The Neural Basis of Competition in Auditory Word Recognition and Spoken Word Production

BY
Giulia Righi
Sc.B. Brown University, 2004

A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPY IN THE DEPARTMENT OF COGNITIVE AND LINGUISTIC SCIENCES AT BROWN UNIVERSITY

PROVIDENCE, RHODE ISLAND
MAY 2010

This dissertation by Giulia Righi is accepted in its present form by the Department of Cognitive and Linguistic Sciences as satisfying the dissertation requirements for the degree of Doctor of Philosophy

Date _____ _____
Sheila Blumstein, Advisor

Recommended to the Graduate Council

Date _____ _____
Michael Tarr, Reader

Date _____ _____
David Badre, Reader

Approved by the Graduate Council

Date _____ _____
Sheila Bonde, Dean of the Graduate School

– GIULIA RIGHI –

Cognitive and Linguistic Sciences
Brown University
Box 1978
Providence, RI 02912

Giulia_Righi@Brown.edu
Office: 401-863-7254
Home: 401-965-9248
137 Metcalf Research

EDUCATION

Brown University (Providence, RI)
Doctor of Philosophy in Cognitive Science, expected Summer 2009
Dissertation title: The neural substrates of competition

Brown University (Providence, RI)
Bachelor of Science, Cognitive Science, May 2004
University Honors

HONORS AND AWARDS

2008	Dissertation Fellowship
2006	Human Brain Mapping Travel Award (Florence, Italy)
2004	Department of Cognitive and Linguistic Sciences Thesis award
2003	Brown Magnetic Resonance Imaging Facility undergraduate fellowship

EMPLOYMENT

Graduate Research Assistant to Sheila Blumstein **9/06 – 5/08**
Brown University, Providence RI
- Used eye tracking and fMRI data to investigate the neural basis of competition

Graduate Research Assistant to Michael Tarr **9/04 – 8/06**
Brown University, Providence RI
- Used behavioral and fMRI data to investigate face processing and perceptual expertise.

Undergraduate Research Assistant to Michael Tarr **9/02 – 5/04**
Brown University, Providence RI
- Used behavioral and fMRI data to investigate face perception.

PUBLICATIONS

– IN PRESS –

Righi, G. Blumstein, S.E.B, Mertus, J., Worden, M.S. (in press). The neural systems underlying lexical competition: an eye tracking and fMRI study. *Journal of Cognitive Neuroscience.*

Righi, G. (in press). Visual Agnosia. In Kreutzer, J.S., DeLuca, J., & Caplan, B. (Eds.) *Encyclopedia of Clinical Neuropsychology*.

Righi, G., Jerskey, B. (in press). Prosopagnosia. In Kreutzer, J.S., DeLuca, J., & Caplan, B. (Eds.) *Encyclopedia of Clinical Neuropsychology*.

Righi, G., Vettel, J.M. (in press). Dorsal Visual Pathway. In Kreutzer, J.S., DeLuca, J., & Caplan, B. (Eds.) *Encyclopedia of Clinical Neuropsychology*.

Righi, G., Vettel, J.M. (in press). Ventral Visual Pathway. In Kreutzer, J.S., DeLuca, J., & Caplan, B. (Eds.) *Encyclopedia of Clinical Neuropsychology*.

– IN PREPARATION –

Righi, G., Peissig, J., Tarr, M.J. (in preparation). The impact of disguises on the recognition and processing of faces.

Righi, G., Vettel, J.M., Lebrecht, S., Tarr, M.J. (in preparation). Individual differences in face processing: establishing a link between brain and behavior.

INVITED TALKS

Righi, G. Tarr, M. J. (2008). Exploring individual differences in face processing: linking brain and behavior. Talk given at the International Conference of Psychology, Berlin, Germany.

CONFERENCE PRESENTATIONS & POSTERS

Lebrecht, S., Righi, G., Vettel, J. M., Tarr, M. J. (2008). Predicting individual differences in cortical activations using behavioral measures. Poster presented at the Society for Neuroscience Meeting, Washington, DC.

Righi, G., Tarr, M. J. (2008). Understanding the nature of the neural tradeoff between faces and objects of expertise. Talk given at the Perceptual Expertise Network XIV, Banff, Canada

Righi, G., Tarr, M. J., Kingon, A. (2006) The neural substrates of chess expertise. Poster presented at Human Brain Mapping, Florence, Italy.

Righi, G., Sheinkopf, S., Tarr, M. J. (2005). Modulation of personal knowledge and familiarity in the fusiform and beyond in ASD subjects and controls. Talk given at the Perceptual Expertise Network X, Pittsburgh, PA

Righi, G., Tarr, M. J. (2004). Are chess experts any different from bird, greeble, or face experts? Poster presented at the Vision Science Society, Sarasota, FL.

Righi, G., Tarr, M. J. (2004). Is chess expertise mediated by the same mechanisms as visual expertise for faces? Talk given at the Perceptual expertise Network Meeting 8, Nashville, TN

TEACHING EXPERIENCE

Neuroimaging and Language, Teaching Assistant **Spring 2008**
Brown University, Providence RI

Language and the Brain, Teaching Assistant **Fall 2007**
Brown University, Providence RI

Language, Truth and Advertising, Teaching Assistant **Spring 2006**
Brown University, Providence RI

Introduction to Cognitive Sciences, Teaching Assistant **Fall 2005**
Brown University, Providence RI

Perception, Teaching Assistant **Fall 2003**
Brown University, Providence RI

Acknowledgments

First of all, I am very thankful to my advisor, Sheila Blumstein, for her guidance and unconditional support. She has been an amazing mentor and role model, and has instilled in me her enthusiasm for research. I would also like to thank my committee member Michael Tarr and David Badre, for their useful comments and suggestions.

I would like to thank all members of the Speech Lab as they have provided useful feedback and have answered my many questions, and have honored me with their friendship. Special thanks go to John Mertus, who provided immensurable help by troubleshooting and programming all the scripts used for the experiments presented in this dissertation. Very special thanks go to Emily Myers, who has been a dear friend and colleague, and never shied away from my many questions and taught me many things about fMRI analysis.

I would like to thank all members of the Tarr Lab for their support and friendship over the last five years.

Lastly, I would like to thank the staff of the MRF at Brown who have provided much support and comic relief during long sessions at the scanner.

Table of Contents

List of Tables

List of Figures

1. CHAPTER: Introduction

The goal of this dissertation is to examine how brain regions respond to different types of competition during word comprehension and word production. I will present three studies that attempt to enhance the current understanding of which brain regions are sensitive to different aspects of competition and how the nature of the stimuli and the context in which they occur can modulate their recruitment. All the studies will use behavioral paradigms in conjunction with fMRI.

1.1 The Competitive Nature of Language Processing

Competition is inherent in language processing. During language comprehension, a listener must match the auditory input to specific items in a lexicon that consists of thousands of words, some of which share sounds structures, others which share meanings. Most models of word recognition suggest that the matching of auditory input onto a lexical representation is an incremental process. That is, the search for the appropriate lexical representation begins as soon as auditory input is received, and as the auditory input unfolds, this information is used to narrow down the set of potential candidates. The result of this incremental process is that at the onset of a word, all of those words that share the initial sound structure are activated. The word candidates that share sound properties with the auditory input remain partially activated until sufficient information is conveyed such that the word is uniquely identified (Marslen-Wilson, 1978; McClelland & Elman, 1986; Norris, 1994; Luce & Pisoni, 1998). During comprehension competition is not only present at the phonological level, it is also present at the semantic

level, because the partial activation of multiple lexical entries also results in the partial activation of their meanings (Marslen-Wilson, 1978).

Competition is present in an analogous manner also during language production. When a speaker is presented with a line drawing of an object that is to be named, its corresponding conceptual representation becomes activated in the lexicon. However, upon the activation of a specific conceptual representation, others that are semantically related to it will also receive partial activation. Moreover, interactive models of word production suggest that the activation of multiple conceptual representations results in the partial activation of multiple word candidates and also of all of their phonological codes (Dell et al., 1997; Starreveld & La Heij, 1996), such that competition is present across all levels of the grammar, until a target is ultimately selected and articulated.

To summarize, models of language processing suggest that competition is pervasively present during both word comprehension and production. Moreover, they suggest that the competition is an inherent property of the functional architecture of language.

1.2 Language-driven competition in the brain

The study of the competitive nature of language processing has produced an extensive literature that examines the neural systems recruited under various conditions of competition and those areas involved in its resolution. Previous studies have shown that the introduction of competition can modulate the recruitment of a network of regions that are commonly associated with language processing, which include temporal/parietal

and prefrontal regions. Temporo/parietal regions have been traditionally associated with processes that are specialized within specific linguistic domains or levels of the grammar. For example, the inferior parietal region has been associated with phonological processes, while the middle temporal region has been associated primarily with semantic processes (Hickok & Poeppel, 2004; Indefrey & Levelt, 2004; Price, 2000). Under conditions of competition, these regions have been shown to respond selectively to these specific linguistic domains (e.g. Gold & Buckner, 2002; Prabhakaran et al., 2006; Gold et al., 2005).

More debate remains regarding the role of prefrontal regions under conditions of competition. The prefrontal cortex has been traditionally associated with cognitive control, goal-directed behavior, and the retrieval of information (see Miller & Cohen, 2001 for a review). Moreover, it has been shown that this region is recruited under conditions that require the resolution of competition among multiple potential responses, in order to select the most task-relevant response (see Badre & Wagner, 2007 for a review).

Studies of competition during language processing have specifically focused on the role that a portion of the prefrontal cortex, namely the left inferior frontal gyrus (IFG), plays under conditions of competition. Several theories have been proposed with regard to the specific role of this region. Thompson-Schill and colleagues have suggested that the left inferior frontal gyrus (IFG) is involved in the resolution of competition among conceptual representations, and that its degree of activation reflects the amount of competition present among activated representations (Thompson-Schill et al., 1997; 1999; Kan & Thompson-Schill, 2004; Spalek & Thompson-Schill, 2008; Snyder et al.,

2007). Others have suggested that this region is not functionally homogenous. Several studies have observed greater activation during semantic processing tasks in the anterior portion of the IFG (~BA 47/45), and greater activation during phonological processing tasks in the posterior portion of the IFG (~BA 45/44; Poldrack et al., 1999; Buckner et al., 1995; Bokde et al., 2001; McDermott et al., 2003; Burton et al., 2003), thus suggesting a domain-specific organization of the left IFG.

An alternative subdivision of this region has been recently put forth by Badre & Wagner (2007). They have suggested that the left IFG implements two pivotal mechanisms that contribute to the instantiation and resolution of competition. More specifically Badre & Wagner (2007) have suggested that the more anterior portion of the IFG is involved in the controlled retrieval of multiple semantic representations, (~BA 47), while the more posterior portion is primarily responsible for the resolution of competition among the retrieved representation and thus response selection (~BA 45).

To summarize, previous findings have shown that several brain structures are sensitive to competition and are involved in its resolution. More specifically, posterior temporal and parietal regions seem to be primarily sensitive to the specific source of competition (semantics vs. phonology), while the prefrontal regions are primarily responsible for resolving competition. However, there is still an ongoing debate regarding the functional organization of the prefrontal regions recruited under conditions of competition. The experiments described in this dissertation will attempt to contribute to this debate.

1.3 The current studies

As mentioned in the previous section, several studies have shown that the left IFG is recruited under conditions of competition in language processing. Nevertheless, the large majority of these studies have focused on competition that is created by the manipulation of semantic relationships between multiple representations (e.g. Thompson-Schill et al., 1997; Kan & Thompson-Schill, 2004; Schnur et al., 2006; Spalek & Thompson-Schill, 2008; Thompson-Schill et al., 1999; Moss et al., 2005; Thompson-Schill et al., 1998; Grindrod et al., 2008). Yet, as mentioned in a previous section, models of language processing predict that competition takes place among phonologically similar representations, in a manner analogous to competition among semantic representations. Thus, it is reasonable to believe that the left IFG should also be recruited under conditions of phonological competition. The goal of experiment 1 is to investigate whether phonological competition also recruits the left IFG in tasks involving word comprehension. This study will be relevant in order to establish whether the left IFG responds in a domain-general way to competition during language comprehension.

A second type of competition that has been largely overlooked in studies of language processing is competition that is intrinsic to a stimulus and not dependent on the context in which a specific stimulus is presented. In other words, the majority of studies have relied on competition created by the direct presence of multiple representations within the context of the task (e.g. Snyder et al., 2007; Thompson-Schill et al., 1997; Bedny & Thompson-Schill, 2008). Nevertheless, models of language processing suggest that the activation of multiple competing representations is intrinsic to the structure of language and thus it is not dependent on the overt presence of competitors. Thus, given the

properties of the lexicon, would we expect to find activation in the prefrontal cortex when competition is induced implicitly and is not overtly present among the stimuli? Experiment 2 will address this question. More specifically, Experiment 2 is designed to study how brain regions respond to competition when it is intrinsic to a stimulus and not dependent on the task context in word comprehension.

Experiments 1 and 2 are concerned with trying to expand the current understanding of the role of the prefrontal cortex under different types of competition that arise in language comprehension. In contrast, Experiment 3 aims to address similar questions in the context of language production. Much less is known about the neural systems underlying competition in spoken word production. As described in the previous section, word production is also susceptible to competition at both the phonological and semantic levels. Nevertheless, the majority of studies of competition during word production have focused on semantic competition. Results of these studies have shown that semantic competition recruits the left prefrontal cortex (e.g. Kan & Thompson-Schill, 2004; Spalek & Thompson-Schill, 2008; Moss et al., 2005; de Zubicaray et al., 2001; Thompson-Schill et al., 1999; Schnur et al., 2008). Studies of phonological competition in production are fewer and have shown incongruent results with regard to the recruitment of prefrontal cortex (de Zubicaray et al., 2002; Abel et al., 2008; Bles & Jasma, 2008). Thus, the first goal of Experiment 3 is to directly compare semantic and phonological competition during word production to better understand whether this region responds in a domain-specific way to competition during production. As mentioned above, competition during production can also arise because of the intrinsic properties of words, giving rise to implicit semantic and phonological competition. Nevertheless, it has remained an open

question whether these two types of implicit competition during production will recruit the same areas that are sensitive to direct competition and whether the same areas are recruited as those in auditory word recognition. Thus, the second goal of experiment 3 is to investigate the neural bases of implicit competition during language production.

1.4 Summary

The three studies presented in this dissertation are designed to address several specific questions regarding the role of brain regions, specifically the left prefrontal cortex, in the resolution of competition during language processing. First of all, these studies are designed to directly compare competition created across language domains (semantic vs. phonology) in order to determine those areas which might respond to competition in a domain-general way, and those regions which might respond to competition in a domain-specific way. Secondly, these studies will also examine whether direct and implicit types of competition are processed in analogous ways in the brain. That is, they will explore whether regions that are sensitive to direct competition show a qualitatively or quantitatively different response under conditions of implicit competition. Third, the use of both comprehension and production tasks will provide evidence as to how the domain in which competition is created (semantic vs. phonological) and its nature (direct vs. mediated) interact with the specific type of task-response required (comprehension vs. production).

2. CHAPTER 2: Neural systems underlying lexical competition: an eyetracking and fMRI study

2.1 Introduction

In retrieving information in the service of a specific goal, there are many instances in which more than one stimulus representation may be accessed (Desimone & Duncan, 1995; Duncan 1998; Miller & Cohen, 2001). Thus, competition is created among these multiple representations. However, typically only one of the active representations is appropriate as a response. As a consequence, competition needs to be resolved in order to achieve a specific goal or carry out a discrete response. This scenario is not specific to any one cognitive domain, but rather the maintenance of multiple representations, the resolution of competition, and ultimately response selection are functions associated with the domain general mechanisms of cognitive control. Converging evidence from neuropsychology and neurophysiology suggests that the prefrontal cortex is involved in cognitive control (cf. Miller & Cohen, 2001).

The resolution of competition is critical for the processing of language. In order to recognize a word, for example, the listener must select the appropriate word candidate from the thousands of words in the lexicon, many of which share sound shape properties. Most models of word recognition suggest that as the auditory input unfolds over time, this information is used online to continuously pare down the set of potential competitors. That is, at the onset of a word, all of those words which share onsets are initially

activated; as the auditory input unfolds those word candidates that share sound properties remain partially activated until sufficient auditory information is conveyed such that the word is uniquely identified (Marslen-Wilson, 1978; McClelland & Elman, 1986; Norris, 1994; Luce & Pisoni, 1998). Not only is the sound shape of lexical competitors partially activated but so are their meanings. For example, using a cross-modal priming paradigm, subjects show semantic priming for words that share onsets (Marslen-Wilson, 1987). Presentation of a word such as *general,* which has an onset competitor word *generous,* primes *gift* when the prime word is presented before the input string is disambiguated (i.e. *gener...*).

Recently effects of lexical competition have been found using an eye tracking or visual world paradigm (e.g. Spivey-Knowlton, 1996; Tanenhaus et al., 1995, Allopenna et al., 1998). In this paradigm, subjects are presented with a visual array of objects and are asked to find specific targets as their eye movements are monitored. One of the advantages of this technique over priming and lexical decision judgments is that it provides information about the time course of lexical access. Tanenhaus et al. (1995) have shown that there is a systematic correspondence between the time course of processing a referent name and the eye movements to a referent object, indicating that monitoring eye movements over time provides a continuous measure of how word recognition unfolds (cf. Yee & Sedivy, 2006). Moreover, the eye tracking paradigm allows for the investigation of lexical processing in a more "ecologically valid" manner than most other paradigms used to investigate word recognition, as subjects are not required to make a meta-linguistic judgment about the lexical status, the sound shape, or meaning of a stimulus (cf. Yee & Sedivy, 2006).

Previous studies have shown that when subjects are presented with an auditory target (e.g. *beaker*) and a visual display of the target object (e.g. *beaker*), an onset competitor (e.g. *beetle*), and two more phonologically and semantically unrelated objects (e.g. *shoe, hammer*), they show increased looks to the onset competitor compared to the unrelated items before looking consistently at the correct target (Allopenna et al., 1998; Dahan et al., 2001a; Dahan et al. 2001b; Tanenhaus et al., 1995). These findings suggest that as the auditory input unfolds, both the target stimulus and its onset competitor are partially activated, and that the subject must resolve this competition among this set of potential lexical candidates in order to select the correct item in the visual display.

Despite the richness of the literature investigating lexical competition effects with behavioral methods, less is known about the neural systems underlying the resolution of lexical competition. The present study set out to investigate the neural basis of phonological onset competition using fMRI coupled with the eye tracking paradigm. The paradigm used required subjects to find a target object named auditorily within a visual display containing four objects while their eye movements were being tracked. In some trials, two of the object names shared phonological onsets, while in other trials no competitor was present in the visual display.

A recent study by Yee and colleagues (2008) provides some suggestions about the brain areas that might be recruited under conditions of onset competition. Using the same eyetracking paradigm with Broca's and Wernicke's aphasics, they showed that both groups demonstrated pathological patterns. Specifically, they found that Broca's aphasics with frontal lesions including the inferior frontal gyrus (IFG) showed a very weak onset competitor effect. That is, they made few fixations towards the onset competitor in the

visual display. On the other hand, Wernicke's aphasics with temporo-parietal lesions including the posterior portions of the superior temporal gyrus (STG) showed a larger competitor effect than age-matched controls. These results suggest that both anterior and posterior language processing areas are influenced by phonological onset competition. However, the differences between these two subject groups also suggest that these regions might have different functional roles.

Posterior temporo-parietal brain structures are involved in the initial processing of a lexical entry both at the phonological and the semantic level. Hickok and Poeppel (2000) have proposed that mapping from sound to meaning recruits a network of regions including the posterior superior temporal gyrus (STG), the supramarginal gyrus (SMG), and the angular gyrus (AG). The left temporo-parietal region, including the SMG and the AG, is also involved in mapping of sound structure to a phonological representation and in storing this representation (Paulesu et al., 1993). These regions have also been shown to be sensitive to phonological competition. In particular, using a lexical decision paradigm, Prabhakaran et al. (2006) showed increased activation in the left SMG when subjects performed a lexical decision task on words that were from high density neighborhoods (i.e. had a lot of phonological competitors) compared to words from low density neighborhoods (i.e. had few phonological competitors) (cf. Luce and Pisoni, 1998 for discussion of behavioral effects of neighborhood density on word recognition).

While posterior regions appear to be involved in processing the sound structure and meaning of words, as discussed earlier, frontal regions appear to be involved in "executive control functions" (e.g. Duncan, 2001; Duncan & Owen, 2000; Miller & Cohen, 2001; Smith & Jonides, 1999). Within prefrontal cortex there is evidence that the

left IFG is recruited in the resolution of competition and in the ultimate selection of the appropriate response. Thompson-Schill and colleagues (1997; 1998; 1999) have suggested that the left IFG is involved in making a selection among competing conceptual representations. In a recent study, Snyder and colleagues (2007) showed increased activation in the left IFG as a function of semantic conflict during both semantic and phonological tasks. Similarly, Gold and Buckner (2002) found increased activation in the same portions of left inferior prefrontal cortex during controlled retrieval of both semantic and phonological information.

While the IFG is clearly involved in 'executive control', several recent proposals have suggested that there is a functional division within the IFG. Some have proposed that the left IFG is partitioned as a function of linguistic domain with a phonology-specific processing mechanism in the posterior portion of the IFG and a semantic-specific processing mechanism in the anterior portion of the IFG (Buckner et al., 1995; Burton et al., 2003; Burton, 2001; Fiez et al., 1997; Poldrack et al., 1999). Others (Badre & Wagner, 2007) have proposed that the left IFG can be divided on the basis of different functional processes. They propose that the most anterior portion is responsible for the maintenance of multiple conceptual representations that have been activated either by top-down or bottom-up processes, and the more posterior portion of the IFG is responsible for selecting the appropriate task-relevant representation (Badre & Wagner, 2007).

The goal of this study is to investigate the neural bases of phonological onset competition. Based on the findings reviewed above, it is hypothesized that both posterior regions, specifically the left SMG, and anterior regions, specifically the left IFG, will be

recruited under conditions of phonological onset competition. While the role of the SMG is uncontroversially related to phonological analysis and access of lexical form, the role of the IFG in resolving phonological competition is less clear. Prabhakaran et al. (2006) failed to show increased IFG activation as a function of phonological competition, suggesting that this area may be recruited only in resolving competition among conceptual representations. Activation should occur in the IFG in the current study because the appropriate conceptual representation needs to be selected from the competing conceptual representations in order to look at the correct object in the visual array. However, IFG activation could also be modulated by phonological competition, independent of semantic/conceptual competition. In that case, the IFG would appear to play a domain general role in resolving competition not only as a function of competing conceptual representations but also as a function of competing phonological representations. Given that in our paradigm, competition is based upon similarities in the phonological form among words, and that no specific semantic or phonological judgment is required, we hope to provide evidence to further specify the role of the left IFG in the resolution of lexical competition.

2.2 Methods

2.2.1 Norming Experiments

Two preliminary norming experiments were conducted in order to select easily identifiable visual exemplars for each of the object names to be used as stimuli in the eye tracking experiment.

2.2.1.1 Subjects

Forty college-aged subjects were tested. All subjects were recruited from the Brown University community and were paid for their participation. All subjects were native speakers of American English and had either normal or corrected to normal vision and no hearing or neurological deficit.

2.2.1.2 Materials

Sixty names of highly pictureable common objects served as target words. Each of the target words was paired with a highly pictureable noun that shared either the entire first syllable or the onset and the vowel of the first syllable with it (e.g. lamb-lamp) to create a set of sixty onset competitors. The target-onset competitor pairs were chosen from those used in previous experiments and unpublished data that have investigated the behavioral effects of phonological onset competition (McMurray, personal communication; Yee & Sedivy, 2006; Yee et al., 2008). An additional, 120 highly pictureable nouns were selected to serve as filler items. The filler items were chosen from the MRC psycholinguistic database (The University of Western Australia, AU), such that there were no significant differences, as assessed by t-tests, in mean word frequency, number of syllables, concreteness, and imageability scores between the sets of targets, onset competitors, and fillers. The visual stimuli consisted of two distinct color photographs of each target, onset competitor, and filler object. The color photographs were taken from the Hemera Photo Object database (Hemera Technologies, Toronto, ON) and Google Images.

2.2.1.3 Procedure

The first preliminary experiment was a naming task designed to make sure that subjects consistently named each of the pictures chosen, and that the name given to each object corresponded to the name intended to be associated with each picture.

Twenty participants divided into two groups participated in this experiment. Each subject group saw only one exemplar per object, for a total of 240 images. In each trial subjects saw a picture of an object on a white background, and were asked to type the name of the object they thought it represented. The picture remained on the screen for 1s, and subjects had unlimited time to type the name. If more than 1/3 of the subjects misidentified a picture, a new image was selected to be paired with the object in question.

The second preliminary experiment was conducted to validate the new set of images that contained the images that met the identification criterion from the previous experiment plus the new exemplars selected to replace those that did not meet the above specified criterion. In this second experiment, subjects were asked to make a yes/no judgment about the word/picture pairs to provide a measure of identification accuracy, and a measure of ease of identification by recording reaction time latencies.

