The Role of Broca's Area for Phonology During Visual Word Recognition: Investigations using Magnetoencephalography and Transcranial Magnetic Stimulation

Katherine Louise Wheat

PhD

University of York
Department of Psychology
January 2012

Abstract

This thesis explored a possible role of Broca's area (specifically the pars opercularis of left inferior frontal gyrus and neighbouring precentral gyrus; LIFGpo/PCG) in accessing sublexical phonology during visual word recognition. In Experiments 1 to 4, behavioural masked sublexical phonological priming effects were tested during lexical decision and reading aloud in English. No sublexical phonological effects were found during the lexical decision tasks, but significant sublexical phonological priming effects were found during reading aloud. In Experiment 5, masked sublexical phonological priming effects were then tested during a silent reading task using magnetoencephalography. Sublexical phonological priming effects were localised to LIFGpo/PCG within ~200 ms for real word targets and within ~75 ms for nonword targets. This indicates an early sensitivity to sublexical phonological information at LIFGpo/PCG during silent reading of English. In Experiment 6 chronometric functional magnetic resonance imaging guided transcranial magnetic stimulation was used to create focal and transient virtual lesions to LIFGpo/PCG in order to test the hypothesis that the putative early sublexical phonological representations seen at LIFGpo/PCG are functionally necessary for visual word recognition. Dutch participants underwent transcranial magnetic stimulation during reading aloud as compared to picture naming. An early disruption to word reading that was not present for picture naming would be evidence in favour of a necessary role of LIFGpo/PCG during early visual word recognition processes, as opposed to disruption of later speech production processes that are common to reading and naming. Experiment 6 failed to demonstrate that this region is functionally necessary for reading aloud prior to 200 ms in Dutch. The combination of findings in this thesis lead to many possible interpretations, which cannot be ruled in or out without further investigation. As yet, the functional significance of this early LIFGpo/PCG activation, therefore, remains unclear.

Contents

List of Tables

List of Figures

Acknowledgements

First and foremost, I would like to sincerely thank my supervisor, Dr Piers Cornelissen, for his support and encouragement over the past four years. I could not have come so far without his patient teaching and occasional tough love, and without him I probably would not have discovered such a love of research.

Thank you to my research committee, Prof Andy Ellis and Dr Philip Quinlan, for setting the bar high and inspiring me to strive to reach it; to University of York for funding my research; and to Department of Psychology for becoming my second home.

To Prof Leo Blomert and all my colleagues in Maastricht, thank you for providing a warm welcome, along with new challenges and a fresh perspective.

Many thanks to all of the staff at YNiC, including Andre, Becky, Mark, Michael, Garreth, and Sam; none of the work in this thesis could have been conceived without the foundations you provide.

To all of the friends I have made along the way, thank you for providing so much joy through times that were not always joyful. My Friday nights are not the same without you (Jodie, Chris, Yvonna, Pádraig, Annelies, Shane, Alex, Alice, Megan, and everyone else I have met at York, past and present).

To Jon, your unfaltering support has helped me to endure the tough times and enjoy the good times. Thank you for those perfect little things you do every day that drive me crazy and make me giggle.

Finally, many huge thanks go to my loving family, without whom I could never have begun this journey. Mum, Dad, Rachel and Sarah, for inspiring, teasing, distracting, feeding, loving, and understanding me.

Declaration

This thesis comprises the candidate's own original work and has not, whether in the same or different form, been submitted to this or any other University for a degree. Selected aspects of the research described in this thesis have been presented elsewhere.

Wheat, K. L., Cornelissen, P. L., & Hansen, P. C. (2010, June). *Further MEG explorations of early activation in Broca's area during visual word recognition*. Poster presented at 16th Annual Meeting of the Organization for Human Brain Mapping, Barcelona, Spain.

Wheat, K. L., Cornelissen, P. L., & Hansen, P. C. (2011, July). Exploring early activation of Broca's area during visual word recognition using magnetoencephalography. In B. Boets (Chair), *In search for neural correlates of reading and dyslexia*. Symposium conducted at 18th Annual Meeting of the Society for the Scientific Study of Reading, Tampa, FL, USA.

Chapter 1

Overview of the Thesis

This chapter presents an introduction to the research questions addressed by this thesis and an overview of the following chapters.

1.1 Introduction

Literacy is an invaluable ability in modern society. Traditionally, written language has provided the means to communicate ideas across time and space like nothing else. Even in the current era of mobile telephones and video messaging, much of the information we take in daily is in written form. Without basic literacy, therefore, functioning successfully in society becomes very difficult, if not impossible. Job prospects become limited, having a knock-on effect on self-esteem and health (e.g., Vogel & Holt, 2003).

The goal of successful reading is to access meaning from print. The foundations of successful reading lie in the ability to recognise single words (Palmer, Brown, Petersen, & Schlaggar, 2004). This means, first, visually analysing the print to determine the identity and the position of letters within a string. Letter identity is important in distinguishing between words such as *trail* and *train*; position allows distinction between words such as *trail* and *trial*. Later, the letter string must be associated with phonological and semantic information in order to read the word aloud and to understand its meaning. Subsequent processes, leading eventually to sentence comprehension and beyond, are dependent on the core skill of visual word recognition (Palmer et al., 2004). Contextual reading adds many further levels of complication, such as storing a phrase or sentence in working memory and applying knowledge of syntax (Palmer et al., 2004).

In asking ‘how do we read?’ the question is, therefore, ‘how do we extract meaning from a printed stimulus?’ (Rapp, Folk, & Tainturier, 2001). The stimulus in question could be a single word, a sentence, or even a whole novel. Single word reading paradigms allow the study of basic word recognition processes, affording the simplicity and control over experimental designs that could not be achieved with sentence reading due to the extra influence of syntax, sentential semantics, and working memory (Palmer et al., 2004).

The ability to read is not acquired automatically. Although as a skilled reader, reading may feel effortless and automatic, learning to read is a slow and effortful process requiring years of instruction. Speech emerged as the prevailing form of communication around 50000 years ago (DeFrancis, 1989), with the earliest alphabetic writing systems not becoming dominant until less than 5000 years ago (Millard, 1986). This means that, unlike oral communication, evolution has probably not prepared the human brain for the demands of reading. Nevertheless, 90% of people learn to be effective readers; however, despite proper instruction many people show specific problems in acquiring this invaluable skill (Blomert, 2011).

Approximately 10% to 15% of school age children show extreme difficulty grasping basic reading and literacy skills despite having at least average intelligence and being without general learning difficulties (Shaywitz, Escobar, Shaywitz, Fletcher, & Makuch, 1992). These children, whose reading difficulties are not due to sensory acuity deficits, socioeconomic, or other extraneous factors, are often diagnosed with *dyslexia* or *specific reading disability* (Vellutino, Fletcher, Snowling, & Scanlon, 2004). One step towards understanding how to improve reading education and interventions aimed at remediating and possibly preventing the developmental deficits that result in dyslexia is to understand the process of skilled reading (Palmer et al., 2004). Findings from skilled readers can then be used, in combination with investigations into the preconditions for learning to read and the learning process itself, to inform educational practices for teaching reading at all levels, for both typically developing and struggling readers (Rayner, Foorman, Perfetti, Pesetsky, & Seidenberg, 2001).

Deficiencies in phonological awareness and related skills, such as the application of letter–sound correspondence rules, have been shown to be critical predictors of reading difficulties (e.g., Bradley & Bryant, 1983). Phonological awareness is the understanding and awareness that spoken words comprise individual speech sounds (phonemes) and combinations of these sounds (Vellutino, et al., 2004). Numerous studies have shown that training children in phonological awareness benefits word identification, spelling, and general reading ability (for a review see e.g., Vellutino, et al., 2004). Understanding how these improvements relate to neural processes will allow a deeper understanding of the reading network and its normal and disordered functioning; however, important questions regarding phonological access in normal readers remain under debate. As will be explored in Chapter 2, questions regarding when and where in the brain phonological access occurs have yet to be answered.

The aim of this thesis was to explore phonological access during skilled visual word recognition. Phonological access was explored in experimental settings during single word reading, allowing simple experimental manipulations to give insight into the complexities of basic word recognition processes. Although the mature reading system reflects years of instruction, practice and experience, resulting in significant changes to the way visual and auditory information is processed (Blomert, 2011), it remains an important component in the study of reading development (Rayner et al., 2001). Furthermore, the study of the neural processes involved in skilled reading could provide insights not only into disordered reading, but also reveal neural aspects of cognitive representation, computation, and problem solving (Rapp et al., 2001).

The question addressed by this thesis was ‘What is the role of Broca’s area for phonology during visual word recognition?’ The main research directions that arose from this question were (1) an investigation of the nature of any phonological representations that can be seen at Broca’s area during visual word recognition, and (2) an investigation of the functional role of any phonological representations for the task of visual word recognition. In exploring these research directions, the temporal and spatial aspects of phonological representations in Broca’s area were considered. The specific functional necessity of Broca’s area during visual word recognition was also probed.

1.2 Overview of the Following Chapters

1.2.1 Chapter 2: Literature Review

This chapter examines the role of phonology during visual word recognition and how Broca’s area might contribute to phonological processes during visual word recognition. The possible non-linguistic functions of Broca’s area are also reviewed. Evidence from psycholinguistic models, behavioural studies, neuropsychology, and the neuroimaging literature is considered.

1.2.2 Chapter 3: Experiments 1–4

The chapter reports four behavioural experiments which explore the conditions under which masked phonological priming can be achieved in normal adult readers. The two aims of these experiments were to explore behavioural sublexical phonological priming and to design a suitable test of sublexical priming for use in a magnetoencephalography (MEG) experiment. Experiments 1 and 2 used a lexical decision task and Experiments 3 and 4 used a reading aloud task.

1.2.3 Chapter 4: Experiment 5

This chapter reports an investigation of the masked phonological priming using a silent naming task in MEG. The aim was to test whether sublexical phonological priming effects can be seen at Broca’s area by using nonword targets. The timing of these effects was explored in comparison with similar priming effects for real word targets.

1.2.4 Chapter 5: Experiment 6

This chapter reports a transcranial magnetic stimulation (TMS) investigation of the role of Broca’s area during reading aloud as compared with picture naming. Participants were native Dutch speakers reading aloud Dutch nouns and naming the pictures of those same nouns. The target site was selected based on an fMRI localiser task. fMRI-guided chronometric TMS stimulation was then administered during task performance.

1.2.5 Chapter 6: Summary and General Discussion

This chapter presents a summary of the main findings and conclusions from the preceding experiments. The implications and future directions are discussed in light of these and previous findings.

Chapter 2

Literature Review

This chapter examines the role of phonology during visual word recognition and how Broca’s area might contribute to phonological processes during visual word recognition. The possible non-linguistic functions of Broca’s area are also reviewed. Evidence from psycholinguistic models, behavioural studies, neuropsychology, and the neuroimaging literature is considered.

2.1 Introduction

The aim of this review is to explore what is currently understood about the role of Broca’s area during visual word recognition. In order to address this question, first an introduction to the study of visual word recognition will be presented, with a specific focus on the phonological aspects of reading models and behavioural experiments. Second, Broca’s area will be examined, starting with a discussion of Broca’s area and visual word recognition in the neuropsychological literature, followed by a discussion of Broca’s area and visual word recognition in the neuroimaging literature. There will be a specific focus on phonology, but evidence for other linguistic and non-linguistic functions of Broca’s area will be examined. In the final section, the temporal dynamics of word recognition processes will be explored. Here, evidence will be evaluated that asserts Broca’s area as a key neural node in phonological access at an earlier timing than might previously have been predicted. The specific research questions addressed in the following chapters will then be presented, based on the evidence from this review.

2.2 Visual Word Recognition

2.2.1 Introduction

Visual word recognition refers to the basic processes involved in the identification of a single word; namely, the visual analysis of the stimulus, and the recognition of the name and meaning of the word (Rapp et al., 2001). Contextual reading involves many additional processes, such as working memory, but it cannot operate without the successful recognition of single words (Palmer et al., 2004). However, even these most fundamental components of successful fluent reading are not yet been fully understood. Much research is dedicated to asking this key question of visual word recognition; ‘how, where, and when in the brain are individual words recognised?’ (Sereno & Rayner, 2000). In this section, the study of visual word recognition will be explored from models of how the brain might recognise words to experiments exploring word recognition behaviour. From these studies, researchers have aimed to infer *how* the neural systems operate. Later sections of this review will then explore how neuropsychological and neuroimaging studies have been used to provide additional evidence of *where* and *when* in the brain the basic processes of visual word recognition might take place.

2.2.2 Models of Visual Word Recognition

The field of modelling has progressed from simple “verbal models” (Jacobs & Grainger, 1994) to complex computational models aiming to reproduce the actual behaviours of human participants (Coltheart, Rastle, Perry, Zeigler, & Langdon, 2001). Verbal models are depicted in text or a diagram and are often incomplete or under-specified (Jacobs & Grainger, 1994; Coltheart et al., 2001), such as Just and Carpenter’s (1980) model of reading comprehension. The model describes the process controlling eye fixations during reading a passage and includes processes such as extracting the visual features of a word and placing in working memory, activating an internal semantic representation of a word from long-term memory, determining the relationships between words in a sentence, and integrating knowledge across sentences. Although it is a model of reading comprehension, this model is particularly relevant because the authors designed a model of reading comprehension and eye movements that did not explicitly define how the process of visual word recognition is achieved. As shown in Figure 2.1, the model jumps from the stage of extracting the physical features of the text to encoding the word and accessing the lexicon. These processes have been the focus of entire computational models of word recognition, but are shown here as just two boxes. Just and Carpenter's model has since received criticism on levels other than under-specification (Rayner, 1998), however, it serves to illustrate the disadvantage such "box and arrow" diagrams have compared to computational models. Although verbal models allow the expression of creative ideas and the organisation of experimental findings, they also tolerate gaps and inconsistencies in the specification of a theory (Jacobs & Grainger, 1994).

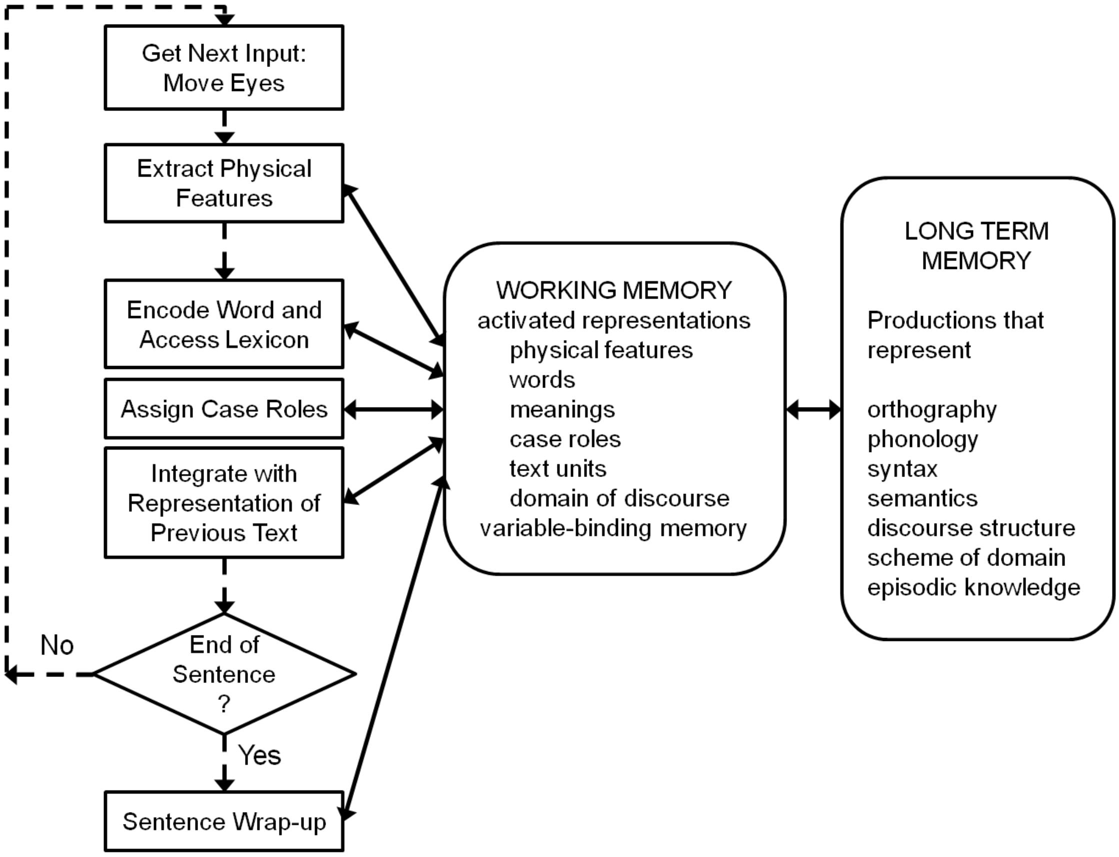


Figure 2.1 The reader model: From eye fixations to comprehension. This model exemplifies the tendency of verbal models to be under-specified. Adapted from Just and Carpenter (1980).

Computational models are programmed simulations of how a system works. They allow theories about a system to be shaped based on mismatches between the performance of the program and observed human behaviour (Coltheart et al., 2001). These models, therefore, provide a test of theoretical assumptions by reproducing specific behaviours, and can also be used to simulate reading disabilities and different teaching and learning methods (Harm & Seidenberg, 1999; Seidenberg, 2005). Because computational models are executable programs, they must be fully specified in order to run, forcing the theorist to address any gaps and inconsistencies (Coltheart et al., 2001). The two computational approaches that will be described here provide examples of two different ways of implementing the structure of the underlying programming, and two different groups of theoretical assumptions on which the computational models are based. These approaches are the dual-route cascaded (DRC) model (Coltheart et al., 2001) and the connectionist, triangle, or parallel distributed processing (PDP), approach (e.g., Harm & Seidenberg, 2004; Plaut, McClelland, Seidenberg, & Patterson, 1996; Seidenberg & McClelland, 1989). First, the basic structure of each approach will be described, before the two approaches are compared and contrasted.

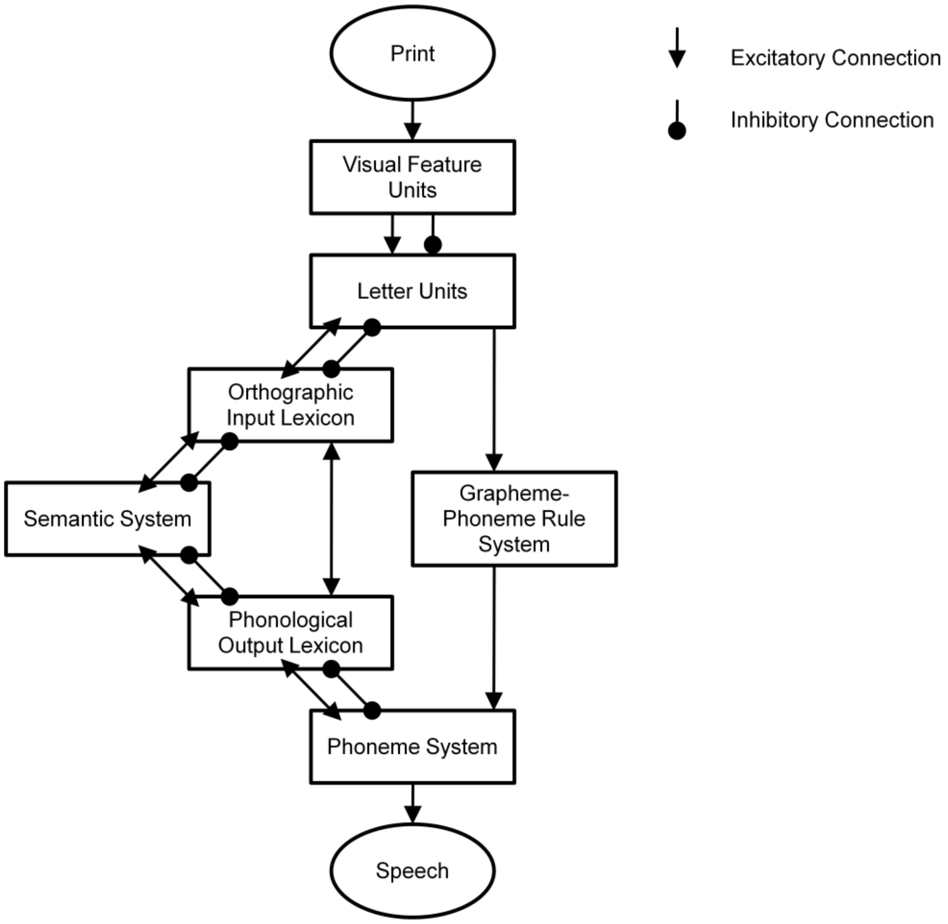


Figure 2.2 Basic architecture of the dual-route cascaded (DRC) model. Adapted from Coltheart et al. (2001).

