The Neural Substrates of Phonological Processing: An Examination of Neuroimaging Research

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1. Introduction

Recent advances in neuroimaging technology have added a new dimension to the study of cognitive processes, enabling researchers to manipulate and observe on-line processing in the human brain. Imaging procedures, such as positron emission tomography, functional magnetic resonance imaging, and magnetoencephalography, have become widely used in the study of language processes and many studies have focused specifically on investigating the neural regions activated during phonological processing (Klein, et al., 1995; Shaywitz, et al., 1995; Price, et al., 1997; Zouridakis, et al., 1998). Phonological processing involves the encoding and analysis of the phonological attributes of a stimulus (e.g., the segmental and prosodic properties of an utterance) and can be elicited by tasks involving speech perception or phoneme discrimination (e.g., rhyme judgement tasks). Despite the use of standardized testing techniques designed to isolate phonological processes, previous attempts to localize the neural regions associated with phonological processing have produced highly variable results. The purpose of the present research is to integrate the results of a broad range of neuroimaging studies in order to identify the neural correlates of phonological processing.

In previous research, the use of positron emission tomography (PET) to determine the neural substrates of phonological processing has proved problematic. In a comparative analysis of PET imaging studies, Poeppel (1996) revealed that the majority of findings did not converge on similar regions of cortical activation, despite the use of tasks specifically designed to recruit phonological processes. In fact, across these studies, no single region was consistently implicated in the computation of phonological information, a finding that Poeppel termed a "no-overlap result" (pp. 321) for the domain of phonological processing. Although Poeppel attributed some of the variability in these results to insufficient task-control matching and problems inherent in the application of PET methodology, he also claimed that another significant contributing factor was that none of the studies were motivated by a particular theoretical framework. Consequently, Poeppel suggested that the 'no-overlap' result may actually reflect the selective activation of different aspects of phonological processing, but that, in the absence of a guiding theoretical model, the way in which the phonological tasks in these studies map onto linguistic representations during the retrieval of lexical information remains unclear.

Indefrey and Levelt (2000) proposed a model of word production that provides a theoretical foundation for the study of processes involved in lexical retrieval (see also Levelt & Indefrey, 2000). This model consists of a succession of 'core' processing components that are directly involved in the generation of words, including components specific to phonological processing. The core components each represent a characteristic processing operation, drawing clear distinctions between the linguistic functions involved in word production. For phonological processing operations, this model segregates segmental from metrical processing, with independent core components for phonological retrieval and phonological encoding. The word production model also contains a series of 'lead-in' processing components that trigger the activation of the core components at various stages in the generation of words. These lead-in processes are types of cognitive operations (e.g., visual word recognition) that are selectively activated by different kinds of cognitive tasks (e.g., word reading). As a result, these processes provide a mechanism with which to map word perception tasks onto specific linguistic representations using a model of word production.

Using their model, Indefrey and Levelt conducted a meta-analysis of a group of neuroimaging studies, focusing predominantly on PET and evoked response potential (ERP) research. They predicted that the processing components in their word production model would provide a structure for the resolution of inconsistent data from the neuroimaging research. The meta-analysis revealed a convergence of the patterns of activation observed in these studies onto a specific network of cortical regions. As a result, Indefrey and Levelt proposed that this cortical network subserves the processes involved in the generation of words and suggested that, within this network, there was functional specialization for the various processing stages of word production depicted by their model. Indefrey and Levelt concluded that their word production model provides a guiding theoretical framework for the study of language processes in neuroimaging research.

Although Indefrey and Levelt limited their meta-analysis mainly to PET and ERP research, studies using functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG) to localize the neural substrates of phonological processing have also yielded divergent results (Pugh, et al., 1996; Simos, et al., 1998; Zouridakis, et al., 1998; Poldrack, et al., 1999). The present study applies the word production model proposed by Indefrey and Levelt to a sample of fMRI and MEG studies investigating phonological processing. The first step involves decomposing the phonological tasks in these studies, using a task decomposition procedure similar to Poeppel (1996), with the assumption that these tasks involved the same processes as the phonological processing components of Indefrey and Levelt's model. If the tasks used to engage phonological processing in these studies map onto the tasks that activate the lead-

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in processing components outlined in the word production model, then this model will provide a theoretical framework for the integration of results from the fMRI and MEG literature. The hypothesis of the present study is that the regions of activation found in the fMRI and MEG studies will parallel the neural regions in the cortical network described by Indefrey and Levelt. This finding would suggest that current evidence for the localization of phonological processing is not inconsistent, but merely reflects activation in the various cortical regions corresponding to the different stages of phonological processing.

After a comparison of the neuroimaging techniques used to study language processes, I will describe Poeppel's review of PET methodology in previous investigations of phonological processing. Then, I will introduce Indefrey and Levelt's model of word production and compare it to alternative accounts of lexical representation, with an analysis of how each of these theories accounts for issues related to the retrieval and use of lexical information. Next, I will describe Indefrey and Levelt's meta-analysis of the data from a group of neuroimaging studies. I will then apply Indefrey and Levelt's model to the data from a sample of fMRI and MEG studies to integrate the results from these studies. An analysis of the cortical regions activated during phonological processing will follow, with a discussion about the implications of these findings for the word production model.

2. Comparison of Neuroimaging Techniques

2.1. Positron Emission Tomography (PET)

One of the first neuroimaging techniques to become widely used in the investigation of cognitive processes was positron emission tomography (PET). As a result, PET studies comprise a majority of the current empirical literature on the neural basis of cognition, in particular, research investigating the cortical regions underlying language processes (Jaeger, et al., 1996; Demb, Poldrack, & Gabrieli, 1999). Although the present study focuses on fMRI and MEG research, a description of the PET technique is useful to provide a basis for the review of previous research using this methodology and to introduce the paired subtraction paradigm used in PET research, as its application extends to the use of alternative neuroimaging techniques.

PET technology takes advantage of the fact that increased neuronal activation creates an increase in the metabolic requirements of the activated cells, such that the subsequent elevation in the regional levels of oxygen and glucose can be traced and recorded (Rugg, 1997). Monitoring changes in regional haemodynamic variables is made possible by the introduction of specific radioactive tracers into the blood stream via the injection of glucose labeled with a positron-emitting isotope (Logan, 1994). When glucose is taken up by an activated cell, positron-electron annihilation events are produced by the rapid

decay of this isotope, causing positrons to radiate from the cell. As positrons are emitted from activated cells, a three-dimensional image of the cortex is generated, in which the intensity of any given neural region is proportionate to the amount of blood flow in that region (Rugg, 1997). This technique allows researchers to use haemodynamic variation as an indirect measure of relative neural activity in determining the functional neuroanatomy of various cognitive domains.

PET imaging has the advantage of producing a clear spatial representation of the cortical regions activated during a given task and, until only very recently, it was the preferred method for the assessment of cognitive function in the brain. Despite this advantage, PET imaging technology has a number of disadvantages. Although PET can provide an image with high spatial resolution, its temporal resolution is very poor. The effects of haemodynamic variation can only be observed when the increase in neural activity is sufficient enough to produce a change in the overall metabolic demands of the neuron population (Rugg, 1997). As a result, differences in the *timing* of the neuronal activity cannot be captured and the functional importance of such differences cannot be measured. Moreover, even if these effects could be observed with only a minimal increase in neural activity, because the haemodynamic response itself is delayed in relation to synaptic activity among the neurons, the observable effect would still be slower and more diffused, producing an image with poor temporal resolution.

Additional disadvantages related to PET's temporal resolution stem from the fact that changes in the haemodynamic properties of a neuron population may not necessarily produce a strong physiological signal. Because PET constructs a neural representation by capturing these changes, it requires many trials over a certain length of time to record the image. Demonet, et al., (1993) determined that the fastest rate at which PET scanning acquires an image is approximately ten seconds. These limitations on PET imaging's temporal acquisition capabilities pose a problem for the study of cognitive processes, like phonological processing, which occur in mere milliseconds.

In order to maximize the signal-to-noise ratio and reduce the effects of the limitations on data acquisition, researchers have developed a methodological strategy termed the Paired-Image Subtraction Paradigm (for a review see Fox et al., 1988; Posner et al., 1988; Friston et al., 1993). This paradigm requires the presentation of two minimally different tasks: a control task and an experimental task. The experimental task is a more complex extension of the control task, assumed to engage all of the cognitive processes activated by the control task, plus an additional process of interest. The control image is then subtracted from the experimental image and the resulting area of activation is argued to be the neural substrate for the process by which the two tasks differ. Although this paradigm creates an adequate signal-to-noise ratio, in order to obtain enough statistical power to interpret subtle changes in this signal, it is necessary for the

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data to be averaged across participants (Fox et al., 1988). One limitation with this procedure is that pooling the data requires each image to be compared with a 'standardized' image. These comparisons fail to take into account individual differences in cortical structure, as averaging the images across subjects decreases the quality of their spatial resolution. As a result, the paired subtraction paradigm precludes the study of individual differences observed in the patterns of activation associated with each task.