Two groups of 10 new subjects participated in this experiment. Each subject group saw only one visual exemplar per object name, for a total of 240 images. Each picture appeared on the screen for 1 sec, and was followed by a visually presented word that was either the correct name for the object presented or a different object name. Subjects were asked to decide whether the word they read was the correct name for the object presented or not. Accuracy and reaction times (RT) were measured. Items were eliminated from the stimulus set on the basis of 3 criteria: 1. if more than 1/3 of the subjects gave

incorrect answers in the word/picture matching trials; 2. if more than 1/3 of the subjects had RT latencies longer than two standard deviations over their individual mean RT latencies for correct responses; 3. if the across-subjects mean RT for the correct responses to a specific item was more than two standard deviations above the across-subjects mean for the set of correct responses for the matching trials.

Based on the results of the two norming experiments, fifty-four target word-object pairs, fifty-four objects depicting phonological onset competitors, and one hundred and eight filler items were selected as stimuli for the eyetracking experiment. The stimuli used in the experiment are listed in the Appendix.

2.2.2 fMRI and Eye tracking Experiment

2.2.2.1 Participants

Eighteen participants (14 females) ranging in age from 18 to 32 (mean age = 23) took part in one scanning session. Participants were all right-handed as assessed by the Oldfield handiness inventory (Oldfield, 1971). Participants reported normal hearing and normal or corrected-to-normal vision, and no neurological impairment. All participants gave written informed consent according to the guidelines of the Human Subjects Committee of Brown University. All participants were screened for MR safety prior to the scanning session. The data from one participant was excluded from both the behavioral and fMRI analyses because of technical difficulties.

2.2.2.2 fMRI acquisition

Scanning was done on a 3T Siemens TIM Trio scanner at Brown University, using a standard 8-channel head coil, outfitted with a mirror for back projection, an infrared illuminator, and an infrared mirror for eye tracking. High-resolution anatomical images were collected using a 3D T1-weighted magnetization prepared rapid acquisition gradient echo sequence (TR = 2.25s, TE = 2.98ms, 1 mm^3 isotropic voxel size). Functional images were acquired using a multislice, ascending, interleaved EPI sequence (TR = 2.7s, TE = 28 ms, FOV = 192, 45 slices, 3mmX3mm in-plane resolution, 3mm slice thickness). A total of 164 volumes were acquired during each run. In addition, two "dummy" volumes were acquired at the start of the run to allow the MR signal to reach steady state; these volumes were discarded by the scanner.

2.2.2.3 Materials

The stimulus set consisted of 54 target auditory stimuli (mean duration = 480 ms), and 108 visual displays. The auditory target stimuli were recorded by a male speaker in a sound attenuated room. Each visual display consisted of a 3x3 grid on a white background containing four pictures, one picture in each of the corners of the grid. The visual grid subtended 16x16 degrees of visual angle, with each cell being approximately 5x5 degrees of visual angle.

The competitor trials consisted of 54 visual displays containing four objects corresponding to the target auditory stimulus (e.g. *beaker*), the onset competitor (e.g. *beetle*), and two fillers (e.g. *train, hammer*) (see Figure 1).

The remaining fifty-four displays served as the no-competitor trials and contained an object corresponding to the target auditory stimulus (e.g. *beaker*) and three filler objects

that were phonologically, semantically, and visually unrelated to the target (e.g. *ship, marble, comb*). Each auditory target token was paired with two displays, one containing both the target and the onset competitor and two fillers (competitor trial), and one containing the target and three fillers (no-competitor trial).

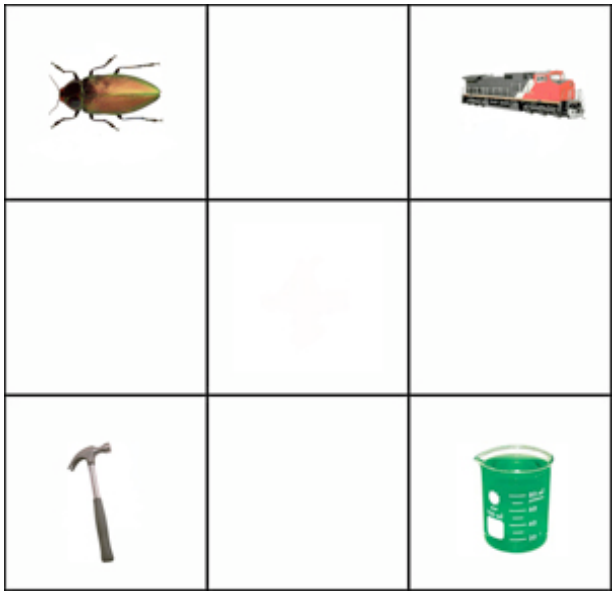

Figure 1. Example of a competitor trial display. The target object (beaker) shares the onset with one of the objects in the display (beetle), while the other two objects are unrelated semantically and phonologically.

While each auditory token was repeated across the two conditions, none of the object pictures was seen more than once. That is, subjects saw two different exemplars of each object, one in the competitor trials and one in the no-competitor trials. The position of targets and competitors within the grid was counterbalanced, such that targets and competitors appeared an equal number of times in all four positions. Moreover, all repeated types (i.e. there were two visual exemplars for each object) never appeared in the same location across runs.

2.2.2.4 Procedure

An SMI iView X MRI (SensoMotoric Instruments Inc., Needham, MA) eye tracker was used. An infrared camera located at the edge of the MRI bed was used to monitor participants' eye movements. The camera recorded the participant's eye movements at 60Hz, with accuracy of greater than 1 degree of visual angle. Stimuli were presented with Bliss software (Mertus, 2002) on a Dell laptop, connected to an LCD projector, and back-projected to the head coil mirror, and through sound attenuating pneumatic headphones.

Subjects participated in two experimental runs of an event-related design, each consisting of 54 stimulus presentations. In each run they saw an equal number of target-competitor and target-fillers displays in random order and were exposed once to all of the auditory targets; one-half of the targets were paired with target-competitor displays and the other half were paired with target-filler displays. Hence, if an auditory target were paired with a target-competitor display in the first run, the same auditory target would be paired with a target-filler display in the second run. The occurrence of target-competitor and no-competitor displays was counterbalanced across conditions. Overall, subjects were presented with fifty-four target-competitor trials and fifty-four target-filler trials.

Each trial began with the presentation of the four-picture array in order to provide the subject with a chance to briefly scan the display. One second later a red fixation cross appeared in the center of the screen, and the objects disappeared. Participants were instructed to fixate on the cross when it appeared. The fixation cross remained on the screen for one second followed by the reappearance of the four objects with the simultaneous auditory presentation of the name of one of the objects present in the display (target). The four objects remained on the screen for 1.5 s. Subjects were

instructed to find and look at the object that had been named until it disappeared. Presentation of stimuli was jittered according to a uniform distribution of nine trial onset asynchronies (TOA values ranging from 4.5 to 11.8 s in .9s steps). During the TOA intervals, the screen was left blank. Each TOA bin was used an equal number of times in each run, and an equal number of competitor and non-competitor trials were assigned to each TOA bin in each run.

2.3 Data Analysis Methods

2.3.1 fMRI data preprocessing

fMRI data was analyzed using AFNI (Cox, 1996; Cox & Hyde, 1997). Preprocessing steps included slice acquisition time correction for each run separately. The runs were then concatenated for each subject to carry out head motion correction by aligning all volumes to the fourth collected volume using a 6-parameter rigid body transform. These data were then warped to Talairach and Tournoux space (1998), and resampled to 3-mm isotropic voxels. Lastly, the data were spatially smoothed using a 6-mm full-width half maximum Gaussian kernel.

2.3.2 fMRI statistical analysis

Each subject's preprocessed EPI data were regressed to estimate the hemodynamic response function for the two experimental conditions (competitor condition vs. non-competitor condition). Response functions were estimated by convolving vectors containing the onset times of each auditory stimulus with a stereotypic gamma-variate

hemodynamic response function provided by AFNI (Cox, 1996; Cox & Hyde, 1997). The calculation of the raw fit coefficients for each voxel was carried out using the AFNI 3dDeconconvolve program. The raw coefficients were then converted to percent signal change by dividing each voxel coefficient by the experiment-wise mean activation for that voxel. Because of the repetition of auditory targets across the two runs, a group analysis was carried out by entering the percent signal change data into a mixed factor 2-way ANOVA, with subject as a random factor, and condition (competitor vs. no competitor), and run (1^{st} run vs. 2^{nd} run) as fixed factors. The resulting statistical maps were corrected for multiple comparisons using Monte Carlo simulations. A voxel level threshold of $p< 0.025$ and a cluster level threshold of $p<0.05$ (48 contiguous voxels) was used for all comparisons. The atlases used to locate the anatomical structures were the Anatomy Toolbox atlases (Eickhoff *et al.*, 2005; 2006; 2007).

2.4 Results

2.4.1 Eye tracking results

Eye tracking data were initially processed by counting the number of fixations that each subject made on target, competitor, and filler objects in each trial, sampled every 17 ms. Only fixations initiated after the onset of the auditory target, and lasting longer than 100ms were included in the analysis. We defined four regions that contained target, competitor, and filler object pictures. Each region was a 3.5x3.5 degrees of visual angle square in each of the four corners of the display. A fixation to a specific object was defined as consisting of the time that a saccade moved the eye into the specific region

until a saccade moved the eye out of that region. Thus, saccades in which the eye did not move out of the region were included as part of the fixation time for that region.

If the subject did not fixate on the target by the end of the trial, that trial was excluded from the analysis. On average, 4% of the trials were excluded for fifteen out of the seventeen subjects. The remaining two subjects proved to be difficult for the eye tracker to calibrate. Thus approximately one third of their trials were excluded from the analysis. For each subject, the proportion of fixations to target, competitor and filler objects was computed by averaging the number of fixations to each object in seven 200ms windows, and dividing it by the total number of fixations across all objects in the same time window. This analysis was performed on the data of both runs averaged together, and on the data from each run alone. Figure 2a shows the mean proportion of looks to the target, onset competitor, and the average of the two unrelated pictures in the competitor trials across both runs, figure 2b shows the same analysis done on the data from the first run, and figure 2c shows the results of the same analysis from the second run.

The data were statistically analyzed to determine whether a significant competitor effect emerged and to ascertain the time course of this effect. For the purpose of the analysis, a trial was defined as starting 200 ms after auditory stimulus onset, since it takes about 200 ms to launch a saccade (Altman & Kamide, 2004; Hallet, 1986), and ending when the display disappeared from the screen. A two-way repeated measures ANOVA of the proportion of looks with object (competitor, filler) and time bin (seven 200 ms bins) as factors revealed a marginally significant main effect of condition $F(1,16) = 4.04$, $p < 0.07$, showing that overall competitors were fixated on more often than filler items.

There was no significant main effect for time bin, $F(6,16) = 1.7$, $p < 0.13$. Moreover no significant interaction was found, $F(6,96) = 1.6$, $p < 0.16$.

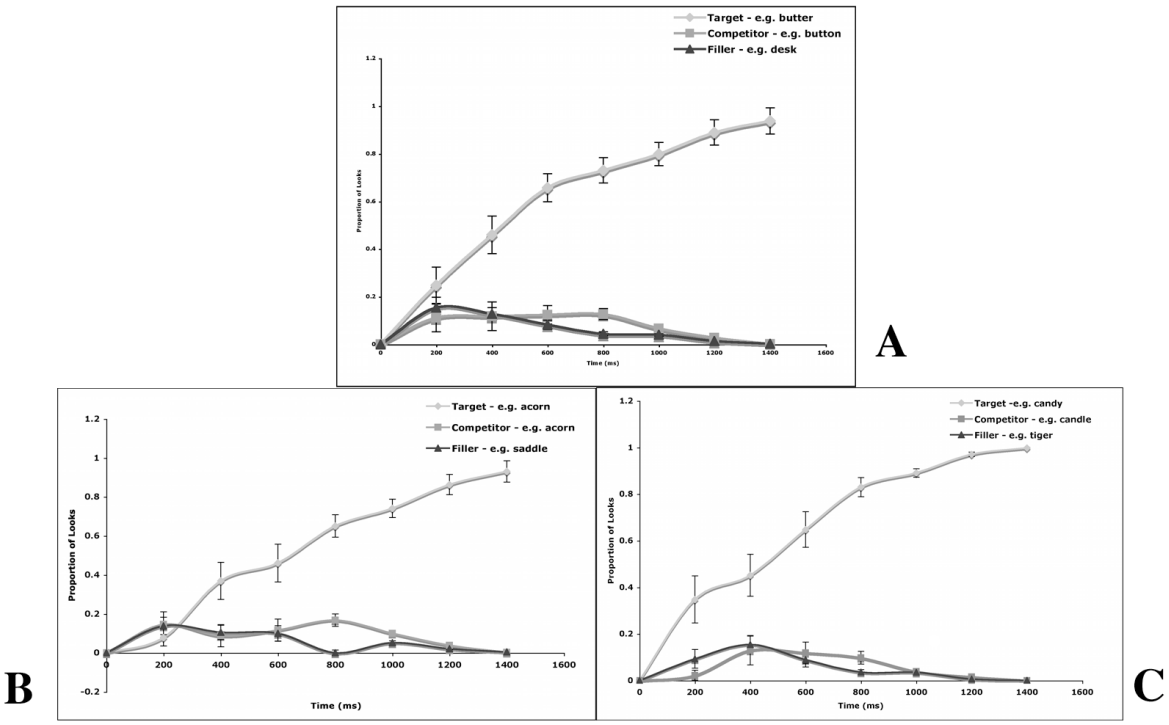

Figure 2. Proportion of fixations over time to the target, the onset competitor, and the average of the two unrelated items in competitor trials. Zero corresponds to the onset of the auditory target. Standard error bars are shown for every data point. (A) Data averaged from both runs. (B) Data from the first run. (C) Data from the second run.

In order to assess the presence of competitor effects across the two runs, separate two way (Condition x Time Bin) repeated measures ANOVAs were also conducted. Results for the first run revealed a significant main effect for condition, $F(1,16) = 5.8$, $p < 0.05$, showing that competitors were fixated on significantly more than filler objects. The analysis also revealed a marginally significant main effect for time bin, $F(6,16) = 1.9$, $p <$

0.08, but no significant interaction, $F(6,96) = 1.5$, $p < 0.2$. Results from the second run revealed no significant main effect for condition, $F(1,16) = 0.4$, $p < 0.6$, and no significant interaction, $F(6,96) = 1.7$, $p < 0.12$. However, there was a marginally significant main effect for time bin, $F(6,16) = 2.1$ $p < 0.06$.

2.4.2 fMRI results

Table 1 provides a summary of the results of the two-way (Condition X Run) ANOVA. Table 1a lists those clusters that showed a main effect of condition and Table 1b lists those clusters that showed a main effect of run ($p < 0.05$, corrected). No clusters showed a significant condition x run interaction. The focus of discussion will be on those clusters falling within regions previously identified to be involved in language processing (see Figure 3).

Several clusters showed a significant effect of condition with greater activation for competitor trials than no-competitor trials. As Figure 3 shows, the left inferior frontal gyrus (LIFG) contains two clusters of activation that responded more strongly in the competitor condition compared to the no-competitor condition. The largest of these clusters was located primarily within the pars Opercularis (BA 44, 71% of active voxels), but also extended into the pars Triangularis (BA 45, 20% of active voxels). The second cluster was located primarily within the pars Triangularis (BA 45, 95% of active voxels), and extended marginally into the middle frontal gyrus (4% of active voxels). A third frontal cluster was located primarily in the left insula (56% of active voxels), but extended into the pars orbitalis (BA 47, 28% of active voxels). It is important to note that, despite the proximity of these three frontal clusters, they are anatomically distinct.

Table 1a. Significant clusters activated in the Condition X Run ANOVA

			Talairach Coordinates		
Cortical Region	*Brodmann's Area*	*Cluster Size*	*x*	*y*	*z*
Competitor > No-Competitor					
Left Supramarginal Gyrus	40/2/13	139	58.5	46.5	35.5
Left Inferior Frontal Gyrus	44/45	118	49.5	-4.5	17.5
Left Cingulate Gyrus	24/23	77	1.5	4.5	38.5
Left Inferior Frontal Gyrus	45/46/10	70	46.5	-43.5	11.5
Right Inferior Parietal Lobule	40	69	-49.5	43.5	50.5
Left Insula	13/47	51	31.5	-13.5	-9.5
Competitor < No-Competitor					
Left Cuneus	18/17	59	4.5	91.5	26.5
Left Lingual Gyrus	18/17	55	19.5	97.5	-6.5
Right Lingual Gyrus	18/17	50	-10.5	82.5	-6.5

Main effect of condition. Clusters thresholded at a cluster-level threshold of $P < 0.05$ with a minimum of 48 contiguous voxels, and at a voxel-level threshold of $P < 0.025$, $t = 2.459$ (corrected). Coordinates indicate the maximum intensity voxel for that cluster in Talairach and Tournoux space. The first Brodmann area listed corresponds to the location of the maximum intensity voxel. If the cluster extended into other Bas, those are also listed (see text for details).

Table 1b. Significant clusters activated in the Condition X Run ANOVA

			Talairach Coordinates		
Cortical Region	*Brodmann's Area*	*Cluster Size*	*x*	*y*	*z*
First Run > Second Run					
Left Declive	17/18	330	1.5 7	3.5	-12.5
Right Superior Parietal Lobule	7/2/40	145	-34.5	46.5	62.5
Right Middle Temporal Cortex	37/19	127	-52.5	61.5	-0.5
Left Superior/Inferior Parietal	7	109	31.5	55.5	56.5
Left Middle Occipital Gyrus	18/19/37	90	25.5	88.5	11.5
Left Postcentral Gyrus	3/40/22	81	58.5	25.5	35.5
First Run < Second Run					
Posterior Cingulate	31/23/7	510	1.5	49.5	17
Left Superior Parietal Lobule	7/5/39	160	37.5	64.5	50.5

Main effect of run. Clusters thresholded at a cluster-level threshold of P < 0.05 with a minimum of 48 contiguous voxels, and at a voxel-level threshold of P < 0.025, t = 2.459 (corrected). Coordinates indicate the maximum intensity voxel for that cluster in Talairach and Tournoux space. The first Brodmann area listed corresponds to the location of the maximum intensity voxel. If the cluster extended into other BAs, those are also listed (see text for details).

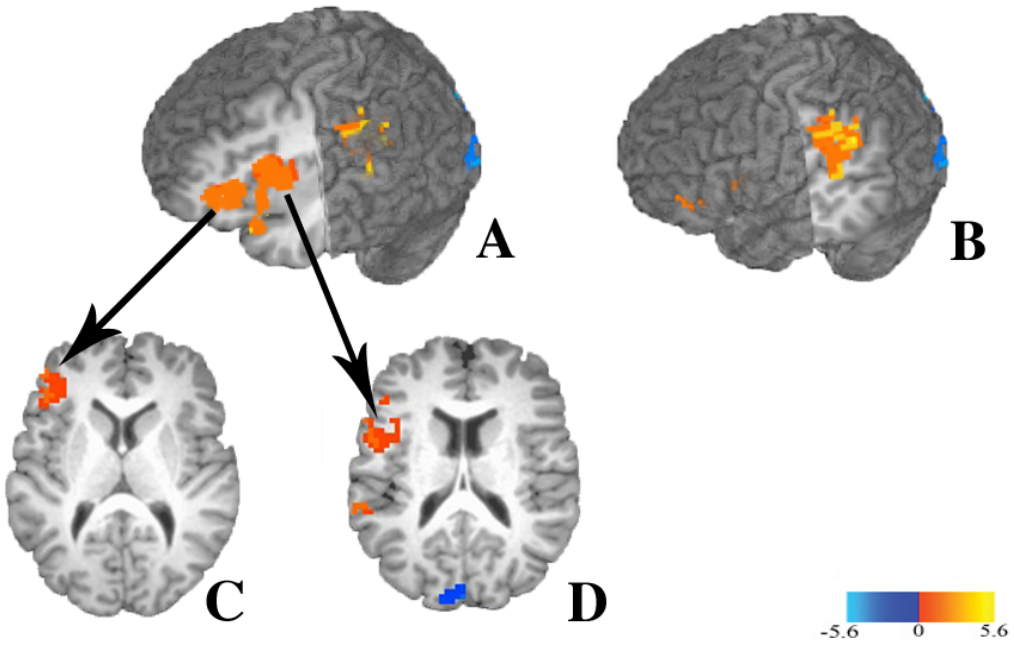

Figure 3. Maps thresholded at a voxel-level threshold of p < 0.025, t = 2.459, and clusters shown correspond to a corrected significant level of p <0.05. (A) Clusters in the left inferior frontal gyrus showing greater activation for competitor trials compared to no-competitor trials. Sagittal slice shown at x = 35, and coronal cut shown at y = 15. (B) Cluster in the left inferior frontal gyrus (BA 45). Axial slice shown at z = 11. (C) Cluster in the left inferior frontal gyrus (BA 44/45). Axial slice shown at z = 17. (D) Cluster in the left temporo-parietal region showing greater activation for competitor trials compared to no-competitor trials. Sagittal slice shown at x = 50, coronal slice shown at y = 20.

Beyond the frontal regions, there were also significant clusters of activation in the left and right temporo-parietal region showing increased activation in the competitor condition compared to the no-competitor condition. The left hemisphere cluster was located within the supramarginal gyrus (SMG, 50% of active voxels). This cluster extended into the inferior parietal lobule (22% of active voxels), and the posterior portion of the left superior temporal gyrus (STG, 7% of active voxels). The right hemisphere

cluster was primarily located in the right SMG (71% of active voxels), and extended into the inferior parietal lobule (27% of active voxels). No clusters emerged in language areas in which there was greater activation in the non-competitor condition than the competitor condition.

The two-way ANOVA also revealed several clusters that showed a significant main effect of run. The clusters that showed a stronger response in the first run compared to the second run were located in the left middle occipital cortex, the superior parietal lobules bilaterally, the left postcentral gyrus extending into the posterior portion of the STG, and the right middle temporal cortex extending into extrastriate visual cortex. The clusters showing a larger response in the second run compared to the first run were located in the left superior parietal lobule and the posterior cingulate cortex

2.5 Discussion

In the present study, the neural bases of phonological onset competition were investigated. The results show that lexical competition induced by shared phonological onsets recruits both frontal structures, i.e. the left inferior frontal gyrus, and posterior structures, i.e. the supramarginal gyrus.

2.5.1 Behavioral Findings

The behavioral results replicate previous findings showing that subjects look more at pictures of objects that share onsets with an auditory target than to pictures of unrelated objects (Allopenna et al., 1998; Dahan et al., 2001a; Dahan et al. 2001b; Tanenhaus et al.,

1995). This effect was marginally significant across both runs, and statistically significant in the first run. The lack of significance in the second run suggests that the repetition of auditory targets reduced the strength of the competition effect. However, as shown in Figure 2c, even in the second run the proportion of looks between competitors and filler items showed greater looks to competitor trials than to no-competitor trials. Thus, the presence of an onset competitor in the stimulus array affects access to the auditorily presented lexical target. It is worth noting that the initial divergence between the proportion of looks to the competitor and filler items emerged about 200-400 ms later than that reported in previous studies. Previous studies have shown that a divergence between looks to the competitor and filler objects emerges as early as 200ms after word onset (Yee & Sedivy, 2006; Yee et al., 2008).

In the current study, the delay of the onset competitor effect may be due to a number of methodological differences. First, traditionally a small number of competitor trials are presented together with a larger number of no-competitor trials to ensure that the subject remains unaware of the experimental manipulation. In the present study, an equal number of competitor and no-competitor trials was used, because the addition of more no-competitor trials would have lengthened significantly the amount of time subjects had to spend in the scanner. It is possible that the shift in the ratio of competitor to no-competitor trials influenced the size and latency of the competitor effect observed here. Second, earlier studies required subjects not only to look at the target but also to overtly point to the target with their finger or with a mouse. In the current study, subjects were only required to look at the target picture. The coupling of a motor and visual action may have a facilitatory effect on subjects' responses that is not observed when only a visual

response is required. Third, in contrast to earlier studies that used a head-mounted eye tracker that allowed subjects to move their heads as they were doing the task, participants were unable to move their heads in the scanner. This difference might have affected the ease with which subjects moved their eyes, as it is more natural to follow eye movements with head movements. Lastly, the stress of doing the task while in the scanner might have also affected the ease with which participants launched eye movements. In fMRI studies it is not uncommon to find slower reaction times in behavioral tasks while in the scanner compared to the same tasks outside of the scanner. For example, reaction time latencies in a lexical decision task were on the order of 200-300 ms slower in the scanner than outside the scanner (cf. Prabhakaran et al., 2006 and Luce and Pisoni, 1998 where the same stimuli were used). It is possible that eye movements are subject to a similar phenomenon.

