the primate frontal cortex. In: Roberts AC, Robbins TW, Weiskrantz L, editors. *The prefrontal cortex, executive and cognitive functions*. Oxford: Oxford University Press. p 103–116.
- Postle BR, Berger JS, D’Esposito M (1999): Functional neuroanatomical double dissociation of mnemonic and executive control processes contributing to working memory performance. *Proc Natl Acad Sci USA* 96:12959–12964.
- Price CJ, Wise RJS, Watson JDG, Patterson K, Howard D, Frackowiak RSJ (1994): Brain activity during reading: the effects of exposure duration and task. *Brain* 117:1255–1269.
- Price CJ (1998): The functional anatomy of word comprehension and production. *Trends Cogni Sci* 2:281–288.
- Price CJ, Wise RJS, Frackowiak RSJ (1996): Demonstrating the implicit processing of visually presented words and pseudowords. *Cereb Cortex* 6:62–70.
- Rademacher J, Galaburda AM, Kennedy DN, Filipek PA, Caviness VS (1992): Human cerebral cortex: localization, parcellation, and morphometry with magnetic resonance imaging. *J Cogni Neurosci* 4:352–374.
- Rumsey JM, Horwitz B, Donohue B, Nace K, Maisog JM, Andreason P (1997): Phonological and orthographic components of word recognition: a PET-rCBF study. *Brain* 120:739–759.
- Strupp JP (1996): Stimulate: A GUI based fMRI Analysis Software Package. *NeuroImage* 3:607.
- Swick D (1998): Left temporal-parietal lesions impair repetition priming for nonwords, but not words. *Academy of Aphasia Meeting. Brain Lang* 65:144–146.
- Warrington EK, Shallice T (1980): Word-form dyslexia. *Brain* 103:99–112.
- Zatorre RJ, Evans AC, Meyer E, Gjedde A (1992): Lateralization of phonetic and pitch discrimination in speech processing. *Science* 256:846–848.
- Zatorre RJ, Meyer E, Gjedde A, Evans AC (1996): PET studies of phonetic processing of speech: review, replication, and reanalysis. *Cereb Cortex* 6:21–33.