Another important drawback of PET methodology is that there is a limit to the number of times a participant can undergo this testing procedure (Rugg, 1997). Positrons are not emitted very frequently from cells and, as such, numerous scans may be required from each participant in order to obtain interpretable results. For PET, the need for multiple samples is particularly problematic, as it is a relatively invasive procedure, and each participant can only undergo a restricted number of scans in order to maintain safe levels of radiation exposure. Due to its drawbacks, the use of PET imaging has declined for the study of cognitive processes, however, another haemodynamic method that has become widely used to image both the structure and the function of the brain is functional magnetic resonance imaging (fMRI). Since the majority of the studies in Indefrey and Levelt's (2000) meta-analysis involved the use of PET scanning, the present research focuses, in part, on fMRI studies investigating the structure and function of the cortical regions involved in phonological processing.

2.2. Functional Magnetic Resonance Imaging (fMRI)

One type of fMRI procedure that enables researchers to map cortical structure and function is the 'blood oxygenation level dependent' (BOLD) method (Ogawa et al., 1990, 1992). The BOLD method involves indexing the variability in the levels of blood oxygenation in the cortex, such that the effect of oxygen concentration on various types of haemoglobin in the blood serves as a measure of neural activity. When the metabolic demands placed on cortical cells are increased due to greater neuronal activation, the corresponding increase in the levels of oxygen in the blood supply exceeds what is necessary to meet these metabolic demands. This excess creates regions of richly oxygenated cells. Oxygenation levels affect the magnetic properties of haemoglobin agents in the blood and, when placed within a magnetic field, deoxyhaemoglobin has a greater magnetic susceptibility than oxyhaemoglobin (Rugg, 1997). As the concentration of deoxyhaemoglobin decreases, a signal that is sensitive to these changes will reflect the ratio of deoxy- to oxyhaemoglobin within the blood, providing information about the density of activated neurons in the region and the intensity of their activation. This information can be used to construct an image of the cortex in response to various stimulus types.

fMRI technology presents a number of improvements over PET imaging. Most notably, because fMRI is a non-invasive procedure, there is no limit on the number of scans that can be obtained from a single participant (Rugg, 1997). This increases the reliability and power of within-subject effects and allows for the analysis of individual differences in the patterns of cortical activation. The data acquisition abilities of fMRI technology are also more advanced, increasing the speed of image acquisition from approximately ten seconds per image for PET scanning, to only three seconds per image using fMRI. fMRI also offers the advantage of high spatial resolution in its images. Although PET produces an image with high spatial quality, it records strictly functional responses, whereas fMRI produces a fine-grained representation of the anatomical structure of the cortex. The benefits associated with fMRI technology have extended its application to the study of many cognitive domains and it is increasingly employed to isolate the neural correlates of language function.

Despite its broadening application as a more advanced imaging technique, fMRI also suffers from some significant disadvantages. One drawback, inherent to the BOLD methodology, is that the BOLD signal undergoes degradation from cells in certain cortical regions that are sensitive to variation in magnetic properties other than those changes produced by blood oxygenation (Rugg, 1997). As a result, fMRI is not equally sensitive to the distribution of neuronal activation across all regions of the cortex. Another factor that contributes to the degradation of the signal quality is head movements. This is problematic for the experimental use of most imaging techniques, including fMRI, as it limits the kinds of testing procedures used in the design (e.g., even the minimal movements involved in speech production tasks introduce artifacts into the data) and requires participants to remain very still throughout the experiment.

Additionally, although fMRI offers an improvement over PET in the speed of image acquisition, fMRI images still have very poor temporal resolution. Despite their spatial capabilities, all imaging techniques that rely on haemodynamic variation to provide an indirect indication of neural activity are severely restricted in their ability to index the time course of this activity. An alternative to the use of haemodynamic imaging methods is the application of electrophysiological techniques that have the ability to measure the neural correlates of processing in real time. One such technique, that measures electromagnetic responses in the cortex, is magnetoencephalography (MEG). MEG has yet to become widely used in the study of cognitive function and, as such, very few studies in Indefrey and Levelt's meta-analysis involve the use of this technique. The present study involves an analysis of MEG research, in addition to studies using fMRI, to provide an overview of current evidence for the localization of the neural substrates of phonological processing from multiple research perspectives.

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2.3. Magnetoencephalography (MEG)

When regional neuronal activity exceeds the threshold of background activity levels, electrical currents in the population of activated neurons produce a detectable electromagnetic field. The magnetic flux associated with this electromagnetic field can be measured using magnetoencephalography (MEG) (for a review see Hämäläinen et al., 1993). MEG takes advantage of the fact that neurons, when activated, undergo a change in polarity, becoming either polarized or depolarized (Rugg, 1997). This process produces electrical currents in the neurons that generate magnetic fields. The strength of these magnetic fields is measured in proportion to the electroencephalographic waves emitted by neuron populations in the brain during cortical activation. The measured responses are represented as waveforms of varying frequencies that can be quantitatively analyzed to produce topographic maps of the intensity and direction of the brain's magnetic fields, which may be used to infer the localizations of current dipoles in the cortex.

The greatest benefit associated with MEG technology is the high temporal resolution of the images it generates. The ability of MEG to track the correlates of on-line cognitive processing allows researchers to establish an initiation point for stimulus discrimination. When coupled with well-established behavioural results (e.g., reaction time studies), these studies of the temporal properties of neural activity can only serve to enhance our understanding of information processing. Another advantage of MEG is that it provides another non-invasive alternative to the study of cortical activity. Just as with fMRI, this allows for the application of an experimental design with numerous conditions, as each participant may undergo multiple recording sessions.

One important limitation for MEG, however, is that the magnetic recordings are sensitive only to fields generated by current dipoles in the neurons orientated *tangentially* to the scalp (see Figure 1) (Rugg, 1997).

(1)   Figure 1.

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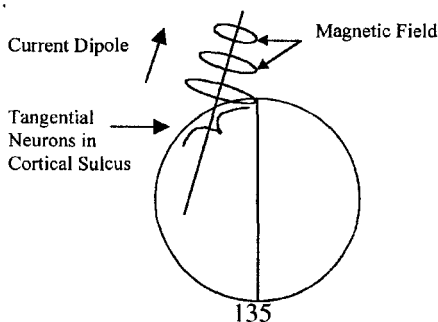
As a result, the majority of MEG recordings capture activation localized exclusively to cortical sulci and reflect a minimal contribution from activity in the cortical gyri. Since a significant portion of the cortex is comprised of gyral neurons, this restricts the usefulness of MEG in many contexts. However, Phillips et al. (1995) argued that much of the activation related to auditory language phenomena is localized to the lateral sulcus and, as a result, this type of language processing can be easily measured using MEG.

In summary, neuroimaging techniques, such as PET, fMRI and MEG, provide a valuable tool for the analysis of on-line processing in the human brain. These techniques provide researchers with the potential to make more direct observations of various cortical language functions that previously could only be inferred indirectly from lesion studies or developmental disorders. With new technological capabilities, however, comes a new set of methodological issues. The application of neuroimaging methodology to the study of language processing has produced variable results and a review of previous neuroimaging research demonstrates that current evidence for the cortical localization of phonological processing remains unreliable.

3. Previous Research

Previous attempts to isolate the neural correlates of phonological processing using neuroimaging technology have yielded divergent results. Poeppel (1996) examined some of these results in a review of PET studies investigating the neural basis of phonological processing and revealed that many questions remain about the functional neuroanatomy of phonological processing.

3.1 Poeppel (1996)

Poeppel (1996) conducted a critical review of five PET studies designed to locate the neural correlates of phonological processing (see Table 1). Although all of the studies used PET methodology combined with experimental task paradigms designed to recruit phonological processing, Poeppel observed that each study reported different, *non-overlapping*, regions of cortical activation. In order to determine the cause of such varying results, Poeppel conducted a decomposition of the experimental tasks employed in these studies. For the task decomposition, Poppel analyzed each of the studies, focusing on how the tasks of each experiment were designed to engage phonological processing specifically. The following sections summarize the conclusions drawn by the authors of each of these studies about the neural basis of phonological processes and Poeppel's analysis of these conclusions.

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(2)   Table 1.

Study	Task Type	Stimulus Type	Modality	Area of Activation
1. Petersen et al. (1989)	Rhyme Judgement Task	Word Pairs	Visual	• Temporoparietal cortex
2. Zatorre et al. (1992)	Rhyme Judgement Task	Word and Non-Word Pairs (CVCs)	Auditory	• Left posterior temporal and parietal regions • Broca's area
3. Sergent et al. (1992)	Rhyme Judgement Task	Single Letters (Consonants)	Visual	• Prefrontal areas
4. Demonet et al. (1992)	Phoneme-Monitoring Task	Non-Words	Auditory	• Superior, middle and inferior temporal gyri • Broca's area
5. Paulesu et al. (1993)	Rhyme Judgement Task	Single Letters (Consonants)	Visual	• Superior temporal gyrus • Broca's area • Temporoparietal cortex

3.1.1. Petersen et al. (1989)

Petersen et al. (1989) were among the first to investigate language processes using PET imaging methodology, and phonological processing was only one of the experimental processes in this large-scale study designed to investigate the neural basis of language. In order to recruit phonological processing specifically, Petersen et al. used a rhyme judgement task in which participants were visually presented with a pair of words, one above and one below a fixation point, and were asked to indicate whether the word pair rhymed. The stimuli consisted of either visually similar, rhyming, word pairs (e.g., dog-bog) or visually dissimilar, nonrhyming, word pairs (e.g., dog-cat). As a control condition, participants were presented with the same stimuli, but were not required to make a response.