The DRC (Coltheart et al., 2001) comprises two possible routes from visual input to naming a word aloud. The first is a direct (lexical) route. This route is so called because the visual-orthographic input directly activates the associated orthographic word-form entry in the mental dictionary, or lexicon, from which the appropriate pronunciation can then be accessed, or "addressed". The other, secondary, route takes the visual-orthographic input and uses a rule-based grapheme-to-phoneme mapping process to slowly and serially "assemble" the appropriate pronunciation. This secondary route is termed the "sublexical" route as a whole-word orthographic form is not required to produce a pronunciation, unlike the direct route, where each word is represented by a node in the network from which all information about that word can be retrieved. A verbal model of the basic theoretical architecture underlying the model is shown in Figure 2.2. The two routes allow the model to identify words with irregular pronunciations like *yacht* (via the direct route), and to pronounce newly encountered words and nonwords by rule-based grapheme-to-phoneme mapping (via the sublexical route). Word pronunciation occurs when all of the phonemes of a string have been sufficiently activated, either via the lexical route, or the sublexical route, or by a combination of both routes; though, the lexical route always has a head start. Different activation thresholds and criteria have been used to allow the models to simulate different behaviours (Coltheart et al., 2001).

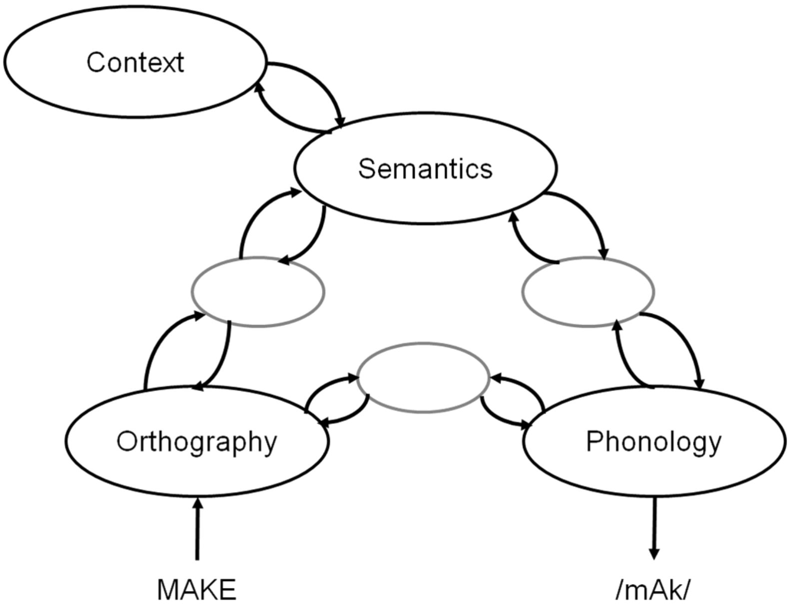


Figure 2.3 The triangle model of Seidenberg and McClelland (1989). Grey ovals represent hidden units in the computational model. Various instantiations of the model have included different subsystems of the basic framework.

In the PDP approach (Harm & Seidenberg, 2004; Plaut et al., 1996; Seidenberg & McClelland, 1989), there are no distinct routes for different types of words. The pronunciations for all strings are generated via a network of weighted connections and "hidden units" in a parallel distributed processing architecture. The "triangle" framework on which the PDP models are based is shown in Figure 2.3. Investigations into the workings of instantiated models have verified that the models do not self-organise into separate routes for reading different types of words, rather, the same weighted connections are used to varying degrees for pronouncing both irregular words and nonwords (Harm & Seidenberg, 2004).

The dual-route (e.g., DRC) and the connectionist (e.g., PDP) frameworks represent divergent views of how the reading system encodes written words. Dual-route theorists propose two separate mechanisms; one for recalling memorised whole words, and one for decoding novel words. The two subsystems of word recognition are proposed to have different governing principles, to be acquired by different mechanisms, and to be located in different brain regions (Seidenberg, 2005). The connectionist framework, on the other hand, has only one mechanism for pronouncing any string and so has been argued to take into account the partial regularities that can be found in irregular words (Seidenberg, 2005). For example, an irregular word such as *pint* shares pronunciation with the regular words *pine* and *pant.* Seidenberg (2005) proposed that dual-route theories fail to make use of the overlaps between regular and irregular words by processing them in completely separate subsystems.

As well as differing in their underlying theoretical framework, the two types of models differ in their computational implementation. For example, the architecture of the DRC model is hard-wired by the model builders in advance, unlike the PDP connectionist models, which use a learning algorithm to progressively adjust the weights of the connections based on a training corpus of stimulus–response pairs (Coltheart et al., 2001). Furthermore, the DRC model contains a "lexicon" of local units for each word the model can read, whereas in PDP models, non-localised representations of words are distributed across multiple units. Because of these differences, the two types of models are able to account for different behavioural phenomena. For example, PDP models are better able to account for consistency effects (inconsistent words have a different pronunciation to other words with the same spelling and are slower to name than consistent words; e.g., *have* shares spelling but not pronunciation with *gave* and *save*) and for the alternative pronunciations seen when participants name nonwords than the DRC model (Zevin & Seidenberg, 2006). However, both models claim to account for the anomalies seen in acquired surface and phonological dyslexia (Coltheart et al., 2001; Harm & Seidenberg, 1999).

Although these and other models can account for many behavioural phenomena exhibited by human participants, this is not sufficient to demonstrate that the model replicates the word recognition system of the brain. Different models can closely simulate human word and nonword reading behaviours via different theories and mechanisms, demonstrating that the same results can be produced from different underlying systems. Models are, however, a useful way to formalise and test theories of visual word recognition, and can be used to make predictions about human behaviour based on the performance of the model.

2.2.3 The Role of Phonology in Visual Word Recognition

The models presented in the previous section stem from different perspectives about how the brain uses and coordinates the different types of information that are potentially available during single word recognition. Here, the specific role of phonological information will be examined in more detail using additional evidence from behavioural studies, including an introduction to the behavioural priming paradigm.

2.2.3.1 Strong Versus Weak Phonology

Most theories of visual word recognition are based around the three components of orthography (letter information), phonology (abstract word–sound information) and lexico-semantics (knowledge of word meanings); the debate comes from how these subsystems interact in skilled reading (Pugh et al., 1996). The three most basic theories of how these subsystems could work together are graphemic-encoding, phonemic-encoding, and dual-encoding (Meyer, Schvaneveldt, & Ruddy, 1974). In graphemic-encoding theories, meaning can be computed directly from the visual representation of the word, without any prior access phonological information; however, there is a broad consensus that phonological information has a role in visual word recognition (Coltheart et al., 2001; Frost, 1998; Rastle & Brysbaert, 2006), ruling out a purely graphemic-encoding approach.

Phonemic-encoding theories propose that the visual representation *must* be converted into a phonological code before the meaning can be accessed. These theories, known more commonly as strong-phonological theories, predict mandatory sublexical phonological processing of written words regardless of the task, in other words, visual word recognition cannot take place in the absence of a phonological representation (Frost, 1998; Rastle & Brysbaert, 2006).

Dual-encoding, or weak-phonological, theories involve both direct-lexical (phonology addressed after word identification) and phonological-sublexical (phonology assembled via grapheme–phoneme mapping) processes. As exemplified by the DRC and PDP models discussed above, dual-encoding models can make use of orthographic and phonological information in different ways, either as two separate routes (i.e., DRC) or in a connectionist network (i.e., PDP). The DRC model is a particularly good example of the weak-phonological perspective that a direct lexical route takes precedence and is supported by a slow, secondary, and nonessential phonological coding route (Coltheart et al., 2001; Rastle & Brysbaert, 2006). From this perspective, phonological encoding processes would only be seen in tasks that explicitly require it, such as rhyme judgements (Frost, 1998).

A pseudohomophone Stroop test has been used to present evidence in favour of automatic phonological processing. In the traditional Stroop test, participants are shown colour words but asked instead to name the colour of the ink, for example, to say *red* for the word *green* printed in red ink. Difficulty in naming the ink rather than reading the word demonstrates automatic word processing. In the pseudohomophone version of the task, the printed words are pseudohomophones; nonwords that are pronounced the same as real words. In this version, the printed word *green* is replaced by the pseudohomophone *grean*. Due to the phonological relationship between the two, if *grean* produces the same interference effect as *green*, this indicates that the phonological code of *grean* has been accessed; necessarily involving sublexical processes, due to the nonlexical status of *grean*.

Dennis and Newstead (1981) showed such a Stroop interference effect for pseudohomophones of colour words. Pseudohomophones slowed participants’ reactions when naming the ink of an incongruent colour word. However, pseudohomophones did not perform as well as real words when the ink and colour word were congruent. Colour words produce a facilitatory effect when naming congruent ink, but this was not true for pseudohomophones. This was presented as evidence that computation of phonology is automatic, even when it interferes with the task, but that it is slower than the direct lexical access available to real colour words. A variation of the Stroop test was also used by Tzelgov, Henik, Sneg and Baruch (1996) with cross-script homophones in Hebrew–English bilinguals. Tzelgov et al.’s task showed that if a nonword written in Hebrew script was phonologically identical to an English colour word (or vice versa) a Stroop interference effect was found. This provides further evidence of automatic phonological processing. A criticism of the Stroop task could be that it requires naming and therefore mandatory computation of phonology in order to complete the task. However, a distinction should be made between the phonological input/encoding processes required to access the pronunciation of *grean* and the phonological output processes required for naming any string. The output code to be computed is that of the coloured ink and the competing phonological code of the written word (which can only be accessed sublexically) is detrimental to the task (Frost, 1998). The evidence, therefore, is in favour of an automatic but slow phonological access, but evidence from tasks that do not require a naming response and show fast access to phonology would provide stronger support for a strong-phonological theory.

A pseudohomophone effect has also been shown in lexical decision experiments. In this case, if the nonword list contains pseudohomophones then participants show slower reaction times when rejecting these pseudohomophones than when rejecting other visually controlled nonwords (e.g., Coltheart, Davelaar, Jonasson, & Besner 1977; Rubenstein, Lewis, & Rubenstein, 1971). This suggests that sublexical phonological information is available to influence the decision process and could be seen as support for fast automatic sublexical phonological access. However, Coltheart (1978) argued that slower reactions times to pseudohomophones provide evidence that because no matching word can be found via a lexical route, slower sublexical processes have sufficient time to occur before a lexical decision can be made, supporting a dual-encoding approach. Van Orden (1987) has since argued that a semantic categorisation task improves on the lexical decision task. Van Orden showed that for a semantic category prompt, such as *FLOWER*, a higher proportion of false alarm errors was seen when the target to be classified was a homophone of a member of that category, such as the target *ROWS*, which is homophonic with *rose*. Because a meaning must be identified, responses cannot be based on perceived stimulus familiarity as they could in lexical decision (see e.g., Besner, Coltheart, & Davelaar, 1984). Also, the task does not require nonwords, the inclusion of which could induce a greater degree of phonological encoding than found in normal skilled reading. Furthermore, in Van Orden's semantic categorisation task, the homophone effect is inferred based on false positives, rather than slower *no* responses in lexical decision. Thus, Van Orden argued this is evidence of automatic and fast access to phonology. Although, in fact, this experiment does not show that this rapid access occurs via sublexical mechanisms because the same result could occur via an output phonological code generated by the direct-lexical route if that code backwards activated alternative meanings, as is possible in the schematic of the DRC (see Figure 2.2). A replication of the experiment by Van Orden, Johnston, and Hale (1988) that extended the finding to pseudohomophones (e.g., falsely categorising *SUTE* as an article of clothing), however, does imply that fast sublexical phonological encoding must be taking place, in disagreement with the slow sublexical route of the DRC.

Finally, evidence in support of a strong-phonological theory where the task does not require computation of any phonological code comes, for example, from Ziegler and Jacobs (1995). Participants were given a target letter (e.g., *I*) and asked whether it was present in the target string. The task only requires the participant to visually search the letters and not to pronounce the string. Where the target string was a pseudohomophone, participants made errors based on the spelling of the real word. For example, a false alarm when presented with *BRANE* due to the presence of *I* in the real word *BRAIN*, and a miss error for *TAIP* due to the absence of *I* in the real word *TAPE*. In this case, the results can be interpreted as the pronunciation of the pseudohomophone activating a shared phonological representation of the real word, and eventually activating the real word orthographic form. The (necessarily) sublexical computation of the phonology of the pseudohomophone is unnecessary for, and detrimental to, the graphemic task, providing further evidence for a strong automatic connection from orthography via sublexical phonology to meaning.

Coltheart et al. (2001) argued that according to their interpretation, the strong-phonological perspective suggests that there must be no direct lexical route. They argued that since there has been no confirmation that such a route does not exist, the evidence for automatic sublexical phonological access is insufficient support for a strong-phonological theory. This is because automatic sublexical phonological access could take place under the weak-phonological perspective that all tasks involve both direct-orthographic and phonologically-mediated processes. In fact, Dennis and Newstead’s (1981) finding of an automatic but slow phonological access could support such a weak-phonological theory. However, Van Orden, Pennington, and Stone (1990) conversely argued that there is no convincing evidence of a direct route in visual word recognition, and that the burden of proof lies with the theorists proposing such a route.

In the preceding sections, models of visual word recognition and the debate surrounding the involvement of phonology have been introduced. Ultimately, theorists use these models and behavioural studies in order to infer properties of the underlying neural organisation of processes involved in reading. As has been shown, multiple models of reading systems can replicate the same phenomena, and behavioural testing does not conclusively support any one theory. Therefore, the evidence presented thus far does not favour any particular model of visual word recognition, and is not sufficient to support either the weak- or strong-phonological perspective. Another paradigm that has yet to be discussed, but that has been widely successful in investigating the role of phonology during visual word recognition, is the behavioural priming paradigm.

2.2.3.2 Masked Priming and Phonology

In behavioural priming, the response to a second stimulus (the “target”) is altered due to the previous presentation of another stimulus (the “prime”). For example, Meyer, Schvaneveldt, and Ruddy (1974) presented pairs of words in a lexical decision task and showed that reaction times to the second member of the pair could be altered based on the relationship between the two words. When graphemic and phonemic information were shared (as in the prime–target pair *bribe–TRIBE*) reaction times to the second item were significantly faster than to controls, and when graphemic but not phonemic information was shared (e.g., *couch–TOUCH*) reaction times were significantly slower than to controls. Furthermore, lexical decisions are also faster when targets are primed by the relevant semantic category (e.g., *bird–ROBIN;* Neely, 1977) or a semantically related word (e.g., *bread–BUTTER;* Meyer, Schvaneveldt, and Ruddy, 1972). Priming effects can also be seen when multiple stimuli intervene between the prime and target. In a perceptual identification task with visible primes, Humphreys, Besner, and Quinlan (1988; Experiments 1 & 2B) showed a significant advantage of repetition priming (e.g., *lost–LOST*) in the percentage of correct target identifications. This was true even when the prime and target were separated by seven trials, such as *lost–NEAR* followed seven trails later by *xxxx–LOST*. This effect of repetition priming within a list was also shown by Forbach, Stanners, and Hochhaus (1974) where, in a lexical decision task, the response time to words decreased on subsequent presentations of the same word. In all of these examples the primes were clearly visible and required a response from the participant. In visual word recognition, therefore, shared properties such as phonology, semantics, and identity can influence the speed or accuracy of the response to a subsequently presented target word. This type of priming has been used to argue, for example, that phonology plays a significant role in visual word recognition (Meyer et al., 1974). However, the visible primes leave open the alternative interpretations that participants are able to respond strategically by predicting the target on the basis of the prime, or that episodic memory effects influence the results (Evett & Humphreys, 1981).

In *masked* behavioural priming, the prime stimulus is presented for a brief duration and preceded (sometimes also followed) by a pattern mask, such as a row of hash marks. The presentation procedure masks the identity of the prime and the participant is usually unable to report its' presence. The specific masking procedures vary and the targets can either be clearly visible, as in a lexical decision task (e.g., *mask–prime–target*; Forster & Davis, 1984), or masked, as in a perceptual identification task (e.g., *mask–prime–target–mask*; Evett & Humphreys, 1981). As in unmasked priming, the degree of overlap between the prime and target is varied, and the effect on a behavioural response to the target is measured. The premise behind masked behavioural priming is that if the response to the target can be affected without awareness of the prime, automatic and unconscious processes can be studied without interference from any strategic or memory effects (Dehaene et al., 2001). The idea being that the response to the target will be affected by the previous presentation of the prime where the two share neural processes. For example, if a neural representation of the prime has been partially or fully activated when the target is presented, then a representation of the target may be more easily or less easily available for activation (depending on how they are related) resulting in a change in reaction time or accuracy of response.

Here, the focus will be on masked *phonological* priming, although, masked priming has also been used to study other components of visual word recognition. For example, repetition or identity priming (where prime and target are the same, but usually presented in different cases to minimise visual feature overlap, e.g., *lost–LOST*) looks at whole-word processing (e.g., Evett & Humphreys, 1981). This type of priming is thought to investigate general mechanisms of visual word recognition (Humphreys et al., 1988). Orthographic processes have been studied, for example, using transposed letter priming. Forster, Davis, Schoknecht, and Carter (1987) found that priming effects for transposed letter primes (e.g., *anwser–ANSWER*) were no different from identity primes, and stronger than for one-letter-different controls (e.g., *antwer–ANSWER*), which has important consequences for models of orthographic encoding (see e.g., Perea & Lupker, 2003). Semantic processes have been studied by using masked primes with a semantic or associative link to the target word. For example, Fowler, Wolford, Slade, and Tassinary (1981; Experiments 5 & 6) showed that semantically related masked primes (e.g., *ocean–WATER*) resulted in faster lexical decisions than for unassociated pairs (e.g., *ocean–BEGIN*).

Lukatela and Turvey (1993) demonstrated masked phonological priming using homophonic words. Their prime stimuli were homophones of words that have a semantic relationship to the target. For example, *toad* and *towed* are homophonic, but only *toad* is semantically related to *frog*. Because priming occurred for *towed–FROG* (demonstrated by faster reaction times for naming *frog* primed by *towed*, than for the orthographic control condition *trod–FROG*), Lukatela and Turvey argued that the phonological relationship between *towed* and *toad* allowed semantic priming of *frog* via mandatory computation of a phonological code. Furthermore, because the time between the onset of the prime and the onset of the target (stimulus onset asynchrony; SOA) was only 100 ms, the authors claimed that a phonological code was rapidly available to influence subsequent processing, though a distinction between input and output phonology cannot be made.

Further evidence of mandatory, rapid computation of phonology comes from priming studies using masked pseudohomophone primes. For example, a series of masked pseudohomophone priming experiments from Ferrand and Grainger in French (1992; 1993; 1994) and Lukatela, Turvey and colleagues in English (Lukatela, Eaton, Lee, & Turvey, 2001; Lukatela, Eaton, Sabadini, & Turvey, 2004; Lukatela, Frost, & Turvey, 1998) have demonstrated that for a word target such as *CLIP*, reaction times on a lexical decision task were faster when preceded by a pseudohomophone prime (e.g., *klip*), compared to an orthographically matched control prime (e.g., *plip*). Because the primes must be accessed sublexically and are not available for conscious report by the participant, this suggests that sublexical phonological input is rapidly encoded, outside of strategic conscious control.

The use of strategic control by the participant in phonological priming effects was further ruled out in a masked priming study by Ferrand and Grainger (1992; Experiment 2). In previous primed lexical decision experiments (e.g., Ferrand & Grainger, 1992; Experiment 1), a pseudohomophone prime was always followed by a real word target and never by a nonword target. Although the primes were masked, if the participants were in fact aware of the identity of the prime, they might use strategies to predict the identity of the target from the prime, influencing reaction times. Thus, the authors added primed pseudohomophones to the target list of a lexical decision task; for example, prime target pairs such as *coue—COUS* (French nonwords that are homophonic to each other and to the real French word *coup*). A pseudohomophone prime could then be followed by either a real word target or a pseudohomophone target, so both *yes* and *no* lexical decision responses would be possible following a pseudohomophone prime. The results showed that pseudohomophones continued to facilitate *yes* responses to real words compared to orthographic controls, despite the fact that pseudohomophone primes were no longer predictive of a *yes* response. Even if the participants were able to identify the primes, they could not use this information to their advantage, thus demonstrating a process outside of the conscious control of the participant.