2.5.2 The effects of competition in temporo-parietal structures

The comparison between competitor and no-competitor trials showed increased activation in the left posterior STG and SMG. Activation of the left STG and SMG has been previously identified to be involved in phonological processing (e.g. Binder & Price, 2001; Gelfand & Bookheimer, 2003 Hickock & Poeppel, 2000). More recently, it has been shown that the left SMG is recruited under conditions of phonological competition (Prabhakaran et al., 2006). Prabhakaran and colleagues (2006) observed increased activation in the SMG when subjects performed a lexical decision task on words with many phonological competitors compared to words with few phonological competitors. Of interest, the current study not only showed activation in the left SMG but

also in the right SMG. However, it is worth noting, that although not discussed, other studies have shown that the right SMG is also recruited in phonological tasks (Price, Moore, et al., 1997). That the right SMG is activated in the current study suggests that right hemisphere mechanisms are also recruited under conditions of phonological competition.

The present findings confirm the recruitment of the SMG under conditions of competition driven by similarities in phonological form. However, these results differ from those of Prahbhakaran et al. (2006) in two important ways. First, the findings of the current study show that the SMG is not only recruited in a task requiring access to lexical form but it is also recruited in a task that requires access to the conceptual representation of a word. In the Prabhakaran et al. (2006) study, participants had to make a lexical decision on a singly presented auditory target stimulus. Thus, the subjects had only to overtly access the lexical form of the word to make a decision. In contrast, in the current study, subjects were required to look at a named picture. In order to do so they had to access the conceptual representation of the picture in order to match its shape to the auditorily presented target. Second, the findings of the current study show that the SMG is not only recruited when phonological competition is implicit, but is also recruited in a task in which competition is explicitly present in the stimulus array. That is, in the Prabhakaran et al. study the phonological competitors were never presented, whereas in the current study the phonological competitors were presented in the stimulus array. Thus, findings of the present study indicate that the left SMG is sensitive not only to phonological competition intrinsic to a stimulus, but also to phonological competition that is reinforced by conceptual representations. The influence of conceptual

representations on activation in the SMG could result from two-way connections with frontal areas assumed to be involved in the manipulations of these representations. This is not surprising given that a previous study (Gold & Buckner, 2002) has shown that the left SMG coactivates with domain-general frontal regions when subjects are performing a controlled phonological judgment.

2.5.3 The effects of competition in frontal structures

There is a large body of evidence suggesting that ventrolateral portions of prefrontal cortex, which include the IFG, are involved in guiding response selection under conditions of conflict or competition (cf. Badre & Wagner, 2004; Desimone & Duncan, 1995; Miller & Cohen, 2001). Selection is undoubtedly present in our task. Thus, it is not surprising that increased left IFG activation was found. However, there are a number of experimental factors that could have contributed to the modulation of IFG activation. In the present task, the presence of an onset competitor in the stimulus array results not only in the activation of the phonological form of the target stimulus and its phonological competitor, but also in activating the conceptual representations of these competing stimuli. Thus, competition needs to be resolved at both phonological and conceptual levels of representation.

Thompson-Schill and colleagues (Thompson-Schill et al, 1997, 1998, 1999) have proposed that the left IFG is a domain general mechanism that guides selection among competing conceptual representations. In support of this hypothesis, a recent study by Snyder and colleagues (2007) found increased activation in the left IFG when multiple semantic representations were competing regardless of whether the subject performed a

phonological or semantic judgment task (Snyder et al., 2007). Thus, in their study competition was driven by semantic factors. In the current study, competition was driven by phonological factors, and activation of the IFG was modulated by the presence of phonological onset competition. Taken together, these findings support the hypothesis that the IFG is domain-general in that it is responsive to phonological as well as semantic/conceptual competition and it is recruited even when the response is not dependent on either semantic or phonological judgments.

Nonetheless, competitor trials elicited more activation than non-competitor trials in the current study in two non-overlapping clusters in the left IFG. The largest cluster was located primarily within BA 44 (71% of active voxels), and the second cluster was located within BA 45 (95% of active voxels). A third cluster in the insula extended into BA 47. The presence of these distinct clusters of activation suggests that there is a functional division of the IFG. It is to this issue that we now turn.

There are several neuroimaging studies showing a functional distinction between anterior and posterior IFG on the basis of whether semantic or phonological information is processed. These studies have shown that the anterior portion of the left IFG, corresponding to BA 45/47 is activated in tasks requiring semantic processing, while the posterior portion of the left IFG, corresponding to BA 44 is activated in tasks requiring phonological processing (Bucker et al., 1995; Burton et al., 2000; Fiez et al., 1997; Poldrack et al. 1999). This framework would suggest that the clusters found in the present study are responding separately to competition at the semantic/conceptual level and at the phonological level. Thus, the emergence of a cluster in BA 44 is consistent with the view that it is responsive to phonological factors, whereas the emergence of clusters in BA 45

and including BA 47 is consistent with the view that they are responsive to semantic/conceptual factors. Given that the presence of phonological competition appeared to activate more than one conceptual representation, thus increasing conceptual competition in the competitor condition, it is reasonable to suggest that BA 45/47 and BA 44 are tightly coupled.

Other researchers have proposed that there is a functional subdivision of the IFG based upon different processes involved in cognitive control. Badre & Wagner (2007) suggest that within the IFG two distinct subregions perform two different functions: controlled retrieval and post-retrieval selection (Badre & Wagner, 2007). Controlled retrieval refers to the top-down activation of semantic knowledge relevant to the task at hand and it is suggested to recruit BA47. If more than one knowledge representation becomes active, post-retrieval selection is needed to resolve competition, regardless of the form of these representations (e.g. semantic, phonological, and perceptual). In this framework post-retrieval selection is implemented in BA45.

In the current study, BA 47 (which was part of a larger cluster including the insula) could be recruited by the activation of task-relevant semantic knowledge. The increased activation found in BA 47 for competitor trials could reflect the higher number of semantic representations that are activated in the competitor condition. Namely, not only are the semantic representations associated with the target stimulus activated but in addition the semantic representations of the phonological competitor are as well. The cluster found in BA 45 could reflect the domain general post-retrieval selection mechanism. As to the role of BA 44, Badre and Wagner (2007) agree with its involvement in phonological processing, and further suggest that its proximity to speech

production regions might implicate it as a selection mechanisms tied with a specific overt response (Badre & Wagner, 2007). Thus, the activation found in BA 44 could be interpreted as involved in carrying out response-related selection.

To summarize, the present study showed that the left IFG is sensitive to competition driven by phonological similarity, and not only to competition among semantic/conceptual factors. Moreover, the activation found in the left IFG is consistent with a functional segregation of this region in anterior and posterior portions both on the basis of linguistic domain and on the basis of different processes involved in cognitive control. Further studies will be necessary to determine whether these interpretations are mutually exclusive, or whether the IFG can be functionally divided according to both models.

3. CHAPTER 3: Neural responses to competition mediated by phonological similarity and semantic relatedness: and eye tracking and fMRI study

3.1 Introduction

The study of how the brain deals with competition has produced an extensive literature that spans across cognitive domains. Competition plays a critical role in cognitive control. In particular, interactions in the world require the ability to process multiple stimuli at any given time, and more importantly to ultimately select the appropriate stimulus in favor of the others. The neural mechanisms involved in the retrieval of multiple stimulus representations and in making a selection among these representations have been studied using a variety of methodological approaches. These studies have shown that the posterior parietal cortex and the prefrontal cortex are recruited under conditions of competition, with the former being primarily involved in the retrieval and maintenance of information, and the latter being primarily involved in the selection of information (Casey et al., 2000; Corbetta & Shulman, 2002; Milham et al., 2001; Miller & Cohen, 2001).

Particular attention has focused on the role of the left prefrontal cortex, in particular the left inferior frontal gyrus (IFG), in tasks that require the resolution of competition. Thompson-Schill and colleagues conducted a series of studies showing that the left inferior frontal gyrus (IFG) is recruited when response selection demands are increased by the activation of multiple related semantic representations. Using three different tasks, Thompson-Schill and colleagues (1997) found that the left IFG responded more strongly when subjects had to choose a single response when presented with stimuli that elicited

multiple related semantic representations. Kan and Thompson-Schill (2004) found increased left IFG activation when subjects were asked to name objects that had several alternative names compared to objects that had a single specific name. Bedny and colleagues (2008) showed increased left IFG activation when subjects were asked to make semantic judgments on word pairs that contained ambiguous words, such that multiple interpretations were possible. And Snyder and colleagues (2007) demonstrated that the left IFG is recruited under conditions of semantic conflict, even when subjects were asked to make a judgment about the phonological properties of words.

Despite the variety of tasks used to study competition in the prefrontal cortex, there are still questions that remain unanswered. First, the majority of experiments created competition by manipulating the semantic relationship between stimuli. What is not clear is the extent to which competition effects which emerge in the prefrontal cortex are domain specific. That is, will prefrontal cortex be activated under conditions of phonological competition as well as semantic competition?

To our knowledge, only one recent study by Righi et al. (in press) has studied competition induced by phonological similarity in auditory word recognition. Using an eyetracking paradigm paired with fMRI, they presented subjects with a visual display containing four pictures of common objects and asked them to find a specific target object named auditorily. Target objects appeared in two types of response sets. In competitor trials, a target was presented in a display that contained an object whose named shared the phonological onset (initial consonant and vowel) with that of the target (e.g. *beaker- beetle)* and two unrelated objects. In the no-competitor trials, a target was presented in a display that contained three objects that bore no phonological or semantic

relationship to it. Behavioral results showed more looks to the phonological onset competitor than to the unrelated foils. The fMRI data showed sensitivity of the left IFG to this type of competition, showing stronger activation for the competitor condition compared to the no-competitor condition. Thus, it appears as though prefrontal cortex is recruited across different levels of language and in this sense is domain general.

Secondly, the majority of tasks used, including that of Righi et al. (in press) created competition by presenting both targets and competitors in the response set. Thus, it is not clear whether the prefrontal cortex, in particular the IFG, is recruited even when competition is induced implicitly within a stimulus, and no direct competitor is present in the response set.

The present study examines how the brain responds to competition that is implicit to a stimulus when direct competitors are not present among the set of potential responses. Of particular interest, is the sensitivity of the IFG to this type of competition, because a positive finding would extend the role of this region. In particular, it would suggest that cognitive control processes are engaged in selection processes that may not be driven solely by choices based on the environmental context

Lastly, the majority of tasks employed to study the role of the IFG have involved "controlled retrieval processes". That is, they have asked subjects to retrieve specific information about a stimulus that might have not been an automatic stimulus-driven association (cf. Moss et al., 2005). Alternatively, other tasks have relied on the employment of working memory. Thus, the present experiment can provide further evidence as to whether the left IFG is recruited even in the absence of controlled retrieval process, as subjects are simply ask to locate a specific object in a visual display. .

In order to create implicit competition, we can rely on the properties of language processing. There are several current models of language processing that propose interactions between phonological and semantic levels of processing (e.g. Dell et al., 1997; Marslen-Wilson, 1987; Peterson & Savoy, 1998). These models suggests that upon hearing a word, not only does its phonological form become activated, but so do phonological forms similar to it; furthermore, these models predict that partial activation will spread from these multiple phonological forms to their lexical semantic networks. An example of the interactive nature of the language processing system has been shown using an eyetracking paradigm. Yee and Sedivy (2006) presented subjects with visual displays containing four objects and asked them to identify a target object that was named auditorily. Experimental trials consisted of an auditory target such as *hammer* that possessed a phonological onset competitor (*e.g. hammock)*, a semantic associate of the target's phonological competitor (*e.g. nail)* and two fillers that were neither phonologically nor semantically related to the target. Eye movement patterns were compared to the presentation of the same auditory target and 3 fillers, unrelated phonologically and semantically to the target.

Their results showed that during the first 600-800ms of the competitor trials subjects looked more at the semantic associate of the target's phonological onset competitor (henceforth called semantic onset competitor), rather than at the two unrelated objects. Yee and Sedivy showed that lexical competition is not dependent on the explicit presence of competitors. Rather the partial activation of multiple lexical-semantic entries takes place rapidly during comprehension in a bottom-up manner and while it is influenced by context, it is not dependent on it (cf. Yee and Sedivy, 2006).

The paradigm used by Yee and Sedivy (2006) seems particularly appropriate to answer the present experimental question, because it can examine potential modulation of activation induced by the implicit phonological similarity between the target object and its competitor, without having to present a direct competitor in the response set. That is, looks to the semantic onset competitor serve as evidence for the implicit partial activation of the target's phonological onset competitor.

As stated above, sensitivity to mediated competition would extend the role of the left prefrontal cortex as a response selection mechanism that is sensitive to competition even when direct competitors are absent from the response set. Moreover, the specific anatomical location of the sensitivity to mediated competition could provide further insight into functional organization of the left IFG. While Thompson-Schill and others have suggested that the IFG as a whole is sensitive to selection demands (Moss et al., 2005; Snyder et al., 2007; Thompson-Schill et al., 1997), others have proposed that this regions can be subdivided into subregions either sensitive to selection demands in specific domains (see Fiez, 1997 for a review) or implementing different functions (Badre & Wagner, 2007). The domain-specific hypothesis suggests that posterior portion of the IFG, roughly corresponding to BA44/45, is primarily associated with controlled phonological processing, while the ventral/anterior portion, roughly corresponding to BA47/45 is primarily associated with controlled semantic processing (Bokde et al., 2001; Burton et al., 2003; Poldrack et al., 1999). Badre and Wagner (2007) have suggested that the controlled retrieval of multiple semantic representations and response selection are implemented respectively in the more anterior portion of the IFG (~BA 47) and in the mid-ventral portion (~BA 45).

While focus on the literature has been on the IFG and its role in competition, recent studies have shown that temporo-parietal areas are involved in the representation of potential stimulus responses under condition of conflict and/or competition (Bunge et al., 2002; Casey et al., 2000; Hazeltine et al., 2000;). More specifically, tasks involving language processing have suggested that the posterior parietal cortex functions as a retrieval and storage mechanism for phonological information (Awh et al., 1996; Gold & Buckner, 2002; Hickok et al., 2003; Paulesu et al., 1993; Ravizza et al., 2004). Two recent studies have shown that this region is also recruited under conditions of phonological competition. Prabhakaran and colleagues (2006) found increased activation in the left supramarginal gyrus (SMG) for words that shared sounds structure with many other words, compared with words that shared sound structure with few other words, when subjects performed a lexical decisions task. Righi and colleagues (in press) found increased activation in the left SMG when subjects were presented with a visual array containing four objects and were asked to identity a target object in the presence of its phonological competitor, compared to when the a target object was presented without any of its competitors. Given these findings, we would expect to find increased activation created by mediated competition in the left temporo-parietal region, induced by the automatic retrieval of multiple phonological representations.

3.2 Methods

3.2.1 fMRI and Eye tracking Experiment

3.2.2 Participants

Nineteen participants (12 females) ranging in age from x to y (mean age = 22 $\pm$ 7.5) served as subjects. All participants were right-handed as assessed by the Oldfield Handedness Inventory (Oldfield, 1971), and reported normal hearing, normal or corrected-to-normal vision, and no neurological impairment. All participants gave written informed consent according to the guidelines of the Human Subjects Committee of Brown University and were screened for MR safety prior to the scanning session. The data from one participant was excluded from both the behavioral and fMRI analyses because of technical difficulties with the calibration of the eye tracker.

3.2.3 fMRI acquisition

Scanning was done on a 3T Siemens TIM Trio scanner at Brown University, outfitted with a standard 8-channel head coil, a mirror for back projection, an infrared illuminator, and an infrared mirror for eye tracking. The high-resolution anatomical images were collected using a 3D T1-weighted magnetization prepared rapid acquisition gradient echo sequence (TR = 2.25s, TE = 2.98ms, 1 mm^3 isotropic voxel size). The functional images were acquired using a multislice, ascending, interleaved EPI sequence (TR = 2.7s, TE = 28 ms, FOV = 192, 45 slices, 3mmX3mm in-plane resolution, 3mm slice thickness). The experiment consisted of two experimental runs, each consisting of 164 volumes. In addition, two "dummy" volumes were acquired at the start of the run to allow the MR signal to reach steady state; these volumes were discarded by the scanner.

3.2.4 Materials

Experimental materials consisted of 54 auditory target stimuli and 108 visual displays. The auditory target stimuli were recorded by a male speaker in a sound attenuated room. The visual displays consisted of a 3x3 grid on a white background containing four objects pictures, positioned in the corners of the grid. The visual grid subtended approximately 16x16 degrees of visual angle, with each cell being approximately 5x5 degrees of visual angle.

Fifty-four competitor trials consisted of visual displays containing four objects corresponding to the target auditory stimulus (e.g. *hammock*), a semantic associate of the phonological onset competitor of the target (e.g. *nail*), and two fillers (e.g. *peach, cab*) (see Figure 4).

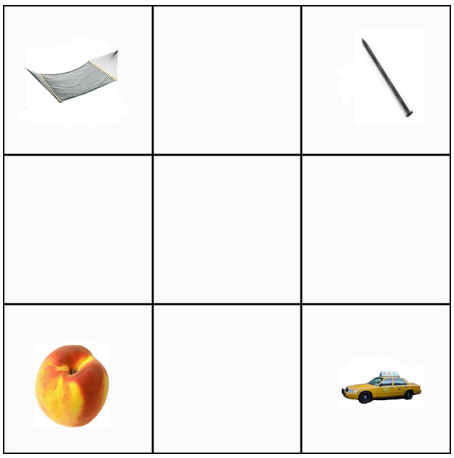

Figure 4. Example of the visual display used in the competitor condition. The target (hammock) is paired with the semantic associate of its onset competitor (nail, via the implicit activation of hammer), and two unrelated filler items.

Another set of fifty-four displays served as the no-competitor trials and contained an object corresponding to the target auditory stimulus (e.g. *hammock*) and three filler objects that were phonologically, semantically, and visually unrelated to the target (e.g. *slippers, onion, fish*). Thus, each auditory target token was used with two displays: one containing both the target and the onset competitor and two fillers (competitor trial), and one containing the target and three fillers (no-competitor trial). The object pictures were seen only once, so that subjects saw two different exemplars of each object, one in the competitor trials and one in the no-competitor trials. The positions of targets and competitors were counterbalanced within the grid, appearing an equal number of times in all four corners; all repeated stimuli (the two visual exemplars corresponding to each object) never appeared in the same location across runs.

The stimulus set consisted of fifty-four target-competitor taken from those used in previous experiments that have investigated the behavioral effects of mediated phonological competition (Yee & Sedivy, 2006; Yee et al., 2008). An additional 108 highly pictureable nouns were selected to serve as filler items; these items were chosen from the MRC psycholinguistic database (The University of Western Australia, AU), such that there were no significant differences, as assessed by t-tests, in mean word frequency, number of syllables, concreteness, and imageability between the sets of targets, competitors, and fillers. All object pictures were two distinct color photographs of each target, competitor, and filler object. The color photographs were collected from the Hemera Photo Object database (Hemera Technologies, Toronto, ON) and Google Images. The images were all normed in a previous study to make sure that they were all easily identifiable as the intended objects (Righi et al., in press).

3.2.5 Procedure

The eye tracker used was an SMI iView X MRI (SensoMotoric Instruments Inc., Needham, MA). The set-up consisted of an infrared camera located at the edge of the MRI bed to monitor participants' eye movements. The camera recorded the participant's eye movements at 60Hz, with accuracy of greater than 1 degree of visual angle. The visual stimuli were presented with Bliss software (Mertus, 2002) on a Dell laptop, connected to an LCD projector, and back-projected to the head coil mirror. The auditory stimuli were presented through sound attenuating pneumatic headphones.

An event-related design was used with two experimental runs, each consisting of 54 stimulus presentations. Subjects saw an equal number of target-competitor and target-fillers displays in each run. The two trials types were presented in random order. In each run one-half of the targets were paired with target-competitor displays and the other half were paired with target-filler displays such that if an auditory target were paired with a target-competitor display in the first run, the same auditory target would be paired with a target-filler display in the second run.

Stimulus presentation was jittered according to a uniform distribution of nine trial onset asynchronies (TOA values ranging from 4.5 to 11.7 secs in 0.9 secs steps). The screen remained blank during the TOA intervals. Each TOA bin was used an equal number of times in each run, and an equal number of competitor and non-competitor trials were assigned to each TOA bin in each run.

Each trial began with the presentation of the four-picture array that lasted one second followed by a red fixation cross appearing in the center of the screen. The fixation cross remained on the screen for one second, and subjects were instructed to fixate on it for its

duration. The four objects then reappeared simultaneously with the auditory presentation of the name of one of the objects present in the display (target). The objects remained on the screen for 1.5 seconds. Subjects were told to find the object named in the display and keep looking at it until it disappeared.

3.3 Data Analysis Methods

3.3.1 Eye Tracking Data Analysis

The analysis consists of measuring the looks that subjects made to the four objects in the display sampled every 17 ms. We defined 4 regions, each 3.5x3.5 degrees of visual angle, around of each of the four objects present in the display. A fixation to a specific region was defined as the time that a saccade moved the eye into the specific region until a saccade moved the eye out of that region. Saccades in which the eye did not move out of the region were included as part of the fixation time for that region. Only the fixations initiated after the onset of the auditory stimulus and lasted at least 100 ms were counted Fixations falling into each of the four regions were calculated. The data were then resampled into 100ms time windows. For each subject for each 100ms time window, the average number of fixations to each object type was computed and the proportion of looks was calculated by dividing the number of fixations by the total number of fixations across all objects within the same time window. Average proportion of looks were then calculated for each subject for each object type across all time windows.

3.3.2 fMRI data preprocessing

fMRI data was analyzed using AFNI (Cox, 1996; Cox & Hyde, 1997). Data were preprocessed by correcting for slice time acquisition for each run; then motion correction was carried out by aligning all volumes to the fourth collected volume using a 6-parameter rigid body transform. Motion corrected data were then warped to Talairach and Tournoux space (Talairach 1988), and resampled to 3-mm isotropic voxels. Lastly, the resampled data were spatially smoothed using a 6-mm full-width half maximum Gaussian kernel.

3.3.3 fMRI statistical analysis

The preprocessed EPI data were regressed to estimate the hemodynamic response function for the two experimental conditions (competitor condition vs. non-competitor condition). The response functions were estimated by convolving a stereotypic gamma-variate hemodynamic response function provided by AFNI (Cox, 1996; Cox & Hyde, 1997) with vectors containing the onset times of each auditory stimulus. AFNI 3dDeconconvolve program was used to calculate raw fit coefficients for each voxel for both conditions. The input stimuli for each subject included regressors for the competitor trials, for the no-competitor trials, and for trials that did not meet a specific criteria derived from an item analysis, which will be discussed below, and for the 6 motion correction parameters computed during preprocessing. The raw coefficients of the competitor and no-competitor conditions were converted to percent signal change by dividing each voxel coefficient by the experiment-wise mean activation for that voxel.

A mixed factor one-way ANOVA was computed on the percent signal change data, with subject as a random factor, and condition (competitor vs. no competitor) as fixed factors. The resulting statistical maps were corrected for multiple comparisons using Monte Carlo simulations. All comparisons were submitted to a voxel level threshold of $p< 0.05$ and a cluster level threshold of $p<0.05$ (75 contiguous voxels). The atlases used to locate the anatomical structures were the Anatomy Toolbox atlases (Eickhoff 2005; Eickhoff 2006; Eickhoff 2007).

A region of interest (ROI) analysis was also carried out to examine the role of the left inferior frontal gyrus (IFG) in more detail. Three functional ROIs within the IFG were selected. These ROIs had been identified in a previous study by Righi and colleagues (in press) which examined the activation elicited by phonological onset competition using the same visual world paradigm as used in the current study. These functional regions have the following characteristics: region 1 consists of 118 voxels distributed among BA 44 (71%) and the posterior portion of BA 45 (20%), region 2 consists of 70 voxels primarily located within BA 45 (95%) and marginally into the middle frontal gyrus (4%), and region 3 consists of 51 voxels distributed among the left insula (56%) and BA 47 (28%). For each ROI, mean percent signal change was extracted for every participant for both experimental conditions, and submitted to paired t-tests.

Subjects vary in the extent to which their selection of the target word is modulated by the presence of a mediated competitor. That is, the proportion of looks to the competitor varies across subjects, and the magnitude of this competitor effect presumably reflects the extent of the selection demands made on the subject. In order to examine whether the amount of activation in the IFG is related to the magnitude of the competitor effect and

thus it is modulated by the amount of selection required, a regression analysis was run between the magnitudes of the competition effect for each subject in the behavioral eye tracking task and the difference in percent signal change in the fMRI data between the competitor and no-competitor conditions. For each subject, a behavioral competition score was computed by taking the difference between the mean proportion of looks to the competitor and the mean proportion of looks to the average of the two fillers across all competitor trials. For the neural data, a difference score was computed for each subject by extracting the mean percent signal change for the competition and no-competitor conditions and taking the difference. This operation was performed separately in each of the three ROIs. The behavioral and neural scores were then correlated using simple linear regression.