A number of regions displayed a significant increase in regional blood flow during the experimental condition. Once Petersen et al. subtracted the control condition from the test condition, the resulting pattern of cortical activation was localized to left temporoparietal regions (see Figure 2). As a result, Petersen et al. argued that the left temporoparietal cortex mediates phonological processing or encoding.

(3)   Figure 2.

Petersen et al. (1989)
Temporoparietal Cortex
B39, B40
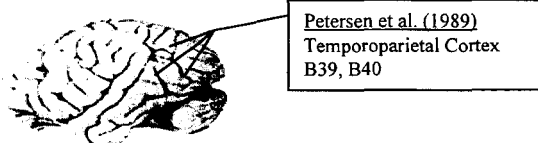
3.1.2. Zatorre et al. (1992)
Zatorre et al. (1992) investigated which cortical regions were sensitive to speech stimuli by auditorily presenting word and pseudo-word pairs consisting of consonant-vowel-consonant (CVC) strings. In the experimental condition, designed to isolate phonological processing, participants had to judge whether the final consonants in the CVC pair were the same (e.g., bag-big) or different (e.g., tig-lat). As a control, they conducted a passive-listening condition, in which participants were presented with the stimuli from the experimental condition, but were not required to generate a response. Poeppel argued that this design did not allow Zatorre et al. to isolate phonological processing, as presumably participants would still make a same-different judgement, regardless of whether or not they articulated that judgement. However, Zatorre et al. argued that this design would activate phonological processing and used the paired subtraction paradigm to determine the localization of activation for the phonological condition.

Their results for the phonological condition indicated a significant increase in the regional blood flow to left-lateralized regions, including Broca's area and temporo-parietal cortex (see Figure 3). Zatorre et al. suggested that this pattern of activation implicates a cortical network underlying phonological processing involving left posterior temporal and parietal regions and Broca's area.

(4)   Figure 3.

Zatorre et al. (1992)
Broca's Area
B44, B6

Zatorre et al. (1992)
Temporoparietal
Cortex
B40, B7

3.1.3. Sergent et al. (1992)
In an attempt to replicate the results of Petersen et al. (1989) or Zatorre et al. (1992), Sergent et al. (1992) also conducted a study using a rhyme judgement task, however, they maintained that the only way to isolate one specific aspect of linguistic processing, such as phonological processing, was to use stimuli that were not subject to interference from other linguistic information, such as semantic, or orthographic, codes. Accordingly, they used letter stimuli in a letter-sound task, where participants were required to make a rhyme judgement between individual, visually presented letters and an auditorily presented speech sound (e.g., does <e> rhyme with [iy]). Sergent et al. argued that this task would isolate the visual and phonological codes of the letter without generating interference from other types of linguistic processing.

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Using the paired subtraction paradigm, Sergent et al. devised two control conditions for subtraction from the experimental condition. To subtract out activation from semantic codes, they used an object task, involving a forced-choice categorization about the 'living' status of line-drawings that depicted either living (e.g., a person) or non-living objects (e.g., a house). In order to control for interference from orthographic codes, the second control condition was a letter-spatial task, involving visually asymmetrical consonants that either rhymed (e.g., <b-c-d-g-p-z>) or did not rhyme (e.g., <f-j-k-l-n-r>) with the auditorily presented speech sound (e.g., [iy]). These letters were either oriented normally or in an upright mirror-reversed position and participants were required to make a forced-choice orientation judgement.

Importantly, the results of this replication study did not converge with those found by either Zatorre et al. (1992) or Petersen et al. (1989). Instead, after the subtraction of both control conditions, Sergent et al. observed significant activation in three prefrontal areas of the cortex (see Figure 4). Sergent et al. attributed this pattern of activation to the involvement of regions specialized for the programming of articulatory gestures, yet Poeppel argued that this explanation was insufficient, considering the fact that neither the experimental or control condition required any explicit articulation. It is apparent that this attempt to replicate previous neuroanatomical findings for the domain of phonological processing only contributed to the discrepancy among PET results.

(5)   Figure 4.

Sergent et al. (1992)
Frontal Areas
B11, B45, B46
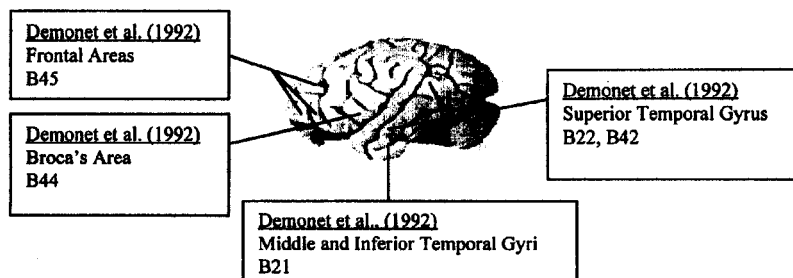
Sergent et al. (1992)
Superior Temporal Gyrus
B42

3.1.4. Demonet et al. (1992)

Demonet et al. (1992) investigated whether or not separate cortical regions were implicated in semantic and phonological processing. In order to isolate phonological processing, they employed a "phoneme-monitoring" task using auditorily presented multisyllabic nonwords. Participants were required to monitor the stimulus for the presence of a specific sequence of speech sounds (e.g., a [d] followed by a [b]). A non-speech sound control condition involved groups of pure tones, in which the participants were required to determine if there was a rising pitch in the third tone.

The results of the subtraction showed an increase in the regional blood flow to the superior, middle and inferior temporal gyri and Broca's area (see

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Figure 5). The authors attributed the most significance to activation in regions of the superior temporal cortex. They concluded that phonological processing activates auditory association cortex in the left superior temporal gyrus and the anterior part of Wernicke's area, but suggested that Broca's area may also play a role in phonological processing.

(6)   Figure 5.

Demonet et al. (1992)
Frontal Areas
B45

Demonet et al. (1992)
Broca's Area
B44

Demonet et al. (1992)
Superior Temporal Gyrus
B22, B42

Demonet et al.. (1992)
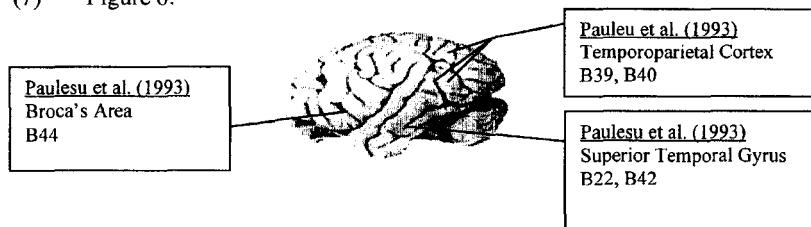Middle and Inferior Temporal Gyri
B21

3.1.5. Paulesu et al. (1993)
Although the research of Paulesu et al. (1993) focused on the verbal components of working memory, they also made specific claims about the neural substrates of phonological processing. In their memory model, based on Baddeley (1992), phonological processing is a combination of phonological encoding and rehearsal operations and, as such, their experiment employed two language conditions designed to capture these processes. The first verbal task consisted of a sequence of six visually presented consonants that were phonologically dissimilar (e.g., <k-l-m-p-q-s>). In a dual-task paradigm, participants were required to maintain this string of consonants by subvocal rehearsal to activate both phonological encoding and subvocal rehearsal processes, while monitoring for a visually presented probe stimulus (e.g., <f>). The second was a rhyme judgement task for visually presented letters that was intended to activate only phonological encoding (e.g., does the target rhyme with /iy/). The results from these two language tasks were combined and then compared to a control condition, in order to separate the memory component from the verbal component.

The results of the verbal component indicated patterns of activation in areas including Broca's area, superior temporal gyrus, the supramarginal gyrus of the temporo-parietal cortex and the insulae in primary auditory cortex (see Figure 6). Paulesu et al. concluded that phonological encoding can be localized to the supramarginal gyrus of the left hemisphere and that areas in the superior temporal gyrus and frontal cortex may also be involved in phonological processing.

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(7)   Figure 6.

Paulesu et al. (1993)
Broca's Area
B44

Pauleu et al. (1993)
Temporoparietal Cortex
B39, B40

Paulesu et al. (1993)
Superior Temporal Gyrus
B22, B42

The results of the Paulesu et al. study are particularly striking in comparison to the experiment conducted by Sergent et al. (1992). These two experiments used exactly the same type of task to recruit phonological processing (e.g., a rhyme judgment task in the visual modality) with single consonant stimuli, but the localization results are dramatically different. Where Sergent et al. reported activation in prefrontal areas for phonological processing, Paulesu et al. concluded that phonological processing is localized to regions in the temporal and temporoparietal cortex and Broca's area. This comparison illustrates the high degree of variability among studies using PET methodology to identify the neural substrates of phonological processing.

3.2. Summary
Poeppel's comparison of PET results revealed that, despite our ability to combine cognitive testing with neuroimaging technology, current data for the cortical localization of phonological processing is highly variable. Poeppel (1996:321) termed this a 'no-overlap' result for the domain of phonological processing and concluded that it is premature to infer which cortical areas mediate phonological processing from PET research. In his analysis, Poeppel argued that problems with the experimental designs in these studies and in the application of PET methodology may account for some of the variability in the PET data. However, he also observed that none of the experiments in his review were motivated by a particular theoretical model. As a result, Poppel argued that the lack of reference to a specific theoretical framework may account for a *significant* amount of the variability in these results. Indeed, Poeppel proposed that a possible explanation for the no-overlap result could be that the tasks in these studies engaged different aspects of phonological processing, but that, without a theoretical model detailing the various aspects of phonological processing, the results appear inconsistent.