Because the pseudohomophones are not words, and therefore could not be read via a direct-orthographic lexical route, this suggests that pseudohomophone priming occurs due to sublexical phonological access. Lukatela et al., (2001) further investigated the nature of the phonological representations that are primed during masked priming. They used prime target pairs such as *zea—SEA* and *vea—SEA* to investigate whether the shared phonetic features of the alveolar fricatives /z/ and /s/ would produce faster reaction times than an initial consonant sharing fewer phonetic features, such as the labio-dental fricative /v/. The results confirmed a reaction time advantage for primes with a greater degree of phonetic feature overlap in their initial consonant. A further experiment verified that the effect was not due to overlap of visual features (using the letter feature analysis of Evett & Humphreys, 1981); therefore reinforcing the inference that phonological priming effects occur via sublexical mechanisms.

There has, however, been debate around whether masked phonological priming effects are simply false positives, and if not, whether they are relevant to normal visual word recognition processes (Coltheart et al., 2001; Rastle & Brysbaert, 2006). This debate has been fuelled by the sometimes fragile effects of phonological priming, which have been disrupted by factors such as the proportion of related primes and targets (Brysbaert & Praet, 1992; Verstaen, Humphreys, & Olson, 1995) or the lighting conditions of the test room (Lukatela et al., 1998; Lukatela, Frost, & Turvey, 1999; Frost, Ahissar, Gotesman, & Tayeb, 2003). Rastle and Brysbaert (2006), therefore, created and tested a typical masked phonological priming paradigm, based on their meta-analysis of masked priming studies in English, spanning 22 years of research. The authors' meta-analysis revealed a small to medium effect size (r = .20–.30) for masked phonological priming, and their initial priming experiment confirmed the existence of a masked phonological priming effect in a lexical decision task. The authors strictly controlled for the amount of orthographic overlap between the primes and targets to ensure the effect was not, in fact, due to orthographic priming. They also conducted a further lexical decision experiment where pseudohomophones were included in the target list; similar to the procedure of Ferrand and Grainger (1992) described above. Participants were significantly faster to make lexical decisions for words preceded by masked phonological primes than graphemic controls, even in the case where phonological encoding is discouraged by the presence of pseudohomophone targets, suggesting an automatic process. Because pseudohomophones primes could be followed by a word or a nonword, this confirmed that participants were not using knowledge about the pseudohomophone primes to strategically respond to the target word.

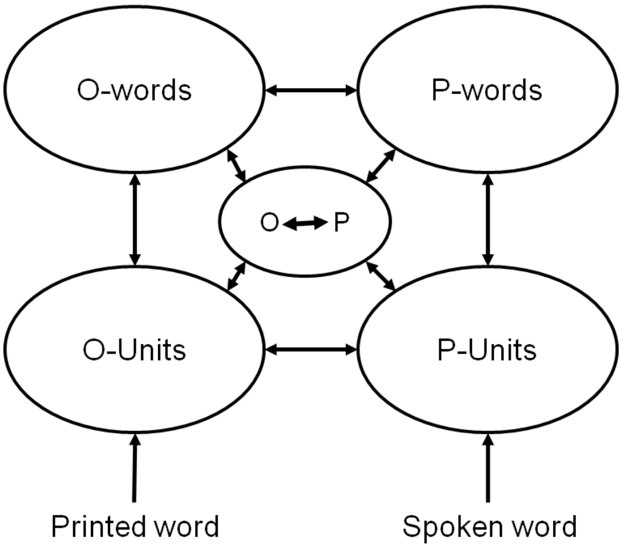


Figure 2.4 Basic architecture of a bimodal interactive-activation model of word recognition. The architecture extends that proposed by Grainger and Ferrand (1994) by including a central process for orthography-to-phonology mapping, which receives activation from orthographic input units (O-units) and phonological input units (P-units), and sends on activation to whole-word orthographic (O-word) and phonological (P-word) representations. Adapted from Grainger, Muneaux, Farioli, & Ziegler (2005).

Rastle and Brysbaert’s (2006) study also attempted to simulate masked phonological priming effects using the DRC model of Coltheart et al. (2001). The authors concluded that the standard DRC model parameters were unable to reproduce phonological priming during lexical decision, as the influence of the orthographic aspects of primes was too great and the phonological aspects were processed too slowly. Further simulations were carried out after changing the properties of the model such that

(1) the phonologically mediated route operated in a parallel rather than serial way, (2) the relative contribution of the phonological route was strengthened, and (3) orthographic inhibition processes were reduced. After significant modifications, the model came close to simulating fast phonological priming effects, but only at the expense of the model's ability to read aloud exception words. The model therefore cannot account for both of the human behaviours of phonological priming and irregular word reading using the same set of parameters.

The interactive activation group of models, however, has evolved in order to account for the priming of heterographic homophones (words with different spellings but pronounced identically, e.g., *threw–through*). The basic architecture stems from McClelland and Rumelhart's (1981) interactive activation of orthographic encoding, adapted by Grainger and Ferrand (1994), resulting in the bimodal interactive-activation framework for word recognition (Ferrand & Grainger, 2003; Grainger & Ferrand, 1994; Grainger, Diependaele, Spinelli, Ferrand, & Farioli, 2003; Jacobs, Rey, Ziegler, & Grainger, 1998; Ziegler, Muneaux, & Grainger, 2003) In the bimodal interactive-activation model (BIAM; see Figure 2.4), a printed word first activates a sublexical orthographic code (O-units). The orthographic code then activates the central orthography-to-phonology mapping process. It is this fast parallel sublexical mapping of letters onto phonemes that allows the model to simulate fast phonological priming effects (Diependaele, Ziegler, & Grainger, 2010). Crucially, in the BIAM, orthography is rapidly mapped to an input phonological code, rather than the output phonological code of the DRC. Thus the model is able to account for masked phonological priming effects, whilst still being able to discriminate between words and nonwords via an orthographic route (Diependale et al., 2010).

Finally, masked priming is similar to, but distinct from, backward masking (e.g., Allport, 1977; Kahneman, 1968; Naish, 1980; Perfetti, Bell, & Delany, 1988; Raab, 1963; Spencer & Shuntich, 1970). In backward masking, a target is presented, immediately followed by a masking stimulus. The participant sees a presentation sequence such as *target–masking-stimulus–pattern-mask* (where the target and masking-stimulus are shown very briefly) and is asked to report any words they saw. Whereas the prime in masked priming might facilitate the response to the target when they are related, the masking stimulus is said to produce less disruptive masking when it is related to the target. For example, under phonological masking conditions, Naish (1980) presented participants with target words such as *ewe* masked by a homophone, such as *you*, or a pseudohomophone, such as *yoo*. The masking conditions made the target difficult to identify, but identification performance was better in the phonological masking conditions (65.8% and 86.5%) compared to a neutral masking stimulus, such as *bag* (52.5% and 72.0%).

Based on evidence from both backward masking and masked priming, Berent and Perfetti (1995) proposed their two-cycles model of phonological assembly. The two-cycles model is so-called because consonant and vowel phonology are assembled by separate processes. Consonant phonology is assembled in an initial automatic process, and vowel information is added in a second, slower and controlled process. The model supports a strong role of phonology in visual word recognition, as it assumes that initial activation is always based on the assembled consonant phonology, which is supported, but cannot be overridden, by a direct-lexical route. Vowel phonology is then computed using lexical information. The claims of the two-cycles model were supported in a series of priming and backward masking studies by Berent and Perfetti (1995; Berent, 1997), though the model has not been implemented in a computational form. However, Lukatela and Turvey (2000) argued that their series of masked primed lexical decision experiments did not support the two-cycles' claim that consonant phonology is assembled first. Though, their data did not rule out the multilinear phonological theory that assembled phonology consists of levels of structural organization and therefore multiple levels of orthographic-to-phonological mapping.

2.2.4 Summary

This section has explored the contribution of models and behavioural studies to the field of visual word recognition. Computational models have significant advantages over verbal models, which can be incomplete and under-specified. Computational models can be used to simulate and predict human behaviours, allowing researchers to make inferences about how the brain might perform these processes. However, no model is able to reliably reproduce all of the human behaviours seen during visual word recognition tasks. In particular, masked phonological priming has been a source of difficulty. The masked phonological priming task has been used as evidence to support the strong-phonological perspective that initial access to phonology is a rapid and mandatory process of visual word recognition. The DRC model, a weak-phonological model, was unable to reproduce these masked phonological priming effects, bolstering support for the strong-phonological theory. However, the fast parallel mapping of the

BIAM is able to account for these effects without compromising nonword reading ability.

The evidence presented is thus far inconclusive. There is evidence to suggest that a phonological code is quickly accessed without intention or strategic control, corroborating the strong-phonological theory. Though, these findings alone cannot support the claim of strong-phonological theories that phonological coding is the only route to visual word recognition, as this argument would need to be substantiated by evidence from neuropsychological or transcranial magnetic stimulation studies showing that visual word recognition is impossible without phonological processing (Rastle & Brysbaert, 2006).

This section has addressed theories and studies that aim to infer *how* visual word recognition might operate. The next section additionally examines evidence of *where* in the brain visual word recognition takes place by exploring the contribution of neuroimaging studies and neuropsychology. This section will include an introduction to the region known as “Broca’s area”.

2.3 Visual Word Recognition in the Brain

2.3.1 Introduction

Returning to the key question of visual word recognition; how, where, and when in the brain are individual words recognised? (Sereno & Rayner, 2000), the studies presented in the previous section aimed to infer *how* the brain might work to recognise single words. These inferences have been drawn from verbal models, computational models, and behavioural studies, all of which attempt to look inside the ‘black box’ of the brain and understand how these complex cognitive processes take place. In this section, neuropsychological and neuroimaging evidence of the visual word recognition network in the brain will be presented, in order to examine what is currently known about *where* visual word recognition processes take place in the brain.

2.3.2 Neuropsychology and Reading Disorder

Neuropsychological case studies have been used to make inferences about the processes involved in normal reading. One group of disorders from the neuropsychological literature that have been particularly informative for the study of reading and visual word recognition are the acquired dyslexias. Unlike developmental dyslexia, which hinders the acquisition of fluent reading skills from the outset, acquired dyslexia occurs after brain damage and is studied in previously literate adults. There are many varieties of acquired dyslexia, such as deep, phonological, letter-by-letter, surface, and visual dyslexia (see e.g., Marshall & Newcombe, 1973; Patterson, 1981). Each is characterised by the presence or absence of difficulty with particular types of word properties, such as irregularity, concreteness, frequency, and so on (Patterson, 1981).

A key finding from the neuropsychological literature on acquired dyslexia comes from Marshall and Newcombe’s (1973) six case studies of patients, categorised into three varieties of acquired dyslexia; deep, visual, and surface dyslexia. Marshall and Newcombe reported a distinction between patients who were able to read nonwords, but completely unable to read irregularly spelled words (e.g., *debt*), and patients who showed the opposite pattern. This “double dissociation” between patients showing the reverse pattern of deficit and spared function (in situations where the two functions are sufficiently closely related to draw meaningful conclusions) has been described as the gold standard for cognitive neuropsychology (Patterson & Plaut, 2009), and has been particularly relevant to the debate surrounding phonological access in visual word recognition. Theorists have argued that the dissociation between patients who are unable to read nonwords and patients who are unable to read irregular words demonstrates damage to two distinct word recognition routes (e.g., Coltheart et al., 2001). One set of patients show damage to the direct lexical route, but a spared grapheme–phoneme route, and vice versa for the other group of patients. Evidence of spared word reading in patients apparently completely unable to use a phonological route to reading—as indicated by an inability to read nonwords aloud, inability to judge whether two words rhyme without using visual clues, and an inability to judge whether words are pseudohomophones—contradicts the strong-phonological position that word recognition can only take place via phonological access.

There are, however, caveats that must be considered when interpreting neuropsychological evidence. First, in considering a single case study, the patient’s prior level of functioning is not usually known, damage can include multiple brain regions, and patients can have a number of confounding health problems (Patterson & Plaut, 2009). The damaged areas may also be involved in general functions other than the functions that appear to be impaired (Démonet, Thierry, & Cardebat, 2005). For example, a region that is highly specialised for a particular role in language may also have other more general cognitive functions. A further limitation of lesion deficit case studies is that lost abilities may be a direct result of damage to the lesioned area or a result of the disconnection of undamaged areas (Price, 2000). Therefore, it cannot necessarily be inferred that a damaged area is necessary for a particular function, as the deficit may result from damaged connections that coincidentally pass through the observed damaged region. The accumulation of evidence from multiple patients with corresponding brain lesions and similar behavioural symptoms is therefore useful in cognitive neuropsychology; however, in comparing patients there may be confounds such as response bias effects. For example, if one patient prioritises accuracy but another thinks it is more important to produce any response at all, they might show a difference in the rates and types of errors, even though they have the same underlying deficit (Patterson & Plaut, 2009). Furthermore, unlike in studies of undergraduates, groups of patients are not necessarily of similar ages, premorbid intelligence, or background (Shallice, 1988). Double dissociations are particularly useful, because a difference in performance between two tasks does not on its own imply that the two tasks result from different processes; one task may just be easier than the other (Shallice, 1988). Dissociations have been used primarily to infer that two tasks are performed by separate mental functions, modules, or processes (Dunn & Kirsner, 2003). However, Plaut (1995) and Juola and Plunkett (2000) have shown that lesions to connectionist models, which do not specify clear divisions of functions or modules, can also produce double dissociations, demonstrating that a connectionist, rather than modular, neural organisation is also a valid interpretation of patient data (Davies, 2010). Though, the lesions of Plaut were, in fact, specifically applied to different aspects of the network in order to produce the different deficits. The lesions of Juola and Plunkett, however, were applied randomly across the connections of the network. Finally, the pattern of behaviours exhibited by a patient or group of patients may result from a complex interaction between any deficits due to the particular damage and any coping strategies developed (intentionally or otherwise) by the patient following the injury, including any neural reorganisation or compensation by other brain regions (see e.g., Saur et al., 2006).

2.3.2.1 Introduction to Broca's Area

Leaving the limitations of neuropsychology aside, another important finding from the lesion deficit literature (which, though not specifically related to visual word recognition, is relevant for this review) comes from patients with aphasia. In 1861, Broca reported a 51 year old man with severely impaired speech articulation, but with other mental abilities relatively intact (Broca, 1861a; 1861b). This patient was the first of a group of patients with similarly impaired speech articulation who were found, post-mortem, to have similar regions of brain damage (Broca, 1863; 1865). Later, Wernicke (1874) reported patients who showed impaired speech comprehension and who had a different pattern of brain damage. The dissociation of these acquired disorders, termed Broca's and Wernicke's aphasia, led to the formulation of several general principles: (1) brain damage does not cause a general reduction in language ability, but disrupts particular aspects more than others, (2) the type of disruption is linked to the location of the damage, and (3) this selective disruption is related to the organisation of language in the brain (Berndt & Caramazza, 1980). This represented a significant advancement in the understanding of the organisation of language, and the organisation of the brain in general. Broca's and Wernicke's areas, as they have come to be known, are shown in Figure 2.5.

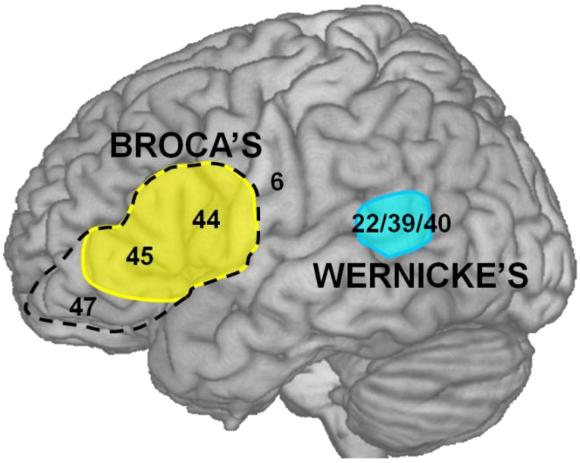


Figure 2.5 Broca's and Wernicke's areas. Broca's area (yellow) covers Brodmann areas (BA) 44 and 45 and Wernicke's area (blue) covers parts of BA 22, 39 and 40. Broca's area covers part of the inferior frontal gyrus (black dashes), which also includes BA 47. BA 6 is the precentral gyrus.

Broca's area is particularly important for this review because, as will be seen in the next section, neuroimaging studies have associated it with phonological processes during visual word recognition. The region encompasses the pars opercularis and pars triangularis of the left inferior frontal gyrus (IFG), which are covered by Brodmann's areas (BA) 44 and 45, respectively (see e.g., Nishitani, 2005). The cytoarchitecture of

Broca's area is unique in that it contains both the granular nerves cells (usually seen in prefrontal regions) that undertake associative, multimodal, and amodal roles, and the agranular nerves cells that are usually seen in motor-premotor unimodal regions (Judaš & Cepanec, 2007). This dual-nature of Broca's area's cytoarchitecture, shown by its intermediate position between granular and agranular cortex, is an unresolved issue in neuroscience, as it remains unclear whether to classify IFG (also including pars orbitalis; BA 47) as a unique whole region, or as being composed of other cytoarchitectonic regions (Judaš & Cepanec, 2007).

More recently, there has been debate surrounding the homogeneity of both the structural damage and the aphasic symptoms of Broca's aphasics (see e.g., Keller, Crow, Foundas, Amunts, & Roberts, 2009, for a review). For example, although Broca focused on reporting damage to the surface of the cortex, many of the patients also showed extensive subcortical damage extending beyond the region typically defined, since Broca's reports, as Broca's area (Keller et al., 2009). Furthermore, it has been argued that Broca's aphasia in fact covers a range of aphasic syndromes (Alexander, Naeser, & Palumbo, 1990) and damage to Broca's area can produce a variety of speech and language deficits, in modes other than speech production (for reviews see e.g., Davis et al., 2008; Grodzinsky & Amunts, 2006).

Word and nonword reading performance are not typically tested or described in case studies of Broca's aphasia (Fiez & Petersen, 1998) and testing reading proficiency in aphasics is difficult due to the potential confound of speech production problems on measures of reading aloud (Boccardi, Buzonne, & Vignolo, 1984). However, Benson (1977) reported that out of 61 patients with Broca's aphasia, 51 also presented with alexia. Although, Benson did concede that deficits other than a literal alexia could be behind the apparent reading difficulty, such as gaze paresis, an inability to maintain verbal sequences, or an inability to comprehend syntactic structure. Boccardi et al., (1984) therefore, tested their group of 42 mild to severe Broca's aphasics using non-verbal tests of word and sentence reading. In the word reading test, patients were asked to choose the appropriate picture to match a written word. In the sentence reading test, patients were instructed to follow a written command. No patients were found to have severe alexia (<50% on both tests), 25 patients had mild to moderate alexia, and 17 patients showed no alexia (>80% on both tests). Thus, Boccardi and colleagues showed co-occurrence of aphasia and alexia, but did not find as strong an association as Benson. Braber, Patterson, Ellis, and Lambon Ralph (2005) suggested that Broca's aphasics show a general phonological impairment that is evident in repetition and reading of words and nonwords and in sentence completion. In all three tasks, the patients made more errors for nonwords than words, as would be expected for a phonological deficit. Patients also showed more difficulty with the reading task than the repetition task and only 5 out of 10 patients were able to complete all aspects of the most difficult sentence completion task. These tasks all required spoken responses, which must be impaired for a diagnosis of Broca's aphasia. However, the results demonstrated that, rather than a global production deficit, the nature of errors made by Broca's aphasics in speech production is sensitive to lexicality and other linguistic and phonological aspects of the task and stimuli.

2.3.2.2 Summary

As discussed above, neuropsychology has provided the fields of reading, psycholinguistics, and visual word recognition with significant advancements in the understanding of how and where in the brain these processes occur. Some important caveats in the interpretation of lesion deficit studies have been discussed, including the limitation of double dissociations in distinguishing between modular and connectionist type neural organisation. Furthermore, when inferring the localisation of functions from lesion deficit cases, it is important to remember that this may be of limited use in cases where brain damage is extensive and where there has been time for neural reorganisation since the damage occurred. Despite these caveats, lesion deficit studies represent a major contribution to cognitive neuroscience, particularly before the advent of neuroimaging techniques. However, Shallice (1979) argued that the most reliable understanding comes from combining patient data with data from normally functioning participants and revealing corroborating findings. With this in mind, in the next section the functional neuroimaging of visual word recognition will be discussed.

2.3.3 Neuroimaging and the Visual Word Recognition Network

In this section, an overview of findings from functional neuroimaging will be presented in order to explore what these methods can tell us about visual word recognition in the brain. Although contradictions in the literature exist, a broad consensus of the nodes of the reading network has arisen from many neuroimaging studies, building on the foundations of knowledge from neuropsychological assessments (Mainy et al., 2008). As Fiez and Petersen (1998) argued, neuroimaging has an obvious role in localising regions that are active during task performance, but using this knowledge to infer how reading takes place presents a greater, yet more rewarding, challenge.