3.4 Results

3.4.1 Eye tracking results

The competitor effect was examined by comparing the proportion of looks to the competitor object and the average of the two fillers over the entire trial. For the purpose of this analysis, a trial is defined as starting 200 ms after the onset of the auditory stimulus and ending 1300 ms after the onset of the auditory stimulus, which is when the display became blank. As Figure 5a shows, there are greater looks to the competitor than to the unrelated filler. Nonetheless, this effect was not significant, $t(17) = 1.07$, $p < 0.31$.

An item analysis revealed that a number of the stimulus pairs failed to elicit a competitor effect across subjects. In particular, computing the percentage of subjects that looked at each competitor item for each competitor trial revealed that 15 out of 54

competitor items elicited looks in fewer than 10% of the subjects. These items were excluded from the data and a second analysis was conducted comparing the proportion of looks to the mediated competitor compared to the two filler items (see Figure 5b).

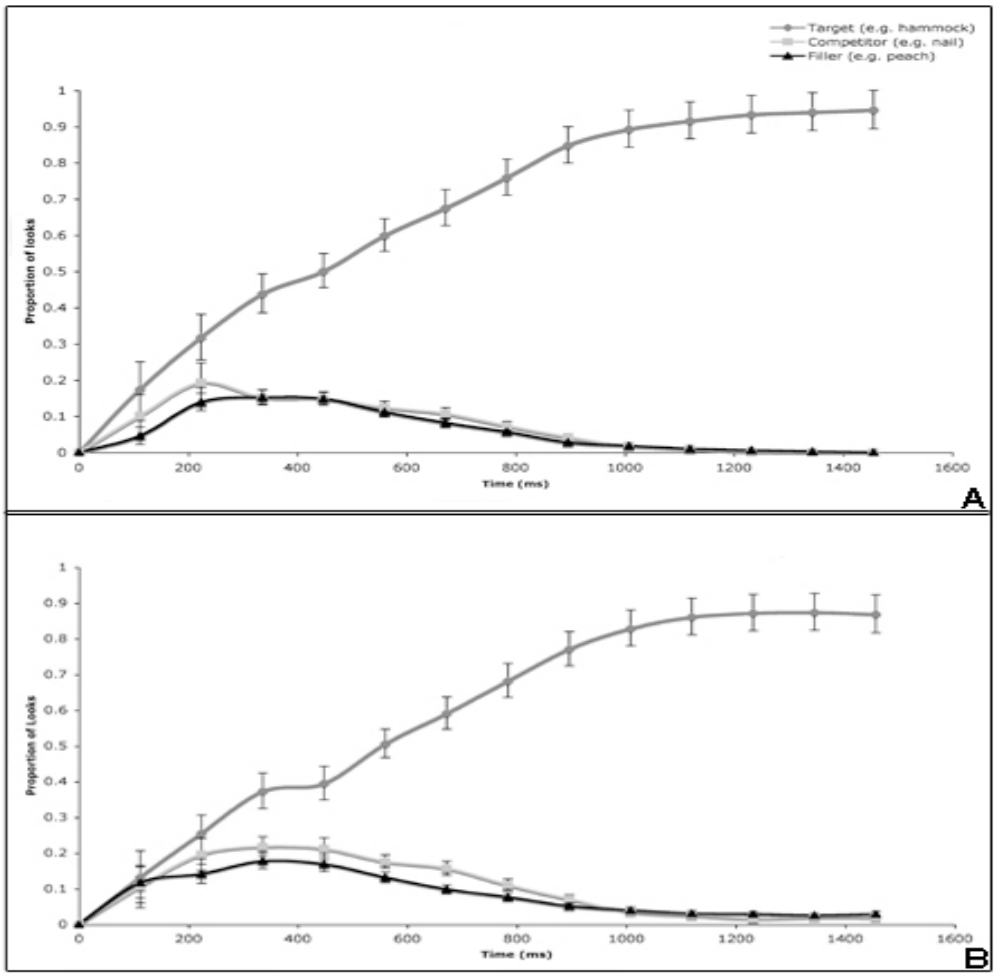

Figure 5. Average proportion of fixations over time to the target, the semantic associate of the onset competitor, and the average of the two unrelated items in competitor trials. Zero corresponds to the onset of the auditory target. Standard error bars are shown for every data point. (A) Data when all trials are included in the analysis. (B) Data when 15 items are excluded after the item analysis.

This analysis revealed a significant difference between the mean proportion of looks to the competitor and the mean proportion of looks to the average of the two filler items in the competitor trials, $t(17) = 2.25$, $p < 0.04$.

3.4.2 fMRI results

Given that the goal of this experiment is to investigate the neural substrates of mediated phonological competition, the data used in all of the analyses reported included only the stimulus pairs that elicited looks to the competitor in least 10% of the subjects. Thus, the fMRI data used corresponded to the behavioral data used in the second analysis of the eye tracking data and included 39 trials per condition. Several analyses were then conducted on the fMRI data.

3.4.2.1 Whole-brain analysis

The first analysis contrasted activation in the competitor condition to the no-competitor condition across the whole brain. Table 2 provides a summary of the results of the one-way ANOVA, and Figure 6 shows the location of the left hemisphere clusters. This analysis revealed several clusters of activation that responded more strongly to the competitor than the no-competitor condition at a corrected cluster-level threshold of $p < 0.05$. No clusters showing the opposite pattern survived thresholding. The analysis revealed one cluster located in the right prefrontal cortex extending from the middle frontal gyrus (MFG) into the inferior frontal gyrus (IFG) and precentral gyrus. Two more clusters emerged in the left superior/middle frontal region, one more anterior extending towards the anterior cingulate and one more posterior extending into the precentral gyrus.

There was also a significant cluster located primarily within the left inferior parietal lobule (IPL), extending into the SMG, and partially anteriorly into the postcentral gyrus.

Table 2. Significant clusters activated in the one-way ANOVA

			Talairach Coordinates		
Cortical Region	*Brodmann's Areas*	*Cluster Size*	*x*	*y*	*z*
Competitor > No-Competitor					
L. Caudate/Putamen		307	-1.5	7.5	14.5
L. Hippocampus		154	19.5	16.5	-9.5
R. Hippocampus		123	-25.5	-10.5	41.5
R. Middle/Inferior Frontal Gyrus	46/45/44	121	7.5	1.5	50.5
L. Superior/Middle Frontal Gyrus	9/8/6/46	113	-22.5	16.5	-6.5
L. Middle Frontal Gyrus	10/46/	80	16.5	-52.5	35.5
L. Inferior Parietal	40/2	77	49.5	28.5	38.5

Results of one-way ANOVA. Clusters thresholded at a voxel-level threshold of $p < 0.05$ and cluster level threshold of $p<0.05$ (minimum cluster size 75 voxels). Coordinates indicate the maximum intensity voxel for that cluster in Talairach and Tournoux space. The first Broadmann area listed corresponds to the location of the maximum intensity voxel. If the cluster extended into other BAs, those are also listed (see text for details).

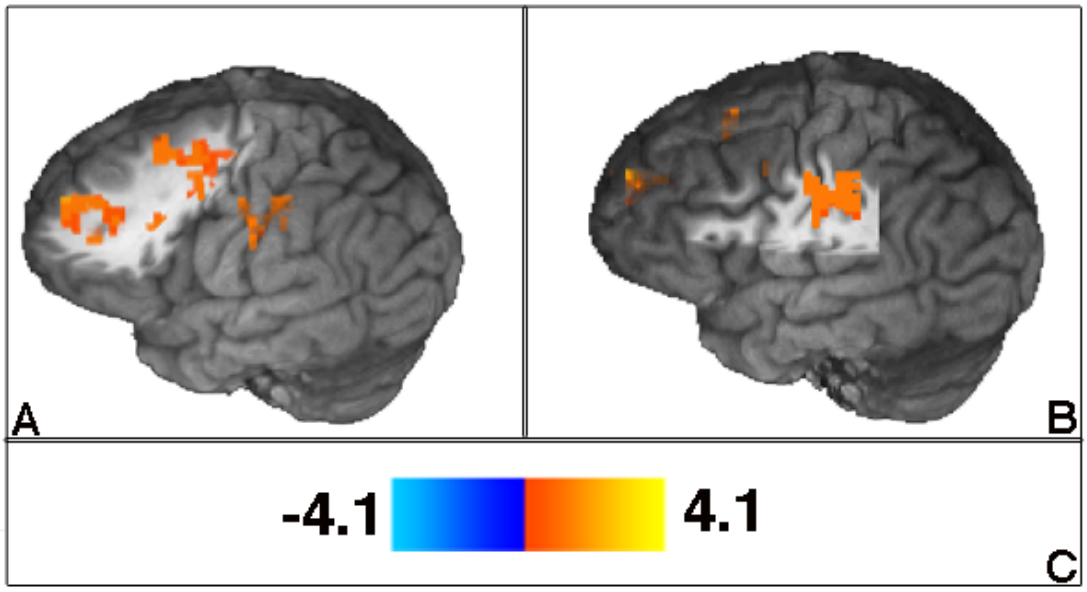

Figure 6. Results of the one-way ANOVA comparing the competitor and no-competitor trials across the whole brain. Areas in yellow-orange show increased activation for the competitor condition compared to the no-competitor condition. Maps are thresholded at a voxel level threshold of p< 0.05, t = 2.1, and clusters shown correspond to a corrected significance level of p<0.05. (A) Clusters in left middle and superior frontal gyri. Sagittal slice shown at x = 45, and coronal cut shown at y = 15. (B) Cluster in left inferior parietal region. Sagittal slice shown at x = 10, and coronal cut shown at y = 45 and axial cut shown at z = 30.

No significant activation emerged in the left IFG using the p<.05 threshold corrected for multiple comparisons. However, if the statistical threshold was relaxed to p <.1, corrected, significant activation emerged in the left IFG. Thus in order to examine the pattern of activation in the left IFG and the potential differences in the subareas of the IFG (BA44, BA45, BA47), three ROI analyses were performed.

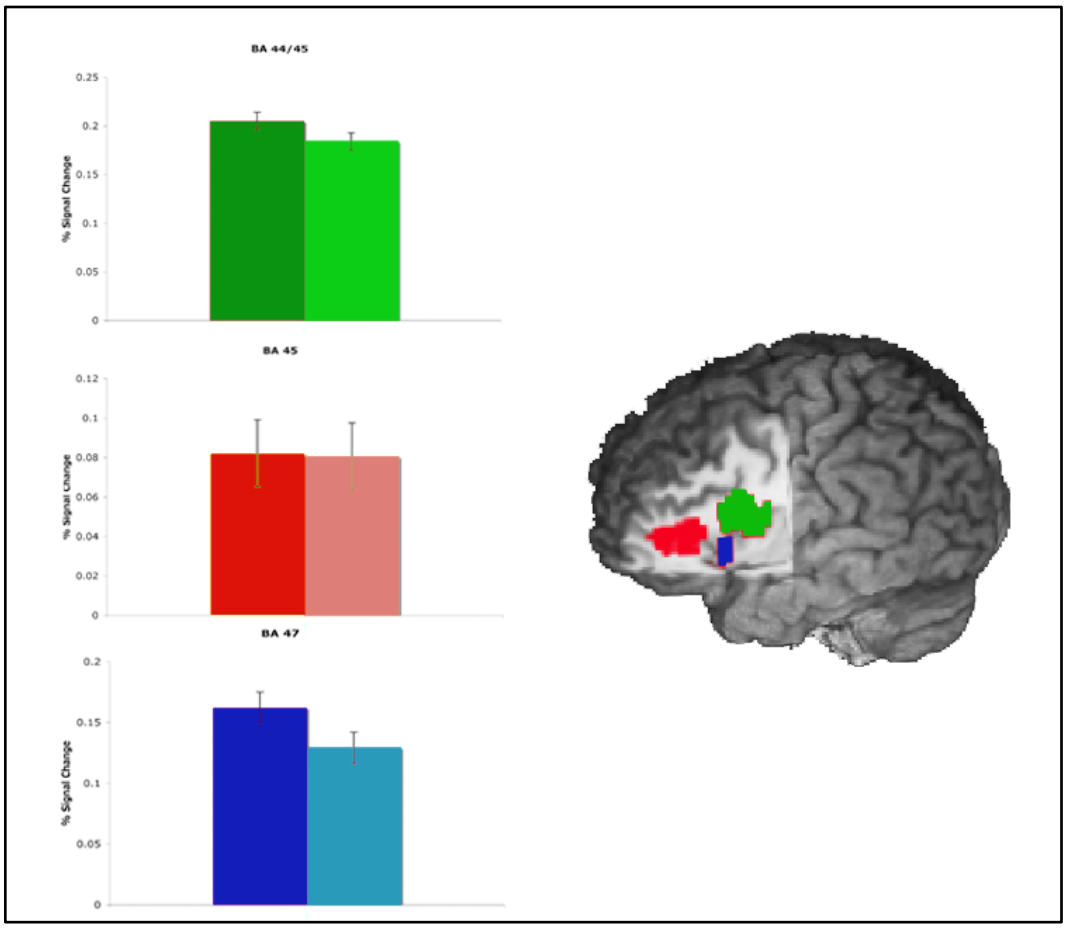

Figure 7. Results of ROI analysis. (A) Location of the three ROIs. (B) Average percent signal change for competitor (dark green) and no-competitor (light green) conditions in region 1. (C) Average percent signal change for competitor (dark red) and no-competitor (light red) conditions in region 2. (D) Average percent signal change for competitor (dark blue) and no-competitor (light blue) conditions in region 3.

3.4.2.2 ROI Analyses

Paired t-tests were performed in all three left IFG ROIs including BA44, 45, and 47. Figure 4 shows the location of the ROIs and the mean percent signal change for the two experimental conditions in each of the ROIs. Significant differences between competitor and no-competitor trials were observed in region 1 (including primarily BA44; ($t(17) = 2.26$, $p < 0.04$) and in region 3 (including BA47; $t(17) = 2.45$, $p < 0.03$). No significant

difference was found in region 2 (including primarily BA45; $t(17) = 0.09$, $p < 0.93$). Linear regressions were computed between the behavioral and the neural competitor effect in all three IFG ROIs. A significant correlation emerged only in region 2 (BA 45; $r(17) = 0.55$, $p < 0.02$).

3.5 Discussion

In the present study, the neural bases of mediated phonological-semantic competition were investigated. The results show that mediated competition induced by presenting a target object (e.g. *hammock*) in a context containing an object that is a semantic associate (*nail*) of the target's phonological competitor (*hammer*) results in increased brain activation bilaterally in prefrontal regions and in the left posterior temporo-parietal region.

3.5.1 Behavioral Findings

The behavioral results replicate previous findings showing that subjects look reliably more at pictures of objects that are semantic associates of the target's phonological competitor than at unrelated objects (Yee & Sedivy 2006; Yee et al., 2008). The magnitude of this effect was smaller than that shown originally by Yee and Sedivy (2006), and only emerged statistically when items that failed to show the effect for at least 10% of the subjects were removed. It is worth noting that the magnitude of the mediated competitor effect is considerably smaller than that shown when the phonological competitor is present in the stimulus set (Yee and Sedivy, 2006). Not surprisingly, analogous findings occur in the scanning environment as well.

3.5.2 Mediated competition in the Prefrontal Cortex

The present study showed that prefrontal regions, are sensitive to phonological competition, even when competitors are implicit and absent from the set of potential responses. This result extends previous findings showing that the prefrontal cortex is sensitive to competition created by the direct manipulation of conflict in the response set (i.e. Bedny et al., 2008; Snyder et al., 2007) or by conflict created by the number of potential semantic associations that a word may have (i.e. Kan & Thompson-Schill, 2004; Thompson-Schill et al., 1997). Moreover, they also provided further evidence that the prefrontal cortex is sensitive to competition even in the absence of controlled processes (Moss et al., 2005).

The whole-brain analysis revealed sensitivity to mediated competition manipulation in the right medial/ventrolateral prefrontal cortex and in the left medial/superior prefrontal cortex (as shown in figure 6). Weaker activation was also found activation in the left IFG, although this activation did not survive the statistical correction threshold. Nevertheless, an ROI analysis revealed a significant competitor effect with increased activation in the phonologically mediated semantic competitor condition compared to the no competitor condition in the left IFG (as shown in figure 7). This pattern of results suggests that in the absence of a direct competitor from the response set competition is present, but it is substantially weaker than when a direct competitor if overtly present.

The competition effect found in this experiment relies upon the partial activation of the phonological competitor of the target, which in turn partially activates its semantic associates. The significant competition found in the middle frontal gyrus (MFG) and in

the superior frontal gyrus (SFG) could reflect implicit semantic priming of the semantic associate of the mediated phonological competitor, and potentially the partial reinforcement of its activation because of its presence in the visual display. Previous studies have shown that the SFG and MFG are activated when subjects are asked to judge the semantic relationship among words (McDermott et al., 2003) and in semantic priming studies (Kotz et al., 2002; Raposo et al., 2006; Rissman et al., 2003).

There is evidence suggesting that the left prefrontal cortex is involved in guiding the selection of a response under conditions of conflict or competition (Barde & Thompson-Schill, 2002; Bedny et al., 2008; Kan & Thompson-Schill, 2004; Moss et al., 2005; Thompson-Schill et al, 1997) However, the specific location of activation among studies investigating response selection under conditions of competition varies. Thompson-Schill and colleagues (1997) identified clusters of activation that were sensitive to semantic conflict in BA 45/44 using noun classification and verb generations task. Using a naming task, Moss and colleagues (2005) reported sensitivity to selection demands in clusters anterior and inferior to those reported by Thompson-Schill et al. (1997). A recent study by Snyder and colleagues (2007) found sensitivity to selection demands in the entire anatomically defined IFG, regardless of whether subjects were making a judgment on phonological or semantic attributes of the stimuli. Interestingly, when they subdivided the IFG, they found more sensitivity to increased selection demands in anterior portions of the IFG when subjects were performing a semantic judgment, while sensitivity to selection demands regardless of task was found in the mid-to-posterior areas of the IFG (Snyder et al., 2007). These results have been taken as evidence for the fact that selection processes are implemented across the left IFG (Moss et al., 2005). Consistent with this

proposal are the results from the ROI analysis, which showed an overall difference between competitor and no-competitor condition in the more anterior and more posterior portions of the IFG.

Nonetheless, the results of the ROI analysis also support the proposal that the IFG could be partitioned into sub-regions that are either sensitive to specific stimulus characteristics, or implement different functional mechanisms, or both. In the present study regional differences were found within the left IFG. First, a difference between competitor and no-competitor conditions emerged in the more posterior region (BA 44/45) and in the more anterior region (BA 47/13). Second, a significant positive correlation was found in BA 45 between a behavioral measure of competition and the neural sensitivity to competition. This graded activation presumably reflected individual differences across subjects in the extent to which the target stimulus induced competition. These results are consistent with the view that the more anterior and posterior portion of the IFG have different a different functional role from that of BA 45. In particular, activation in BA44 and 47 could be due to either the partial activation of multiple phonological/semantic representations, or to the increased selection demands imposed by competition, or both. In contrast, the positive correlation found in BA 45 could reflect the varying amounts of selection demands that the stimuli posed for each subject. In order to provide support for our interpretation of the present results, we turn to the discussion of two theories proposing a functional subdivision of the left IFG.

There are several neuroimaging studies showing a functional distinction between anterior and posterior IFG based on whether semantic or phonological information is processed (see Fiez, 1997 for a review). For example, Poldrack and colleagues (1999)

found increased activation in the anterior portion of the IFG (~BA 47/45) for semantic judgments, and increased activation in the posterior portion for phonological judgments (~BA 44/45). Burton and colleagues (2003) presented participants with lists of words and asked them to monitor either the semantic relationship between words or whether they rhymed. They found more activation for semantic processing compared to phonological processing in the anterior left IFG, and the opposite pattern in the posterior left IFG. McDermott and colleagues (2003) presented subjects with words pairs that could either be semantically related or rhymed with one another, and found that the processing of semantic relationships elicited activation in BA 47 and BA 45/44 within the IFG, while the processing of phonological relationships elicited activation in a more posterior region in BA44/6. In the current study, activation of BA47/45 and BA44/45 could reflect the fact that competition was induced both semantically/conceptually (between the semantic associate of the phonological competitor and the target) and phonologically (between the mediated phonological competitor and the target), thus activating both BA47 and BA44/45

An alternative to the hypothesis that the IFG is functionally subdivided in terms of domain-driven specialization is the hypothesis that the IFG is functionally subdivided in terms of different executive control functions. Badre & Wagner (2007) suggest that within the IFG two distinct subregions perform two different functions: controlled retrieval and post-retrieval selection (Badre & Wagner, 2007). Controlled retrieval refers to the top-down activation of semantic knowledge relevant to the task at hand and it is suggested to recruit anterior ventrolateral PFC (~BA47). If more than one knowledge representation becomes active, post-retrieval selection is needed to resolve competition,

regardless of the form of these representations (e.g. semantic, phonological, or perceptual). In this framework post-retrieval selection is implemented in mid-ventrolateral PFC (~BA45); BA 44 is not involved in either selection or retrieval processes, but rather it is suggested to be associated with "response level representations" (cf. Badre & Wagner, 2007).

The present results support a hybrid of these two proposals with regard to the role of the left IFG in the resolution of competition during language comprehension, as this region might have both domain-specific components and a domain-general selection mechanism. The activation found in BA 47 and in BA 44/45 could reflect the retrieval of multiple semantic representations and multiple phonological representations respectively, consistent with the hypothesis that the IFG is partitioned into domain specific functions. In contrast, the quantitative sensitivity across subjects found in BA 45 for competition is consistent with the view that this area recruits post-retrieval selection mechanisms, sensitive to selection demands imposed by a task.

To summarize, in the present study we show that the left IFG is sensitive to competition even when it is created implicitly by phonological similarity, and no direct competitor is present in the response set. Nevertheless, the neural response to mediated competition is weaker in the absence of a direct competitor form the response set. The data are in agreement with proposals of the left IFG as a functionally heterogeneous region, embodying both domain specific retrieval processes and a selection mechanism. Lastly, the present results also show that the recruitment of the IFG under condition of competition takes place also under non-controlled retrieval processes.

3.5.3 Mediated competition in temporo/parietal structures

Mediated phonological-semantic competition elicited increased activation in the left inferior parietal lobule (IPL) and in the left supramarginal gyrus (SMG), extending slightly into the precentral gyrus. These results are in agreement with previous findings showing sensitivity to phonological competition in this region (Prabhakaran et al., 2006; Righi et al, in press), presumably resulting from the partial activation and maintenance of multiple phonological forms (Awh et al., 1996; Gold & Buckner, 2002; Paulesu et al., 1993).

Nonetheless, in the present experiment the majority of significantly activated voxels in this region were located within the left IPL, whereas the left temporo-parietal cluster identified by Righi and colleagues was primarily located within the left SMG. The left IPL is commonly found activated in studies of language comprehension (Crinion et al., 2003; Price, 2000; Spitsina et al., 2006). Moreover, it also appears to be recruited when participants are required to make a variety of linguistic judgments. This region has been found to be responsive when subjects are asked to make phonological judgments on word pairs (McDermott et al., 2003), and when subjects are asked to make semantic judgments on single words (Dapretto & Bookheimer. 1999; Demonet et al., 1992). It is also recruited when the semantic relationships between stimuli was manipulated by presenting a target and its semantic associate simultaneously (deZubicaray et al., 2001). Given its involvement in both phonological and semantic processing, it is not surprising that significant activation was found in the left IPL in the current study. The variation in the cluster's distribution between the present study and Righi et al. (in press) could result from the interaction of phonological and semantic factors in the current experiment as

well as the implicit nature of both phonological and semantic competition. While in Righi et al. (in press) the relationship between target and distractor was direct (both appeared in the stimulus array) and the relationship was driven only by phonological similarity, in the present experiment both semantic and phonological associations were present but were implicit in the relation between the target and the distractor. Thus, the sensitivity to mediated competition found in the left posterior parietal region could result from the increased activation of both phonological forms and their semantic associates created by the competitor trials, and the maintenance of these representations while the subject is looking for the target in the visual display.

4. CHAPTER 4: The Neural substrates of competition during word production

4.1 Introduction

Object naming relies on a series of stages: recognition of the item to be named, activation of the conceptual representation of the item, mapping the conceptual representation onto its phonological form, and converting this abstract phonological representation into a phonetic plan for articulation. Nonetheless, the selection of a word for naming requires that it be selected from the thousands of words in the mental lexicon, many of which share properties of meaning and sound. As a consequence, selection of a word is carried out under conditions of competition. In fact, studies of speech errors and of naming latencies have shown that word selection is affected by phonological and semantic similarities between the candidate word and other words in the mental lexicon (see Levelt, 1999 for a review).

A paradigm that has been extensively used providing evidence for competition effects in word production is the picture-word-interference (PWI) task (Lupker, 1979; Rosinski, 1977). In this paradigm, subjects are presented with a picture of a common object and either a written word positioned across the picture or an auditory word presented before, during, or after the display. Subjects' task is to name the picture as quickly as possible ignoring the visual or auditory word distractor. Using a visually presented distractor, Rosinski (1977) showed that when an object was paired with a semantically related word, reaction times naming latencies (RT) were significantly longer, compared to when subjects were asked to read the word, ignoring the object. Lupker (1979) explored further the attributes of semantic interference effects showing that reaction times were the most impaired when a distractor belonged to the same basic category as the object (e.g. mouse-

dog), and that this effect was not influenced by either word frequency or category typicality.