The benefit of contact with a theory of phonological processing for these experiments is that theoretical models provide independent evidence for what processes are involved in language function and how these processes interact.

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Phonological processing does not involve a single operation, but a complex combination of operations related to the analysis of phonological information. As a result, phonological tasks, although they may appear similar, may actually be activating very different types of phonological processes. For instance, a task that involves word reading may activate processes related to the retrieval of phonological information for specific word forms from the lexicon. By contrast, a task that involves the identification of non-words, which have no existing lexical form, may activate processes associated with the conversion of graphemes to phonemes. The patterns of cortical activation for each of these types of phonological processes may be localized to different regions of the cortex. As a result, reference to a theoretical model of language processing may account for apparently divergent neuroimaging results.

4. Theoretical Background
There is a large body of literature in linguistics devoted to lexical and phonological theory and many of these theories provide detailed models of the functions involved speech production and perception, including the retrieval and use of phonological information. Indefrey and Levelt (2000) proposed a theory of word production involving a staged succession of processing operations activated during the retrieval of lexical information. In the following sections, I will introduce and describe Indefrey and Levelt's word production model and then compare it to alternative accounts of lexical representation from the linguistics literature.

4.1. The Word Production Model
The model of word production proposed by Indefrey and Levelt (2000) depicts a succession of stages involved in the generation of a phonological word from a conceptual base (see Figure 6). This model, based on Levelt's (1989) theory of word production, involves a series of processing components that function in staged succession throughout the generation of speech. This succession contains a group of 'core' processing components (e.g., phonological code retrieval) and a corresponding set of 'lead-in' processes (e.g., visual word recognition). The core components are directly involved in the generation of words, whereas the lead-in processes enter into the word production model at various stages in the succession of the core processing components and indirectly influence the process of word production. The lead-in processes are selectively activated by different kinds of cognitive tasks (e.g., word reading) and, as such, provide a mechanism with which to map these tasks onto linguistic representations.

(8)   Figure 6.

The processing stages involved in the generation of words (core processes) and the processes activated by various experimental word production tasks (lead-in processes), as depicted by Levelt & Indefrey (2000: 80).

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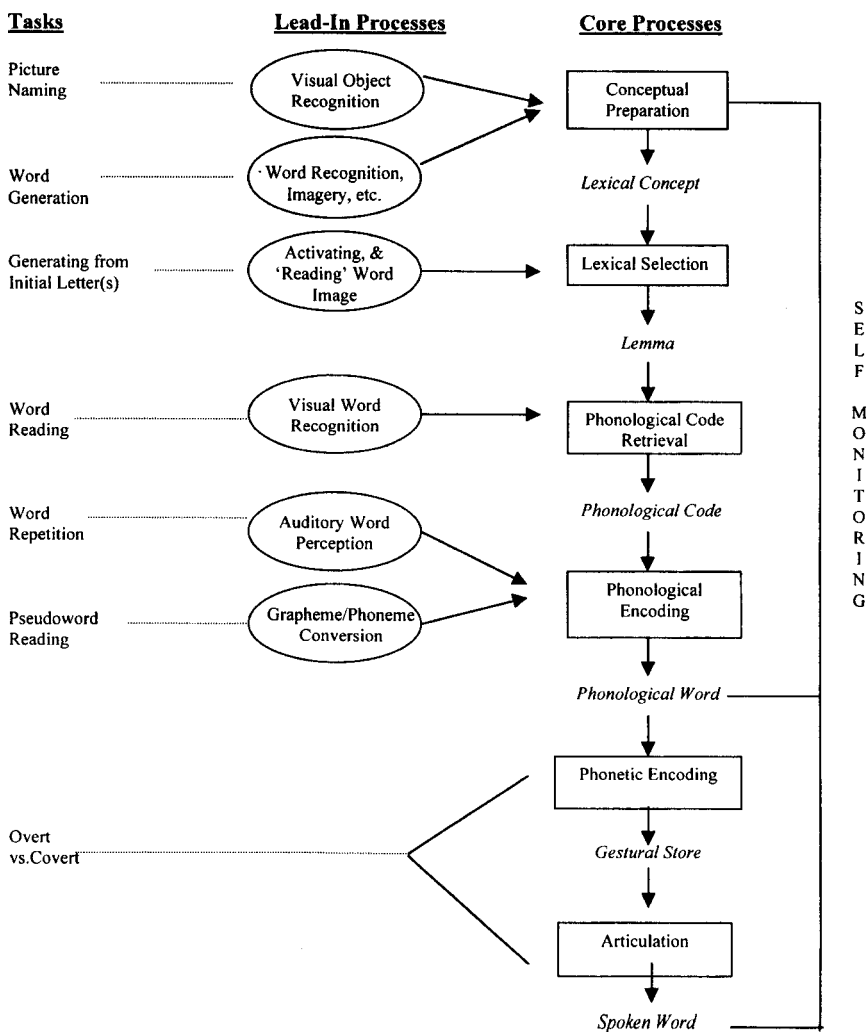
In this model, the core processing components each have a characteristic linguistic input. Each core component selects its characteristic input and performs a computation on that input, which generates the linguistic output for that component. This linguistic output then functions as the input for the next core processing component. Each lead-in process involves a specific type of on-line perceptual processing (e.g., visual word recognition) that enters the word production mechanism at a specific stage in the sequence of core processes and triggers the activation of the core process at that stage. The type of on-line perceptual task determines which lead-in process is activated and at which level this process enters the word production mechanism. If a lead-in process activates a core process in the middle of the word production mechanism, only the processing components subsequent to this component will, in turn, be activated. Importantly, it is the differentiation between the core and lead-in processes in this model that enables studies of word *perception* to be analyzed in terms of a word *production* model. Many studies have used perceptual task designs to investigate specific aspects of language processing, such as phonological processing, and the word production model has core components designed to account for the processing of phonological information.

4.1.1. Phonological Processing

The core processing components of the word production model include two processing units specialized for phonological processing. The first, phonological code retrieval, selects a 'lemma' as its characteristic input (e.g., the noun lemma 'CAT + plural'). Lemmas are syntactic words characterized by a syntactic frame. The lexical concepts for verbs and function words each have a lemma whose syntactic frame specifies how the information in the lexical concept (e.g., semantic information) should be mapped onto syntactic category information (e.g., transitive verb). The syntactic frames of the selected lemmas (e.g., verbs and nouns) undergo the late insertion of phonological information as they combine to incrementally generate the syntactic pattern of the phrase, known as the 'surface structure'. This process of syntactic construction begins as soon as the lemma is retrieved (Indefrey & Levelt, 2000: 847). In order to generate the appropriate output, the phonological code retrieval component must retrieve the phonological codes from the selected lemma. The selection of the lemma triggers the activation of the phonological code for each of its morphemes (e.g., 'CAT + plural' activates /kæt/ + /-z/). The newly generated phonological code is the output of the phonological code retrieval processing component and, as such, becomes the input for a second phonological processing component, phonological encoding.

In the phonological encoding component, the primary function of the phonological code is to provide information for the generation of syllabic

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structure. The process of syllabification is dependent, in part, on inflectional morphology. When the lemma activates the phonological code, the inflectional information contained in the lemma indirectly influences the syllabification process. The domain of syllabification is the phonological word and as these words are syllabified, they become the output of the phonological encoding processing component. In subsequent syntactic processes, phonological words may be incrementally syllabified into connected speech and, as the surface structure expands, these words may combine to form larger units, such as phonological phrases.

The 'lead-in' process that engages the word production mechanism at the level of phonological code retrieval is visual word recognition. Visual word recognition is a type of perceptual processing that is activated during any number of word reading tasks. The lead-in processes that trigger activation at the level of phonological encoding are auditory word perception and grapheme/phoneme conversion. The process of auditory word perception occurs during tasks of word repetition and grapheme/phoneme conversion processes are utilized for pseudoword reading.

In summary, Indefrey and Levelt's theory of word production is based on a complex system of processing components that allow cognitive testing techniques to be mapped directly onto the linguistic representations involved in lexical retrieval. There are a number of issues that a theory of lexical representation must account for in order to characterize the processes involved in the retrieval and use of lexical information. Some of these issues relate to lexical access in general, such as modularity and the specification of features in the lexicon, and some relate specifically to the processing of phonological information, such as the time course for the insertion of phonological information. Indefrey & Levelt integrate these issues into their model of word production and, in the next section, I will compare their model to alternative accounts of lexical representation from the linguistics literature.

4.2. Theories of Lexical Representation

Many linguistic theories of lexical representation propose modular systems of representation for the linguistic functions involved in accessing information from the lexicon. In modular models of lexical retrieval, the individual components of the model each conduct linguistic operations independent of one another, usually within a serial processing framework. For example, in Indefrey and Levelt's model of word production, each processing component, or module, has a characteristic input, on which it conducts a specific processing operation in order to generate the input for the next module in the system. Current morphological theories also advocate a modular approach to lexical representation, beginning with how information is represented and processed within the lexicon.