Although task differences (in particular, the choice of control task) and variations of imaging technique have resulted in some discrepancies across studies (Palmer et al., 2004), functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have been fundamental in moving forward the investigation of single word reading and building on the knowledge of the reading network gained from neuropsychological and computational modelling approaches. Sophisticated manipulation of task and stimuli can further reveal not just where in the brain activity can be seen, but how that pattern of activity changes according to different experimental conditions (Palmer et al., 2004). Converging evidence from many neuroimaging studies has given a broad view of the brain regions involved in the different aspects of visual word recognition (for reviews see, e.g., Dehaene & Cohen, 2011; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Turkeltaub, Eden, Jones, & Zeffiro, 2002; Vigneau et al., 2006; Visser, Jefferies, & Lambon Ralph, 2010). For example, visual-orthographic analyses are generally localised to left occipitotemporal regions (Dehaene & Cohen, 2011; Jobard et al., 2003; Turkeltaub et al., 2002) and semantic and phonological processes have been broadly linked to left anterior temporal, left inferior parietal, and left inferior frontal regions (Bookheimer, 2002; Vigneau et al., 2006; Visser et al., 2010). These three aspects of visual word recognition will be discussed in turn, with a particular focus on phonology and Broca’s region.

2.3.3.1 Neuroimaging and Orthography

Reading begins with the visual information conveyed by marks on a page that conform to the orthographic rules of the language. A fundamental question for theorists is how, where, and when the brain recognises that visual input as print. As reading is relatively recent in human history, it is unlikely that this happens in a genetically pre-determined process via an evolutionarily dedicated cortical system (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2011). However, research has shown that literacy is related to significant changes in the brain’s response to written language (Dehaene et al., 2010), thus exposure and learning may have resulted in cortical regions that are exclusively devoted to visual word recognition.

A key brain region for visual word recognition is the left ventral occipitotemporal cortex (vOT). Many studies have shown that vOT responds more strongly to written words and orthographically legal letter strings than to false fonts or consonant strings (e.g., Cohen et al., 2000; Baker et al., 2007; Reinke, Fernandes, Schwindt, O'Craven, & Grady, 2008; Woodhead, Brownsett, Dhanjal, Beckmann, & Wise, 2011). Furthermore, researchers have demonstrated progressive neuronal tuning to orthographic information along the occipitotemporal gyrus (also known as the fusiform gyrus); from visual features more posteriorly (Dehaene et al., 2004), through to whole word forms at a specific patch of cortex typically localised around MNI coordinates $x = -44$, $y = -58$, $z = -15$ (Jobard et al., 2003). However, this patch of cortex, often termed the "visual word form area" (VWFA), is a source of controversy for theorists. The central argument is whether this region is a highly specialised site of orthographic knowledge (e.g., Dehaene & Cohen, 2011) within a serial feedforward word recognition system, or whether it performs a more general role in allowing visual stimuli such as writing and pictures to access the predominantly left-lateralised language system within a bidirectional interactive network (e.g., Hellyer, Woodhead, Leech, & Wise, 2011).

Evidence in favour of feedforward word recognition at vOT includes the finding by Dehaene, Le Clec'H, Poline, Le Bihan, and Cohen (2002) of VWFA activation during a same-different task in fMRI. VWFA showed a consistent event-related response profile for written words that was independent of the semantic category of the words, and was consistent despite variations in the size and case of the stimuli. A strong response was also seen for written pseudowords, but no response was seen for auditory presentations of words or pseudowords. Thus, the authors concluded that VWFA carries out prelexical coding of visual orthographic information, invariant of location, font, and size.

Kronbichler et al. (2004) showed that, during a silent reading task in fMRI, VWFA activity was modulated by the frequency of the presented word, which they argued showed that the VWFA is involved in recognising whole words rather than prelexical coding. Their study showed decreasing activation in VWFA (and other occipital and frontal regions) in response to increasing word frequency, with the lowest level being pseudowords. The authors controlled for other stimulus properties such as string length, syllable length, and bigram frequency. The effect of bigram frequency may, however, have confounded the results. The authors reported that they controlled for this variable, but did not report any statistical test to say that the bigram frequencies were not significantly different across groups, and the values reported show a trend for bigram frequency to increase as word frequency decreases. Although, the trend does not appear strong enough to rule out a whole-word interpretation of the results presented by Kronbichler et al. Moreover, Glezer, Jiang, and Riesenhuber (2009) showed neural tuning to whole real words at VWFA using an fMRI rapid adaptation paradigm. Glezer et al. demonstrated that for real words there was significantly more adaptation for repetition (e.g., *boat–boat*) than for one-letter-different (e.g., *coat–boat*), which produced the same amount of adaptation as a completely different word (e.g., *fish–boat*). However, for pseudowords, although repetition produced the most adaptation (e.g., *soat–soat*), the one-letter-different condition (e.g., *poat–soat*) showed significantly more adaptation than a completely different pseudoword (e.g., *hime–soat*). The authors proposed that the results indicated tight neuronal tuning to whole words in VWFA, with broader tuning to pseudowords, which would be compatible with an experience-driven improvement in tuning through extensive exposure to real words.

In contrast, other studies have shown that the same vOT region is active in tasks other than visual word recognition, suggesting that the label *VWFA* may be inappropriate. Price and Devlin (2003) presented a review of 18 studies that showed activation within 6 mm of the site Dehaene et al. (2002) reported as VWFA. Price and Devlin showed that this region was active, for example, when viewing, naming and performing actions to pictures of objects (e.g., Moore & Price, 1999), when reading Braille (Büchel, Price, & Friston), and when repeating and making decisions to auditory words (Price, Winterburn, Giraud, Moore, & Noppeney, 2003; Thompson-Schill, Aguirre, D’Esposito, & Farah, 1999). As activity was seen when no visual stimuli were presented, Price and Devlin, therefore, argued that this vOT region is not exclusively devoted to either visual form or visual word form processing. The authors presented three possible alternatives for the functional role of vOT: (1) There are different populations of cells with different functions within vOT; (2) There is a single cognitive function that underlies all responses that must account for the tactile and auditory responses of vOT; (3) The same population of cells perform different functions depending on interactions with other brain regions. Thus, the authors concluded that vOT is a polymodal area that is involved in visual word recognition but is not specific for visual word forms.

Devlin, Jamison, Gonnerman, and Matthews (2006) further argued against vOT as a store of visual word forms in a feedforward word recognition system. Instead, they proposed that vOT acts as an interface between visual information and higher order properties, such as the sound and meaning of a stimulus. In a primed lexical decision task in fMRI, Devlin et al. looked for effects of lexicality, orthographic priming and semantic priming at a vOT region of interest based on Dehaene et al.'s (2002) VWFA. A lexicality effect was found, as shown by repetition priming of real words (e.g., *cabin–CABIN)* but not pseudowords (e.g., *solst–SOLST*) at vOT, in contrast with a prelexical role of vOT. Devlin et al. also manipulated the prime–target relationship for real words such that they could be related in either form (e.g., *fasten–FAST*) or meaning (e.g., *profit–GAIN*) or both (e.g., *deadly–DEAD*). A significant interaction between form and semantic effects was revealed. The form priming effect at vOT was reduced when meaning was also shared compared to when form alone was shared. The authors argue that this semantic modulation of form priming is not compatible with the claim that prelexical letter combinations are stored in vOT. They argue that vOT activity is modulated by both bottom-up and top-down processes, allowing the integration of visual and nonvisual information.

The findings of nonvisual effects at vOT, including Braille reading, and semantic modulation, therefore contradict the hypothesis of VWFA as an exclusive orthographic representation region in a feedforward word recognition system. Additional evidence in favour of an interactive bidirectional word recognition system that includes vOT comes from Hellyer et al. (2011). Hellyer et al. used number words and digits as their stimuli in a number decision task and a phoneme decision task in fMRI. During passive viewing, a main effect of stimulus type was seen, with significantly greater activity to number words than digits in VWFA (in both anatomically and functionally defined sites). During the active tasks, a main effect of task (number decision or phoneme decision) was seen at VWFA, with significantly stronger activation for the phoneme task, whether the task was performed on number words or digits. The activation seen during presentation of digits was, therefore, modulated by task. Thus, the authors concluded that the results are consistent with an interactive or parallel distributed processing reading system, and not with a feedforward orthographic processing role of so-called VWFA.

Finally, Dehaene and Cohen (2011) proposed a number of interesting questions for future research in this area: (1) What are the neural codes in the vOT and how are they influenced by language rules? (2) What are the roles of top-down influences on the vOT and literacy? (3) What is the connectivity profile of vOT before and after learning to read? (4) What are the relationships between the fusiform face area and word recognition; does reading recycle the face recognition system? As yet, the specific role(s) of vOT and the supposed VWFA remain(s) uncertain, however, that this region is relevant for visual word recognition and responds to the orthographic properties of words is clear.

2.3.3.2 Neuroimaging and Semantics

In building up a picture of the visual word recognition system in the brain, another important question is how and where meaning is accessed. There are key differences between orthographic and semantic information. Orthographic input necessarily comes from visually presented words and letter strings. Semantic input, on the other hand, can come from a variety of visual and auditory sources, such as written words, pictures, and spoken words. Orthography can be studied outside of language by using pseudowords and unpronounceable letter strings, whereas semantic information is necessarily tied to real language. Semantic knowledge can occur outside of literacy and, unlike orthography, is learned via other means prior to learning to read. Therefore, semantic concepts must be shared across input modalities, requiring either multimodal or amodal brain regions or multiple semantic areas serving different modalities. This is suggestive of a highly complex and interactive semantic network; an idea supported by Devlin et al.'s (2006) finding of a semantic influence on the orthographic processing in vOT. There was no main effect of semantics at vOT, so this region is not itself sensitive to semantics, suggesting interactive connectivity with semantic regions or processes. Spitsnya, Warren, Scott, Turkheimer, and Wise (2006) also showed convergence of spoken and written input along the superior temporal sulcus and at the temporal pole and angular gyrus. These regions were hypothesised to connect unimodal spoken and written language input to anatomically distributed stores of knowledge about objects and concepts. The authors suggested that these stores lie mainly in the temporal lobe, with frontal activations relating to metalinguistic processes.

Binder, Desai, Graves, and Conant (2009) reviewed 120 PET and fMRI studies of semantic processing of spoken and written stimuli. The authors found seven brain regions associated with semantic processes: (1) posterior inferior parietal lobe (angular gyrus and portions of supramarginal gyrus), (2) lateral temporal cortex (middle temporal gyrus and portions of inferior temporal gyrus), (3) ventral temporal cortex (mid-fusiform and adjacent parahippocampal gyrus), (4) dorsomedial prefrontal cortex, (5) IFG, (6) ventromedial prefrontal cortex, and (7) posterior cingulate gyrus. Their findings suggest a widespread semantic network (see Figure 2.6) and revealed specific subsystems of semantic knowledge relating to actions, manipulable artefacts, abstract concepts, and concrete concepts. The authors proposed that more posterior (temporal and parietal) components of the network relate to storage, whereas frontal components relate to retrieval of semantic information. This semantic network was broadly similar to the network shown by Pulvermüller, Kherif, Hauk, Mohr, and Nimmo-Smith (2009) using fMRI. Pulvermüller et al. also showed evidence of overlapping category-specific semantic networks, but did not make a distinction between posterior and frontal aspects of these distributed networks.

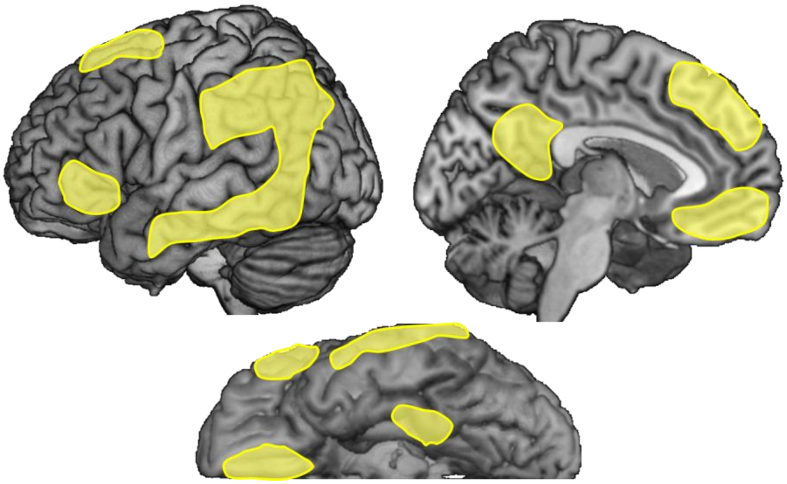


Figure 2.6 The semantic network. Left hemisphere regions shown by PET and fMRI studies to be associated with semantic processes. Adapted from Binder et al. (2006).

2.3.3.3 Neuroimaging, Phonology, and Broca's Area

This section will examine the contribution of functional neuroimaging to phonology; a visual word recognition process that is especially important for this thesis. Phonological input, like semantics, can come from both written and spoken language. Therefore phonological processes might also be expected to involve a complex, anatomically distributed network of brain regions. Broca's area has been implicated in speech output processes since neuropsychological case studies by Broca (1861a; 1861a; 1863; 1865) and this section will explore whether this region is also relevant for phonological input processes, as well as other proposed functions of this region.

In a meta-analysis of 129 fMRI and PET studies, published between 1992 and 2004, Vigneau et al. (2006) examined 45 studies that included phonologically relevant contrasts. This analysis revealed 125 peaks of activation in the left frontal lobe and 122 peaks across the left temporal and inferior parietal areas, though a limitation of this meta-analysis is that these regions were selected a priori and peaks outside these areas were not examined. Nonetheless, the large number of contrasts revealing activation across these areas demonstrates their importance for phonological processes. This widely distributed network overlapped with the networks for semantics and sentence processing examined in the same meta-analysis, though, the centres of mass for each process were significantly different (as verified by *t*-tests). In a review of fMRI studies of semantics, Bookheimer (2002) also demonstrated the close proximity of phonological, semantic, and syntactic processes in inferior frontal cortex. The peaks of IFG activity tended to be located more anteriorly for semantically related tasks, clustering around BA 47 (pars orbitalis); syntactic tasks showed peaks around BA 44/45 (pars triangularis) and phonologically related peaks occurred in posterior IFG, clustered around the border of BA 44 and BA 6 (pars opercularis and precentral gyrus). Figure 2.7 shows the clusters of phonological activity revealed by Vigneau et al. (2006) and the IFG peaks revealed by Bookheimer (2002).

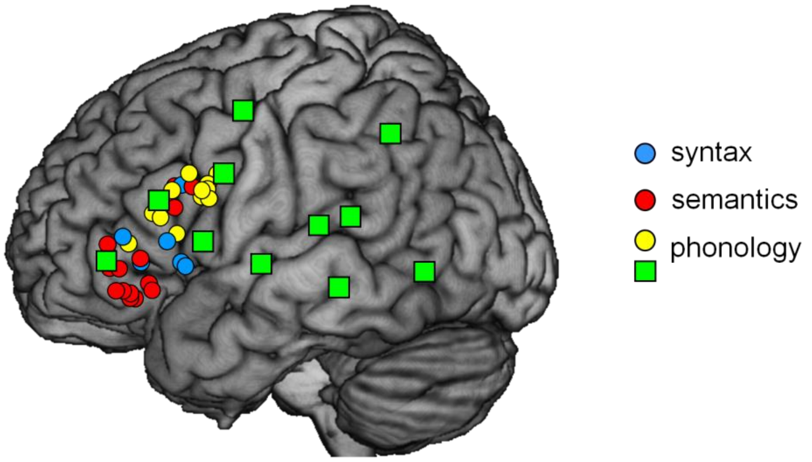


Figure 2.7 Summary of phonological and IFG activations. Approximate IFG Brodmann areas indicated. Adapted from Bookheimer (2002; circles) and Vigneau et al. (2006; squares).

The studies reviewed by Vigneau et al. (2006) and Bookheimer (2002) included auditory presentation of stimuli, and other studies have shown a close relationship between phonological processing of auditory and visual stimuli. For example, Poldrack et al. (2001) showed pars opercularis and pars triangularis activation both for rhyme judgements on visually presented words and for intelligible speech; Haist et al. (2001)

showed activation of primary auditory cortex during a visual phonological lexical decision task, which they speculated related to top-down activation during phonological word form analysis; and Burton, LoCasto, Krebs-Noble, and Gullapalli (2005) showed increased activity in pars opercularis to phonologically related tasks for both written and spoken words. However, of particular interest for this thesis are regions that respond during visual word recognition and that can be linked to phonological encoding processes.

A number of studies have looked at the dissociation of phonological and semantic processes specific to visually presented words. For example, Gold, Balota, Kirchhoff, and Buckner (2005) used an fMRI adaptation paradigm to look at phonological and semantic processing of written words. In fMRI adaptation, behavioural priming responses are correlated with a reduced hemodynamic response. This is thought to reflect increased efficiency of processing on subsequent trials where neural processes are shared (see e.g., Henson, 2003, for a review). In the phonological adaptation task, participants were asked to produce the regular pronunciation of irregular words, such as pronouncing *pint* to rhyme with *mint* and *hint*. The semantic task required participants to generate appropriate verbs corresponding to nouns. The results showed that more posterior IFG (BA 44/6) was related to phonology and more anterior IFG (BA 45/47) was related to semantics. A region of interest (ROI) approach restricted the main analyses to the prefrontal cortex, though exploratory whole-brain analyses also revealed phonological effects at the supramarginal gyrus (BA 40). However, in this study, the tasks and contrasts were particularly chosen to reveal cognitive control aspects of phonology and semantics. The results, therefore, did not show a broad network, such as that seen by Vigneau et al. (2006) The results also do not support a role for Broca’s area in input phonological processes, such as in grapheme-to-phoneme conversion.

In order to dissociate phonological and semantic processes during a more implicit task that did not require overt phonological or semantic judgements, Mechelli, Josephs, Lambon Ralph, McClelland, and Price (2007), used an unmasked priming task in fMRI. The authors contrasted phonological and semantic priming of words and pictures, where participants were asked to read or name both items in a prime–target pair. The results for prime–target pairs with shared phonology (relative to semantically related or unrelated) showed activation in the bilateral insula; the medial aspect of IFG, but outside of the region typically labelled as Broca’s area. This result was independent of stimulus modality, and there were no effects specific to phonological processing of words but not pictures. Shared semantics revealed activation in left pars orbitalis of IFG, middle temporal gyrus, angular gyrus, and superior frontal gyrus. The semantic results were also no different for words or pictures. The authors concluded that reading words and naming pictures rely on shared phonological and semantic systems. Mechelli et al. did not show Broca's area activity in the phonological contrasts, supporting Gold et al.'s (2005) interpretation of Broca's area as a region of phonological control, rather than relating to phonological input.

Wilson, Tregellas, Slason, Pasko, and Rojas (2010) made the phonological aspect of their fMRI study even more implicit by using masked priming. Wilson et al. used homophone (e.g., *pause–PAWS*) and pseudohomophone (e.g., *jurm–GERM*) masked primes in a lexical decision task. The study revealed phonological priming effects (reduced hemodynamic response) in bilateral superior and middle temporal gyri, precuneus, superior frontal gyrus, supramarginal gyrus and angular gyrus, but did not reveal any inferior frontal regions of activity. Overall, these studies have revealed a widespread phonological network, but the contribution of Broca's area as revealed by functional neuroimaging studies has been mixed. Bookheimer (2002) and Vigneau et al. (2006) showed clearly dissociable activity for phonological and semantic processes in this region, as revealed by data from over 150 fMRI and PET studies. However, what level of phonological process these activations relate to (from the early input encoding level up to speech output) is unclear. As Gold et al. (2005) suggested, these activations may relate to phonological aspects of cognitive control; an interpretation also supported by the results of Mechelli et al. (2007) and Wilson et al., which did not show IFG activity during implicit phonological tasks.

2.3.3.4 What Other Roles for Broca's Area?

Moving beyond visual word recognition, Broca's area has been implicated in a wide range of linguistic and non-linguistic functions. Such non-linguistic roles of Broca's area include motor-imagery (Binkofski et al., 2000; Gerardin et al., 2000), object manipulation and grasping (Binkofski et al., 1999), motor preparation (Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998; Rushworth, Krams, & Passingham, 2001), planning (Fincham, Carter, van Veen, Stenger, & Anderson, 2002), action understanding (Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001; Rizzolatti, Fogassi, & Gallese, 2002) and imitation (Meltzoff & Decety, 2003).