In addition to effects of semantic factors in influencing naming latencies, there are influences of phonological similarity between a target word and distractor on naming latencies. For example, Lupker (1982) showed that if target and distractor are similar in their phonological form, subjects were slower in naming a target with its related distractor compared to naming in isolation, but were faster in naming a target with a phonologically related distractor compared to naming a target presented with an unrelated distractor.

There are two sources of interference that come into play in the PWI paradigm. One source of interference is "response conflict" which originates from conflict between two different potential responses, one for the visual target and the other for the distractor. A second source of interference is the extent to which there is competition between the target and distractor. Thus, response conflict is inherent in the selection of a target word from two potential responses; but the extent of this conflict is modulated by the nature of the relationship between target and distractor. For example, if the target and distractor are semantically related, greater resources will be needed to select the target word from the two highly activated stimuli than if the target and distractor do not share any semantic properties.

Competition is inherent in the structure of a number of recent models of spoken word production. Fully interactive models propose that activation at one level of the grammar spreads not only within that level but also influences activation across levels of processing (Caramazza, 1997; Dell et al., 1997; Starreveld & La Heij, 1995). Thus, the

conceptual representation of a word (e.g. *car*) will activate associated conceptual representations (e.g. *truck, bus, etc*), and also activate their associated phonological forms (e.g. *cab, cat, trunk, bug, etc*). Thus these models predict that competition arises not only when the relationship between target and distractor is directly phonological or semantic (*car* is semantically related to *truck* and phonologically related to *cab*), but also when the relationship is indirect (*car* is 'related' to and hence will partially activate *trunk* via its semantic relationship to *truck*). Given the fully interactive nature of these models, they predict that naming latencies using the PWI paradigm should be affected not only when the picture of a car is presented with *truck* (semantic) or *cards* (phonological) as distractors, but also if the distractor were to be, for example, *poker* (semantic associate of the target's phonological competitor) or *trunk* (phonological competitor of the target's semantic associate).

In the case of a target-distractor pair like *car-poker*, the functional architecture of the interactive spoken word production models would predict that *car* will produce partial activation of its conceptual representations and its semantic associates (*cab, bus, truck, etc.)* and also to its phonological form and those of its semantic associates. At the same time *poker* will also provide partial activation to its semantic associates (e.g. *cards*), and in turn these semantic associates will project partial activation to their phonological codes. Because of the phonological similarity between the semantic associate of the distractor (*cards*) and the target (*car*), the shared phonological segment will receive a boost in activation, which should result in faster naming latencies (facilitation) compared to unrelated target-distractor pairs. A few studies have provided evidence for facilitation under these conditions (Cutting & Ferreira, 1999; Ferreira & Griffin, 2003; Peterson &

Savoy, 1998). For example, Peterson and Savoy (1998) had subjects name line drawings of objects (e.g. *couch*). On a small percentage of trials, they presented a written word together with the object and asked their subjects to read the word instead of naming the object. For example, when the target was the picture of a couch, the distractor word could be either phonologically related to the name of the target (e.g. *count*), or phonologically related to a synonym of the object name (e.g. *soda,* which is a phonological competitor of sofa, which is a synonym of couch). They found that response latencies were facilitated for both the phonologically related distractors (e.g. *couch-count*) and also for words that were phonologically related to a synonym of the object name (e.g. *couch-soda;* henceforth dubbed phonological-semantic competitor).

Fully interactive models of language processing also predict that naming latencies using the PWI paradigm should be affected even when the relationship between target and distractor is mediated semantically, although these models do not make predictions about mediated priming. For example, these models predict that pairs such as *lion-tire* (henceforth dubbed semantic-phonological competitors) should also produce naming latencies different from unrelated target-distractor pairs. In the case of a pair like *lion-tire*, the target will activate its conceptual representation and its semantic associates (e.g. *tiger*) and also all the relevant phonological codes of these associates. Tiger thus will activate the set of phonologically similar words such as tire. Thus, *tiger* will receive partial activation from the target itself, and also from the phonologically similar distractor tire. These models predict that this increase in competition among semantically associated words should result in slower naming latencies compared to cases in which target and competitor only share phonological similarity. Nevertheless, phonological

similarity between the semantically mediated competitor and the distractor suggest that naming latencies should still be facilitated. Studies of semantic interference using PWI have shown slower response latencies when both target and distractor represent context-appropriate responses (Costa et al., 2000; Costa et al., 2003; Lupker, 1979). For example, in the case of a pair like *dog-cat*, both target and distractor could be considered appropriate responses, as they are both at the same level of categorization, they are both domestic animals, etc. In contrast, when target and distractors are semantic associates but are not both "response-relevant" (Lupker, 1979), such as pairs like *car-tire*, naming facilitation is observed compared to unrelated pairs, because the relationship between the target and distractor produces priming.

As stated above, fully interactive models of language processing predict that word production will be influenced by both direct and mediated semantic and phonological competition. Thus, we could expect to find sensitivity to all of these types of competition during word production in brain regions that are sensitive to competition.

There are several studies showing increased brain activation under condition of semantic conflict in the left prefrontal cortex using the Stroop task (Banich et al., 2000; Barch et al., 2001; Milham et al., 2001; Peterson et al., 2002; Roelofs et al., 2002; Van Veen et al., 2005). Several studies of word production have also shown increased activation in the left inferior frontal gyrus (IFG) and the temporo-parietal structures under conditions of semantic competition (Abel et al., 2008; Barch et al., 2000; de Zubicaray et al., 2001 Kan & Thompson-Schill, 2004; Moss et al., 2005; Schnur et al., 2009; Spalek & Thompson-Schill, 2008; Thompson-Schill et al., 1997). Two recent studies using PWI also found increased activation in the left IFG and in temporal structures when targets

were presented with semantically related distractors, compared to unrelated distractors (Abel et al., 2008; de Zubicaray et al., 2001).

Several brain regions have also shown to be sensitive to phonological competition in production. Two previous studies using PWI with phonologically related target-distractor pairs found increased activation in the left inferior parietal region (Abel et al., 2008; de Zubicaray et al., 2002). A recent study using picture-picture target-distractor pairs also found increased activation in the left IFG when the names of the two objects represented in the pictures were phonologically related (Bles & Jasma, 2008).

Taken together, these results show that both direct semantic and phonological competition recruit brain regions in posterior temporo-parietal cortex and prefrontal cortex during word production. Moreover, they suggest that posterior brain regions might be sensitive to the specific domain in which competition is created with temporal structures recruited under conditions of semantic competition and parietal structures recruited under conditions of phonological competition. In contrast, the IFG might be recruited regardless of the specific type of competition. What is not clear is whether mediated competition will recruit the same areas as those recruited under direct conditions of direct competition.

The goal of the present study is to examine how different types of competition affect the recruitment of neural structures. The current study will directly compare the effects of semantic and phonological competition, both when competition is created directly and when its effects are mediated by both phonological and semantic factors. The paradigm chosen to achieve these goals will be a PWI task with visually presented distractors.

Given the results of previous studies, we expect to find effects of direct phonological and semantic competition in posterior temporo-parietal regions and in the prefrontal cortex. To our knowledge, no prior studies have investigated the neural systems underlying mediated competition during production. Nevertheless a recent experiment by Righi and colleagues (in preparation) that investigated mediated phonological-semantic competition in word comprehension showed that increased activation in the left prefrontal cortex and posterior temporo-parietal cortex, albeit to a lesser extent than direct phonological competition. Thus, we would expect that mediated competition should also elicit activation in these same regions, eve though the strength of the neural response might be weaker compared to that elicited by direct competition. Activation in prefrontal cortex under such conditions is of particular interest since such findings would indicate that response selection does not require the direct presence of a competitor. Rather response selection is influenced by structural properties inherent in the grammar, even when those properties are indirectly activated.

4.2 Methods

4.2.1 Behavioral Pilot Experiment

A behavioral pilot experiment was conducted to assure that we were able to replicate the semantic and phonological interference effects shown in the literature (Caramazza & Costa, 2000; Caramazza & Costa, 2001; Damian & Martin, 1999; Jescheniak & Schriefers, 2001; Lupker, 1979; Lupker, 1982; Rosinski, 1977; Starreveld & La Heij, 1996) and to test whether mediated competition also affects naming latencies, as it suggested by fully interactive models of language processing (Dell et al., 1997). The pilot

experiment was designed to mirror the conditions and timing parameters to be used in the fMRI experiment.

4.2.1.1 Participants

Ten participants took part in one experimental session. All participants gave written informed consent according to the guidelines of the Human Subjects Committee of Brown University.

4.2.1.2 Materials

The stimulus set consisted of 336 visual displays. Each visual display contained a line drawing of a common object taken from the either Snodgrass and Vanderwart (1980) corpus or from Google Images. The line drawings were taken from several semantic categories such as fruits and vegetables, furniture, musical instruments, tools, animals, vehicles, clothing, and professions. Each picture was presented in two conditions. In the "conflict" condition, the picture was presented with a word superimposed through its midline. The font used for the letter strings was Times New Roman in size 36 in upper case.

The experiment consisted of 6 conditions (see figure 8 for examples of stimuli), one baseline condition and 5 conflict conditions. In the "baseline" condition, the picture to be named was presented with a string of Xs superimposed through its midline. The "conflict" trials consisted of five different manipulation conditions, with each target appearing once as a picture and once as a distractor word in two different conflict conditions. The five conflict conditions included 1) semantic interference (S): target and distractor were taken from the same semantic category and were at the same level of the

category hierarchical structure (e.g. car-truck); 2) phonological interference (P): target and distractor shared their phonological onset (e.g. hammer-hammock); 3) mediated phonological-semantic interference (PS): target and distractor were related such that a semantic associate of the distractor word shared its phonological onset with the target (e.g. hammock-screwdriver, where *hammer* is the implicit phonological competitor of the target which is semantically related to the distractor (screwdriver); 4) mediated semantic-phonological interference (SP): target and distractor were related such that a semantic associate of the target shared its phonological onset with the distractor word (e.g. sofa-cherry, where *chair* is the implicit semantic associate of the target which shares a phonological onset with the distractor cherry); 5) response conflict (U): target and distractor are unrelated both semantically and phonologically (e.g. raft-dime).

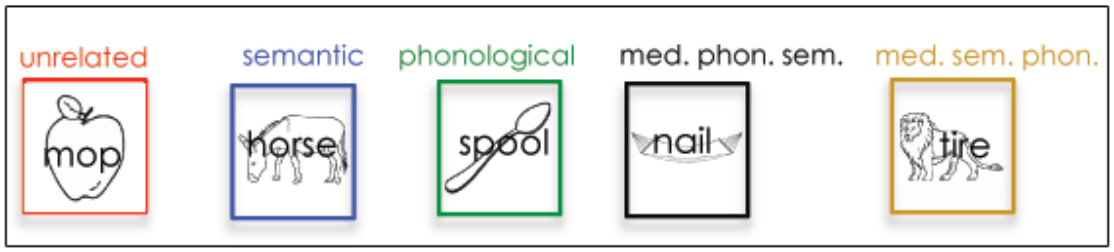

Figure 8. Example of stimuli for each experimental conflict condition used in both the behavioral pilot and fMRI experiment.

4.2.1.3 Procedure

The experiment consisted of 168 "conflict trials" and 168 "baseline" trials, presented in a random intermixed order, equally distributed across four experimental runs, such that each run contained a total of 84 trials (42 "conflict" trials and 42

"baseline" trials). Within each run, the number of "conflict" trials was broken down into the five conflict conditions, such that there were 9 trials of each of the S, P, PS, and SP conditions and 6 trials of the U condition. Overall there were 36 trials for the S, P, PS, and SP conditions and 24 trials for the U condition. The reason for choosing slightly unmatched number of trials was to limit of repetitions for each item and also to make sure that each item was repeated an equal number of times. Targets were unique to each run, such that subjects never saw the same line drawing more than once in each run. The order of the runs was randomized across subjects.

The experiment was programmed in Bliss (Mertus, 2002) and run on a Lenovo laptop. Each trial began with the presentation of a fixation cross for 0.25 seconds, followed by the visual display that remained on the screen for 1.75 seconds. Subjects were required to name the object presented on the screen as quickly as possible. Vocal responses were recorded on a digital recorder (Edirol, Roland, USA), which also recorded via a beep at the onset of the stimulus presented on the screen. Naming latencies were determined by automated voice key software, which measured the onset of each naming response relative to the presentation of the experimental stimulus (Mertus, in preparation).

Prior to the beginning of the actual experiment, subjects performed a practice run that consisted of 10 unrelated trials, in order to get accustomed to the visual displays. The objects and distractors used during the practice were unique to this phase.

To mirror the experimental set up that would be used in the scanner, presentation of stimuli was jittered according to a uniform distribution of three trial onset asynchronies (TOA values of 3s, 6s, 9s). During the TOA intervals the screen was left blank. Each

TOA bin was used an equal number of times in each run, and an equal number of items for each condition was assigned to each TOA bin in each run.

4.2.1.4 Results

Trials in which participants provided an incorrect name, or failed to name the object, were removed from the analysis. When the error occurred on only one of the occurrences of each item (e.g. in a conflict condition), its counterpart in the baseline condition was also removed. For each subject, naming latencies that were more than three standard deviations above the mean reaction time for that condition were excluded from data analysis. For each subject, mean naming latencies times for each experimental condition were computed. Table 3 reports the mean reaction-time naming latencies (RT) for all experimental conditions.

Table 3. Naming Latencies for Behavioral Pilot

Condition	*Mean*	*Standard Deviation*
Baseline	834	48.74
Semantic	997	57.69
Phonological	902	50.85
PS	869	41.9
SP	909	48.77
Unrelated	956	43.75

Average Naming Latencies (Mean) and standard deviations reported in ms. for the behavioral pilot.

A repeated measures one-way ANOVA revealed a significant effect of condition ($F(5,9) = 31.34$, $p < 0.0001$). Planned comparisons were conducted to examine the effects of the different conflict conditions. First of all, all conflict conditions produced significantly longer reaction times compared to the baseline condition. Comparing the effects of competition with that of response conflict (U condition) revealed the following results: the RT latency in naming words in the S condition compared to the U condition was marginally significant ($t(9) = 1.9$, $p < 0.08$), showing a semantic interference effect. There was a significant phonological facilitation effect with significantly faster naming latencies for words in the P condition compared to the U condition ($t(9) = 3.36$, $p<0.009$). Both mediated conditions showed faster naming latencies compared to the U condition (PS vs. U: $t(9) = 5.3$, $p< 0.0006$; SP vs. U: $t(9) = 2.8$, $p< 0.03$). The PS condition was significantly faster than P ($t(9) = 3.45$, $p<0.008$), but there was no significant difference between SP and P ($t(9) = 0.64$, $p<0.6$). However, a significant difference emerged between PS and SP conditions ($t(9) = 4.32$, $p<0.002$), with SP trials producing longer naming latencies than PS trials.

4.2.1.5 Discussion

The results from the behavioral pilot replicated previous findings, showing interference in the present of semantic associates and facilitation in the presence of phonological competitors compared to unrelated distractors (Lupker, 1979; Lupker 1982; Rosinski, 1977). The findings also revealed that the two mediated conditions produced naming facilitation. Conditions similar to the PS condition have been used in a few experiments and have shown varied results, with some experiments showing facilitation (Cutting &

Ferreira, 1999; Ferreira & Griffin, 2003; Peterson & Savoy, 1998) and others showing no effect (Damian & Martin, 1998; Miozzo et al., 2003).

To our knowledge no prior experiment used a condition similar to the SP condition. As was discussed in the introduction, this condition was also expected to produce faster naming latencies than the U condition.

Taken together, the results of the behavioral pilot test support interactive models of language processing and suggest that the implicit semantic and phonological competitors are being activated and are influencing naming response latencies (Caramazza, 1997; Dell et al., 1997; Starreveld and La Heij, 1996).

4.2.2 fMRI Experiment

4.2.2.1 Participants

Nineteen participants (13 females) ranging in age from 18 to 34 (mean age = 23 $\pm$ 5) took part in one scanning session. Participants were all right-handed as assessed by the Oldfield handedness inventory (Oldfield, 1971). Participants reported normal hearing and normal or corrected-to-normal vision, and no neurological impairment. All participants gave written informed consent according to the guidelines of the Human Subjects Committee of Brown University. All participants were screened for MR safety prior to the scanning session. The data from two participants were excluded from both the behavioral and fMRI analyses because of excessive motion during the acquisition of functional images.

4.2.2.2 fMRI Acquisition

Scanning was done on a 3T Siemens TIM Trio scanner at Brown University, using a standard 8-channel head coil, outfitted with a mirror for back projection. High-resolution anatomical images were collected using a 3D T1-weighted magnetization prepared rapid acquisition gradient echo sequence (TR = 2.25s, TE = 2.98ms, 1 mm^3 isotropic voxel size). Functional images were acquired using a multislice, ascending, interleaved EPI sequence with sparse acquisition (TR = 3s, TE = 28 ms, FOV = 192, 16 slices, 3mmX3mm in-plane resolution, 3mm slice thickness). A sparse sampling acquisition technique was utilized as it allowed for the recording of naming responses in relative silence for later analysis, and also for the acquisition of functional images after subjects had finished their vocal response. The experiment consisted of four runs of 173 volumes each, for a total of 519 functional volumes. In addition, two "dummy" volumes were acquired at the start of each run to allow the MR signal to reach steady state. These volumes were discarded by the scanner.

4.2.2.3 Materials

The stimulus set was identical to the one used in the preliminary behavioral experiment, with the exception of a few changes in the line drawings chosen following feedback from the participants in the pilot experiment. The number of items, trials, and distributions of the conditions was identical to that described in the behavioral pilot.

4.2.2.4 Procedure

Immediately prior to the experimental session, subjects underwent a familiarization phase outside the scanner during which they were shown each line drawing that was to be used in the scanning experiment paired with its correct name. The name was provided in written form and positioned below the line drawing. Each object-name paired was shown for 4 seconds. Subjects were told to study each object and silently rehearse its name.

Once inside the scanner the subjects were given a short practice session to familiarize them with the experimental task. Stimuli included line drawings of a total of 10 objects paired with unrelated distractors, none of which were part of the experimental set. Subjects were instructed to name the object depicted in the drawing as quickly and as accurately as possible. Upon conclusion of this phase, subjects were provided feedback on their performance and were again given the instructions before the experiment proper began.

The numbers of experimental trials and the design of the experiment was exactly the same as the pilot experiment (see Materials and Procedures above)

4.3 Data Analysis Methods

4.3.1 Behavioral Data Analysis

Participants' recorded responses were analyzed first by listening to each response and determining whether they correctly named the picture. Trials in which participants provided an incorrect name, failed to name the object, or were not able to complete their utterance prior to functional image acquisition were removed from the analysis. When the

error occurred on only one of the occurrences of each item (e.g. in a conflict condition), its counterpart (e.g. in the baseline condition) was also removed. For the remaining correct trials naming latencies were determined by measuring the onset of each naming response relative to the onset of the presentation of the experimental stimulus using automated voice key software developed by John Mertus. For each subject, naming latencies that were more than three standard deviations above the mean reaction time for that specific condition were excluded from data analysis. For each subject, mean naming latencies times for each experimental condition were computed, and these data were submitted to a repeated-measures one-way ANOVA followed by a set of planned comparisons.

4.3.2 fMRI data preprocessing

fMRI data was analyzed using AFNI (Cox, 1996; Cox & Hyde, 1997).Functional data was corrected for slice time acquisition by run. The runs were concatenated and motion correction was performed by aligning all volumes to the fourth collected volume using a 6-parameter rigid body transform. The motion corrected data were then warped to Talairach and Tournoux space (Talairach 1988), and resampled to 3-mm isotropic voxels. Lastly, the data were spatially smoothed using a 6-mm full-width half maximum Gaussian kernel.

4.3.3 fMRI statistical analysis

Each subject's preprocessed EPI data were regressed to estimate the hemodynamic response function for each of the experimental conditions (S, P, PS, SP, U, baseline) and

also for the naming errors. The response functions were estimated by convolving vectors containing the onset times of each image acquisition sequence that followed the naming response with a stereotypic gamma-variate hemodynamic response function provided by AFNI (Cox, 1996; Cox & Hyde, 1997). AFNI 3dDeconconvolve program was used to compute the raw fit coefficients associated with each experimental condition. The raw coefficients for all conditions were converted to percent signal change by dividing each voxel coefficient by the experiment-wise mean activation for that voxel. The whole-brain group analysis was carried out by entering the percent signal change data into a mixed factor ANOVA, with subject as a random factor, and experimental conditions as fixed factors. Correction for multiple comparisons was carried out using Monte Carlo simulations to determine minimum cluster size that would be reliable at a corrected p value of 0.05. Anatomical structures were identified using the Anatomy Toolbox atlases (Eickhoff 2005; Eickhoff 2006; Eickhoff 2007).

4.4 Results

4.4.1 Behavioral Results for fMRI session

Table 4 shows the mean RT naming latencies for all experimental conditions from the scanning session. Comparison of the overall naming latencies for participants in the scanner to those in the pilot behavioral experiment indicated similar response latencies, with an average naming latency of 907 vs. 911 ms. Turning to the results in the scanner, a repeated measure one-way ANOVA revealed a significant effect of condition ($F(5,16) = 12.96$, $p < 0.0001$).

A series of planned comparisons revealed the following results. All conflict conditions produced significantly slower naming latencies compared to the baseline condition. Although naming latencies were slightly slower for S compared to U conditions, this difference was not significant ($t(16) = 0.39$, $p < 0.8$). There was a significant effect between P and U ($t(16) = 2.9$, $p< 0.02$), showing a phonological facilitation effect. There were faster naming latencies for PS vs. U conditions, ($t(16) = 3.33$, $p<0.005$), showing that PS trials caused facilitation. Similarly, SP trials also resulted in facilitation of naming latencies compared to unrelated trials, ($t(16) = 2.44$, $p<0.03$). . There were no significant differences between P and either of the mediated conditions (P vs. PS, $t(16) = 0.28$, $p<0.8$; P vs. SP, $t(16) = 0.66$, $p<0.6$) nor did any difference emerge between PS and SP ($t(16) = 0.62$, $p<0.6$).

Table 4. Naming Latencies for scanning session

Condition	*Mean*	*Standard Deviation*
Baseline	865	77.89
Semantic	944	102.48
Phonological	895	95.57
PS	897	98.59
SP	904	100.47
Unrelated	939	75.83

Average Naming Latencies (Mean) and standard deviations reported in ms.from the scanning session.

4.4.2 fMRI Results

Several analyses were carried out to decouple brain activations that were sensitive to response conflict alone from brain activations that were sensitive to the lexical factors creating competition and to identify the neural areas modulated by the different competitor conditions. All analyses report clusters that were statistically significantly activated at $p < 0.05$, corrected.

To determine those neural areas sensitive to response conflict, i.e. conflict between two different potential responses, one for the visual target and the other for the distractor) in the absence of phonological or semantic competition, the unrelated condition (U) was compared to the baseline condition (B). Table 5 shows a list of the significantly activated clusters in this comparison. Increased activation for U compared to B was found in the left posterior parietal lobe, in the left prefrontal cortex, and in the left ventral/inferior temporal cortex.

Table 5. Clusters of activation sensitive to stimulus conflict.

			Talairach Coordinates		
Cortical Region	*Brodmann's Area*	*Cluster Size*	*x*	*y*	*z*
Unrelated > Baseline					
Left Ventral/Temporal cortex	37/19/18	523	43.5	70.5	-15.5
Left Prefrontal Cortex	45/46/44	298	46.5	-10.5	35.5
Left Posterior Parietal	7/19/39	177	28.5	73.5	47.5
Baseline > Unrelated					
Anterior Cingulate	32/9	873	-1.5	-25.5	2.5
Posterior Cingulate	31/7	863	1.5	37.5	47.5
Right Superior Temporal	40/13	196	-55.5	40.5	44.5
Right Superior Temporal	21/22/38	108	-61.5	16.5	-0.5

Clusters thresholded at a cluster-level threshold of $P < 0.05$ with a minimum of 100 contiguous voxels, and at a voxel-level threshold of $P < 0.05$, $t = 2.13$ (corrected). Coordinates indicate the maximum intensity voxel for that cluster in Talairach and Tournoux space. The first Brodmann area listed corresponds to the location of the maximum intensity voxel. If the cluster extended into other BAs, those are also listed (see text for details).