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Morphological theories of lexical representation offer a number of alternative suggestions about the nature of the information in the lexicon. In the majority of models, lexical items are comprised of a set of stems and a set of affixes that are stored in the lexicon and projected into the syntax during the generation of word forms. However, differences in these models emerge concerning exactly what type of information these lexical items are specified for. Lieber (1992) proposed a model with affixes fully specified for feature information (e.g., number, lexical category, tense). By this account, the items in the lexicon provide enough information to generate the correct structures for the syntax. By contrast, in Indefrey and Levelt's model of word production, lexical items are not specified for feature information and, as such, combine with both inflectional and derivational information prior to leaving the lexicon. Similarly, in Wunderlich's model of inflectional morphology, termed 'Minimalist Morphology' (1997), lexical items are maximally underspecified for feature information. Feature underspecification minimizes the amount of information to be stored in the lexicon, but also usually requires that lexical items combine with morphological information prior to entering the syntax in order to generate the appropriate structure for syntactic processing.

Some morphological models support the notion that the addition of derivational and inflectional information is restricted to the lexicon, while others suggest that the combination of elements occurs outside the lexicon. In 'lexicalist' approaches to morphology, the realization of elements in the syntax is governed by the lexicon. For example, in their lexicalist models, both Indefrey and Levelt, and Wunderlich, proposed that processes combining roots with morphological information occur strictly within the lexicon, prior to entering the syntax. In Wunderlich's model, both morphosyntactic and morphophonological features are added into the lexicon via morphological operations and subsequent syntactic mechanisms (e.g., agreement and case checking) are based on the availability of this information in the word forms. Although Indefrey and Levelt advocate the early insertion of morphosyntactic information, the addition of morphophonological information occurs later, in the phonological processing components of their model.

Like these lexicalist models, Lieber (1992) also proposed that lexical items combine within the lexicon to form words that undergo syntactic operations. By this account, the insertion of morphophonological information occurs early in the system. However, for Lieber, this morphological information combines with lexical roots via syntactic processes, initiating a departure from the traditional lexicalist view of morphology and lexical representation.

Halle and Marantz (1993) proposed an alternative to the lexicalist approach with their 'Distributed Morphology' model that focuses on the syntax, rather than the lexicon. For Halle and Marantz, morphological operations are

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distributed among several different components in the grammar and both derivational and inflectional morphology are inserted after the lexicon. In this account, morphosyntactic features are added in the syntax via syntactic operations (e.g., merge and movement operations: Chomsky, 1993), whereas, like Indefrey and Levelt, the addition of morphophonological features occurs later by vocabulary insertion in the morphology/phonology components of the system.

Another model that departs from lexicalist views is the 'a-morphous', or affixless theory of morphology (Anderson, 1992). This view is based on the notion that the lexicon does not contain affixes, but is composed of roots and word formation rules only. In this approach, there is a separation of derivational and inflectional information, where derivational information is added to the roots in the lexicon and inflectional information is inserted in the syntax via word formation rules. Although Anderson's model supports the early insertion of derivational morphophonology, again there is a division in this model, as, unlike Indefrey and Levelt and Halle and Marantz, the addition of *inflectional* morphophonology occurs later in the system.

In summary, the word production model proposed by Indefrey and Levelt combines aspects of Wunderlich's 'Minimalist Morphology' approach and the 'Distributed Morphology' model of Halle and Marantz. Indefrey and Levelt's theory is similar to Wunderlich, as both offer models in which word roots combine with derivational and inflectional information in the lexicon. However, these models diverge on the issue of phonological insertion. Wunderlich proposes that all morphological information, including morphophonological information is inserted in the lexicon, but Indefrey and Levelt make the assumption that morphophonological information is inserted late, or outside of the lexicon. On this issue, Indefrey and Levelt's model of word production is more like the 'Distributed Morphology' model. Halle and Marantz also maintain that morphophonological information is inserted late, but, unlike Indefrey and Levelt, the combination of lexical items with morphological information occurs in the syntax and not in the lexicon. The model of word production proposed by Indefrey and Levelt provides a detailed account of the processes involved in the retrieval of lexical information. If, for a given processing component, there is an underlying region of cortical function, then this region should be activated by any task involving the processes for that component. To test this claim, Indefrey and Levelt conducted a meta-analysis of a group of neuroimaging studies in an attempt to identify the neural substrates of the different processing components described in their model.

4.3. The Meta-Analysis

Indefrey and Levelt (2000) conducted a comprehensive meta-analysis of cerebral activation results from fifty-eight brain imaging experiments. Of these studies, the

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majority used PET or ERP methodology and only five studies employed fMRI or MEG techniques. In order to combine data from methods with varying resolution capabilities, Indefrey and Levelt used a double reference system to determine the significance of an activation. This system involved the comparison of localizations at both gross and fine-grained divisions of the cortex. They accepted the convergence of evidence onto a certain region only if the chance level given by a binomial distribution was below 10%. This strict threshold for significance meant they considered the agreement of reports of activation in a certain region to be coincidental unless their statistical analysis proved that there was a less than 10% chance that the convergence of these results would occur. The results of their statistical analysis showed a significant pattern of convergence onto a specific network of cortical structures. This finding revealed that Indefrey and Levelt were successfully able to determine reliable localizations for the different processes in their model.

Indefrey and Levelt made specific claims about the cortical regions activated by the core processing components of the word production model. They proposed that a left-lateralized word production network, involving both cortical and subcortical structures, subserves the core processes of word production up to and including phonological encoding. This network consists of the posterior inferior frontal gyrus (Broca's area), the mid-superior and middle temporal gyri, the posterior superior and middle temporal gyri (Wernicke's area), and the left thalamus. For the lead-in processing components, Indefrey and Levelt implicated cortical regions within the general word production neural network and suggested that different patterns of activation within this network reflect the activation of different lead-in processes.

The phonological components of the word production model displayed characteristic patterns of cortical activation. For phonological code retrieval the lead-in process is visual word recognition. In these studies, tasks of word reading that actively engaged the process of visual word recognition generated activation in the left posterior superior and middle temporal gyri (e.g., Wernicke's area) and the left thalamus. As a result, Indefrey and Levelt identified these regions as the neural substrates of phonological code retrieval. The lead-in processes for phonological encoding are auditory word recognition and grapheme/phoneme conversion. Indefrey and Levelt determined that no specific pattern of activation corresponded perfectly to these processes, but the trend in studies using word repetition and pseudo-word reading tasks to engage these processes was activation in the left mid superior temporal gyrus and the left inferior frontal gyrus (e.g., Broca's area). Indefrey and Levelt proposed that these are likely the regions underlying the core process of phonological encoding.

The processing of information in the stages of word production requires a certain amount of time. Once Indefrey and Levelt determined the cerebral

localization of the component processes in their model, they proposed that the temporal properties of the regional activations should be compatible with timing estimates from previous electromagnetic studies (Levelt et al., 1998, Van Turennout, et al., 1997, 1998). Estimates from these studies implicate a time window between 275 and 400 msec for the lexical phonological code retrieval and phonological encoding processing components. Indefrey and Levelt suggested that the data available on the time course of word production is supported by the temporal sequence of processing components outlined in their model.

4.4. Summary
The word production model proposed by Indefrey and Levelt (2000) clearly distinguishes the various stages of processing involved in the generation of speech. In their model, processing begins with the combination of roots and derivational/inflectional information in the lexicon. From the lexicon, word forms are projected into the syntax to undergo syntactic operations and the subsequent insertion of morphophonological information. With such a detailed account of these processes, this model provides a framework that illustrates how cognitive tasks map directly onto linguistic representations. As a result, this model allows researchers to interpret perceptual processing studies in terms of a theoretical model of word production. Indefrey and Levelt applied this model to the data from a group of neuroimaging studies and observed significant activation patterns within a network of cortical regions corresponding to the processing components of their model. The present study extends this model to data from research involving fMRI and MEG neuroimaging methodology. The goal is to determine if the neural correlates and temporal sequencing of phonological processing identified by Indefrey and Levelt hold across tasks using alternative neuroimaging techniques.

5. fMRI and MEG Studies of Phonological Processing
The purpose of the present research is to determine if Indefrey and Levelt's model of word production can account for inconsistencies in the results of fMRI and MEG studies of phonological processing. To this end, I will integrate the results of fMRI and MEG research and compare them to the word production model to determine if the regions of activation from these studies match the cortical network for the processing components of this model.

5.1. fMRI Research
Phonological processing has received much attention in the functional neuroimaging literature. A number of studies using fMRI methodology show different patterns of activation for the computation of phonological information.

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Shaywitz et al. (1995) reported activation restricted to the superior aspect of the inferior frontal gyrus and concluded that this area was uniquely associated with phonological processing. In a similar study, Pugh et al. (1996) observed activation in the inferior frontal gyrus and the middle and superior temporal gyri for the phonological task and concluded that phonological processing makes the heaviest demands on these regions of the cortex. Poldrack et al. (1999) determined that the posterior and dorsal region of the inferior frontal gyrus may be specialized for phonological processing. Although Lurito et al. (2000) observed some frontal activation, localized to Broca's area, their results also showed significant activation in temporal regions. Burton ct al. (2000) found activation in superior temporal regions and determined that phonological processing does not necessarily recruit frontal areas. Based on the differences in the fMRI data, it is evident that there are still many potential locations for the specialization of phonological processing (see Table 2). The present research predicts that a reanalysis of this data, using Indefrey and Levelt's model of word production, will reveal that these studies have captured different aspects of phonological processing that correspond to the phonological components in this model.

(9)   Table 2.