In a linguistic context, but outside of basic word recognition processes, Broca's area has been linked to the semantic integration of observed gestures with heard speech (Willems, Özyürek, & Hagoort, 2006) and in the unification of syntactic, semantic, and phonological information (Hagoort, 2005). This unification is said to occur on a syntactic level by matching written or spoken input to stored syntactic frames of reference, on a semantic level by selecting and integrating word meanings of unfolding discourse into a representation of the preceding context, and on a phonological level by unifying phonological segments into multi-word utterances and monitoring intonational phrase (Hagoort, 2005).

A similar argument is that Broca's area is involved in conflict resolution, such as between competing phonological forms. January, Trueswell, and Thompson-Schill (2009) provided evidence for this top-down conflict resolution in an fMRI study. Participants were presented with pictures that were paired with spoken instruction sentences creating varying degrees of conflict. High conflict was created, for example, by playing the sentence *clean the pig with the* ***leaf*** alongside a picture of a pig holding a leaf and sitting next to a sponge. In this case, the participant is likely to anticipate *clean the pig with the* ***sponge*** but the sentence in fact should be interpreted as *clean the pig* ***that has*** *the leaf*. The participants were also tested with a Stroop task, as this task is known for involving a high level of cognitive control. The authors found linearly increasing activation in BA 44/45 in line with the predicted level of conflict in the picture–sentence task. This region overlapped with activity relating to the cognitive control aspect of the Stroop task, indicating that the recruited processes responded to general cognitive control demands, and were not specific to the syntactic ambiguity created by the picture–sentence pairs.

Finally, in a recent meta-analysis of neuroimaging studies, Liakakis, Nickel, and Seitz (2011) looked at 485 studies published between 1991 and 2007 that showed activity in IFG or insular cortex. The studies were categorised by task into seven groups: (1) semantic processing, (2) syntactic processing, (3) phonological processing, (4) working memory, (5) listening and lip-movement observation, (6) fine movement control, and (7) perceptive processing with empathy. The analyses revealed three significant, spatially distinct clusters in the left hemisphere and one in the right hemisphere. The authors defined the right hemisphere cluster as relating to fine movement control. The three left hemisphere clusters were said to relate to: (1) working memory, such as verbal and digit recall tasks, at BA 44, (2) empathy, such as evaluating emotional expressions, at BA 47, and (3) semantics and phonology, such as synonym and rhyme generation tasks, at BA 45/46. Notably, unlike previous meta-analyses (e.g., Bookheimer, 2002, Vigneau et al., 2006), Liakakis et al. were unable to dissociate phonological and semantic processes in their analyses.

In sum, phonological processes have been linked to a broad network of regions across the left temporal and inferior parietal lobes, and IFG. The specific role of Broca's area in phonological processing during visual word recognition has not been clarified by neuroimaging studies and Broca's area and IFG in general have been linked to a wide range of linguistic and non-linguistic roles. As argued by Price and Devlin (2003), regarding the function of vOT/VWFA, there are at least three possible ways that the many reported functions of Broca's area might be resolved: (1) There are different populations of cells occupying the same cortical region, but with different functions; (2) there is a single cognitive function that underlies all Broca's area activation; (3) the same population of cells perform different functions depending on interactions with other brain regions.

2.3.4 Summary

This section on 'visual word recognition in the brain' has introduced neuropsychology and neuroimaging as tools for studying visual word recognition that can go beyond the capabilities of models and behavioural studies by exploring where in the brain these processes take place. In models of word recognition, researchers create hypothesised functional modules or connections, but these do not necessarily reflect the organisation of the brain. Neuropsychology, in particular double dissociations, can lead to insights about processes that are anatomically and functionally distinct. This can inform theory about normal functioning, but there are many important caveats that must be considered when interpreting lesion deficit data.

Broca's area has been introduced, both from a neuropsychological and neuroimaging perspective. As a classic key component of the speech and language network, it is important for reading research in general, but neuroimaging studies have additionally revealed phonologically specific aspects to the role of Broca's area in visual word recognition. The linguistic aspects of Broca's area, however, are not the full picture, as it also appears to have roles in action, planning, and cognitive control.

Functional neuroimaging evidence of the general regions responsible for visual word recognition processes in the brain has been discussed. Neuroimaging, particularly when combined with sophisticated task design, has led to important insights into how the brain might process single words; however, the question of *when* has yet to be answered. In understanding how these brain regions result in visual word recognition, it is important to know how they interact. Knowing when things happen helps to establish causal links between brain regions and processes, for example, phonological encoding could not be a necessary process in word recognition if it were found to only ever occur after semantic access (Perfetti & Bolger, 2004).The final section of this review will focus on the temporal dynamics of the neural network and discuss Broca's area as, potentially, a key brain region for phonological access, drawing on evidence from the priming literature, electroencephalography (EEG), and magnetoencephalography (MEG).

2.4 The Time Course of Phonology

2.4.1 Introduction

When the eyes are presented with print, a complex sequence of processes ensues. This temporal sequence is essential to the understanding of how visual word recognition takes place in the brain (Perfetti & Bolger, 2004) and, therefore, will be explored in this final section. The timing of word recognition processes have been studied in many ways, for example, the priming paradigm has been used behaviourally to infer the relative time courses of orthographic and phonological processing. Priming tasks have also been combined with the high temporal resolution of EEG and the high spatio-temporal resolution of MEG, leading to a broader understanding of how the processes of visual word recognition may interact.

2.4.2 Temporal Investigation with Behavioural Priming

As discussed above, Ferrand and Grainger (1992; 1993; 1994) used masked pseudohomophone priming experiments to explore the nature of phonological access during visual word recognition. In a primed lexical decision task, Ferrand and Grainger (1993) parametrically varied the prime exposure duration in order to explore the relative time courses of orthographic and phonological contributions. Orthographic and phonological priming were defined as a having significantly faster reaction times than unrelated control primes. The strongest orthographic priming effects occurred at prime exposure durations of 17 and 33 ms, whereas phonological effects peaked at prime durations of 67 ms. However, while this experiment shows a clear early influence of phonological information that is preceded by orthographic effects, shedding light on the temporal sequence of events, it does not necessarily show that phonological processing therefore takes place by 67 ms. Although it is tempting to draw this conclusion, the experiment only shows that 67 ms of prime exposure provides sufficient input to the system for phonological effects to take place at some time, as evidenced by a change in lexical decision reaction times around 500 ms later. In this case, the phonological processing could therefore take place any time between the prime onset and the reaction time. Furthermore, Frost Ahissar, Gotesman, and Tayeb (2003) and Tzur and Frost (2007) demonstrated that there is a significant interaction between prime duration and luminance (in accordance with Bloch’s law; Hood & Finkelstein, 1986) in determining the amount of energy that is provided to the cognitive system. While the luminance of the stimulus determines this energy directly, the exposure duration allows the amount of energy to be summed over time. Therefore, the minimum prime exposure duration (at a particular luminance) needed to show an effect cannot be taken as the minimum amount of time needed by a process.

The main disadvantage of using behavioural experiments to probe the workings of the brain is that with these tasks only the input and the resulting output are known for certain. Sophisticated task designs, such as that of Ferrand and Grainger (1993), make it possible to infer the temporal sequence of processes in the brain. However, it is difficult to infer absolute timings from these experiments. Behavioural paradigms, such as masked priming, have therefore been combined with the high temporal resolution of EEG, leading to fuller insights into the neural processes involved.

2.4.3 Temporal Investigation with Electroencephalography

EEG allows online recording of electrical potentials from the scalp, which are a direct reflection of the electrical currents produced by active populations of neurons. PET and fMRI measure indicators of cerebral blood flow in order to indirectly gauge the level of neuronal activity. This affords EEG a much higher temporal resolution than hemodynamic methods, although, due to the low conductivity of the skull (1/80–1/100 that of the brain; Hämäläinen & Hari, 2002), the electrical potentials measured by EEG are prone to distortion, leading to a much lower spatial resolution.

Hauk, Davis, Ford, Pulvermüller, and Marslen-Wilson (2006) took advantage of the high temporal resolution of EEG in order to explore the processing stages of visual word recognition. Participants performed a lexical decision task on words and matched legal pseudowords, where the words varied in the properties of frequency, length, bigram/trigram frequency, and semantic coherence (a measure of how likely it is for particular words to co-occur). Linear regression analyses of event-related potentials (ERPs) revealed effects of word length and bigram/trigram frequency earlier than 100 ms from word presentation, with whole-word frequency effects appearing by 110 ms. The first effects of lexicality and semantic coherence were seen by 160 ms. Source estimation analyses suggested that the surface structure of the word is processed in vOT by around 100 ms, with semantic information interacting with a widely distributed cortical network by 160 ms. From 200 ms onwards the authors demonstrated parallel activations across many brain regions and simultaneous effects of length, frequency, lexicality and semantic coherence.

Results from EEG (e.g., Hauk et al., 2006) have revealed that visual analysis, orthographic, and semantic processes start to occur within a few hundred milliseconds of viewing a word. Although fMRI has revealed detailed anatomical maps of visual word recognition, it cannot uncover this rapidly evolving and overlapping sequence of processes. The temporal resolution of fMRI is limited by many factors. For example, although a single slice of the brain can be acquired quickly, it can take 2 or more seconds (depending on the specific imaging sequence) to acquire a whole brain volume of images. The temporal resolution is further limited by the low signal-to-noise ratio and the variable hemodynamic response time across participants and brain regions (see e.g., Kim, Richter, & Uğurbil, 1997). Modern imaging sequences, high-field MRI scanners, and new analysis techniques help improve the temporal resolution (depending on the specific questions asked of the research), but fMRI cannot compete with the millisecond by millisecond resolution that can be achieved using EEG. Therefore, EEG reveals detailed temporal information that could not be seen using fMRI, and that research (e.g., Hauk et al., 2006) has shown to be relevant for the rapid evolution of visual word recognition processes.

Grainger, Kiyonaga, and Holcomb (2006) combined the high temporal resolution of EEG with masked phonological priming, in order to investigate the time course of orthographic and phonological processing. They used four priming conditions to separately test orthographic and phonological effects. Orthographic priming was investigated using transposed letter primes (e.g., *barin–BRAIN*) compared to controls with replaced instead of transposed letters (e.g., *bosin–BRAIN*). Phonological priming was tested using pseudohomophone primes (e.g., *brane–BRAIN*) compared to controls which shared as many letters with the target word, but were pronounced differently (e.g., *brant–BRAIN*). The event related potential (ERP) results from the silent reading task indicated that during the 150–250 ms window, orthographic priming was taking place at posterior sites, whilst during the later 250–350 and 350–550 ms windows phonological priming was taking place at anterior sites.

Intracranial EEG, recorded from patients with depth electrodes implanted in the brain as part of the clinical evaluation of severe epilepsy, has placed phonologically related processes at around 400–450 ms. For example, Mainy et al. (2008) showed activity in the pars opercularis of IFG under their phonological and semantic tasks, with the strongest activity for the phonological task at around 400 ms after word presentation. Sahin, Pinker, Cash, Schomer, and Halgren (2009) also demonstrated activity at pars opercularis for their phonological task at around 450 ms following a target word. Participants were shown visual cues to either read the following target word, or to complete the sentence using the following target word. For example, in the phonological condition, the cue *those are the* ____, followed by the target word *rock*, would require the participants to say *rocks* silently in their heads. In the two control conditions, either the word did not need changing to fit in the sentence (*that is the* ____) or the instruction was just to repeat the word. The authors, in fact, showed Broca's activity for all three conditions by 200 ms that was significantly stronger for low than for high frequency words. The authors interpreted this 200 ms response as relating to lexical access, however it may relate to initial input phonological processing of the target word, with the later (450 ms) response relating to the phonological aspects of cognitive control processes, as previously shown by Gold et al. (2005) using fMRI. Though, the temporal resolution of fMRI is typically on the order of seconds, thus is it not possible to know the precise timing of the effect seen by Gold and colleagues.

Evidence from ERPs has placed phonologically related processes within 250 to 500 ms of word onset (e.g., Carreiras, Perea, Vergara, & Pollatsek, 2009; Grainger et al., 2006; Holcomb & Grainger, 2006; Holcomb & Grainger, 2007; Mainy et al., 2008; Newman & Connelly, 2004; Sahin et al., 2009) and within the pars opercularis of left IFG (Mainy et al., 2008; Sahin et al., 2009). Ashby (2010) has argued that these findings represent lexical level phonological effects (such as phonological speech output processes) and that this leaves open the possibility of finding earlier sublexical input phonological processes. Ashby, Sanders, and Kingston (2009) provided such evidence by demonstrating processing of sub-phonemic features of visually presented words by around 80 ms. Ashby et al. (2009) recorded EEG as participants read real word targets with voiced and unvoiced final consonants (e.g., *fad*, *fat*), preceded by masked pseudoword primes that were incongruent or congruent in voicing and vowel duration (e.g., *fap*, *faz*). Phonological feature congruency modulated ERPs by 80 ms, indicating that sub-phonemic features can be activated rapidly during word recognition. Similar results were found by Ashby (2010) using syllable priming. Syllable primes were congruent (e.g., *pon###–PONDER* or *po##–PONY*) or incongruent (e.g., *pon#–PONY* or *po####–PONDER*) with the initial target syllable and target words appeared in both congruent and incongruent conditions (counterbalanced across two groups). ERP results showed a main effect of phonological congruency by 100–120 ms during silent reading.

One explanation for the surprisingly early phonological effects found by Ashby et al. (2009) could be due to the nature of the evoked average signal. Event related potentials (ERPs) are based on averaging signals over many trials. This averaging in the amplitude domain across repeated trials cancels out surrounding brain noise and sums together responses. However, this means that only the brain responses that are consistently locked in time to target onset would be observed in the ERP, because any responses that are variable over time would be cancelled out during averaging. Ashby et al. used short monosyllabic stimuli and consistently manipulated only the final consonants of their primes and targets. This may have succeeded in aligned the phases of the cortical responses to individual trials sufficiently to reveal a significant effect of phonological consistency in their evoked averaged analysis, owing to the sequential nature of phonological encoding (Carreiras, Ferrand, Grainger, & Perea, 2005).

EEG results represent an important contribution to the study of phonological processes in visual word recognition. In particular, by extending findings from behavioural paradigms and placing sublexical phonological processes as early as 80 ms after word presentation. The major disadvantage of the technique is the limited spatial resolution. MEG, on the other hand, combines the high temporal resolution of EEG with good spatial resolution and is therefore able to make a significant contribution to the understanding of how visual word recognition takes place by placing it both in space and time within the brain.

2.4.4 MEG and Phonology

Both MEG and EEG detect signals generated by the same neural activity. In the case of EEG these are electrical potentials generated by populations of neurons and for MEG these are the magnetic fields resulting from those electrical potentials. Unlike the electrical potentials of EEG, the magnetic fields measured by MEG pass through the scalp and intervening tissue largely undistorted (Hari & Salmelin, 1997). This affords MEG a much better spatial resolution than EEG, while still taking advantage of the direct measurements of neuronal activity that lead to a much higher temporal resolution than hemodynamic imaging methods. The methods of MEG will be discussed in more detail in Chapter 4.

As discussed above, behavioural priming tasks are based on the principle that processing of the target will be affected by the previous presentation of the prime. When these overlap, for example on an orthographic or phonological level, insights into these processes can be revealed. Combining priming with EEG reveals how brain activity is affected by this overlap, placing the manipulated processes accurately in time. This principle can be extended to MEG, allowing researchers to place the priming effect in both time and space.

Wheat et al. (2010) used a masked pseudohomophone priming task in MEG to investigate the time course and cortical location of phonological access. The authors used three priming conditions (adapted from Grainger et al., 2006); a pseudohomophone prime (e.g., *brein–BRAIN*), an orthographic control prime (e.g., *broin–BRAIN*), and an unrelated control prime (e.g., *lopus–BRAIN*). The pseudohomophone and orthographic primes both shared the same four out of five letters with the target, and the unrelated prime shared no letters. Because the pseudohomophones and orthographic controls shared equal orthographic overlap between prime and target, regions showing greater activity to the pseudohomophone condition that the orthographic condition relate to phonological priming over and above any orthographic priming effects. Whole-brain beamforming analyses showed significant Broca’s area activity for all three conditions, specifically in the pars opercularis of the left inferior frontal gyrus (BA 44) and overlapping with neighbouring precentral gyrus (BA 6), within the first 200 ms from target onset. In a region of interest analysis at the border of left pars opercularis of inferior frontal gyrus and precentral gyrus (LIFGpo/PCG; overlapping with Broca’s area), the authors demonstrated significantly stronger activity for the pseudohomophone condition than the orthographic condition within ~100 ms of target onset. From this critical contrast, it appears that LIFGpo/PCG has a role in processing phonological aspects of visually presented words within 100 ms of word presentation.

Wheat et al. (2010) interpreted the early activation of LIFGpo/PCG during pseudohomophone priming as reflecting sublexical access to phonology during visual word recognition. They also argued that the result suggests that early visual word recognition processes may take place via a direct print-to-speech mapping that is mediated by an articulatory code. There are several lines of evidence in support of this interpretation but also several alternative possibilities that must be argued against. For example, it could be argued that this result is specific to priming and does not relate to any basic visual word recognition processes, although this does not seem to be the case, as early LIFGpo/PCG activity has previously been observed in other tasks. Cornelissen et al. (2009) reported an MEG study in which participants carried out a passive viewing task. These authors found stronger responses to words than consonant strings, false fonts and faces in Broca’s area within 100 ms of stimulus onset. Pammer et al. (2004) also found activation in Broca's area at ~130 ms during a modified lexical decision task. Although these studies were not able to specifically identify a phonological role for Broca’s area, they provide valuable support for the occurrence of rapid activation of this region during non-primed visual word recognition. The timing of Wheat et al.’s finding is also corroborated by the ERP results of Ashby et al. (2009) and Ashby (2010). In these studies, Ashby and colleagues showed a significant effect of sub-phonemic phonological priming within 80–120 ms of viewing a word. As discussed above, the particular stimuli used by these authors may have allowed them to expose early phonological processing that would not usually be revealed by averaging evoked potentials. MEG analysis methods, such as beamforming, allow researchers to access the so called “induced” activity as well as the “evoked” responses that are usually seen using ERPs. The term *induced* relates to oscillatory brain activity that is not locked in time relative to a stimulus. These oscillatory changes would therefore be cancelled out by averaging in the amplitude domain (as with ERP analysis), but can be revealed using frequency domain analyses (this will be discussed in more detail in subsequent chapters). The early priming result of Wheat et al. was induced type activity, supporting the idea that early phonological processes generally take place during visual word recognition, but would not be revealed by the ERP analyses of, for example, Grainger et al. (2006).

Support for Wheat et al.'s (2010) sublexical articulatory code comes, for example, from direct recording in surgical patients (Greenlee et al., 2004) and fMRI studies (Brown, Ngan, & Liotti, 2008) indicating that LIFGpo/PCG is strongly associated with motor control of speech articulators. Further evidence for an association with speech production codes comes from Pulvermüller et al. (2006) who found that when individuals listened to speech sounds, somatotopic representations of articulatory features were activated in precentral gyrus (PCG) which were spatially consistent with the motor representations required for generating those same speech sounds. Finally, activation of this speech–motor region is consistent with findings from behavioural studies suggesting that the phonology accessed in visual word recognition is sensitive to articulatory characteristics of the words (Abramson and Goldinger, 1997; Lukatela et al., 2001; 2004). Alternatively, it is also possible to interpret the results in terms of the conflict resolution mechanisms of January, et al. (2009; see section 2.3.3.4). This would be particularly relevant for phonological priming, where there is a potential conflict to resolve between different orthographic representations activating the same phonological representation (e.g., *brein–BRAIN*) versus two different orthographic and phonological representations (e.g., *broin–BRAIN*). Though, if this were the case, it would leave open the question of when and where the initial phonological input representations are formed prior to any phonological conflict being resolved by ~100 ms at LIFGpo/PCG.

2.4.5 Summary

The temporal aspect of word recognition is an essential component of understanding how the brain reads. This section has introduced three methods that have been used to study the temporal aspects of visual word recognition. The contribution of behavioural priming has been discussed, along with the limitations of behavioural studies for inferring neural timings. EEG has been introduced as a technique with excellent temporal resolution but limited spatial resolution, that when used with elegant word recognition tasks can provide valuable insights into how and when different processes might take place. MEG has been introduced as a technique that combines the excellent temporal resolution of EEG with good spatial resolution. When frequency domain analyses are used, MEG is also able to reveal neural activity that is not usually seen by EEG studies.

Evidence has been presented that places phonological processing in LIFGpo/PCG as early as 80–120 ms after viewing a word. Not all studies, however, are in agreement with the timing of phonological processing; others placing it much later from around 250 ms to 500 ms. As Ashby (2010) argued, these earlier timings may relate to sublexical phonological access. Later activity, therefore, may relate to whole-word phonological processes, such as the phonological cognitive control observed by Gold et al. (2005).