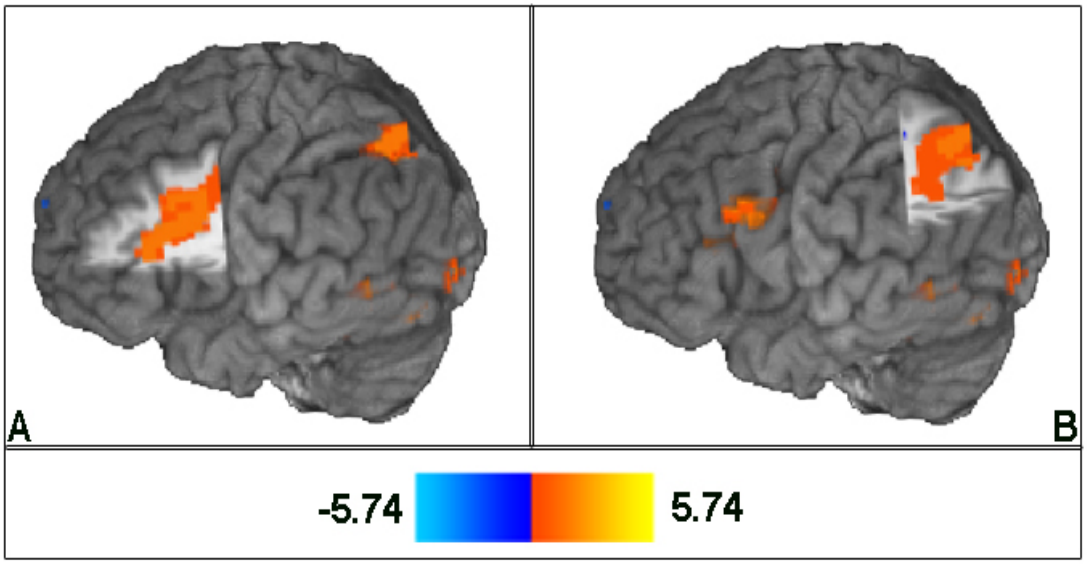

Figure 9. Results of the linear contrast between unrelated and baseline trials. Areas in yellow-orange show increased activation for the unrelated condition. Maps are thresholded at a voxel level threshold of p< 0.05, t = 2.1, and clusters shown correspond to a corrected significance level of p<0.05. (A) Clusters in left inferior frontal gyrus. Sagittal slice shown at x = 30, coronal cut shown at y = 5, and axial cut shown at z = 15. (B) Cluster in left inferior parietal region. Sagittal slice shown at x = 20, and coronal cut shown at y = 50 and axial cut shown at z = 25.

Of particular interest are the first two clusters (see figure 9). The significant cluster located in posterior parietal cortex was situated primarily within the left superior parietal lobule (SPL) and the left inferior parietal lobule (IPL). The significant cluster located in the left prefrontal cortex was situated within the left inferior frontal gyrus (IFG; 36% in BA 45 and 18% in BA 44), and the middle frontal gyrus.

In order to uncover regions that were sensitive to competition and not only to response conflict, each of the lexical interference conditions was contrasted with the unrelated condition. Tables 6a and 6b provide a summary of the all the areas of activation that resulted from these analyses.

Table 6a. Clusters with increased activation for Lexical Competition Conditions

			Talairach Coordinates		
Cortical Region	*Brodmann's Area*	*Cluster Size*	*x*	*y*	*z*
Phonological > Unrelated					
Left Temporo/Parietal	40/39	696	37.5	76.5	41.5
Left Inferior Frontal	45/44/6	691	46.5	-43.5	-0.5
Right Temporo/Parietal	40/39	198	-43.5	64.5	44.5
Semantic > Unrelated					
Anterior and Posterior Cingulate	9/32/7/31	1914	1.5	-49.5	20.5
Left Angular Gyrus	39/40	379	40.5	76.5	38.5
Right Inferior Fontal Gyrus	47	218	-43.5	-40.5	-3..5
Right Temporo/Parietal	39/40	168	-43.5	67.5	44.5
Right Middle Temporal Gyrus	21/38	121	-52.5	7.5	-21.5
Left Middle Temporal Gyrus	21/38	119	61.5	16.5	-12.5
Left Inferior Frontal Gyrus	47	112	40.5	-46.5	-6.5
Semantic-Phonological > Unrelated					
Left Temporo/Parietal	40/39	353	28.5	79.5	44.5
Left Inferior frontal	46/45/47	349	46.5	-43.5	5.5
Right Temporo/Parietal	39/40	157	-40.5	70.5	44.5

Clusters thresholded at a cluster-level threshold of P < 0.05 with a minimum of 100 contiguous voxels, and at a voxel-level threshold of P < 0.05, t = 2.13 (corrected). Coordinates indicate the maximum intensity voxel for that cluster in Talairach and Tournoux space. The first Brodmann area listed corresponds to the location of the maximum intensity voxel. If the cluster extended into other BAs, those are also listed (see text for details).

The phonological interference condition (P) elicited stronger activation than the unrelated condition (U) in the left ventrolateral prefrontal cortex, and bilaterally in the inferior parietal region. The majority of the activation in the left frontal region was located within the left IFG (31% of active voxels in BA 45, 23% of active voxels in BA

44, 13% of active voxels in BA 47), and extended marginally into the precentral gyrus (see figure 10a). Activation in the left temporo-parietal region was located within the IPL, the angular gyrus (AG), and extended into the supramarginal gyrus (SMG). Activation in the right temporo-parietal regions was found primarily in the IPL, and the AG marginally extending into the SMG.

Table 6b. Clusters with increased activation for the Unrelated Competition Condition

			Talairach Coordinates		
Cortical Region	*Brodmann's Area*	*Cluster Size*	*x*	*y*	*z*
Unrelated > Phonological					
Right Cuneus	17	116	-1.5	82.5	17.5
Unrelated > Semantic					
Bilateral Ventral Temporal	37/19/21/22	4696	40.5	70.5	-15.5
Unrelated > Phonological-Semantic					
Left Declive		220	31.5	55.5	-15.5
Right Middle Occipital Gyrus	17/18	203	-34.5	85.5	8.5
Right Declive		104	-25.5	67.5	-12.5
Unrelated > Semantic-Phonological					
Right Precuneus	31/7	108	13.5	19.5	23.5

Clusters thresholded at a cluster-level threshold of P < 0.05 with a minimum of 100 contiguous voxels, and at a voxel-level threshold of P < 0.05, t = 2.13 (corrected). Coordinates indicate the maximum intensity voxel for that cluster in Talairach and Tournoux space. The first Brodmann area listed corresponds to the location of the maximum intensity voxel. If the cluster extended into other Bas, those are also listed (see text for details).

The semantic interference condition (S) elicited stronger activation than U in the anterior cingulate cortex, prefrontal cortex, temporo-parietal region, and bilaterally in the anterior middle temporal gyrus. The frontal cluster of activation was very large and was located within the anterior cingulate (AC) and extended posteriorly towards the posterior cingulate and precuneus. The temporo-parietal activation was located within the left AG, the left posterior MTG, and the left IPL. Activation in prefrontal cortex was found in the right hemisphere in the IFG (47% of active voxels in BA 47), 14% of active voxels in the Insula, 10% of active voxels in the temporal pole, and also in the left IFG (46% of active voxels in BA 47; 5% of active voxels in BA 45), and in the left middle orbital gyrus (see figure 10b).

The phonological-semantic condition (PS) failed to elicit stronger activation than U that resisted statistical correction for multiple comparisons. However, a statistically uncorrected analysis revealed a small cluster in the left IFG, primarily located within BA 45 (see figure 9c).

The semantic-phonological condition (SP) revealed stronger activation than U in the left ventrolateral prefrontal cortex, and bilaterally in the temporo-parietal region (see figure 9d). The frontal cluster of activation was located within the left middle frontal gyrus and the left IFG (31% of active voxels in BA 45, 10% of active voxels in BA 47, 5% of active voxels in BA 44). In the left temporo-parietal region, activation was located primarily within the IPL extending into the AG. In the right temporo-parietal region, activation was also located primarily within the AG extending into the IPL.

The last set of analyses compared the lexical competition conditions, in order to determine the domain-specificity of the neural responses. P was compared to S, to

determine how brain regions respond to different types of direct competition; PS was compared to SP to determine how brain regions respond to the two different types of competition when it is mediated. Table 7 lists all of the significant clusters of activation found in these analyses.

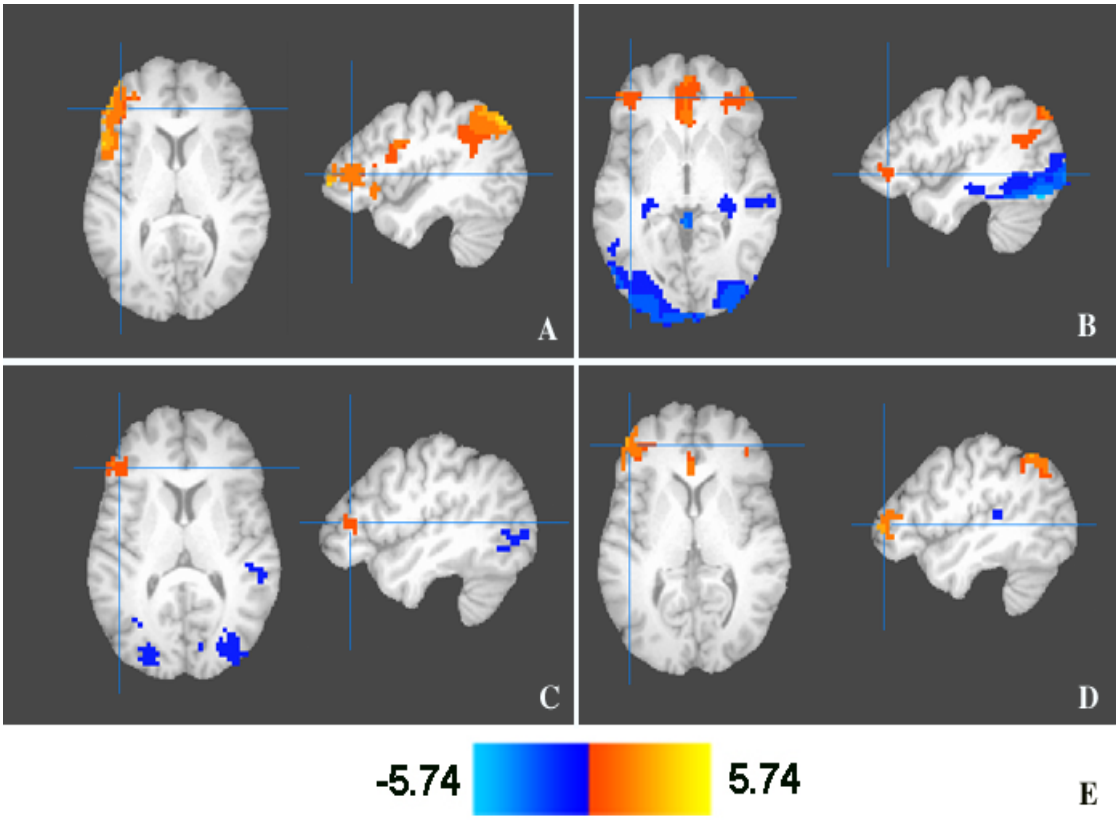

Figure 10. Significant clusters of activation for pairwise comparisons between competition conditions and unrelated condition. Maps are thresholded at a voxel level threshold of p< 0.05, t = 2.1, and clusters shown correspond to a corrected significance level of p<0.05. The crosshairs indicate the clusters of activation located within the left IFG. Areas shown in orange show increased activation for the first condition listed in all comparisons, while areas shown in blue show increased activation for the second condition. (A) P vs. U comparison, axial slice shown at z = 8, sagittal slice shown at y = 36. (B) S vs. U comparison, axial slice shown at z = 1, sagittal slice shown at y = 37. (C). PS vs. U comparison, axial slice shown at z = 10, sagittal slice shown at y = 31. (D) SP vs. U comparison, axial slice shown at z = 6, sagittal slice shown at y = 42.

P elicited greater activation than S over large areas in the left and right prefrontal cortexes, and bilaterally in ventral temporal cortex extending into the posterior parietal lobe (see figure 10a). The significant cluster of activation in the left prefrontal cortex was situated in the left IFG (28% of active voxels in BA 45, 15% of active voxels in BA 44), extending into the precentral gyrus, and slightly into the postcentral gyrus. The significant cluster of activation in the right prefrontal cortex was situated within the right IFG (16% of active voxels in BA 44, 8% of active voxels in BA 45). The significant cluster of activation located in posterior regions extended from extrastriate visual cortex to the IPL and AG, bilaterally.

S elicited greater activation than P over large areas in the posterior cingulate cortex and precuneus, and in the anterior cingulate, extending into the superior medial gyrus. Moreover, greater activation for S was found bilaterally in the anterior portions of the MTG (see figure 10a).

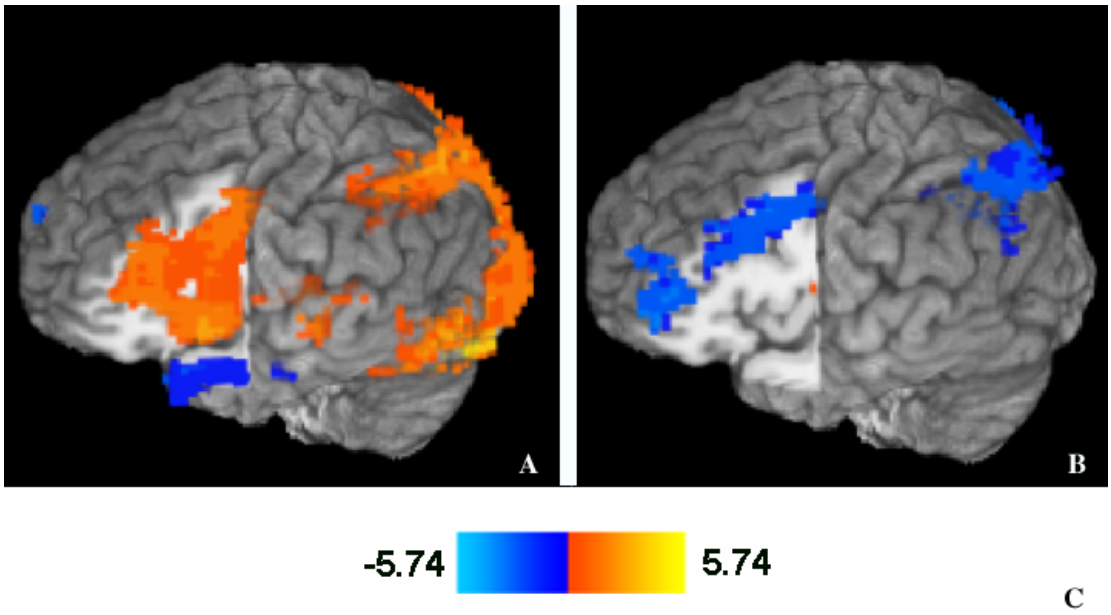

Figure 11. Figure 9. Significant clusters of activation for pairwise comparisons between competition conditions. Maps are thresholded at a voxel level threshold of p< 0.05, t = 2.1, and clusters shown correspond to a corrected significance level of p<0.05. Areas shown in orange show increased activation for the first condition listed in all comparisons, while areas shown in blue show increased activation for the second condition. (A) P vs. S comparison, axial cut shown at z = -3, coronal cut shown at x = 4, sagittal cut show at y = 35. (B) PS vs. SP comparison axial cut shown at z = -3, coronal cut shown at x = 4, sagittal cut show at y = 35

PS elicited greater activation than SP in two clusters (see figure 11b). The largest cluster was located within the right precentral gyrus extending into the cingulate gyrus and the anterior insula. The second cluster was located within the left rolandic operculum and insular lobe.

SP elicited greater activation than PS in several clusters (see figure 11b). The largest cluster was located in the left IPL, AG and SPL. Activation was also found in the right AG and IPL. The third largest cluster was located within the left anterior cingulate. The

smallest cluster was primarily located within the left MFG and the left IFG (22% of active voxels located in BA 45).

Table 7. Comparison of competition conditions

			Talairach Coordinates		
Cortical Region	*Brodmann's Area*	*Cluster Size*	*x*	*y*	*z*
Phonological > Semantic					
Bilateral Ventral/Temporal/Parietal	17/19/37	5347	46.5	61.5	-18.5
Left Prefrontal Cortex	44/45/6	1291	52.5	-10.5	2.5
Right Inferior Frontal	44/45	530	-52.5	-10.5	5.5
Semantic > Phonological					
Posterior Cingulate	23/31	1371	1.5	61.5	11.5
Anterior Cingulate	32	780	1.5	-52.5	20.5
Left Anterior Temporal	21/38	240	37.5	-22.5	-21.5
Right Anterior Temporal	21/38	239	-37.5	-16.5	-15.5
Left Anterior Insula	13	132	28.5	-4.5	-9.5
Phonological-Semantic > Semantic-Phonological					
Right Precentral Gyrus	6	345	-58.5	7.5	29.5
Left Insula	13	114	37.5	22.5	20.5
Semantic-Phonological > Phonological-Semantic					
Left Temporo/Parietal	39/40	351	28.5	79.5	44.5
Right Temporo/Parietal	39/40	270	-37.5	67.5	47.5
Anterior Cingulate	32	260	4.5	-25.5	2.5
Left Prefrontal Cortex	46/45	160	46.5	-7.5	41.5

Clusters thresholded at a cluster-level threshold of P < 0.05 with a minimum of 100 contiguous voxels, and at a voxel-level threshold of P < 0.05, t = 2.13 (corrected). Coordinates indicate the maximum intensity voxel for that cluster in Talairach and Tournoux space. The first Brodmann area listed corresponds to the location of the maximum intensity voxel. If the cluster extended into other Bas, those are also listed (see text for details).

4.5 Discussion

4.5.1 Behavioral findings

Although the behavioral results from the pilot experiment did not completely replicate those in the scanner, the overall pattern between the two was similar (see tables 3 and 4). Any differences are likely attributable to the scanning environment. In particular, it was more difficult for subjects to look at the stimuli and overtly name the pictures while lying down. Additionally, the scanner noise made it more difficult to analyze the naming latency data, likely resulting in less consistent measurements. It is the case that the two experiments differed in the presence of a familiarization phase in the scanner and its absence in the behavioral pilot experiment. However, previous studies using PWI have shown that the presence or absence of a familiarization phase did not change the overall patterns of results (Caramazza & Costa, 2001; de Zubicaray et al., 2001).

Taken together, the behavioral results were similar to those in the literature showing that semantically related distractors produce increased naming latencies (Lupker, 1979; de Zubicaray et al., 2001; Glaser & Dungelhoff, 1984; Lupker, 1979; Starreveld & La Heij, 1996), while phonologically related distractors produce faster naming latencies (de Zubicaray et al., 2002; Damian & Martin, 1999; Jescheniak & Schriefers, 2001;Lupker, 1982 Starreveld & La Heij, 1996). Moreover, both mediated conditions showed faster naming latencies compared to the unrelated condition.

These findings provide strong support in favor of fully interactive models of language processing (Dell et al., 1997). They show that competition is an inherent property of the grammar and that competitors are activated implicitly and affect spoken word production.

Of critical importance, the source of the competition, i.e. whether it is conceptual/semantic or lexical/phonological, and the direction of information flow have different consequences on naming latencies.

In the PWI paradigm, both a target picture and a word distractor are presented. The picture activates the conceptual representation of the word and then activation spreads to the lexical level and the phonological level. The words, in contrast, first activate the sound shape of the word and this information presumably activates in turn its lexical/semantic network. Across all three levels of processing (conceptual, lexical, phonological) activation is never limited to the nodes representing the specific input, but spreads within levels and cascades between levels. Of importance, all competitor conditions show interference effects relative to the baseline condition. Thus, both direct and mediated competition creates interference over naming in isolation, but they do so in different ways.

Direct semantic competition (tiger-lion) creates interference at the conceptual level owing to the activation of two words that are semantically/conceptually associated with each other. In contrast, direct phonological competition (e.g. hammock-hammer) creates facilitation at the phonological level owing to the shared phonological properties and hence converging activation of their onsets.

The mediated conditions create competition at both conceptual and phonological levels but in different ways (see figure 12 for a simplified model of these conditions). In the case of the mediated phonological-semantic condition (e.g. hammock-nail), the conceptual/semantic representation of the picture activates its lexical and phonological form (hammock), which in turn activates the lexical form of those words, which share

phonological properties with it, in this case phonological onsets (/hammer/). This phonological information cascades bottom-up to the semantic/conceptual level activating the representation of the word (hammer) and its lexical semantic network (e.g. nail), creating competition between the target picture, hammock, and the word distractor, nail.

In contrast, in the mediated semantic/phonological condition (e.g. lion-tire), the conceptual/semantic representation of the picture (lion) activates its semantic/conceptual representation, which in turn partially activates its lexical/semantic network. The activation of the semantic/conceptual representation of its semantic associate, in this case tiger, activates its lexical/phonological form which in turn activates those lexical entries which share phonological properties with it, in this case onsets (e.g. tire), creating competition between the target picture, lion, and the word picture, tire.

The relationship between target and distractor in the two mediated condition would suggest different behavioral outcomes. Facilitation in the PS (hammock-nail) condition results from the partial activation of a semantic associate of the distractor (e.g. *hammer*), which, in turn, boosts the activation of the phonological codes that it shares with the target (*hammock*), thus facilitating access to phonetic plans for articulation. In this condition, the majority of the competition is present at the phonological level. However, the absence of the overt presence of the competitor results in overall less activation of the competitor and as a consequence in smaller demands on selection compared to the direct phonological condition. Moreover, in this condition there is no competition at the conceptual level, because the conceptual representations activated by the distractor (nail) are not semantically associated with the target (hammock). Overall, this condition should produce the least amount of competition.

In contrast in the mediated semantic-phonological condition (e.g. *lion-tire*) the distractor activates phonological codes that are partially shared with those associated with a semantic competitor of the target (e.g. *tiger*), also leading to facilitation in naming responses. However, in contrast to the PS condition, the distractor (e.g. tire) boosts the activation of its lexical competitor, tiger, which is semantically related to the target (e.g. lion), leading to increased competition between lion and tire. This boost in activation of the target results in greater selection demands than those in the PS condition resulting in slower naming latencies for the SP condition. However, because the semantic competitor of the target is activated implicitly, it will also slightly boost the activation of the target itself, in a manner analogous to what is observed in semantic priming. Thus, naming latencies in the SP condition are still faster than those produced in the unrelated condition.

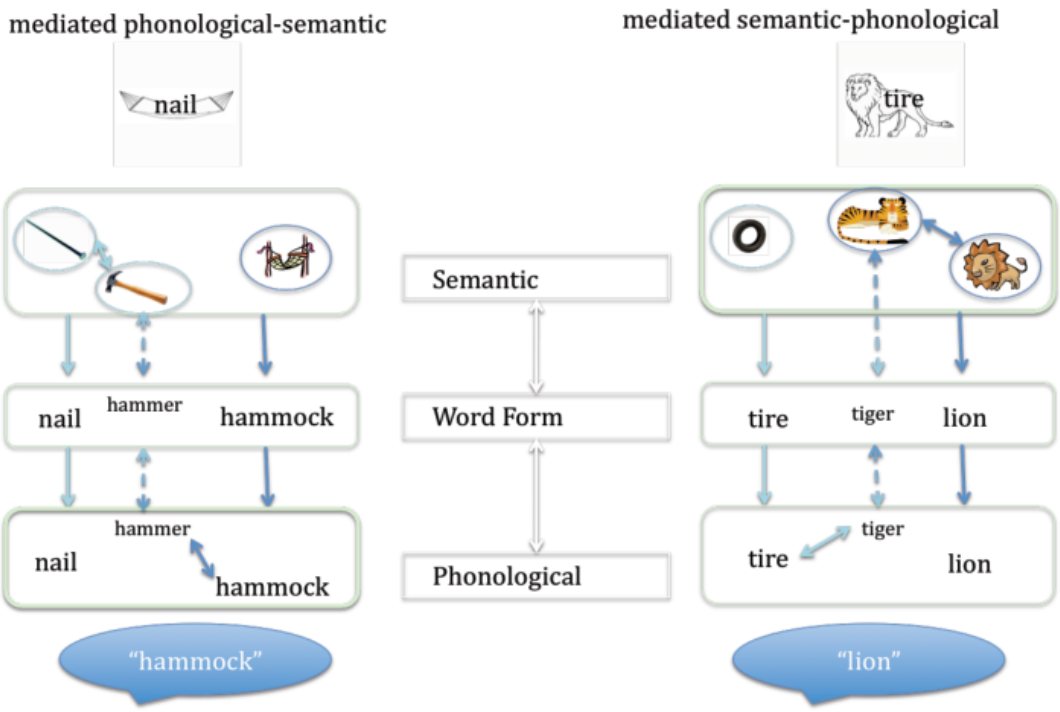

Figure 12. Simplified diagram of processed underlying mediated competition.

4.5.2 The effects of competition on neural structures

4.5.2.1 The influence of response conflict

The first analysis of the neuroimaging data computed a contrast between unrelated and baseline conditions, and was designed to isolate brain regions that were responsive to response conflict in the absence of any specific type of competition. In other words, this contrast highlighted regions that are sensitive solely to the presence of two conflicting representations, and are not dependent on there being a relationship between them.