Study	Task Type	Stimulus Type	Modality	Area of Activation
1. Shaywitz et al. (1995)	Rhyme Judgement Task	Non-Word Pairs	Visual	• Inferior frontal gyrus
2. Pugh et al. (1996)	Rhyme Judgement Task	Non-Word Pairs	Visual	• Inferior frontal gyrus • Middle, superior temporal gyri
3. Poldrack et al. (1999)	Syllable Counting Task	Words and Non-Words	Visual	• Inferior frontal gyrus (posterior and dorsal regions)
4. Lurito et al. (2000)	Rhyme Determination Task	Words	Visual	• Broca's area • Supramarginal gyrus • Superior middle temporal gyrus
5. Burton et al. (2000)	Onset Discrimination Tasks	CVC Word Pairs	Auditory	• Superior temporal gyrus (Exp's 1 & 2) • Frontal regions (Exp 2 only)

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5.1.1 Shaywitz et al. (1995)

The purpose of the Shaywitz et al. (1995) study was to localize the neural regions associated with the component processing operations for reading. In order to engage phonological processing specifically, they used a rhyme judgement task with visually presented pseudoword stimuli. Participants were simultaneously presented with a pair of nonsense letter strings (e.g., LEAT and JETE) and were required to judge whether or not these strings rhymed using a button press response. Shaywitz et al. included an orthographic control condition to account for the influence of orthographic stimulus features on the phonological task. In this condition, the judgement decision was based on the case alternation pattern of a sequence of letters (e.g., <ttTt> and <tTtt>) in two visually presented consonant strings. Shaywitz et al. subtracted the orthographic control condition from the phonological condition using a subtraction paradigm and argued that the resulting pattern of activation reflected the neural substrates of phonological processing.

In this study, the experimental task requires the participants to respond to pseudoword stimuli. Because these stimuli would not correspond to any existing lexical entry, this task would not make any demands on semantic processing. To complete the task, participants would necessarily recruit knowledge about spelling-to-sound correspondences, in order to determine if the orthographic strings corresponded to rhyming syllables. According to the word production model, tasks that involve pseudoword reading engage the lead-in process of grapheme/phoneme conversion. This process accesses the core components of the word production system at the level of phonological encoding. In the word production model, phonological encoding is the second core phonological component, following phonological code retrieval (see Figure 6, pg. 22). The application of this model allows the phonological task in the Shaywitz et al. study to be mapped onto the processing component representing phonological encoding operations. In the cortical network for word production proposed by Indefrey and Levelt, phonological encoding should generate activation in the left inferior frontal gyrus and the left mid superior temporal gyrus.

Shaywitz et al. reported that, after subtraction, the pattern of activation for the phonological task was localized to the superior aspect of the inferior frontal gyrus, including Broca's area, and concluded that these regions are uniquely associated with phonological processing. The localization of phonological processes to the inferior frontal gyrus corresponds to the regions of activation for phonological encoding predicted by Indefrey and Levelt (see Table 3). However, Shaywitz et al. did not observe activation in the mid superior temporal gyrus. A possible explanation is that their task did not involve an auditory component. In the word production model, the core component of phonological encoding may be triggered by the lead-in processes of either auditory word repetition or grapheme/phoneme conversion. The cortical involvement of the mid superior

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temporal gyrus may be exclusive to the auditory lead-in process[1] and, since the phonological task in the Shaywitz et al. study recruited processes including grapheme/phoneme correspondences, activation may have been restricted to the inferior frontal gyrus.

(10) Table 3.

Predicted Localizations	Area of Activation
▪ Left inferior frontal gyrus ▪ Left mid superior temporal gyrus.	✓ ✗

5.1.2. Pugh et al. (1996)

In a similar study, Pugh et al. (1996) used the same experimental paradigm as Shaywitz et al. (1995), with the added contribution of a visual-spatial control. They created a hierarchy of task conditions, each building incrementally on the previous condition. The first was a line-judgement task, designed to activate visual-spatial processing, where participants viewed two sets of four lines, one on top of the other, with right or left orientations and had to judge whether or not the lines displayed the same orientation pattern (e.g., \\\/ and \\/\). The second was a letter case judgement task with consonant string stimuli (e.g., <ttTt> and <tTtt). Pugh et al. argued that this condition makes demands on both visual-spatial and orthographic processing. In order to specifically activate phonological processes, Pugh et al. conducted a rhyme judgment task identical to the phonological task in the Shaywitz et al. study. Participants were presented with two nonsense word strings (e.g., REPE and MEAP) and were required to decide whether or not the nonword strings rhymed. This task was assumed to involve visual-spatial, orthographic and phonological processing. Pugh et al. also included a fourth, semantic, condition designed to involve all component operations, from visual-spatial processing up to semantic processing. Pugh et al. systematically subtracted each condition from the one above it in the hierarchy. To isolate the activation for phonological processing, they subtracted the case judgement task from the phonological task, with the assumption that this would eliminate interference from visual-spatial and orthographic processing.

Like the previous study, the experimental task in this study requires participants to access spelling-to-sound correspondences in order to generate phonological representations for the pseudowords. According to the word production model, this task would engage the lead-in process of

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[1]This assumption may be possible to confirm from Indefrey and Levelt's statistical analysis in their study.

grapheme/phoneme conversion, which would activate the core process of phonological encoding. In this framework, the resulting pattern of activation should occur in the left posterior inferior frontal gyrus (e.g., Broca's area) and the left mid superior temporal gyrus.

Consistent with this prediction, Pugh et al. observed activation for the phonological task in frontal regions, including the inferior frontal gyrus and notably, some activation was reported for the middle and superior temporal gyri (see Table 4). Pugh et al. concluded that the neural correlates of phonological processing involve both frontal and temporal regions of the cortex. Activation in the inferior frontal gyrus confirms the localization of phonological encoding based on the word production model. Despite highly similar experimental designs, unlike the Shaywitz et al. study, Pugh et al. reported activation in the medial and superior temporal gyri. These results are somewhat surprising considering that Shaywitz et al. used essentially the same phonological task and reported no temporal involvement. The possibility that the temporal localizations described in Indefrey and Levelt's cortical network correspond only to the auditory lead-in process for phonological encoding does not seem to hold, as the phonological task in this study did not involve the auditory modality.

(11)   Table 4.

Predicted Localizations	Area of Activation
▪ Left inferior frontal gyrus ▪ Left mid superior temporal gyrus.	✓ ✓

5.1.3. Poldrack, et al. (1999)

Poldrack et al. (1999) conducted a study designed to examine the role of the left inferior prefrontal cortex in semantic and phonological processing, using two different experimental phonological conditions. Both of these conditions were subtracted from a baseline perceptual task to isolate phonological processing. The phonological task in the first condition involved counting the syllables for visually presented mono-, di- or tri-syllabic words and the orthographic task was a case judgement task that required a decision response about the case of the presented words (e.g., uppercase vs. lowercase). The second scan condition compared another phonological syllable counting task, this time with pseudoword stimuli, to the same case judgement orthographic task.

In this study, the experimental task for the first phonological condition recruits a number of phonological operations. Prior to the computation of syllable structure information, participants presumably identify the stimulus as a word

form. According to the word production model, word reading tasks engage the lead-in process of visual word recognition. Inherent to this component is the assumption that word recognition is automatic, even when not explicitly required to complete the task. Support for this assumption comes from other types of cognitive tasks (e.g., the Stroop Task). This process mediates the word production system at the level of phonological retrieval. This step is required because, according to Indefrey and Levelt, word recognition would trigger the retrieval of the lemma associated with each lexical concept, as these lemmas are the characteristic input of the phonological code retrieval processing component. Once selected, these lemmas generate the phonological codes of the word and it is these codes that provide the input for the syllabification of the word. The syllable is one of the constituent units in the core processing component of phonological encoding, so this component would also be activated by the syllable counting task. Consequently, the phonological task in the first phonological condition would involve all levels of phonological processing specified in the word production model. As a result, cortical activation should be widespread in this condition of this experiment. Based on the predictions from Indefrey and Levelt, this activation should involve the left posterior superior and middle temporal gyri (e.g., Wernicke's area) and the left thalamus for phonological retrieval and the left posterior inferior frontal gyrus (e.g., Broca's area) and the left mid superior temporal gyrus for phonological encoding.

The second phonological condition of the experiment also required syllable counting, but this condition used pseudoword stimuli. Unlike the first condition, this condition would not generate the retrieval of phonological code information, as these codes are only associated with items stored in the lexicon. As a result, the phonological codes that provide the input to syllabification would be generated strictly from the translation of orthographic features into phonological features. According to the word production model, pseudoword reading tasks engage the lead-in process of grapheme/phoneme conversion, which, in turn, triggers phonological encoding. As a result, the pattern of activation for the second condition should be restricted to the left posterior inferior frontal gyrus (e.g., Broca's area) and the left mid superior temporal gyrus.

Unfortunately, since the focus of this study was on the role of the inferior prefrontal cortex in language processing, Poldrack et al. restricted their analysis to the scanning range of frontal regions. Despite this fact, the pattern of results observed in this study still appear to be consistent with the localizations found by Indefrey and Levelt in their meta-analysis. For both phonological task conditions, Poldrack et al. observed activation in the dorsal portions of the left inferior frontal gyrus and for the second task, activation was also significant in the posterior sections of the inferior frontal gyrus (e.g., Broca's Area) (see Table 5). These results are consistent with the frontal region correlates of phonological

encoding outlined in the cortical network for word production processes. Poldrack et al. conducted no analysis for activation outside of these frontal regions and, as a result, is it impossible to determine if the patterns of activation produced by these tasks correspond to the localizations predicted for the other components of the word production model.