2.5 General Summary and Conclusion

The aim of this review was to explore what is currently understood about the role of Broca’s area during visual word recognition. The study of visual word recognition in general has been explored, with a specific focus on the phonological aspects of reading models and behavioural experiments. Broca’s area has been introduced as a key region in speech and language from neuropsychology. The sub-regions of Broca’s area have been explored, with a particular focus on the pars opercularis of inferior frontal gyrus in posterior Broca’s area. Neuroimaging evidence for the possible roles of Broca’s area within and outside visual word recognition has also been reviewed.

2.5.1 Key Findings

The key findings from this review were

- Computational models of visual word recognition have significant advantages over verbal models and can be used to simulate and predict human behaviour; however, no model currently accounts for all observed word recognition phenomena.
- The role of phonological processing during visual word recognition continues to be disputed. Evidence suggests rapid and automatic sublexical phonological access that may take place alongside direct-lexical processes. This is in contrast to the slow and secondary phonological route proposed in the DRC model.
- Neuropsychology and neuroimaging go beyond the capabilities of models and behavioural studies by localising word recognition processes within the brain;

however, there are many caveats that must be considered when interpreting neuropsychological evidence.

- Broca’s area has been shown to be a key component of the speech and language network. This region contributes to fluent speech, along with a range of visual word recognition and cognitive control processes.
- The pars opercularis of left inferior frontal gyrus (posterior Broca’s area; LIFGpo/PCG) has been shown to be particularly relevant for phonological processing, as shown during fMRI visual word recognition tasks; however, the inherent limitations of the temporal resolution of fMRI mean that the different levels of phonology (initial encoding processes, later feedback processes, and higher order control processes) cannot necessarily be separated.
- Many EEG studies have placed phonologically relevant processes within 250 to 500 ms of word onset; however recent evidence from EEG and MEG suggests that sublexical phonological information may be processed in the pars opercularis as early as 80 to 120 ms.
- Wheat and colleagues (2010) demonstrated phonological priming at the pars opercularis of left inferior frontal gyrus within 100 ms of word presentation and provided evidence that this activity related to activation of sublexical phonology via an articulatory code.

2.5.2 Research Questions

Based on the evidence presented in this review, it seems that the specific role of phonology during visual word recognition is yet to be defined. There is evidence in favour of a rapid (~100 ms) activation of sublexical phonology during visual word recognition, but this is surprising based on predictions from dual-route theory and some EEG studies. Further investigation is therefore needed to confirm the role of phonology during visual word recognition and place this within the brain in time and space.

The specific research questions that will be addressed by this thesis are; (1) what is the role of Broca’s area for phonology during visual word recognition? For example, is Broca’s area involved in rapid phonological access? (2) What is the nature of the representations at Broca’s? For example, does Broca’s area represent sublexical phonological information? (3) Is Broca’s area necessary for visual word recognition? For example, if sublexical phonological representations are activated at Broca’s area during visual word recognition, do these representations play a necessary functional role in word recognition?

Chapter 3

Experiments 1–4

3.1 Overview

This chapter reports four behavioural priming experiments. The main purpose of these experiments was to test whether sublexical priming effects could be found using nonword stimuli, and whether this was true for both lexical decision and naming. Experiments 1 and 2 used a lexical decision task and Experiments 3 and 4 used a speeded naming task. In all four experiments, we asked whether phonological priming of both word and nonword targets could be produced using nonword primes by manipulating the phonological similarity between the prime and target. A large set of word and nonword stimuli was constructed and tested in order to maximise the behavioural phonological priming effect. Ultimately, these stimuli will also be used to explore sublexical priming effects using MEG.

3.2 Introduction

As seen in Chapter 2, behavioural priming has been combined with EEG and MEG in order to probe the neural processes involved in visual word recognition. Pseudohomophone (Wheat et al., 2010), syllable (Ashby, 2010), and phonetic feature (Ashby et al., 2009) primes have revealed phonological priming effects within around 80 to 120 ms of the target word onset. Furthermore, Wheat et al. used source localisation techniques in MEG to place this priming effect close to the border of pars opercularis of left inferior frontal gyrus and precentral gyrus (LIFGpo/PCG); part of Broca’s area that has been linked to phonological and articulatory processes (e.g., Broca, 1861a; Brown et al., 2008; Vigneau et al., 2006). All three of these studies used nonword primes, providing support for the interpretation that these studies reveal sublexical phonological effects. In particular, Ashby et al.’s (2009) study, which used prime–target pairs that were either congruent in final consonant voicing and vowel duration (e.g., *fap–FAD*) or incongruent (e.g., *faz–FAT*), showed that the similarity (or dissimilarity) between articulatory features of the primes and targets determined the priming effect. However, these studies also had in common the use of real words as targets. This leaves open the possibility that lexical effects also contribute to the phonological priming effect.

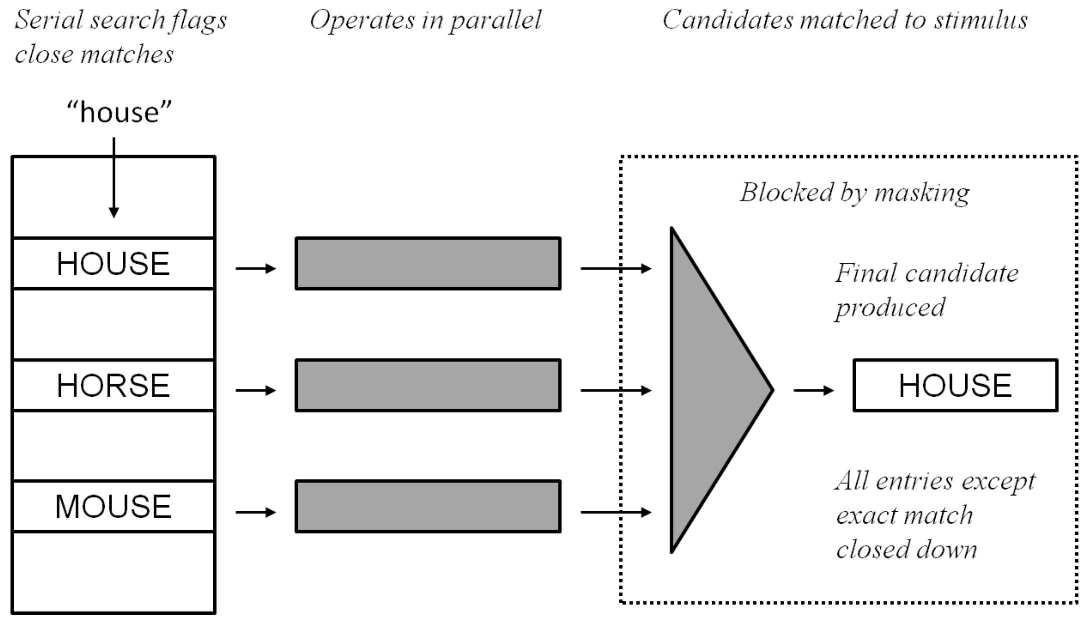


Figure 3.1 The entry-opening account of masked priming. Multiple lexical entries are opened by a word (or closely matching nonword prime), until eventually the matching entry is chosen. Multiple entries are therefore open when a target is presented, resulting in a reaction time advantage if the target is already open. Adapted from Forster (1998).

It has been argued, particularly based on repetition priming of lexical decision tasks (Forster & Davis, 1984), that masked priming effects typically take place at a lexical level. Forster and Davis' "entry-opening" account posits that masked priming of words occurs because identical word primes (or closely orthographically related word or nonword primes) activate one or more possible lexical entries (see Figure 3.1). Residual activation of these entries means that the appropriate target word entry is subsequently faster to re-activate, resulting in faster response times. Phonological behavioural priming effects might also be explained in these terms. For example, pseudohomophone priming might occur because the prime is a close enough match to activate the lexical entry of the following word target via a sublexical route. This pre-activation of the target word's lexical representation by the prime thus facilitates reaction times to the target. Alternative accounts of priming include the "savings effect". The savings effect occurs because the work done to identify the prime can be applied to the target, even if they are not identical (Forster, Mohan, & Hector, 2003). Ultimately, this theory is very similar to the entry-opening account, in that priming eventually results from faster activation of a lexical representation of the target, due to processes that are initiated by the prime. These theories operate within a localist, modular system, such as the DRC model (Coltheart et al., 2001) or the BIAM (Ferrand & Grainger, 2003; Grainger & Ferrand, 1994; Grainger et al., 2003; Jacobs et al., 1998; Ziegler et al., 2003), where whole words are stored in a mental lexicon. They are not compatible with the nonlocalist, distributed representations described by PDP models (e.g., Harm & Seidenberg, 2004; Plaut et al., 1996; Seidenberg & McClelland, 1989) due to the absence of whole-word lexical entry nodes in these models.

Demonstration of priming effects for nonwords would be evidence against an entry-opening or savings theory of masked behavioural priming, as both of these accounts specify that priming occurs at the lexical level. Forster and Davis (1984) did not show any repetition priming of their nonword targets, in line with the predictions of their entry-opening theory. Ferrand and Grainger (1992) also failed to show priming of nonwords in their phonologically primed lexical decision task in French. Homophonic French nonword pairs (e.g., *trat–TRAS*) were not responded to faster than orthographic controls (e.g., *clof–CLON*), whereas for word targets pseudohomophone primes (e.g., *lont–LONG*) produced significantly faster reaction times than orthographic controls (e.g., *lonc–LONG*). This result does not challenge a lexical level account of priming; however, one criticism of Ferrand and Grainger’s stimuli is that different nonword targets were used for the homophonic and control conditions, whereas the same targets were used for both equivalent real word conditions. Although counterbalancing meant a participant still saw a word target only once, the two nonword target conditions may not have been as well matched to each other on baseline unprimed reaction times. This point was conceded in a later lexical decision study (Ferrand & Grainger, 1994) where the nonword analyses were not presented for this reason.

Masked repetition priming effects for nonword targets in lexical decision are typically small and often not significant, and Bodner and Masson (1997) argued that this is because the decision to respond *no* to a nonword suffers from conflicting processes. On one hand, sublexical priming is produced by repetition primes, which speeds up the identification of the nonword target. However, on the other hand, the repetition of the nonwords results in a perceptual fluency that creates a familiarity effect for the primed nonword targets, making it difficult to reject them as nonwords, thus slowing the participants' responses. The net result is, therefore, no repetition priming of nonwords under most circumstances. In their priming task, Bodner and Masson manipulated the case of the targets in order to disrupt this familiarity effect (e.g., *custard–cUsTaRd*). The result was a net repetition priming effect for nonwords that was even larger than for real words (93 ms and 75 ms, respectively). Forster (1998) argued that although this priming task shows evidence of sublexical effects, this is due to the specific nature of the mixed-case stimuli. Forster proposed that mixed-case presentation forces deeper orthographic processing than under normal circumstances and it is the activation of letter entries which are then primed. Ordinarily, Forster argued, these letter entries would not need to be accessed and so no nonword priming would be seen.

In contrast, Perea, Gómez, and Fraga (2010) showed masked repetition priming of nonword targets in Spanish without any specific manipulation of the stimuli. Their lexical decision task showed an 11 ms priming advantage for repeated nonwords, compared to nonwords primed by an unrelated nonword. Furthermore, the authors challenged a popular explanation in the literature for the (usual) lack of priming effects for nonwords. This popular explanation is that priming can only be seen during positive (i.e., *yes*) responses, as negative responses are initiated by a "deadline" criterion. This deadline for rejecting a nonword in lexical decision (as seen in the DRC model, Coltheart et al., 2001, and in the multiple read-out model, Grainger & Jacobs, 1996) means that any sublexical priming cannot be detected, unless the deadline is altered on the basis of the prime (Forster, 1998). Perea et al. challenged this view, not only by demonstrating sublexical repetition effects during lexical decision, but by further demonstrating equivalent nonword priming when the nonwords required a positive response in a go/no-go task. The authors used bootstrapping simulations to show that the 13.5 ms priming effect for nonwords in the go/no-go task was of equal magnitude to the effect in lexical decision. This finding would not be supported by a deadline account.

Two studies in Hebrew also showed nonword priming in a series of lexical decision experiments. Frost, Ahissar, Gotesman, and Tayeb (2003) showed repetition, phonological, and orthographic priming at a smaller magnitude but similar overall pattern to real words. Tzur and Frost (2007) also generated repetition priming for nonwords. Again, this was of a smaller magnitude than for the real word targets, but was still a significant priming effect in two out of three experiments. Unlike Bodner and

Masson (1997), these studies did not use any unusual manipulations of the stimuli in order to produce the nonword priming effects. The BIAM (Grainger & Ferrand, 1994; Grainger et al., 2003; Jacobs et al., 1998; Ziegler et al., 2003) performs well on fast phonological priming tasks due to its sublexical input phoneme mapping (Diependaele et al., 2010). Therefore, this model could potentially account for priming of nonwords via these sublexical phonemic representations; although this has not been tested.

The results of Bodner and Masson (1997), Frost et al. (2003), Tzur and Frost (2007), and Perea et al. (2010) demonstrate that sublexical priming effects can be revealed behaviourally, as evidenced by the priming of nonword targets. In standard repetition priming tasks, it seems likely that a large lexical priming advantage is elicited for real words that cannot exist for nonwords. Forster et al. (2003) suggested that sublexical components probably contribute no more than a 10 ms advantage in repetition priming. This may be confounded by familiarity conflicts for primed nonwords in the lexical decision task, resulting in no overall behavioural priming effect (Bodner & Masson, 1997). The net behavioural priming effect, therefore, probably consists of lexical, sublexical and postlexical effects. The relative contribution of each type of effect being dependent on the task constraints, for example, Bodner and Masson created a strong sublexical orthographic effect by emphasising the importance of individual letters to word recognition.

3.2.1 The Present Experiments

Wheat et al., (2010), Ashby, (2010), and Ashby et al. (2009) have shown phonological priming effects within the first 80–120 ms of word presentation. It has been hypothesised that this relates to the priming of sublexical phonological processes. Wheat et al. further localised this priming effect to the pars opercularis of Broca’s area, which has previously been implicated in phonological and articulatory processes (Broca, 1861a; Brown et al., 2008; Vigneau et al., 2006). If it is the case that Broca’s area has a role in sublexical phonological processes during visual word recognition, then it should be possible to show equivalent priming at Broca’s area for word and nonword targets. If the priming effect previously seen at Broca’s area is sublexical, then the lexical status of the stimuli should not change the pattern of phonological priming seen using MEG. The presence of similar phonological priming of nonword targets would contradict a lexical interpretation of the results, and provide further support for a sublexical phonological role of left IFG in visual word recognition. The following four experiments, therefore, aimed to produce a suitable nonword priming experiment to be used later in MEG.

The important distinction between these behavioural priming effects and the results from EEG and MEG studies is that behavioural experiments only allow the measurement of the output from the system. It seems that lexical effects contribute significantly to the behavioural priming effect, and this seems feasible, as the reaction time is probably based on having finished the entire word recognition process, which will include lexical and postlexical effects, such as orthographic checking (e.g., Lupker, Brown and Colombo, 1997). However, EEG and MEG allow a window into earlier sublexical processes, that contribute greatly within the first 0–200 ms (e.g., Hauk et al., 2006), without the confounding effects of these later processes. Therefore, the mechanisms of behavioural priming are not central to this thesis, as any behavioural effect may be the result of an interaction between sublexical, lexical, and postlexical effects. However, a reliable phonological behavioural priming result will provide a strong basis for investigating sublexical phonological effects using MEG.

In sum, the present experiments serve a dual purpose of investigating sublexical priming effects behaviourally and preparing a suitable test of sublexical effects for use in MEG. Though, the behavioural results will likely include lexical and postlexical effects, evidence of sublexical priming will be a suitable basis for progressing to an MEG investigation of sublexical phonology.

3.3 Experiment 1

Experiment 1 was the first of two primed lexical decision experiments. Previously, lexical decision experiments have been used in English to successfully show phonological priming (e.g., Lukatela et al., 2001; Lukatela et al., 2004; Lukatela et al., 1998). However, none of these experiments have examined the phonological priming effect on nonword targets. The nonword targets in lexical decision experiments in English have included pseudohomophones and illegal letter strings (e.g., Rastle & Brysbaert, 2006), but researchers have treated the nonword trials as foils and discarded them. Only in French (e.g., Ferrand & Grainger, 1992) and Hebrew (Frost et al., 2003; Tzur & Frost, 2007) have the nonword targets been presented under the same phonological priming conditions as the real word targets.

This experiment used the same priming parameters as Wheat et al. (2010); that is, a four-field masking paradigm, with the prime sandwiched between two masks, and the target clearly visible (i.e., *mask–prime–mask–target*). The task was changed from reading aloud in Wheat et al. to lexical decision here in order to incorporate the nonword targets. Lexical decision also provides a stronger test of sublexical effects than reading aloud, because Forster (1998), for example, suggested that behavioural priming effects in reading aloud could be due to priming of postlexical articulatory planning and not to any word recognition processes. This experiment also included the creation of the nonword target and prime stimuli that were used in the four experiments presented in this chapter. Phonological priming was measured as faster reaction times to the phonologically primed (PSEUD) trials than to orthographic controls (ORTH). Targets and primes from both of these conditions always shared all but one letter. Any advantage of the orthographic control prime over an unprimed control condition, consisting of five dashes (UNPRIMED), shows the priming that occurs based on the almost complete orthographic overlap and partial phonological overlap between prime and target. The phonological prime then shows any priming over and above this, in the case where there is the same amount of orthographic overlap but the prime and target sound the same. In other words, equivalent levels of orthographic priming are expected in the orthographic and pseudohomophone conditions, with additional phonological priming in the pseudohomophone condition.

3.3.1 Methods

3.3.1.1 Participants

Twelve native-English-speaking adults (9 females; M_{age} 21.50 years, *SD* 1.57) gave their informed consent to participate on a voluntary basis. All were reported to be right-handed, with normal or corrected-to-normal vision, and with no history of any reading disorder. The experiment was conducted in accordance with the Department of Psychology Ethics Committee, University of York. Participants were paid £4 or awarded course credits. One additional participant took part, but was excluded from all analyses due to a mean error rate >10% with a maximum error rate of 20.5%.

3.3.1.2 Materials

The stimuli were 200 English real-word (*M* freq/million 54.49, *SD* 156.29) and 200 nonword targets matched on length (4-6 letters, mean 5.00), and nonword or pseudohomophone primes that were created from their targets by replacing one letter.

Word and nonword target stimuli were presented in three conditions, denoted by prime–target relationship. Pseudohomophones primes (PSEUD) were designed to sound the same as their target word or nonword and orthographic controls (ORTH) were designed to sound different from their target. In a third, unprimed, condition, the prime was replaced by five dashes (-----). Examples of matched words and nonwords are shown in Table 3.1; the full stimulus list can be seen in Appendix A.

Table 3.1

Examples of Primes and Targets by Position of Letter Switch and Length

	Prime				
Lexicality	PSEUD	ORTH	Target	Position	Length
Word	tipe	tope	TYPE	2	4
Nonword	nirm	narm	NERM	2	4
Word	breef	broef	BRIEF	3	5
Nonword	bokus	bofus	BOCUS	3	5
Word	sitrus	hitrus	CITRUS	1	6
Nonword	ciprin	viprin	SIPRIN	1	6

An initial list of four to six letter nonwords was generated using the WinWordGen 1.0 application (Duyck, Desmet, Verbeke, & Brysbaert, 2004), with the default constraints of number of orthographic neighbours (2–10), minimum legal bigram frequency (30), and minimum onset/suffix bigram frequency (15). Appropriate primes were then generated from the list of nonword targets by replacing one letter so that the pronunciation of the nonword prime was different from or remained the same as the target nonword. Prime–target pairs were then rated according to how well the primes fit the desired constraints of "sounds the same as the target" or "sounds different from the target".

A tiered rating procedure was undertaken, with each experimenter–participant interaction taking place separately. First, the entire stimulus set of prime–target pairs was randomized and then split into one list of primes and another of targets. Three experimenters each asked three different independent participants to read aloud the list of primes, whilst the experimenter viewed a matching list of targets. The experimenter then rated each pronunciation of a prime (as spoken by the participant) as “the same as” or “different from” the appropriate target (as read from their list). Participants were blind to the target spelling and experimenters were blind to the prime spelling. This ensured all stimuli were evaluated for pronunciation without the confounding influence of shared spelling, for example, if a participant read aloud the nonword *bokus* from the list of primes, the experimenter had to identify if the pronunciation they heard matched the written nonword *BOCUS* in their list of targets. Nonword targets were selected for the experiment if they were paired both with a pseudohomophone prime that was rated at least six out of nine times as sounding the same as the target and with an orthographic control prime that was rated at least six out of nine times as sounding different from the target. In other words, *bokus* must rate as sounds-the-same at least six times, and *bofus* must rate as sounds-different at least six times for the target *BOCUS* to be accepted. The intraclass correlation coefficient of the nine participants was .61, 95% CI [.58, .64].