This comparison produced clusters of activation both in posterior temporal and prefrontal cortices (see table 5). A large cluster of activation was present in ventral temporal cortex, in areas associated with object processing. Activation in these regions is

commonly associated with the recognition of objects and words (Grill-Spector et al., 1998; James et al., 2003; McCandliss et al., 2003; Indefrey & Levelt, 2004), thus it is not surprising that the simultaneous presentation of an object and a word elicited more activation than an object and a string of characters. Response conflict also produced increased activation in the left posterior parietal cortex and prefrontal cortex (see figure 9). In the parietal cortex, activation was found in the left SPL and IPL. Previous studies using tasks that create response conflict such as the flanker or Stroop tasks have also reported increased activation in this region under conditions of conflict among multiple potential responses, and it has been suggested that this increase in activation might reflect the need to keep in working memory the multiple response alternatives (Bunge et al., 2002; Casey et al., 2000; Hazeltine et al., 2000; Milham et al., 2001). Thus, the increased activation found in the left parietal region in the present case of response conflict could result from the maintenance of both target and distractor representations while the subject is preparing to make a response.

Activation in the prefrontal cortex was found primarily within the mid portion of the left IFG and the middle frontal gyrus. An influential proposal suggests that the left IFG is recruited under conditions that require response selection because of competition among conceptual representations (Thompson-Schill et al., 1997). Activation in prefrontal cortex is also commonly found when studies employ tasks that involve response conflict, such as the Stroop task (see Duncan & Owen, 2000 for a review). In a recent study Van Veen and colleagues (2005) used a variation on the Stroop task to disentangle the contribution of competition created by the semantic relationship between target and distractor from the contribution of response conflict, which is created because target and distractor lead to

different motor responses. They compared the patterns of brain activation between a condition that included both semantic competition and response conflict and a condition that included only semantic competition. In this analysis they found increased activation in the left IFG and middle frontal gyrus for response conflict (Van Veen et al., 2005). These authors suggested that this portion of the IFG might be specifically sensitive to response conflict, and not to semantic competition (Van Veen et al., 2005). Thus, the results of the present study provide further evidence for the sensitivity of the mid portion of left IFG for response conflict, even in the absence of competition. Thus, this portion of the IFG could implement a mechanism that is sensitive to the fact that multiple response alternatives have been activated and a single one has to be selected, and does not depend on the specific relationship between the competing representations. A more in-depth discussion of the role of the IFG under conditions and conflict and competition will be provided in subsequent sections.

4.5.2.2 The influence of competition in temporal and parietal regions

By comparing each of the five conditions that included both competition and response conflict with the condition that used unrelated distractors we were able to find brain regions that were sensitive to each specific type of competition. The results of this analysis showed that competition at both the semantic and phonological level recruits left temporo-parietal regions during word production (see tables 6a and 6b). Moreover, these results also showed that the recruitment of these regions is not dependent on the overt presentation of both targets and competitors, as mediated competition also elicited significant activation in these regions. More specifically, phonological, semantic, and

mediated semantic-phonological competition elicited activation in left angular gyrus (AG) and inferior parietal lobule (IPL), and these clusters of activation were largely overlapping as it can be seen in figure 13. Phonological-semantic competition also elicited clusters of activation in this region, but these clusters were too small to survive correction for multiple comparisons.

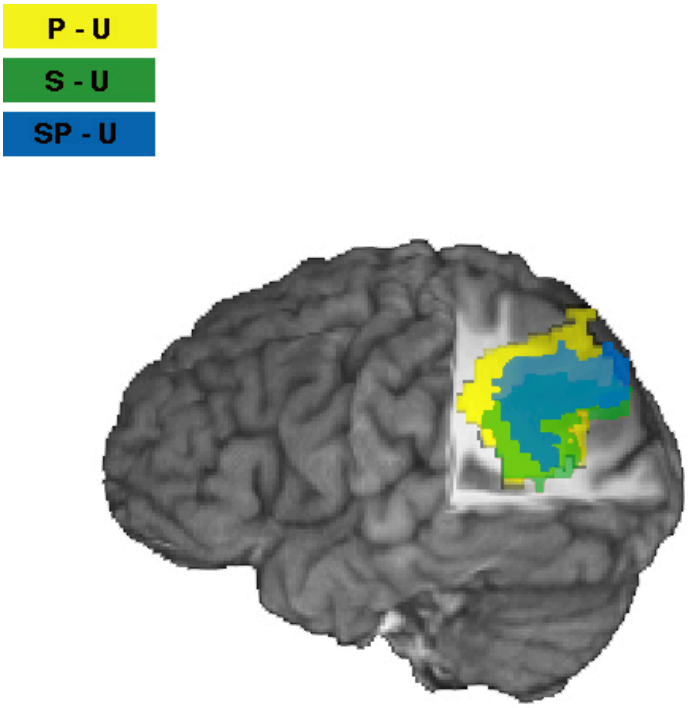

Figure 13. Significant clusters of activation in the left posterior parietal/temporal region for the following contrasts: P-U, S-U, SP-U. The clusters shown were significant at a voxel-level threshold of $p<0.05$ and a cluster-level threshold of $p<0.05$. Sagittal slice taken at x = 15, coronal slice taken at y = 30, axial slice taken at z = 10

As mentioned in the previous section activation in the inferior parietal lobe has been associated with the representation of potential responses in tasks that create response interference (e.g. Banich et al., 2001; Bunge et al., 2002; Casey et al., 2000; Hazeltine et al., 2000; Milham et al., 2001). The increase of activation observed in this region under conditions of competition could suggest that this it is sensitive to the strength of activation that the multiple potential responses are receiving, as under conditions of competition the relationship among targets and distractors is such that they provide one another with partial activation. Moreover, the partial overlap among the clusters of activation across the various conditions of competition could suggest that this region is not sensitive to the linguistic domain in which competition is created.

Only direct phonological competition elicited activation that also extended into the left supramarginal gyrus (SMG), and only direct semantic competition elicited activation in the anterior /mid middle temporal gyrus (MTG). This dissociation also surfaced when direct phonological and semantic competition were compared to one another, showing more activation for phonological competition in posterior inferior parietal regions, while the anterior MTG showed more activation for semantic competition (see figure 11a).

In the literature the MTG is suggested to be sensitive to semantic knowledge and semantic manipulations (e.g. Friederici et al., 2000; Indefrey & Levelt, 2004; Price et al., 1997; Price, 2000), while the SMG has been associated with phonological processing and phonological working memory (Caplan et al., 1995; Hickok et al., 2003; Paulesu et al., 1993). Previous studies of word production under conditions of competition have also found a similar dissociation depending on the domain in which competition was created. Two recent studies using PWI under conditions of semantic competition found increased

activation in the left MTG (Abel et al., 2008; de Zubicaray et al., 2001). Alternatively recent studies of word production under conditions of phonological competition found increased activation in the left SMG (Abel et al., 2008; Bles & Jasma, 2008; de Zubicaray et al., 2002). Thus, the present results provide further evidence for the domain specificity of the SMG and the MTG under conditions of competition during word production.

To summarize, the present results showed that different types of competition all recruited brain regions in the left inferior parietal region that that are commonly associated with representing multiple response alternatives. These regions could be recruited because of the increased activation that target and distractor representations are receiving because of their relationship with one another. Moreover, these regions might not be sensitive to the specific relationship between target and distractor, but simply to the strength of activation of these multiple representation. Alternatively, other regions, namely the MTG and SMG, responded to domain-specific competition, and might be sensitive to the specific direct relationship between targets and distractors.

4.5.2.3 The Influence of Competition in Prefrontal Cortex

Activation in the left inferior frontal gyrus (IFG) was present in all of the competition conditions, with the exception of the phonological-semantic competition condition (although activation was seen in the PS condition when uncorrected). This result supports previous findings showing that the left IFG is sensitive to competition across both semantics and phonology (Gold et al., 2005; Gold & Buckner, 2002; Roskies et al., 2001; Poldrack et al., 1999; Snyder et al., 2007;), and also showing that it is sensitive to both direct and mediated competition (Righi et al., in preparation). However, the different

conditions produced varying extents and amounts of activation in this region (see figure 10), suggesting that despite an overall sensitivity to competition, there are differences in terms of the role that different portions of the IFG might be playing.

Direct phonological competition elicited significant activation in the posterior and mid portions of the IFG (BAs 44 and 45) and in the precentral gyrus, only marginally extending into the most anterior portion of it (BA 47). In contrast, direct semantic competition elicited significant activation in BA 47, and only marginally in BA 45. When phonological and semantic competition were compared directly, the results revealed that former produced higher levels of activation in BA 44 and 45, but no reliable statistical difference was observed in the more anterior portion of the IFG. The two mediated conditions also produced activation in the left IFG: semantic-phonological competition produced activation in BA 46,45 and 47, while phonological-semantic activation was found in BA 45. When compared directly, semantic-phonological competition produced more activation than phonological-semantic competition primarily within BA 45 and 46.

Taken together these results showed that all conditions of competition elicited increased activation within BA 45, and as it can be seen in figure 10, but that semantic competition both mediated and direct showed increased activation in BA 47, while phonological competition showed activation primarily in BAs 44 and 45. It is important to note that phonological-semantic competition produced the weakest activation in the IFG, and despite the fact that in this condition competition was present primarily at the phonological level, no activation was found in BA 44. This could just be the result of the relative weakness of the competition created in this condition.

Several proposals have been put forth describing the role of the left IFG under conditions of competition. Thompson-Schill and colleagues have suggested that the left IFG is recruited when multiple task-irrelevant semantic representations become activated, and act as a response selection mechanism (Thompson-Schill et al., 1997; 1998; 1999). More recently they showed that the recruitment of this region takes place during both semantic and phonological processing under conditions of conflict that produce the activation of multiple conceptual representations, thus suggesting that it is not the level of processing that recruits the IFG but rather the increase in competition among conceptual representations (Snyder et al., 2007). Alternatively, other studies have shown differential responses between the more anterior and posterior portion of the IFG in response to semantic and phonological competition, respectively (Bokde et al., 2001; Burton et al., 2003; Poldrack et al., 1999), suggesting domain-specific responses to competition within the left IFG. A recent proposal has suggested that the left IFG might be subdivided on the bases of different functional mechanisms. More specifically, Badre & Wagner (2007) have suggested that the more anterior portion of the IFG is involved in the retrieval of multiple semantic representations, while the mid portion of the IFG is specifically involved in selection among these retrieved representations.

The results of the present study are in agreement with Thompson-Schill's proposal of the IFG as a response selection mechanism recruited when multiple representations are activated. Nevertheless, the present results suggest that within the IFG the most anterior portion is more sensitive to semantic competition, while the more posterior portion is more sensitive to phonological competition, as BA 47 showed stronger activation for semantic competition while BA 44 was activated primarily by phonological competition.

Further evidence of this potential dissociation during word production has been provided by previous studies using paradigms similar to the one employed in the current study. Using a PWI task with semantic interference de Zubicaray and colleagues (2001) found increased activation in the more anterior portion of the IFG, extending into the middle orbital gyrus under semantic competition. Few other studies using naming under conditions of semantic competition also found increased activation in the more anterior portion of the IFG (Abel et al., 2008; Moss et al., 2005). A recent study in which subjects were presented with pictures of two objects that could be either phonological competitors or unrelated and had to attend to the phonological properties of only one of the two objects, reported increased activation in the posterior IFG (Bles & Jasma, 2008). Thus these previous findings and the present ones would provide further evidence for sensitive to the linguistic type of competition within different subdivions of the IFG.

It is important to mention that two recent studies using PWI and phonologically related distractors failed to find significant activation in the posterior IFG (Abel et al., 2008; de Zubicaray et al., 2002). However, there were some important differences between these two studies and the current one. De Zubicaray and colleagues (2002) used visual distractors, but they mixed phonological and orthographic similarity, such that distractor words were phonological competitors like the ones used in the present experiment only in very few of their trials, while in the majority of trials the distractor words shared orthographical onset with the target name, but not the phonological onset. Abel and colleagues (2008) used auditory distractors instead of visually presented distractors and presented the image 200ms after the onset of the auditory word. Thus, the failure to find activation in the left IFG under phonological competition might be the

result of the specific methodological differences between these two studies and the one presented here.

Despite the fact that the present findings are in agreement with a domain-specific organization of the IFG, they also suggest that BA 45 might be playing a slightly different role compared to BAs 44 and 47. First of all, BA 45 was shown to respond to response conflict in the absence of competition, as it was shown by comparing the unrelated condition to naming without distractors. Secondly all competition conditions produced increased activation in BA 45 when compared to the unrelated condition. Thus this portion of the IFG could be specifically involved in selecting among various types of competing representations, as it has been suggested by Badre & Wagner (2007). The present results would suggest that the recruitment of this region is not dependent on there being a specific relationship among activated representations, but the increase in activation found under conditions of competition suggest that its recruitment might be modulated by the selection demands imposed by a specific task-context. That is, this region responds even when selection demands are created simply because of response conflict, but it will respond more strongly under conditions of competition because the relationship between targets and distractors requires a more effortful selection of the appropriate response.

To summarize, the present results support previous findings showing that the left IFG is recruited under conditions that require response selection. Nevertheless, they also provide evidence for a subdivision within the IFG into a domain-general response selection mechanisms that is recruited under conditions of both response conflict and

competition, and domain-specific components that are sensitive to the specific type of competition introduced, regardless of whether it is direct or mediated.

4.5.2.4 The Influence of Competition in the Anterior Cingulate Cortex

Despite the presence of conflict between targets and distractors across all conditions, only competition at the semantic level elicited activation in the anterior cingulate cortex (ACC). This finding is in agreement with results from previous studies that have utilized the Stroop paradigm in fMRI and have shown increased activation in the ACC under conditions of conflict created by semantic interference (Banich et al., 2001; Casey et al., 2000; Milham et al., 2001; Peterson et al., 1999; Roelofs et al., 2006; Van Veen et al., 2005). Moreover, utilizing a PWI task de Zubicaray and colleagues found increased activation in the ACC under conditions of semantic competition (de Zubicaray et al., 2001), but not in the presence of phonological competition (de Zubicaray et al., 2002).

Several proposals regarding the role of the ACC in executive function have been put forth. The ACC is suggested to play a role as a conflict monitoring mechanism (Miller & Cohen, 2001). Barch and colleagues have expanded this original proposal suggesting that the ACC is recruited when response conflict is present and it is specifically important in situations when subjects need to overcome "prepotent response tendencies" (Barch et al., 2000; Botvinick et al., 2001). Others have suggested that the ACC might play a regulatory function under conditions of conflict (Posner & Rothbart, 2007; Roelofs & Hagoort, 2002; Roelofs et al., 2006). That is, it has been proposed that the ACC acts on the representations that have been activated by a specific task and serve to enhance to activation of the most appropriate among the set of active representations.

These theories make slightly different predictions, with regard to how the ACC would respond to situations of conflict in naming. The conflict-monitoring hypothesis predicts that the ACC will show increased activation when response alternatives are overtly present. The prepotent-response hypothesis suggests that increased activation in the ACC is observed under conditions of conflict between responses, but across similar levels of competition the ACC will show increased activation if a strong response has to be repressed compared to when a less strongly associated response has to be repressed. Alternatively, the regulatory function hypothesis predicts that the ACC will show the most activation when response alternatives are overtly present, but compared to naming in isolation, it will show a decrease in activation if target and distractor are congruent.

In the present experiment the increased activation found in the ACC under conditions of semantic competition could be the result of the need to suppress the reading the distractor, as in this condition the distractor represents a task-appropriate response. No activation in the ACC is found under all other conditions of competition because in all of those cases the distractor is never a viable alternative for the target. Thus, the present result would support a view of the ACC as a conflict detection mechanisms that is specifically sensitive to the relationship among potential responses, such that it responds more strongly when targets and distractors both represent viable response alternatives (Barch et al., 2000; Botvinick et al., 2001).

4.5.2.5 Conclusions

In the present study we have shown that both direct and mediated competition during word production recruits both posterior temporo-parietal and prefrontal regions, primarily

in the left hemisphere. The middle temporal gyrus and posterior portion of the superior temporal sulcus respond selectively to semantic and phonological competition when it is created by presenting directly related target-distractor pairs. Alternatively, inferior parietal regions are sensitive both to competition and response conflict, suggesting that they might be sensitive to the activation of multiple representations elicited by the presentation of incongruent target-distractor pairs. Moreover, this region does not seem to be sensitive to the linguistic domain manipulated, but rather to the strength of the activated representations.

Competition, both direct and mediated, and response conflict also produced significant activation in the left inferior frontal gyrus (IFG). However, within this region, different patterns of responses were observed across conditions. The mid portion of the IFG, roughly corresponding to BA 45, might be responding to the need to select an appropriate response in the presence of incongruent target-distractor pairs. However this region is even more heavily recruited under conditions of both direct and mediated competition as they create increased selection demands. The present results also suggest that the resolution of semantic competition relies on the anterior portion of the inferior frontal gyrus and the anterior cingulate, while the resolution of phonological competition relies primarily on the posterior and mid inferior frontal gyrus.

5. CHAPTER 5: Conclusions

The experiments presented in this dissertation were designed to further the current understanding of how neural structures respond to different types of competition (i.e. semantic vs. phonological), whether the amount of competition (i.e. direct vs. mediated) results in quantitative or qualitative changes in the recruitment of these structures, and how the specific task (i.e. comprehension vs. production) affects which regions are sensitive to competition.

Experiment 1 used a combined eye tracking and fMRI paradigm to study the neural basis of phonological competition during word comprehension. In this experiment subjects were given the name of a target object auditorily and they had to locate it in a visual display that contained four objects. Competition was created by presenting the target (e.g. *hammock*) with its phonological onset competitor (e.g. *hammer*) and 2 phonologically and semantically unrelated distractors. Experiment 2 also used a combined eye tracking and fMRI paradigm to study whether neural structures that were sensitive to the competition created by overtly presenting competitors also responded to mediated competition, i.e. competition in the absence of direct competitors in the visual array. Analogous to Experiment 1, subjects were presented with the name of a target object auditorily and they had to locate it in a visual array that contained four objects. Mediated competition was created by the presenting the target (e.g. *hammock*) in a visual display that contained a semantic associate of the phonological competitor of the distractor (e.g. *nail*) and two other distractor stimuli, which were semantically and phonologically unrelated to the target and competitor.

While Experiments 1 and 2 focused on competition during word comprehension, Experiment 3 investigated the neural structures recruited by different types of competition during word production. Subjects were presented with line drawings of common objects and were asked to name them. Competition was created by introducing written word distractors that were presented simultaneously with the object. These distractors were either semantically or phonologically related to the target objects, and this relationship was either direct, as it was the case in Experiment 1, or mediated, as it was the case in Experiment 2.

Overall, all three studies showed that competition and its resolution recruit a similar network of areas in the posterior tempo-parietal and prefrontal cortices, mostly left-lateralized. This network of regions is recruited when competition is both overt and covert, albeit with different strength of responses. Finally, the present findings show that similar areas were recruited for both word comprehension and word production under conditions of competition.

5.1 Competition in temporo-parietal regions

Competition recruited posterior temporo-parietal regions both during comprehension and production. These regions are commonly found activated in studies using tasks that produce competition and/or interference among potential responses. In Experiment 1 looking for a target object in the presence of its phonological onset competitor recruited the supramarginal gyrus (SMG) and inferior parietal lobule (IPL). In Experiment 2 looking for a target object in the presence of its semantic onset competitor, i.e. in the presence of an object semantically related to a phonological onset competitor of the target

also recruited the SMG and IPL. There was, however, a slight difference in the distribution of activation across the two studies. While in Experiment 1 activation was primarily located within the SMG, in Experiment 2 activation was located primarily the IPL, but extended into the SMG.

In the literature the inferior parietal region, which included the SMG and the IPL, has been associated with the maintenance of information during tasks that require an evaluation of several response options (see Corbetta & Shulman, 2002 for a review). It has been proposed that the SMG is involved in the storage and analysis of phonological information (Awh et al., 1996; Gold & Buckner, 2002; Gold et al., 2005; Hickok et al., 2003; Paulesu et al., 1993; Price et al., 1997; Ravizza et al., 2004). A recent study also found increased activation in the SMG during a lexical decision task when subjects were presented with words that shared sound structure with many other words (Prabhakaran et al., 2006). The increase in activation in the SMG found in Experiments 1 and 2 under conditions of phonological competition provides further evidence for the recruitment of this area when multiple phonological forms become active. Moreover, the present results show that this region is recruited when phonological processing is controlled, as it is the case when words pairs have to be directly evaluated or syllables have to be counted, but also when multiple phonological forms are automatically and implicitly retrieved as is the case during word comprehension. Lastly, the present results show that the recruitment of this region takes place regardless of whether phonological competitors are overtly presented in a task context or not, even though this region responds more strongly when multiple phonological forms are overtly present.

While the SMG has been suggested to be recruited for phonological processing, the IPL has been found to be recruited both when subjects are making phonological judgments on words (McDermott et al., 2003) and when subjects are making explicit semantic judgments (Dapretto & Bookheimer, 1999; Demonet et al., 1992). Given that in Experiment 1 competition was purely phonological and in Experiment 2 both phonology and semantics came into play, it is not surprising that the patterns of activation observed differ slightly in the extent of the recruitment of the SMG and IPL respectively.

The results of Experiments 1 and 2 show that during word comprehension under conditions of competition posterior regions that are sensitive to the linguistic domain in which competition is created are recruited. Moreover, these regions are analogous to those involved in the resolution of competition not only in pointing to a picture but also when the judgments required are metalinguistic in nature (i.e. lexical decision, vowel judgment, syllable count, etc.).

Experiment 3 revealed similar regions sensitive to competition in Experiments 1 and 2. More specifically, when subjects were naming objects with their phonological onset competitors presented as distractors activation was observed in the IPL and SMG. The other competition conditions, all of which involved phonological competition induced in different ways, also revealed areas of activation in proximal regions. In particular, both semantic and mediated semantic-phonological distractor conditions elicited increased activation in the IPL. The only exception was the mediated phonological semantic condition, which elicited very weak activation in this region that did not survive statistical correction for multiple comparisons. The failure of this condition to elicit parietal activation is likely due to the fact that the mediated

phonological competitor boosted the activation of the target, thus reducing the extent of competition in the stimulus array.

Beyond the IPL and the SMG, competition in Experiment 3 elicited activation in the middle temporal gyrus (MTG) under conditions of direct semantic competition, and in the angular gyrus (AG) across all conditions of competition except for mediated phonological semantic competition. The MTG is typically recruited in tasks requiring semantic processing (Hickok & Poeppel, 2004; Indefrey & Levelt, 2004; Price, 2000). Thus, it is not surprising to find that this region responded more strongly to semantic competition, compared to all other conditions. The AG has been given a domain-general role as previous studies have shown that this region is recruited in accessing the names of objects, and, as well in reading the visual forms of words (Mechelli et al., 2003; Price, 2000). Thus, the activation found in this region could simply be the result of nature of our stimuli and the present task.

Overall, the areas of activation that were sensitive to competition were similar across both comprehension and production. Moreover, the same regions responded to both direct and mediated competition, with differences inn strength of response modulated by the extent of competition. Some regions, namely the SMG and the MTG seem to be specifically sensitive to the domain of competition regardless of the task. Other regions, namely the IPL, appears to be more of a domain-general mechanism that supports the retrieval of multiple representations while the subject is in the process of choosing the appropriate one This interpretation regarding the role of the IPL finds support from studies using interference tasks such as the Stroop and the Flanker task, which consistently find activation in the IPL under conditions of competition among multiple

potential responses (Banich et al., 2001; Bunge et al., 2002; Casey et al., 2000; ; Hazeltine et al., 2000; Milham et al., 2001).

5.2 Competition in the prefrontal cortex

The role of prefrontal cortex under conditions of competition has been at the center of the work presented in this dissertation. Numerous studies have found increased activation in the IFG under conditions that increased selection demands during both comprehension (e.g. Bedny et al., 2008; Snyder et al., 2007; Thompson-Schill et al., 1997; 1999;) and production (e.g. Kan & Thompson-Schill, 2004; Spalek & Thompson-Schill, 2008; Moss et al., 2005; Thompson-Schill et al., 1997). The results of all three experiments provide further evidence confirming the involvement of the ventrolateral portion of prefrontal cortex, specifically the inferior frontal gyrus (IFG), under conditions of competition both during word comprehension and word production.

To my knowledge, Experiment 1 was the first experiment to show that competition driven solely by phonological similarity elicited activation in the left IFG when subjects were not asked to perform any specific judgment on the experimental stimuli themselves, but were asked to find a specific object in the visual display. Experiment 2 extended this initial finding showing that the left IFG is recruited even when phonological competition is created in a mediated manner with no direct competitors simultaneously present.