(12)   Table 5.

Predicted Localizations	Area of Activation	
	Word Task	Pseudoword Task
■ Left inferior frontal gyrus	✓	✓
■ Left mid superior temporal gyrus	N/A	N/A
■ Left posterior, superior and middle temporal gyri	N/A	N/A
■ Left thalamus	N/A	N/A

Importantly, however, Poldrack et al. noted that there was much less activation of frontal areas for the syllable counting task involving real word stimuli. They suggested that this was the likely result of activation in posterior regions (e.g., regions in temporal cortex) outside of the scanning range set for this experiment. Poldrack et al. suggested that these regions may have played a primary role in task performance, minimizing the involvement of frontal cortex. This explanation is possible in the context of the word production model, as word reading tasks activate phonological retrieval operations, which are associated with activation in the left posterior superior and middle temporal gyri. However, without activation data for regions outside of the frontal cortex, this explanation is difficult to confirm.

5.1.4. Lurito et al. (2000)
In an analysis of the processes involved in word generation, Lurito et al. (2000) used a silent word rhyming paradigm to activate phonological processing. This paradigm consisted of a rhyme judgment task that was designed to generate subvocal articulation by using orthographically different rhyming word pairs (e.g., 'dial' and 'file') and orthographically similar non-rhyming word pairs (e.g., 'comb' and 'tomb') as stimuli. Participants were required to determine if the two visually presented common English words rhymed and then make a button press response. The control task was a line judgement task, where participants had to judge if a set of lines in different orientations were identical or not (e.g., [\W\] and [∧\\\]). Lurito et al. summed the single subject activation maps and activations

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were considered to be significant only if they exceeded a set threshold in the combined map.

The phonological task in this study was a task of basic word reading. The use of common English words for the rhyme judgment recruits word recognition processes. According to the word production model, word reading invokes the lead-in process of visual word recognition. This process enters the word production system at the core processing level of phonological code retrieval. The pattern of cortical activation associated with phonological retrieval is in the left posterior superior and middle temporal gyri (e.g., Wernicke's area) and the left thalamus.

Lurito et al. reported significant activation in the supramarginal gyrus (superior temporal cortex) and a band of activation deep within the superior region of the left middle temporal gyrus. They concluded that the rhyming task made the greatest demands on peri-sylvian language areas (e.g., Wernicke's area). Activation in these temporal regions confirms the localization of phonological retrieval operations based on the word production model (see Table 6). Although Indefrey and Levelt predicted the activation in the left thalamus, most analyses do not record subcortical structure activation.

(13)   Table 6.

Predicted Localizations	Area of Activation
▪ Left posterior, superior and middle temporal gyri	✓
▪ Left thalamus	N/A

5.1.5. Burton et al. (2000)

To characterize the nature of activation in segmental processing, Burton et al. (2000) conducted two experiments involving 'same/different' judgements for auditorily presented word pair stimuli. In the first experiment, the 'different' word pairs only differed in the voicing feature of the onset (e.g., [dip] and [tip]). As a result, Burton et al. argued that these pairs do not require overt segmentation. By contrast, the second experiment had word pairs that differed by onset voicing and vowel and coda phonemes (e.g., [dip] and [ten]). Burton et al. argued that these pairs required participants to segment the stimuli. Both experiments were subtracted from a tone-discrimination control condition to reveal the regions of activation.

These experiments both involve the computation of phonological information from an auditory speech source. Burton et al. argued that the first experiment

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requires only the perception of the words to complete the judgement task, but that the second experiment involves the additional step of segmenting the speech stream into individual phonemes. In the word production model, there are two lead-in processes associated with phonological encoding: auditory word perception and grapheme/phoneme conversion. In this study, the first experiment only involves the lead-in process of auditory word perception. The second experiment requires the recruitment of processes in addition to auditory word perception, but the processes related to speech segmentation are also associated with phonological encoding operations. In terms of the cortical network proposed in the Indefrey and Levelt study, the results from this study should show activation in the left posterior inferior frontal gyrus (e.g., Broca's area) and the left mid superior temporal gyrus.

Burton et al. reported differential patterns of activation for these two experiments. Both speech conditions displayed activation in superior temporal regions, but only the second condition showed additional activation in frontal areas. From these findings, Burton et al. concluded that phonological processing does not necessarily always recruit frontal areas. This pattern of results is corresponds to the regions specified for phonological encoding in the word production model (see Table 7). The first task only involved auditory word perception and, as such, activation was limited to temporal regions. The second experiment involved additional processing operations which resulted in activation for all areas associated with phonological encoding.

(14)   Table 7.

Predicted Localizations	Area of Activation
▪ Left inferior frontal gyrus	✓
▪ Left mid superior temporal gyrus	✓

The application of Indefrey and Levelt's word production model to the data from this sample of fMRI studies shows that, using a theoretical model of the processes involved in lexical retrieval, it is possible to reliably identify the neural correlates of phonological processing. Although some of the results were not consistent with this model, the majority of findings converged onto the cortical network proposed by Indefrey and Levelt. In the next section, I will apply this model to a group of MEG studies in an attempt to obtain a similar result.

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5.2. MEG Research

MEG has yet to become widely applied to the investigation of language processing. However, in the existing literature using MEG methodology to test the phonological characteristics of language function, there are subtle differences in the patterns of results for phonological processing. Zouridakis et al. (1998) determined that the source of activity was localized to temporal and temporoparietal areas between 200 and 600 msec post-stimulus onset. Simos et al. (1998) observed that the activity sources in their study were localized to the superior and middle temporal gyri, however, differential patterns of response latencies were observed across modalities. Phillips et al. (2000) reported that the localization of their mismatch response was centered in the superior temporal cortex, in the 150-210 msec time window. The results of Phillips et al. (in press) were localized to the supratemporal gyrus in the left hemisphere with the divergence of responses occurring at a series of latency intervals. Evidence from MEG research shows the overall convergence of activation patterns for phonological processing on regions in the temporal cortex, however, differences arise in the temporal properties of this activation (see Table 8.0). The application of the word production model to this data may confirm the localization of phonological processes within the temporal cortices and clarify results associated with the temporal sequencing of such processes.

(15)   Table 8.0

Study	Task Type	Stimulus Type	Modality	Area/Timing of Activation
1. Zouridakis et al. (1998)	Word Identification Task	Word Lists	Visual	• Temporal and temporoparietal regions. • 200-600 msec
2. Simos et al. (1998)	1. Auditory Word Recognition Task 2. Visual Word Recognition Task	Words	Auditory/Visual	• Superior and middle temporal gyri • Auditory: 100, 210, 350 msec • Visual: 350-500 msec
3. Phillips et al. (2000)	Passive Listening Task	Phoneme Sequences	Auditory	• Superior temporal cortex • 150-210 msec
4. Phillips et al. (in press)	Identification Task	Phoneme Sequences	Auditory	• Supratemporal gyrus • 170-230 msec

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5.2.1. Zouridakis et al. (1998)
In order to investigate the degree of hemispheric activation during tasks of language function, Zouridakis et al. (1998) conducted a word identification task using real word stimuli. Participants were required to read a list of real words and identify familiar words in a subsequent recognition memory task. The control condition involved a face recognition task, where participants viewed a series of unfamiliar human face photographs and then completed a
recognition memory test. For each condition, the observed activity was indexed by single equivalent current dipoles (ECD) and a dipole localization algorithm determined which activations were considered significant.

In this study, the word identification task was a task of basic word reading. This task would involve the retrieval of information associated with each lexical form. According to the word production model, word reading engages the lead-in process of visual word recognition. This lead-in process activates the core processing system at the level of phonological code retrieval. This process would involve the selection of a lemma for each lexical concept in the list of word stimuli. Information in the selected lemmas would be used to generate the phonological code for each word. It is this code that would subsequently be recalled for the recognition memory task. Based on the cortical network proposed by Indefrey and Levelt, the pattern of activation for phonological code retrieval should involve the left posterior superior and middle temporal gyri (e.g., Wernicke's area) and the left thalamus and the timing estimates confirmed by the localizations in the Indefrey and Levelt study predict a time window between 275 and 400msec for phonological code retrieval.

Zouridakis et al. identified the localization of dipole activation to superior and middle temporal gyri and temporo-parietal regions for the word recognition task. The average MEG responses for these activations showed that ECDs associated with activation in language areas occurred between 200 and 600 msec after the stimulus onset. The activation in the temporal gyri is consistent with the regions of activation for phonological code retrieval described in the word production model (see Table 9). Although the timing sequence falls mainly within the window predicted by the timing estimates in the Indefrey and Levelt study, responses at the later intervals (>400msec) exceed the bounds of these predictions.

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(16)   Table 9.

Predicted Localizations and Time Course	Area of Activation
▪ Left posterior, superior and middle temporal gyri	✓
▪ Left thalamus	✗
▪ 275 - 400msec	✗

5.2.2. Simos et al. (1998)

Simos et al. (1998) conducted an experiment to explore which cortical areas underlie language comprehension processes. Participants were tested on two continuous recognition memory tasks, the first involving visual word stimuli and the second in the auditory modality. Participants either viewed or listened to a word stimuli list and were required to identify words from the test list in a subsequent recognition memory task. Similar to the previous study, the control condition involved a face recognition task with photographs of unfamiliar human faces used as stimuli.