After the rating procedure, the final list contained 200 nonword targets that were each matched with two nonword primes. The two lists of nonword primes were checked for bigram frequency differences by using the combined token bigram frequency score of primes from each condition. The mean Log$_{10}$ token frequency for PSEUD–NONWORD primes was 5.60 (*SE* 0.03) and for ORTH–NONWORD primes was 5.66 (*SE* 0.03). A paired *t*-test revealed no significant difference between the nonword prime conditions, $t(398) = -1.57$, $p = 0.12$, indicating that neither condition contained primes made up of more frequently occurring letter pairs than the other condition. This ensured any orthographic relationship to British English was controlled for because no prime group was more familiar in terms of spelling than the other group.

The four to six letter word targets were then chosen from a pool of 400 by first using the same rating procedure as for the nonwords to ensure well matched primes. Then the final targets were then chosen from the resulting list of 317 by matching to the nonword list on string length and the position of the letter switch. For example, the pseudohomophone–word pair *br**e**ef–BR**I**EF* would be an appropriate match for the pseudohomophone–nonword pair *bo**k**us–BO**C**US* because both are five letters long and have the letter replacement at position three in the string (shown in bold; see also Table 3.1). The mean Log$_{10}$ token frequency for PSEUD–WORD primes was 5.57 (*SE* 0.03), for ORTH–WORD primes was 5.63 (*SE* 0.02). A paired *t*-test revealed no significant difference between the word prime conditions, $t(382) = -1.63$, $p = 0.10$.

Stimuli were displayed on a Mitsubishi Diamond Pro 19 in. CRT monitor, controlled from a Windows PC. Stimulus sequence was generated and controlled using Presentation Version 14.0 (Neurobehavioral Systems, Inc.), which has the advantage of locking the temporal sequence of events to the vertical screen refresh with microsecond precision. The screen resolution was 1024 x 768 True Colour (64-BIT) with 100 Hz vertical refresh, allowing events to be manipulated in multiples of 10 ms. Responses were made using a bespoke button box via LPT1 port, which performed debouncing in hardware.

3.3.1.3 Design

All participants saw all of the target stimuli three times; once for each of the three prime–target conditions. The experiment therefore used a within-subjects design, with the dependent variable of prime–target relationship and the independent variable of reaction time.

Counterbalancing and pseudo-randomization in the following way ensured that each participant saw a unique stimulus order and controlled for potential order effects created by the repetition of each target three times (once for each stimulus type). First, the stimuli from the six conditions were divided equally into three blocks (A, B, and C) so that a target appeared only once in each block, and with an equal number of prime types in each block. Each participant was then assigned one of six possible block orders (ABC, ACB, BAC, BCA, CAB, CBA) ensuring that any order effects of prime–target pairing were controlled for between participants. Finally, a unique order was created for each participant by randomizing the stimulus order within each block (keeping the block structure in order to preserve prime–target level counterbalancing). This final randomisation also ensured word and nonword trials were shown in an unpredictable order for the lexical decision task.

3.3.1.4 Procedure

The experiment took place in a windowless room with overhead illumination provided by a fluorescent strip light. Each trial lasted 3090 ms (for timings see Figure 3.2) with trials looping continuously. The fixation cross indicated the start of a new trial. Each trial contained a brief lower case masked nonword prime followed by an upper case target, displayed in black on a light grey background. The change in case between prime and target controlled for repetition effects due to visual pattern on the retina. Stimuli subtended ~2.74° horizontal and ~0.65° vertical at a viewing distance of ~70 cm.

Participants were instructed to focus on the centrally presented fixation cross, and to decide as quickly and accurately as possible whether each uppercase target was a real word or a nonsense word and to respond by pressing the appropriate button. Participants responded with their right forefinger for a word and left forefinger for a nonword. Timings of responses were logged by Presentation Version 14.0 (Neurobehavioral Systems, Inc.), which provides an estimate of the temporal precision of each trial. Participants were questioned after the experiment to ensure they were not able to report the primes.

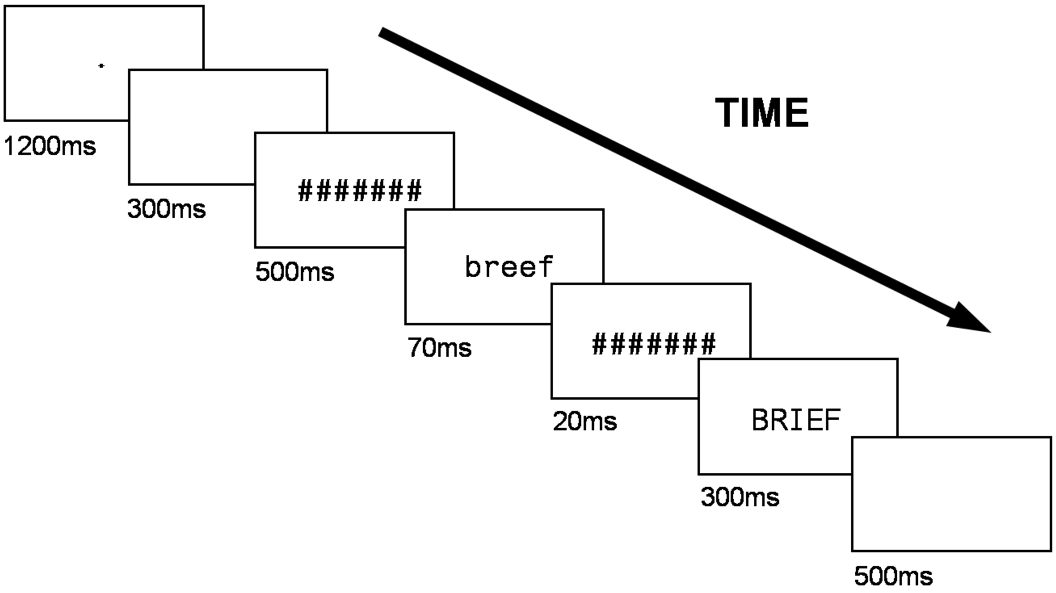


Figure 3.2 The duration of each event within a trial.

3.3.2 Results

Incorrect responses were first removed. The mean error rate was 5.57% (*SD* 2.26). Any trials that were logged by Presentation as having a temporal precision uncertainty of 5 microseconds or greater were also removed (<1% trials). Reaction times (RT) greater or less than 3 standard deviations from the mean (by condition for each subject) or greater than 1100 ms were treated as outlying data points and were excluded from further analysis (<1% of trials; for a discussion of the influence of outliers see e.g., Miller, 1991; Zimmerman, 1994).

As shown in Figure 3.3, there appeared to be a trend for targets primed by pseudohomophones to be responded to fastest, followed by orthographic controls, and unprimed targets responded to slowest. Overall, the real word targets were responded to 37 ms faster than the nonword targets.

3.3.2.1 Reaction Time Analyses by Participants

Reaction time data were analysed using repeated measures ANOVAs (in PASW 18, SPSS Inc., Chicago, IL). Mauchly's test was used to verify that the assumption of sphericity had not been violated and if necessary a correction was applied where stated. A two-by-three repeated-measures ANOVA with the within-subject factors of lexicality and prime–type was conducted. The results showed a significant main effect of lexicality, $F(1,11) = 33.68$, $p < .001$, $\eta_p^2 = .75$, and of prime–type, $F(2,22) = 55.90$, $p < .001$, $\eta_p^2 = 0.84$, and a significant interaction, $F(2,22) = 7.67$, $p = .003$, $\eta_p^2 = .41$.

As there was an interaction between lexicality and prime–type, separate one-by-three ANOVAs were then conducted, splitting the data by lexicality. For real word targets, there was a significant main effect of prime–type, $F(2,22) = 27.89$, $p < .001$, $\eta_p^2 = .72$. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, $F(1,11) = 17.62$, $p = .002$, $\eta_p^2 = .62$, and between ORTH and UNPRIMED, $F(1,11) = 11.18$, $p = .007$, $\eta_p^2 = .50$. For nonword targets, there was a significant main effect of prime–type, $F(2,22) = 31.58$, $p < .001$, $\eta_p^2 = .74$. Planned repeated contrasts revealed no significant differences between PSEUD and ORTH, $F(1,11) = 0.03$, $p = 0.86$, $\eta_p^2 < .01$, but a significant difference between ORTH and UNPRIMED, $F(1,11) = 37.67$, $p < .001$, $\eta_p^2 = .77$.

3.3.2.2 Reaction Time Analyses by Items

Items analyses corroborated the findings. For real words, there was a significant main effect of prime–type, $F(2,392) = 23.52$, $p < .001$, $\eta_p^2 = .11$. Planned contrasts revealed significant differences between PSEUD and ORTH, $F(1,196) = 17.43$, $p < .001$, $\eta_p^2 = .08$, and between ORTH and UNPRIMED, $F(1,196) = 6.86$, $p = .014$, $\eta_p^2 = .03$. For nonwords, there was a significant main effect of prime–type, $F(2,392) = 51.23$, $p < .001$, $\eta_p^2 = .21$. Planned contrasts revealed no significant differences between PSEUD and ORTH, $F(1,196) = 0.12$, $p = .74$, $\eta_p^2 < 0.01$, but a significant difference between ORTH and UNPRIMED, $F(1,196) = 83.37$, $p < .001$, $\eta_p^2 = .30$.

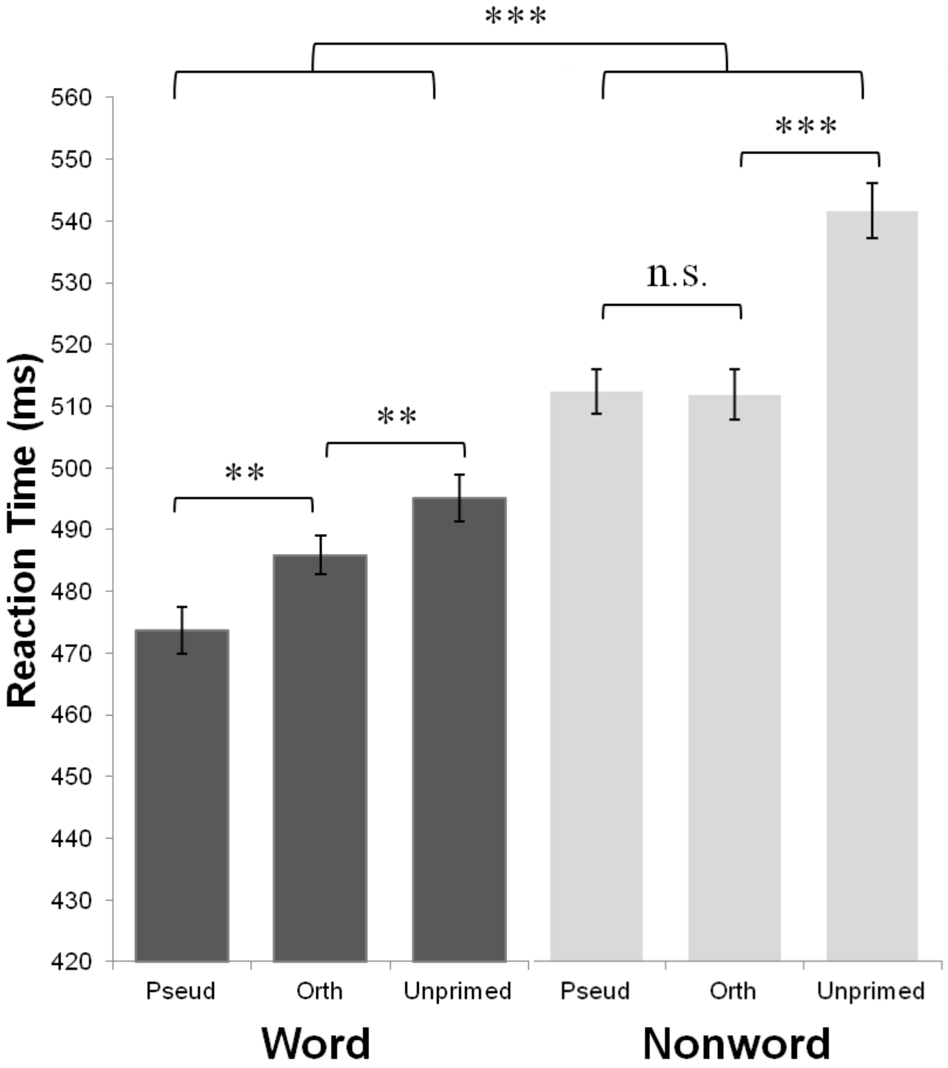


Figure 3.3 Mean reaction times by prime–type and lexicality. Standard error bars, corrected for repeated measures.

*** *p* < .001, ** *p* < .01, n.s. = not significant.

In sum, word targets were responded to faster overall, and show both phonological priming (PSEUD faster than ORTH) and orthographic priming (ORTH faster than UNPRIMED). Nonword trials did not show any phonological priming, but did show orthographic priming.

3.3.3 Discussion

The purpose of Experiment 1 was to explore whether a phonological priming effect could be produced for nonword targets in a lexical decision task. Priming of nonwords would reveal a sublexical component of the behavioural priming effect. However, these sublexical effects may be difficult to demonstrate behaviourally. In

Experiment 1, for nonword targets, no phonological advantage was shown for the pseudohomophone prime over and above the orthographic control prime. Orthographic form priming was, however, shown by significantly faster reaction times to the orthographically primed nonwords than for unprimed nonwords. For the word targets, both phonological and orthographic priming was shown.

At this point, Experiment 1 could have been translated into an MEG experiment. The word targets showed behavioural priming under similar parameters to Wheat et al. (2010), but with a change of task. It could therefore be expected that this experiment would show phonological priming at Broca’s area for word targets. Equivalent nonword priming under these conditions in MEG would be a strong test of the sublexical nature of activity at Broca’s area. However, given that (1) phonological priming of nonwords has not been tested previously in English, (2) the phonological priming effect for words was small, at just 12 ms, compared to 21 ms for Wheat and colleagues, (3) parameters such as lighting conditions, contrast energy, and visibility of the prime have proved critical in producing priming effects (e.g., Frost et al., 2003; Humphreys et al., 1988; Lukatela et al., 1999), and (4) MEG experiments are expensive both in terms of time and resources, we deemed it prudent to further investigate whether a behavioural phonological priming effect could be produced for nonwords in English. A second lexical decision experiment was therefore conducted with slightly altered parameters.

3.4 Experiment 2

In Experiment 2 the priming procedure was altered slightly with the aim of increasing the priming effect for both word and nonwords. One factor that has been shown to impact on the priming effect is the visibility of the prime, for example, Humphreys et al. (1988) showed that within trial priming effects benefit from masked priming procedures, whereas list effects (i.e., subsequent presentations of the same target within a stimulus list) benefit from unmasked procedures. The prime duration used in Experiment 1 was 70 ms. Although Wheat et al. (2010) previously demonstrated that this was not long enough for the participants to be able to identify the prime, some participants from Experiment 1 did report being able to see a flickering pattern before the target was presented.

Forster, et al. (2003) mentioned that in their experience, an intervening mask between the prime and the target can lead to an increased visibility of the prime and to a weaker priming effect. Wheat et al. (2010) used an intervening mask in line with the successful phonological priming task of Grainger et al. (2006). However, the prime and backward mask durations of Grainger et al. resulted in a total SOA of just 67 ms, compared to a total SOA of 90 ms in Experiment 1. Ferrand and Grainger (1993) demonstrated that the optimal SOA for phonological priming in lexical decision task in French is 60–70 ms. At this prime duration (without an intervening mask), there was a decline in the facilitation provided by orthographic overlap and an increase in the facilitation provided by phonological overlap.

In Experiment 2, the intervening mask between the prime and target was removed, in order to make the prime less visible. This is in line with the three-field masking procedure (*mask–prime–target*) used by, for example, Forster and Davis (1984), Ferrand and Grainger (1993), Lukatela, et al. (1998), Frost et al. (2003), and Tzur and Frost (2007). Removing the intervening mask and shortening the prime duration by 10 ms resulted in an SOA of 60 ms, in line with the phonological priming findings of Ferrand and Grainer (1993). Therefore, the stimuli and task remained the same as Experiment 1, but the trial event sequence and timings were modified in order to investigate whether nonwords could be primed under different trial parameters and to try to increase the strength of the word phonological priming effect.

3.4.1 Methods

3.4.1.1 Participants

Twelve native-English-speaking adults (11 females; M_{age} 22.58 years, *SD* 10.05) gave their informed consent to participate on a voluntary basis. All were reported to be right-handed, with normal or corrected-to-normal vision, and with no history of any reading disorder. The experiment was conducted in accordance with the Department of Psychology Ethics Committee, University of York. Participants were paid £4 or awarded course credits. One additional participant took part, but was excluded from all analysis due to a mean error rate >20% with a maximum error rate of 31%.

3.4.1.2 Stimuli, Materials and Design

The stimuli, materials and design were identical to Experiment 1.

3.4.1.3 Procedure

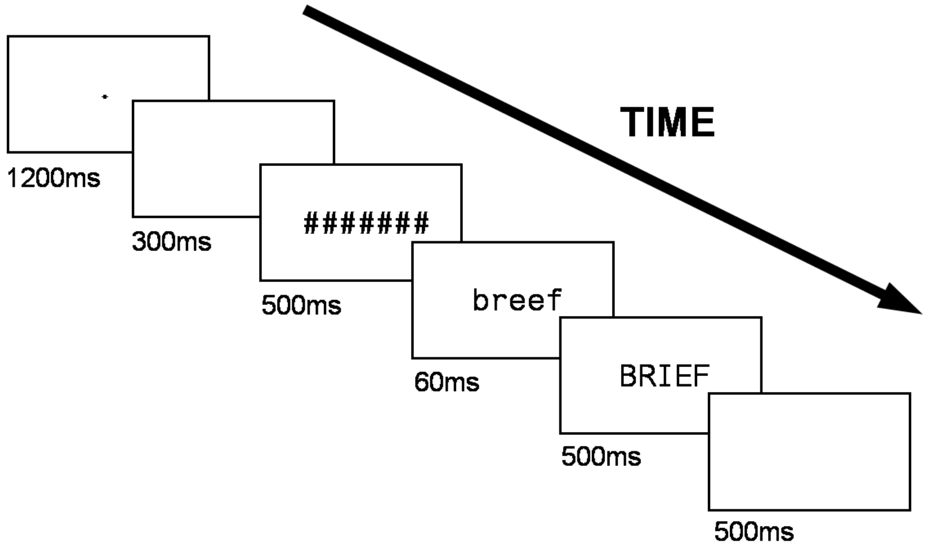


Figure 3.4 The timings of each event within a trial. The second mask has been removed, and the prime duration shortened to create a new SOA of 60 ms.

The procedure was modified from Experiment 1 by removing the backward mask so that the new trial event sequence was *mask–prime–target*. The prime duration was also shortened to 60 ms from 70 ms. These changes resulted in a new SOA of 60 ms, reduced from a 90 ms SOA in Experiment 1. The new trial event timings are shown in Figure 3.4. All other aspects of the procedure remained the same as Experiment 1.

3.4.2 Results

Incorrect responses were first removed; the mean error rate was 8.65% (*SD* 5.34). Any trials that were logged by Presentation as having a temporal precision uncertainty of 5 microseconds or greater were also removed (<1% trials). RTs greater or less than 3 standard deviations from the mean (by condition for each subject) or greater than 1100 ms were treated as outlying data points and were excluded from further analysis (<1% of trials).

Figure 3.5 shows a trend for real word targets to be responded to faster than nonword targets, with a mean RT advantage of 47 ms for words. For real words, targets primed by pseudohomophones appeared to be responded to fastest. For nonwords, targets primed by orthographic controls appeared to be responded to fastest.

3.4.2.1 Reaction Time Analyses by Participants

A two-by-three repeated measures ANOVA with the within-subject factors of lexicality and prime–type was conducted. The results showed a significant main effect of lexicality, $F(1,11) = 44.54$, $p < .001$, $\eta_p^2 = .80$, and of prime–type, $F(2,22) = 9.25$, $p = .001$, $\eta_p^2 = .46$, and a significant interaction, $F(2,22) = 3.56$, $p = 0.046$, $\eta_p^2 = .24$. Due to the significant interaction and the main effect of lexicality, separate one-by-three ANOVAs were then performed for words and nonwords.