The results of the two experiments showed that even though both types of competition recruit the IFG, activation in this region appears to be modulated by the amount of competition created. In particular, weaker responses were elicited when competition was mediated than when it was overt. Moreover, the results of the two

experiments suggest potentially different functional roles for portions of the IFG. In Experiment 1 competition elicited significant activation in three non-overlapping clusters, with the largest one being located in the more posterior portion of the IFG (~BA44/45), the second largest located within the mid portion (~BA45), and the third largest located in the more anterior portion (~BA47). In Experiment 2, competition elicited significant activation in the more anterior and posterior portions of the IFG, while activation in the mid portion showed a positive relationship with a behavioral measure of competition. That is, the individual differences in the extent to which competition affected the performance of individual subjects correlated positively with neural sensitivity to competition.

The differences between the results of Experiments 1 and 2 are in agreement with proposals suggesting that different portion of the IFG, roughly corresponding to its constituent Brodmann areas are sensitive to different aspects of competition. Previous studies have suggested two potential functional organizations within the left IFG. A domain-specific hypothesis has suggested that the more anterior portion of the IFG is more sensitive to controlled semantic processing, while the more posterior portion is more sensitive to controlled phonological processing (Bokde et al., 2001; Buckner et al., 1995; Burton et al., 2003; Poldrack et al., 1999; Wagner et al., 2001). In contrast, Badre and Wagner (2007) have suggested that BA 47 is involved in the controlled retrieval of semantic representations that are relevant for the task at hand, BA 45 is primarily involved in selecting among these retrieved representations, and BA 44 is associated with the representation of potential responses.

In light of these theories, the results of Experiments 1 and 2 suggest that during word comprehension BA 45 is responding to the increased demands for selection created by the introduction of competition, as its response to competition is modulated by the extent to which competition affects the responses of individual subjects. The activation of the more anterior and posterior portions of the IFG appears to reflect the retrieval of multiple representations that are related to the target object. Unfortunately, the lack of a pure semantic condition in the two experiments does not allow for providing evidence as to whether anterior and posterior portions of the IFG are specifically sensitive to semantics and phonology, respectively.

Experiment 3 was designed to test similar hypotheses to Experiments 1 and 2 in word production, thus allowing for the further elucidation of the role of the IFG under conditions of competition. The results of Experiment 3 showed that the IFG was recruited under both direct and mediated semantic and phonological competition in spoken word production, as it is in auditory word comprehension. Analogous to Experiments 1 and 2, the IFG showed increased activation under conditions of direct competition compared to mediated competition. Nevertheless, there were differences in the patterns of activation within the IFG across conditions, providing further evidence that the IFG is a functionally heterogeneous region. In particular, differences in activation patterns were observed between direct semantic and direct phonological competition. Phonological competition recruited a large portion of the IFG that included BA 44 and 45, and only marginally recruited BA 47. In contrast, semantic competition produced activation primarily in BA 47 and 45, and not in BA 44. Thus, these results support the view that different areas of the IFG are recruited as a function of the linguistic domain (phonological or semantic)

with phonological competition recruits the more posterior portions of the IFG and semantic competition recruits the more anterior portions of the IFG. However, the fact that significant activation emerged within BA45 across all conditions suggests that a more general purpose mechanism, presumably a response selection mechanism (Badre & Wagner, 2007) is recruited to resolve competition across these domains.

5.3 Overall Conclusions

The goal of the studies presented in this dissertation was to examine the neural systems recruited under conditions of competition during language comprehension and production. These results showed that competition recruits a network of regions in the posterior temporo-parietal cortex and in the prefrontal cortex, and that these regions are recruited under both direct and mediated competition. The results of all three experiments also showed that analogous networks of regions were recruited during comprehension and production.

Of particular interest was the role of the inferior frontal gyrus under conditions of competition. The present experiments confirm the role of this region as a selection mechanism under conditions of competition, and showed that this region responds to competition across linguistic domains and also to both direct and mediated types of competition. Moreover, the present results provide further support for the functional heterogeneity of the left IFG. More specifically, BA 44 responded to competition created only by manipulating phonological factors. BA 47 responded to competition created by both phonological and semantic factors, but critically this domain-general response was achieved only when the experimental task required selection among conceptual

representations, as it was the case for both experiments 1 and 2. BA 45 showed increased activation across all conditions of competition, regardless of task and of response type. Thus, the present results are in agreement with Badre and Wagner's (2007) proposal suggesting that different functional mechanisms are implemented within the left IFG.

6. References

Abel, S., Dressel, K., Bitzer, R., Kümmerer, D., Mader, I., Weiller, C., et al. (2009). The separation of processing stages in a lexical interference fmri-paradigm. *Neuroimage*, *44*, 1113-1124

Allopenna, P. D., Magnuson, J. S., & Tanenhaus, M. K. (1998). Tracking the time course of spoken word recognition using eye movements: evidence for continuous mapping models. *Journal of Memory and Language, 38*, 419-439.

Altman, G. T. M., & Kamide, Y. (2004). Now you see it, now you don't: meditating the mapping between language and the visual world. To appear in J. Henderson & F. Ferreira (Eds). *The interface of language, vision, and action.* Psychology Press.

Awh, E., Jonides, J., Smith, E. E., Schumacher, E. H., Koeppe. R. A., Katz, S. (1996). Dissociation of storage and reharsal in verbal working memory. *Psychological Science, 7,* 25-31.

Badre, D., & Wagner, A. W. (2004). Selection, integration, and conflict monitoring: assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron, 41*, 473-487.

Badre, D., & Wagner, A. W. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia, 45*, 2883-2901.

Banich, M. T., Milham, M. P., Jacobson, B. L., Webb, A., Wszalek, T., Cohen, N. J., et al. (2001). Attentional selection and the processing of task-irrelevant information: Insights from fmri examinations of the stroop task. *Progressive Brain Research*, *134*, 459-470.

Barch, D. M., Braver, T. S., Sabb, F. W., & Noll, D. C. (2000). Anterior cingulate and the monitoring of response conflict: Evidence from an fmri study of overt verb generation. *Journal of Cognitive Neuroscience*, *12*, 298-309.

Barde, L. H., & Thompson-Schill, S. L. (2002). Models of functional organization of the lateral prefrontal cortex in verbal working memory: Evidence in favor of the process model. *Journal of Cognitive Neuroscience*, *14*, 1054-1063.

Bedny, M., McGill, M., & Thompson-Schill, S. L. (2008). Semantic adaptation and competition during word comprehension. *Cerebral Cortex*, *18*, 2574-2585.

Binder, J. R., & Price, C. J. (2001). Functional neuroimaging of language. In R. Cabeza & A. Kingstone (Eds.), *Handbook of functional neuroimaging* (pp. 187–251). Cambridge: MIT Press.

Bles, M., & Jansma, B. M. (2008). Phonological processing of ignored distractor pictures, an fmri investigation. *BMC Neuroscience*, *9*, 20-29.

Bokde, A. L. W., Tagamets, M. A., Friedman, R. B., & Horwitx, B. (2001). Functional interaction of the inferior frontal cortex during the processing of words and word-like stimuli. *Neuron*, *30*, 609-617.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Reviews of Neuroscience*, *25*, 151-188.

Botvinick, M. M., Carter, C. S., Braver, T. S., Barch, D. M., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Reviews*, *108*, 624-652.

Buchsbaum, B. R., Hickock, G., & Humphreys, C. (2001). Role of the left posterior superior temporal gyrus in phonological processing for speech perception and production. *Cognitive Science*, *25*, 663-678.

Buckner, R. L., Raichle, M. E., & Petersen, S. E. (1995). Dissociation of human prefrontal cortical areas across different speech production tasks and gender groups. *Journal of Neurophysiology, 74*, 2163-2173.

Bunge, S. A., Hazeltine, E., Scanlon, M. D., Rosen, A. C., & Gabrieli, J. D. E. (2002). Dissociable contributions of prefrontal and parietal cortices to response selection. *Neuroimage*, *17*, 1562-1571.

Burton, M. W. (2001). The role of inferior frontal cortex in phonological processing. *Cognitive Science*, *25*, 695–709.

Burton, M. W., Small, S. L., & Blumstein, S. E. (2000). The role of segmentation in phonological processing: An f MRI investigation. *Journal of Cognitive Neuroscience*, *12*, 679–690.

Caplan, D. & Waters, G.S. (1995). On the nature of the phonological output planning processes involved in verbal rehearsal: Evidence from aphasia. *Brain and Language, 48*, 191-220.

Caramazza, A. (1997). How many levels of processing are there in lexical access? *Cognitive Neuropsychology*, 14, 177-208

Caramazza, A., & Costa, A. (2000). The semantic interference effect in the picture-word interference paradigm: Does the response set matter? *Cognition*, *75*, B51-B64.

Caramazza, A., & Costa, A. (2001). Set size and repetition in the picture--word interference paradigm: Implications for models of naming. *Cognition*, *80*, 291-298.

Casey, B. J., Thomas, K. M., Welsh, T. F., Badgaiyan, R. D., Eccard, C. H., Jennings, J. R., et al. (2000). Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 8728-8733.

Costa, A., Caramazza, A., & Sebastián-Gallés, N. (2000). The cognate facilitation effect: Implications for models of lexical access. *Journal of Experimental Psychology: Learning, Memory, & Cognition: 26*; 1283-1296

Costa, A., Mahon, B., Savova, V., & Caramazza, A. (2003). Level of categorization effect: A novel effect in the picture-word interference paradigm. *Language & Cognitive Processes: 18*, 205-233

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201-215.

Costa, A., Alario, F. X., & Caramazza, A. (2005). On the categorical nature of the semantic interference effect in the picture-word interference paradigm. *Psychonomic Bulletin Review*, *12*, 125-131.

Cox, R. W. (1996). AFNI: Software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research*, *29*, 162–173.

Cox, R. W., & Hyde, J. S. (1997). Software tools for analysis and visualization of fMRI data. *NMR in Biomedicine*, *10*, 171–178.

Crinion, J. T., Lambon-Raph, M. A., Warburton, E. A., Howard, D., Wise, R. J. S. (2003). Temporal lobe regions engaged during normal speech comprehension. *Brain: 126;* 1193-1201.

Cutting, J. C., & Ferreira, V. S. (1999). Semantic and phonological information flow in the production lexicon. *Journal of Experimental Psychology: Learning Memory and Cognition*, *25*, 318-344

Dahan, D., Magnuson, J. S., Tanenhaus, M. K., & Hogan, E. M. (2001a). Subcategorical mismatches and the time course of lexical access: Evidence for lexical competition. *Language and Cognitive Processes, 16,* 507–534.

Dahan, D., Magnuson, J. S., & Tanenhaus, M. K. (2001b). Time course of frequency effects in spoken-word recognition: Evidence from eye movements. *Cognitive Psychology, 42,* 317–367.

Damian, M. F., & Martin, R. C. (1998). Is visual lexical access based on phonological codes? Evidence from a picture-word interference task. *Psychonomic Bulletin and Review*, *5*(1), 91-95.

Damian, M. F., & Martin, R. C. (1999). Semantic and phonological codes interact in single word production. *Journal of Experimental Psychology: Learning Memory and Cognition*, *25*, 345-361.

Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, *24*, 427-432.

Dell, G. S., Schwartz, M. F., Martin, N., Saffran, E. M., & Gagnon, D. A. (1997). Lexical access in aphasic and nonaphasic speakers. *Psychological Review*, *104*, 801-838.

Demonet, J. F., Chollet, F., Ramsay, S., Cardebat, D., Nespuolous, J. L., Wise, R., Rascol, A., Frackowiak, R. (1992). The anatomy of phonological and semantic processing in normal subjects. *Brain: 115:* 1753-1768.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193−222. |

de Zubicaray, G. I., Wilson, S. J., McMahon, K. L., & Muthiah, S. (2001). The semantic interference effect in the picture-word paradigm: An event-related fmri study employing overt responses. *Humam Brain Mapping*, *14*, 218-227.

de Zubicaray, G. I., McMahon, K. L., Eastburn, M. M., & Wilson, S. J. (2002). Orthographic/phonological facilitation of naming responses in the picture-word task: An event-related fmri study using overt vocal responding. *Neuroimage*, *16*, 1084-1093.

D'Esposito, M., Postle, B. R., & Rypma, B. (2000). Prefrontal cortical contributions to working memory: evidence from event-related fMRI studies. *Experimental Brain Research*, *133*, 3–11.

Duncan, J. (1998). Converging levels of analysis in the cognitive neuroscience of visual attention. *Philosophical Transcripts of the Royal Society of London B*, *353*, 1307−1317.

Duncan, J. (2001). An adaptive model of neural function in prefrontal cortex. *Nature Reviews Neuroscience*, *2,* 820-829.

Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neuroscience*, *23,* 475-483.

Eickhoff S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage, 25,* 1325-1335.

Eickhoff S. B., Heim, S., Zilles, K., & Amunts, K. (2006). Testing anatomically specified hypotheses in functional imaging using cytoarchitectonic maps. *Neuroimage, 32*, 570-582.

Eickhoff S. B., Paus, T., Caspers, S., Grosbras, M. H., Evans, A. C., Zilles, K., & Amuants, K. (2007). Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. *Neuroimage, 26,* 511-521.

Ferreira, V. S., & Griffin, Z. M. (2003). Phonological influences on lexical (mis)selection. *Psychoogical Science*, *14*, 86-90.

Fiez J. A. (1997). Phonology, semantics, and the role of the left inferior prefrontal cortex. *Human Brain Mapping, 5*, 79–83.

Friederici, A. D., Opitz, B., & von Cramon, D. Y. (2000). Segregating semantic and syntactic aspects of processing in the human brain: An fmri investigation of different word types. *Cerebral Cortex*, *10*, 698-705.

Gelfand, J. R., & Bookheimer, S. Y. (2003). Dissociating neural mechanisms of temporal sequencing and processing phonemes. *Neuron*, *38*, 831–842.

Glaser, W. R., & Dungelhoff, F. J. (1984). The time course of picture-word interference. *Journal of Experimental Psychology: Human Perception and Performance*, *10*, 640-654.

Gold, B. T., & Buckner, R. L. (2002). Common prefrontal regions coactivate with dissociable posterior regions during controlled semantic and phonological tasks. *Neuron, 35*, 803-812.

Gold, B. T., Balota, D. A., Kirchhoff, B. A., & Buckner, R. L. (2005). Common and dissociable activation patterns associated with controlled semantic and phonological processing: Evidence from FMRI adaptation. *Cerebral Cortex*, *15*, 1438-1450.

Grindrod, C. M., Bilenko, N. Y., Myers, E. B., & Blumstein, S. E. (2008). The role of the left inferior frontal gyrus in implicit semantic competition and selection: An event-related fmri study. *Brain Research*, *1229*, 167-178.

Hallet, P.E. (1986). Eye movements. In: K. Boff, L. Kaufman and J. Thomas (Eds.), *Handbook of perception and human performance* (pp. 10-1-10-112). New York: Wiley.

Hazeltine, E., Poldrack, R., & Gabrieli, J. D. E. (2000). Neural activation during response competition. *Journal of Cognitive Neuroscience*, *12*, 118-129.

Hickok, G., & Poeppel, D. (2000). Towards a functional neuroanatomy of speech perception. *Trends in Cognitive Sciences, 4*, 131-138.

Hickok, G., & Poeppel, D. (2004). Dorsal and ventral streams: A framework for understanding aspects of the functional anatomy of language: Towards a new functional anatomy of language. *Cognition*, *92*, 67-99.

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*, 393-402.

James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: An fmri study. *Brain*, *126*, 2463-2475.

Jescheniak, J. D., & Schriefers, H. (2001). Priming effects from phonologically related distractors in picture-word interference. *Quarterly Journal of Experimental Psychology, 54A*, 371-382.

Kan, I. P., & Thompson-Schill, S. L. (2004a). Effect of name agreement on prefrontal activity during overt and covert picture naming. *Cognitive Affective Behavioral Neuroscience*, *4*, 43-57.

Lupker, S. J. (1979). The semantic nature of response competition in the picture-word interference task. *Memory and Cognition*, *7*, 485-495.

Lupker, S. J. (1982). The role of phonetic and orthographic similarity in picture word interference. Canadian Journal of Psychology, 36, 349 376.

Luce, P. A., & Pisoni, D. B. (1998). Recognizing spoken words: the neighborhood activation model. *Ear and Hearing, 19*, 1-36.

La Heij, W., Starreveld, P. A., & Steehouwer, L. C. (1993). Semantic interference and orthographic facilitation in definition naming. *Journal of Experimental Psychology: Learning Memory and Cognition*, *19*, 352-368.

Levelt, W. J. M. (1999). Models of word production. *Trends in Cognitive Sciences*, *3*, 223-232.

Mahon, B. Z., Costa, A., Peterson, R., Vargas, K. A., & Caramazza, A. (2007). Lexical selection is not by competition: A reinterpretation of semantic interference and facilitation effects in the picture-word interference paradigm. *Journal of Experimental Psychology: Learning Memory and Cognition*, *33*, 503-535.

Marslen-Wilson, W., & Welsh, A. (1978). Processing interactions during word-recognition in continuous speech. *Cognitive Psychology, 10,* 29 – 63.

Marslen-Wilson, W. (1987). Functional parallelism in spoken word recognition. *Cognition, 25,* 71 – 102.

McCandliss, B. D., Cohen, L., Dehaene, S. (2003). The visual word form area: expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences: 7,* 293-299.

McClelland, J. L., & Elman, J. L. (1986). The TRACE model of speech perception. *Cognitive Psychology, 18,* 1–86.

McDermott, K. B., Petersen, S. E., Watson, J. M., & Ojemann, J. G. (2003). A procedure for identifying regions preferentially activated by attention to semantic and phonological relations using functional magnetic resonance imaging. *Neuropsychologia*, *41*, 293-303.

Mechelli, A., Gorno-Tempini, M. L., & Price, C. J. (2003). Neuroimaging studies of word and pseudoword reading: Consistencies, inconsistencies, and limitations. *Journal of Cognitive Neuroscience*, *15*, 260-271.

Mertus, J. A. (2002). *BLISS: The Brown Lab interactive speech system*. Providence, Rhode Island: Brown University.

Milham, M. P., Banich, M. T., Webb, A., Barad, V., Cohen, N. J., Wszalek, T., et al. (2001). The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Cognitive Brain Research*, *12*, 467-473.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24*, 167-202.

Miozzo, M., & Caramazza, A. (2003). When more is less: A counterintuitive effect of distractor frequency in the picture-word interference paradigm. *Journal of Experimental Psychology General*, *132*, 228-252.

Moss, H. E., Abdallah, S., Fletcher, P., Bright, P., Pilgrim, L., Acres, K., et al. (2005). Selecting among competing alternatives: Selection and retrieval in the left inferior frontal gyrus. *Cerebral Cortex*, *15*, 1723-1735.

Norris, D. (1994). Shortlist: A connectionist model of continuous speech recognition. *Cognition, 52,* 189–234.

Oldfield, R. C. (1971). The assessment and analysis of handedness: the Edinburgh Inventory. *Neuropsychologia, 9*, 97-113.

Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of the verbal component of working memory. *Nature, 362*, 342-345.

Peterson, B. S., Kane, M. J., Alexander, G. M., Lacadie, C., Skudlarski, P., Leung, H. C., et al. (2002). An event-related functional MRI study comparing interference effects in the Simon and Stroop tasks. *Cognitive Brain Research*, *13*, 427-440.

Peterson, R. R., & Savoy, P. (1998). Lexical selection and phonological encoding during language production: Evidence for cascaded processing. *Journal of Experimental Psychology-Learning Memory and Cognition*, *24*, 539-557.

Poldrack R. A., Wagner A. D., Prull M. W., Desmond J. E., Glover G. H., & Gabrielli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage, 10*, 15–35.

Posner, M. I., Rothbart, M. K., Sheese, B. E., Tang. Y. (2007). The anterior cingulate gyrus and the mechanism of self-regulation. *Cognitive, Affective & Behavioral Neuroscience: 7,* 391-395.

Prabhakaran, R., Blumstein, S. E., Myers, E. B., Hutchinson, E., & Britton, B. (2006). An event-related investigation of phonological-lexical competition. *Neuropsychologia*, *44,* 2209-2221.

Price, C., Moore, C. J., Humphreys, G. W., & Wise, R. J. S. (1997). Segregating Semantic from phonological processes during reading. *Journal of Cognitive Neuroscience, 9,* 727-733.

Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy*, *197*, 335-359.

Raposo, A., Moss, H. E., Stamatakis, E. A., & Tyler, L. K. (2006). Repetition suppression and semantic enhancement: An investigation of the neural correlates of priming. *Neuropsychologia*, *44*, 2284-2295.

Ravizza, S. M., Delgado, M. R., Chein, J. M., Becker, J. T., & Fiez, J. A. (2004). Functional dissociations within the inferior parietal cortex in verbal working memory. *Neuroimage*, *22*, 562-573.

Righi, G. Blumstein, S.E.B, Mertus, J., Worden, M.S. (in press). The neural systems underlying lexical competition: an eye tracking and fMRI study. *Journal of Cognitive Neuroscience, advanced online publications.*

Rissman, J., Eliassen, J. C., & Blumstein, S. E. (2003). An event-related FMRI investigation of implicit semantic priming. *Journal of Cognitive Neuroscience*, *15*, 1160-1175.

Roelofs, A., & Hagoort, P. (2002). Control of language use: Cognitive modeling of the hemodynamics of Stroop task performance. *Cognitive Brain Research*, *15*, 85-97.

Roelofs, A., van Turennout, M., & Coles, M. G. (2006). Anterior cingulate cortex activity can be independent of response conflict in Stroop-like tasks.. *Proceedings of the National Academy of Sciences of the United States of America*, *103*, 13884-13889.

Roskies, A. L., Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (2001). Task-Dependent modulation of regions in the left inferior frontal cortex during semantic processing.. *Journal of Cognitive Neuroscience*, *13*, 829-43.

Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: Convergent neuroimaging and neuropsychological evidence for the function of broca's area. *Proceedings of the National Academy of Sciences of the United States of America*, *1*(322-327).

Shalom, D. B., & Poeppel, D. (2007). Functional anatomic models of language: Assembling the pieces. *Neuroscientist*, *14,* 119-127.

Smith, E. E., & Jonides, J. (1999). Storage and executive processes in the frontal lobes. *Science*, *283*, 1657–1661.

Snodgrass, J. G., Vanderwart, M. (1980). A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Perception and Performance; 6;* 174-215.

Snyder, H. R., Feignson, K., & Thompson-Schill, S. L. (2007). Prefrontal cortical response to conflict during semantic and phonological tasks. *Journal of Cognitive Neuroscience*, *19*, 761-775.

Spalek, K., & Thompson-Schill, S. L. (2008). Task-Dependent semantic interference in language production: An fmri study. *Brain and Language*, *107*, 220-228.

Spitsyna, G., Warren, J. E., Scott, S. K., Turkheimer, F. E., & Wise, R. J. (2006). Converging language streams in the human temporal lobe. *Journal of Neuroscience*, *26*, 7328-7336.

Starreveld, P. A., & La Heij, W. (1996). Time course analysis of semantic and orthographic context effects in picture naming. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 22,* 896 -918.

Starreveld, P. A., & La Heij, W. (1995). Semantic interferen-ce, orthographic facilitation and their interaction in naming tasks. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21,* 686-698.

Spivey-Knowlton, M. K. (1996). *Integration of visual and linguistic information: Human data and model simulations.* Unpublished Ph. D. thesis, University of Rochester, Rochester, NY.

Tanenhaus, M. K., Spivey-Knowlton, M. J., Eberhard, K. M., & Sedivy, J. C. (1995). Integration of visual and linguistic information in spoken language comprehension. *Science, 268***,** 1632 – 1634.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of the inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proceedings of the National Academy of Sciences of the United States of America, 94,* 14792-14797.

Thompson-Schill, S. L., Swick, D., Farah, M. J., D'Esposito, M., Kan, I. P., & Knight, R. T. (1998). Verb generation in patients with focal frontal lesions: A neuropsychological test of neuroimaging findings. *Proceedings of the National Academy of Sciences of the United States of America, 95,* 15855-15860.

Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron*, *23*, 513-522.

Talairach, J., & Tournoux, P. (1988). *A co-planar stereotaxic atlas of a human brain*. Stuttgart, Germany: Thieme.

Van Veen, V., & Carter, C. S. (2005). Separating semantic conflict and response conflict in the stroop task: A functional MRI study. *Neuroimage*, *27*, 497-504.

Wagner, A. D., Maril, A., Bjork, R. A., & Schacter, L. (2001). Prefrontal contributions to executive control: fMRI evidence for functional distinctions within lateral prefrontal cortex. *Neuroimage*, *14*, 1337–1347.

Wagner, A. D., Pare-Blagoev, E. J., Clark, J. & Poldrack, R. A. (2001). Recovering meaning: Left prefrontal cortex guides controlled semantic retrieval. *Neuron*, *31*, 329–338.

Yee, E., Blumstein, S., & Sedivy, J. C. (2008). Lexical-Semantic activation in Broca's and Wernicke's aphasia: Evidence from eye movements. *Journal of Cognitive Neuroscience*, *20*, 1-21.

Yee, E., & Sedivy, J. (2006). Eye movements reveal transient semantic activation during spoken word recognition. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *32*, 1-14.