In this study, the visual task condition triggers the lead-in process of visual word recognition. This process would recruit phonological code retrieval operations, which according to the cortical network for word production, would result in patterns of activation in the left posterior superior and middle temporal gyri (e.g., Wernicke's area) and the left thalamus. The auditory task condition activates the lead-in process of auditory word perception. This process generates phonological encoding processes and, as such, would produce activation in the left posterior inferior frontal gyrus (e.g., Broca's area) and the left mid superior temporal gyrus. Again, the timing estimates from the Indefrey and Levelt study predict responses at 275 and 400msec for both phonological code retrieval and phonological encoding component processes.

For the visual recognition task, Simos et al. reported activation in the superior and middle temporal gyrus and at the temporo-parietal junction. These responses developed between 350 and 500 msec after the onset of the stimulus. For the auditory recognition task, Simos et al. reported activation in the vicinity of the superior and middle temporal gyri. Notably, activation in prefrontal regions was observed for two participants. The auditory responses occurred at three early latency intervals corresponding to 100, 210 and 350 msec post-stimulus onset. The results for both conditions in this experiment converge on the localization evidence based on the word production model. The latency interval for the visual

task slightly exceeds the timing estimates proposed by Indefrey and Levelt and the responses in the auditory condition are earlier than predicted time window.

(17)   Table 10.

Predicted Localizations and Time Course	Area of Activation
• Left inferior frontal gyrus • Left mid superior temporal gyrus • Left posterior, superior and middle temporal gyri • Left thalamus • 275 - 400msec	**? (2 participants)** ✓ ✓ ✗ ✗

5.2.3. Phillips et al. (2000)

Phillips et al. (2000) used a modified mismatch paradigm to determine if phonological category representations are available in auditory cortices. There were two experiments in this study, the first was a phonological condition to determine if the auditory cortex can access phonological category representations and the second was an acoustic condition that manipulated the perceptual category boundary of the stimuli from the main (e.g., phonological) condition. Participants listened passively to a continuum of speech sounds. The phonological condition contrasted stimuli from a /dæ/ - /tæ/ continuum and, in the acoustic condition, the phonological distribution of the stimuli was changed, such that the perceptual category boundary fell between the second and third stimulus.

Both conditions of this study involved a passive listening task for the discrimination of phonological category boundaries. This experiment does not involve the same types of processes as in the previous MEG studies. However, due to the lack of literature using MEG techniques to determine cortical activation for phonological information, I have included these studies, comparing them to processes present in the word production model. In the word production model, there is no lead-in process that corresponds specifically to passive listening tasks, however, the auditory perception of a continuum of phonological stimuli would presumably be comparable to auditory word perception. The lead-in process of auditory word perception activates the core processing component of phonological encoding. In terms of the cortical network proposed in the Indefrey and Levelt study, the results from this study should show activation in the left posterior inferior frontal gyrus (e.g., Broca's area) and the left mid superior temporal gyrus between 275 and 400msec for phonological encoding operations.

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Phillips et al. (2000) reported an early mismatch negativity response in the 150-210 msec latency window localized to auditory cortex. They suggested that their findings support the notion that the phonetic category of voicing is localized to the auditory cortex. Although Phillips et al. did not report activation in frontal regions, their findings do correspond to the temporal regions of the cortical network for word production (see Table 11). The time course of their mismatch response is markedly earlier than the timing estimates provided by the Indefrey and Levelt study.

(18)   Table 11.

Predicted Localizations and Time Course	Area of Activation
▪ Left inferior frontal gyrus	✘
▪ Left mid superior temporal gyrus	✔
▪ 275 - 400msec	✘

5.2.4. Phillips et al. (in press)
In a similar study, Phillips et al. (in press) also used an auditory mismatch paradigm to localize the neural regions associated with phonological classes. Participants initially completed an identification task to establish the perceptual boundaries for each subject across three place of articulation categories (e.g., labial, alveolar, and velar). Again a passive listening task was employed to determine if this category distinction was supported by the auditory cortex. In the phonological feature condition, participants listened to stimuli from these categories randomly dispersed with deviant stimuli. A second acoustic control condition was run to determine if a mismatch response for the first condition could be explained by acoustic properties of the stimuli, rather than properties of the phonological feature categories.

Again, these tasks would activate the lead-in process of auditory word perception. This process would recruit phonological encoding operations. According to the word production model, activation for this operation should be localized to the left posterior inferior frontal gyrus (e.g., Broca's area) and the left mid superior temporal gyrus. The timing estimates from the Indefrey and Levelt study predict that a mismatch response for phonological encoding processes would occur in a latency window between 275 and 400 msec.

Similar to the previous study, Phillips et al. observed a mismatch response at a 170-230 ms time interval. The divergence of responses occurred across the

anterior and posterior channel groups, indicating that the generator of the response was localized in the supratemporal auditory cortex. Again, Phillips et al. did not report activation in frontal regions, however, the patterns of results in temporal cortex remains consistent with cortical network from Indefrey and Levelt's study (see Table 12). The latency interval of the mismatch response in this study is approaching the Indefrey and Levelt's time estimates, but are still slightly earlier than the predicted latency response.

(19)   Table 12.

Predicted Localizations and Time Course	Area of Activation
▪ Left inferior frontal gyrus	✖
▪ Left mid superior temporal gyrus	✔
▪ 275 - 400msec	✖

Similar to the results from the fMRI research, the MEG data for the localization of phonological processing was also consistent with the word production model proposed by Indefrey and Levelt. Although the majority of MEG responses were centered in regions that corresponded to the cortical network for word production, most of the latency results for these responses did not support the timing estimates from the Indefrey and Levelt study. It is likely that the relatively small number of studies in this analysis were not representative of overall latency measures for phonological processing in the MEG literature and it is possible that the analysis of a broader sample of results may show a convergence of latency data with the estimates from Indefrey and Levelt's study.

6. Conclusions, Implications and Directions for Future Research
The investigation of phonological processes using neuroimaging techniques has produced variable results. Poeppel (1996) proposed that much of the variability in PET data investigating phonological processes could be accounted for by reanalyzing the results in terms of a theoretical model of lexical representation. Indefrey and Levelt (2000) applied their model of word production to the results of a sample of mainly PET neuroimaging studies and observed the convergence of these results onto a specific network of cortical regions. They concluded that their model of word production provides a theoretical framework for the analysis of neuroimaging research on the processes involved in the generation of words.

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The purpose of the present study was to apply this model of word production to the results of a group of fMRI and MEG studies to test if these results also corresponded to the cortical network for word production proposed by Indefrey and Levelt (2000). The application of the word production model to results from fMRI and MEG research revealed that the regions of activation in these studies were consistent with the regions outlined in the cortical network from the Indefrey and Levelt study. These results demonstrate that, with this model, it is possible to reliably determine the neural correlates of phonological processing.

The implications of these results for Indefrey and Levelt's theory of word production model are that their processing model can be used as a guiding theoretical framework for the study of phonological processing using neuroimaging techniques. The convergence of evidence from the fMRI and MEG data provide support for the sequence of processing components outlined in this model. In their meta-analysis, Indefrey and Levelt determined that their model provided a theoretical structure for the resolution of inconsistent PET and ERP data on language processing. This study has extended the application of this model to fMRI and MEG research investigating specifically processes associated with the phonological components of the model and confirmed that the resolution of divergent fMRI and MEG data is also possible. Although the results of the fMRI and MEG studies in this analysis were predominantly consistent with the model of word production proposed by Indefrey and Levelt, some of the data remains problematic.

Some of the data from these studies did not converge as expected onto the cortical network proposed in the Indefrey and Levelt study. Although the cortical network for word production predicts activation in both the inferior frontal gyrus and mid superior temporal gyrus for phonological encoding operations, it was rare to find activation in both of these areas for these types of tasks. In fact, only two studies from this analysis reported activation in both of these regions when the lead-in processes of auditory word perception and grapheme-phoneme conversion were activated (e.g., Pugh, et al., 1996; Burton, et al., 2000). Similarly, although Indefrey and Levelt propose activation in the left thalamus for phonological code retrieval processes, none of the studies in this analysis reported subcortical activation in the thalamic regions. The timing estimates from the Indefrey and Levelt study also proved problematic for the MEG research in this study. Indefrey and Levelt predicted latency windows of between 275 and 400 msec for both phonological code retrieval and phonological encoding processing components. Although the latency response data from the MEG studies all showed activation in time windows close to these estimates, most responses were either slightly earlier or later than the window predicted in the Indefrey and Levelt study. It appears that, although the model of word production proposed by

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Indefrey and Levelt accounts for a significant amount of the variability in neuroimaging results, some problems still remain. One possibility for the resolution of remaining issues is the consideration of alternative accounts of language processing.

Psycholinguistic theories of the speech processing propose an interactive system for the generation of complex word forms. Dell (1988) proposed a model of phonological retrieval in which the connections between word and phoneme nodes are bi-directional, allowing feedback between the various levels of representation in the network. This spreading activation allows activated word nodes to retrieve their corresponding constituent phonemes in the lexical network. Connectionist models of phonological processing present an alternative to strictly modular accounts of lexical representation for future research on the cortical basis of phonological processing. Perhaps with greater knowledge of the interactivity between the various types of processes in word production, there can be a better understanding of the neural substrates of phonological processing.

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