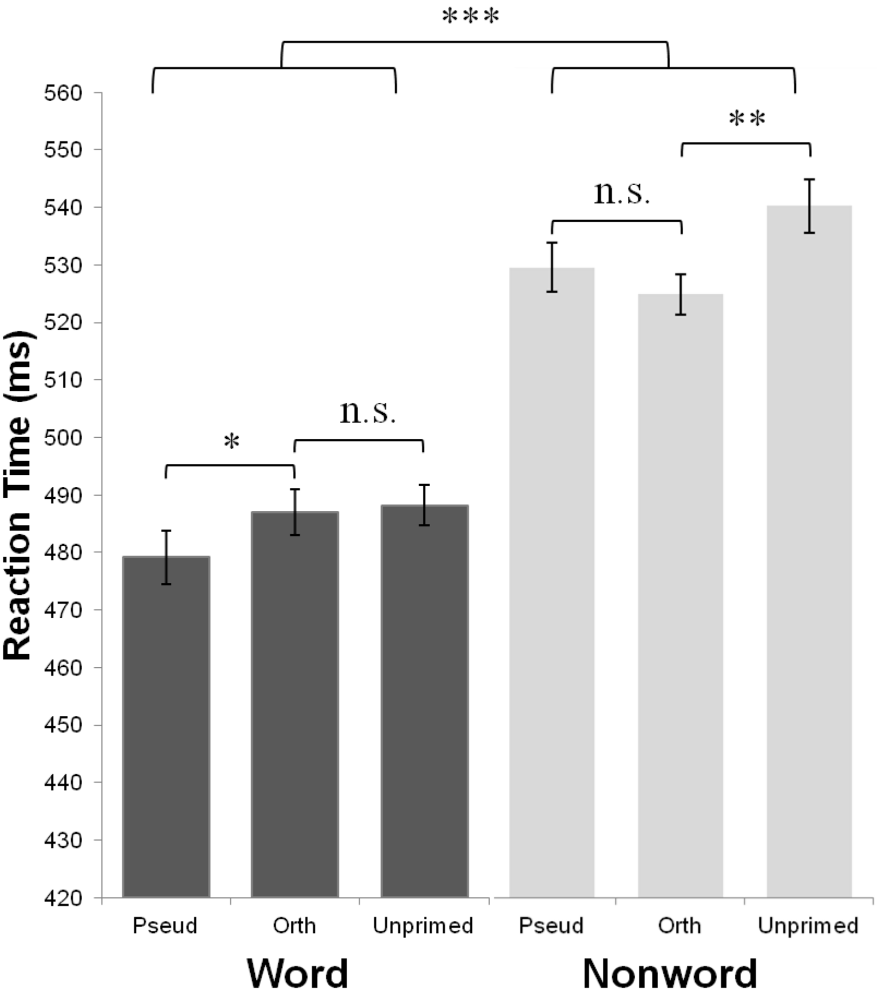


Figure 3.5 Mean reaction times by prime–type and lexicality. Standard error bars, corrected for repeated measures.

*** $p < .001$, ** $p < .01$, * $p < .05$, n.s. = not significant.

For real words, there was a significant main effect of prime–type, $F(2,22) = 3.62$, $p = .044$, $\eta_p^2 = .25$. Planned repeated contrasts revealed a significant difference between PSEUD and ORTH, $F(1,11) = 5.42$, $p = .04$, $\eta_p^2 = .33$, but not between ORTH and UNPRIMED, $F(1,11) = 0.11$, $p = .75$, $\eta_p^2 = .01$. For nonwords, there was a significant main effect of prime–type, $F(2,22) = 7.91$, $p = .003$, $\eta_p^2 = .42$. Planned repeated contrasts revealed no significant difference between PSEUD and ORTH, $F(1,11) = 2.20$, $p = .17$, $\eta_p^2 = .17$, but a significant difference between ORTH and UNPRIMED, $F(1,11) = 16.40$, $p = .002$, $\eta_p^2 = .60$.

3.4.2.2 Reaction Time Analyses by Items

Items analyses corroborated the findings. For real words, there was a significant main effect of prime–type, $F(2,392) = 6.37$, $p = .002$, $\eta_p^2 = .03$. Planned repeated contrasts revealed a significant difference between PSEUD and ORTH, $F(1,196) = 9.87$, $p = .002$, $\eta_p^2 = .05$, but not between ORTH and UNPRIMED, $F(1,196) = 0.08$, $p = .78$, $\eta_p^2 < 0.01$. For nonwords, there was a significant main effect of prime–type, $F(2,392) = 11.03$, $p < .001$, $\eta_p^2 = .05$. Planned repeated contrasts revealed no significant difference between PSEUD and ORTH, $F(1,196) = 0.53$, $p = .47$, $\eta_p^2 < .01$, but a significant difference between ORTH and UNPRIMED, $F(1,196) = 18.21$, $p < .001$, $\eta_p^2 = .09$.

In sum, word targets were responded to faster overall and showed phonological priming (PSEUD faster than ORTH) but not orthographic priming (ORTH equal to UNPRIMED). Nonword trials did not show any phonological priming, but did show orthographic priming.

3.4.3 Discussion

The purpose of Experiment 2 was to explore whether a phonological priming effect could be produced for nonword targets and increased for word targets by modifying the parameters from Experiment 1. However, for nonword targets, no phonological advantage was shown for the pseudohomophone prime over and above the significant orthographic form priming effect. For the word targets, a small but significant phonological priming effect was shown, but there was no advantage shown for orthographic priming alone. Therefore, it seems that under these parameters, words show only a phonological priming effect and nonwords show only an orthographic priming effect without a further advantage for phonological overlap.

That the real word targets show only phonological priming under these parameters is not surprising based on the finding of Ferrand and Grainger (1993) that at an SOA of 60–70 ms the advantage of shared phonology increases and the advantage of shared orthography decreases. It might be surprising that the word effect is smaller than in Experiment 1, however, Frost et al. (2003) and Tzur and Frost (2007) demonstrated using a series of primed lexical decision experiments that SOA does not always determine how successful a prime will be at influencing processing. There is a significant interaction between prime duration and luminance (in accordance with Bloch's law; Hood & Finkelstein, 1986) in determining the amount of stimulus energy that is provided to the cognitive system. The luminance of the stimulus determines this energy directly and the exposure duration allows the amount of energy to be summed over time. The findings of Frost et al. (2003) and Tzur and Frost (2007), therefore, suggest that the specifics of any particular experimental setup (such as screen properties and room lighting) interact with the prime presentation parameters to produce the overall priming effect. Consequently, the prime duration and SOA necessary to elicit priming in any lab may not be expected to be constant across labs. In conclusion, the priming parameters used in Experiment 2 did not result in a phonological priming effect for nonwords or an increase in the priming effect for real word targets.

3.5 Summary: Experiments 1 & 2

The goal of Experiments 1 and 2 was to produce phonological priming of nonwords targets during a lexical decision task in English. Phonological effects for English nonwords have yet to be reported in a primed lexical decision task, although similar effects have been shown in Hebrew (Frost et al., 2003). The overall aim was to produce this behavioural phonological priming effect for nonwords in English in order to translate this into an MEG experiment. This experiment could then be used as a test of the nature of the phonological priming seen by Ashby, (2010) and Ashby et al. (2009) in EEG, and by Wheat et al., (2010) at Broca's area using MEG. The nonlexical status of nonword prime and target pairs allows the investigation of a possible sublexical role of Broca's area during visual word recognition.

Both Experiments 1 and 2 showed significant orthographic priming of nonword targets, but no phonological priming. A lexical level interpretation of priming would not predict any priming when the target is also a nonword. Consequently, these experiments demonstrate sublexical orthographic form priming of nonwords in a lexical decision task in English. However, this is not sufficient for an MEG investigation of sublexical phonology. Experiments 3 and 4 will, therefore, look at how changing the task will affect the priming result in order to extend the phonological priming effect seen with the real words to the nonwords.

3.6 Introduction: Experiments 3 & 4

The lexical decision task is a stronger test of sublexical effects than reading aloud, as it has been argued that priming of nonwords in a reading aloud task could be due to the priming of postlexical articulatory planning and not to any word recognition processes (Forster, 1998). However, the disadvantage of lexical decision is that the task demands are different from basic visual word recognition. The process of rejecting a nonword may be subject to different effects from the decision to accept a real word, such as in the perceptual fluency effect of Bodner and Masson (1997), described above. Lexical decision tasks typically show larger frequency effects and longer reaction times (e.g., Balota & Abrams, 1992; Balota & Chumbley, 1984), which also suggests different processes result in the final response. The choice of task has also been shown to have a significant effect on the type of priming that is found (Kim & Davis, 2003). Therefore, the failure to find an effect of sublexical phonology under lexical decision does not necessarily constitute negative evidence for sublexical phonological involvement in visual word recognition (Johnston & Castles, 2003).

Rastle and Coltheart (1999) found homophonic priming in reading aloud only when either the target or the prime was a real word. Homophonic nonword pairs (e.g., *keff–KEPH*) did not produce any priming. However, in their task, both the prime and the mask were visible and named aloud, with a 900 ms interstimulus interval. As discussed above, prime visibility has been shown to be a critical factor in phonological priming (Humphreys et al., 1988). Therefore, the results of Rastle and Coltheart do not preclude the finding of phonological priming of nonwords when the primes are masked.

Masson and Isaak (1999) demonstrated both repetition and orthographic priming of nonwords in their masked reading aloud paradigm. However, their stimuli did not permit testing for phonological effects. In a four-field (*mask–prime–mask–target*) masked reading aloud task, Horemans and Schiller (2004) investigated sublexical form priming effects in Dutch. The findings demonstrated significant orthographic form priming effects and implied a sublexical basis for the effect, but again phonological priming was not tested. Grainger and Ferrand (1996) compared masked orthographic and phonological effects across different tasks in French; however, the primed nonword targets were only presented in the lexical decision task and showed no priming effects (though, as mentioned above, different nonword targets were used for each prime condition, limiting the conclusions that can be drawn).

Consequently, it is seems that orthographic priming effects can be seen for nonwords in the reading aloud task as in the lexical decision task. However, the phonological priming effect in nonword naming is under explored. Both the lexical decision task and reading aloud may be susceptible to effects that are not related to basic visual word recognition processes, therefore, strong conclusions about the sublexical nature of the effect cannot be drawn from either task. The following two experiments will examine the possibility of producing behavioural phonological priming effects for nonword targets in a reading aloud task.

3.7 Experiment 3

The phonological priming effect for word targets in Experiments 1 and 2 was small compared to the behavioural effect of Wheat et al. (2010). Wheat and colleagues used a speeded naming task rather than the lexical decision task used so far in this chapter. The purpose of Experiment 3 was to replicate the behavioural experiment of Wheat et al. (2010), but including nonword, as well as word, targets. In other words, a direct replication of Experiment 1 in design, but the participants named the word and nonword targets instead of making a lexical decision. As the same experiment parameters were used as in Experiment 1, the participants saw a randomised mix of word and nonword trials.

The priming timings of Experiment 1 were used rather than Experiment 2 because Experiment 1 showed stronger priming effects for words and used the same parameters as Wheat et al. (2010). Although the SOA of 90 ms is longer than some research has shown to be optimal for phonological priming (e.g., Ferrand & Grainger, 1993), as Tzur and Frost (2007) demonstrated, luminance interacts significantly with SOA and can therefore influence the priming effect. Critically, the luminance, SOA and other environmental factors were kept constant across the experimental conditions to be compared; therefore, the exact luminance and exposure durations are not critical to the priming result (Tzur & Frost, 2007). Ultimately, the conditions used by Wheat et al. have shown successful phonological priming in our lab conditions (i.e., longer prime duration, but low screen contrast and mesopic or scotopic viewing conditions), possibly due to the interaction between stimulus luminance and duration (i.e., Bloch’s Law; Hood & Finkelstein, 1986).

One difference between Experiment 3 and the preceding experiments is that this experiment used a subset of the stimuli used in Experiments 1 and 2. Around 100 trials per condition will be needed in the MEG version of the experiment, whereas the lexical decision experiments had 200 stimuli per condition. This allows the stimuli to be selected for the strength of their phonological priming effect based on the significant phonological priming effect of the word targets in Experiment 1.

3.7.1 Methods

3.7.1.1 Participants

Twenty four native-English-speaking adults (6 males; M_{age} 20.13 years, *SD* 3.15) gave their informed consent to participate on a voluntary basis. All were reported to be right-handed, with normal or corrected-to-normal vision, and with no history of any reading disorder.

An additional 4 participants (2 males; M_{age} 19.75 years, *SD* 0.50) were tested, but excluded from all analyses because (1) the fire alarm sounded during testing, (2) they were not a native-English-speaker, (3) the voice key was not activated by the start of the word, or (4) the voice key was set off by breathing noises prior to target word presentation.

3.7.1.2 Materials

In order to maximise the phonological priming effect and to create a suitable set of stimuli for MEG, a refined set of stimuli was selected based on the reaction times from Experiment 1. As there was no phonological priming effect for nonwords, stimuli were selected based on the real word data. First, stimuli were ranked in order of mean phonological priming effect (ORTH minus PSEUD) and selected only if they showed a mean pseudohomophone advantage; that is, at least 1 ms faster mean reaction time for PSEUD than ORTH. This resulted in 123 targets, which were then selected if at least five participants from Experiment 1 showed a pseudohomophone advantage for that target. This left 110 word targets (*M* freq/million 54.15, *SD* 186.66). The mean of Log_{10} bigram token frequency for PSEUD–WORD primes was 5.52 (*SE* 0.04), for ORTH–WORD primes was 5.62 (*SE* 0.03). A paired *t*-test revealed no significant difference between the prime conditions, $t(205) = -1.75$, $p = .08$.

The nonword targets were then selected by matching to the word targets on string length and the position of the letter switch (as in Experiment 1). The mean of the Log_{10} bigram token frequency for PSEUD–NONWORD primes was 5.58 (*SE* 0.03), for ORTH–NONWORD primes was 5.68 (*SE* 0.03). A paired *t*-test revealed a small but significant difference between the nonword prime conditions, $t(218) = -2.07$, $p < .05$, with the orthographic primes being slightly more word like in their orthographic structure.

Stimuli were displayed on a Mitsubishi Diamond Pro 19 in. CRT monitor, controlled from a Windows PC. Stimulus sequence was generated and controlled using Presentation Version 14.0 (Neurobehavioral Systems, Inc.). The screen resolution was 1024 x 768 True Colour with 100 Hz vertical refresh, allowing events to be manipulated in units of 10 ms. Vocal responses were recorded using an Audio-Technica microphone. This is a professional, studio quality microphone that is optimised for recording speech. The analogue to digital conversion of the microphone output was performed by a Soundblaster Xifi card in the Windows PC. Conversion was carried out at 44 KHz with 16-Bit resolution. The recording level of the microphone was set for each participant before testing to ensure appropriate triggering of the voice key (see Appendix B). Timings of responses were logged by Presentation Version 14.0 and sound files of participants' responses were recorded so that the accuracy of responses could be determined offline.

3.7.1.3 Design

All participants were presented with all stimuli from each condition, making a total of 660 trials, with each target seen three times. Stimulus presentation was counterbalanced and pseudorandomised as in Experiment 1.

3.7.1.4 Procedure

The procedure was the same as Experiment 1 with the exception of the instructions given to participants. Participants were instructed to attend the centrally presented fixation marks, and to say each word or made-up word out loud as quickly and accurately as possible.

3.7.2 Results

Incorrect responses were first removed; the mean error rate was 3.99% (*SD* 2.00). Vocal reaction times (VRTs) greater or less than 3 standard deviations from the mean (by condition for each subject) were excluded from analyses. VRTs greater than 1100 ms or less than 200 ms were also excluded. The mean attrition rate after error removal, thresholding, and any trials where the participant did not respond, was 11.41% (*SD* 9.21).

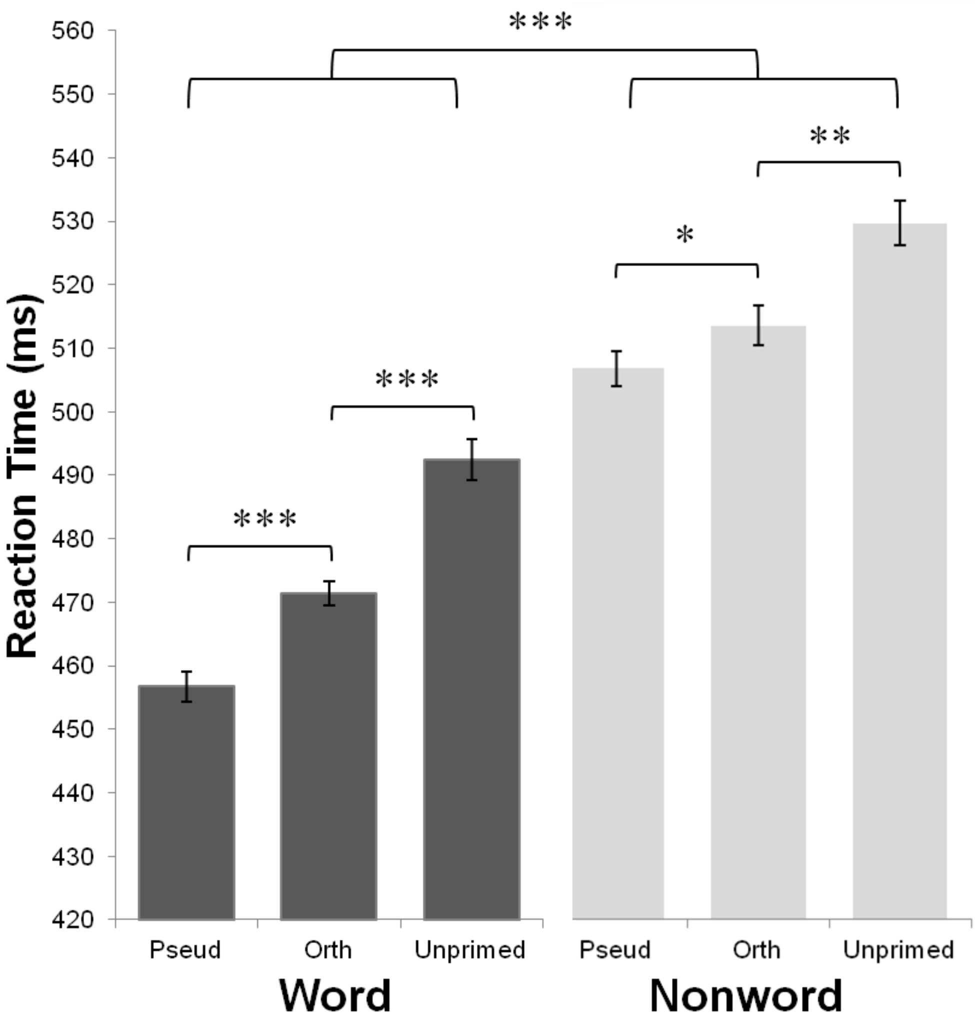


Figure 3.6 Mean reaction times by prime–type and lexicality. Standard error bars, corrected for repeated measures.

*** *p* < .001, ** *p* < .01, * *p* < .05.

As shown in Figure 3.6, there appeared to be a trend for PSEUD to be responded to fastest, followed by ORTH, with UNPRIMED being the slowest. Overall, the real word targets were responded to 43 ms faster than the nonword targets.

3.7.2.1 Reaction Time Analyses by Participants

A two-by-three repeated measures ANOVA with the within-subject factors of lexicality and prime–type was conducted. Mauchly’s test indicated that the assumption of sphericity had been violated for prime–type, $X^2(2) = 8.02$, $p < .05$, and lexicality*prime–type, $X^2(2) = 11.92$, $p < .05$; therefore a Greenhouse-Geisser correction was applied. The results showed a significant main effect of lexicality, $F(1,23) = 148.54$, $p < .001$, Partial $\eta^2 = .87$, and of prime–type, $F(1.53,35.24) = 48.85$, $p < .001$, $\eta_p^2 = .68$, but no significant interaction, $F(1.41,32.43) = 3.36$, $p = .06$, $\eta_p^2 = .13$,.

Separate one-by-three ANOVAs were then conducted, splitting the data by lexicality. For real words, Mauchly's test indicated that the assumption of sphericity had been violated, $X^2(2) = 6.94$, $p < .05$; therefore a Greenhouse-Geisser correction was applied. The results showed a significant main effect of prime–type, $F(1.57,36.21) = 61.64$, $p < .001$, $\eta_p^2 = .73$. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, $F(1,23) = 39.62$, $p < .001$, $\eta_p^2 = .63$, and between ORTH and UNPRIMED, $F(1,23) = 39.78$, $p < .001$, $\eta_p^2 = .63$.

For nonwords, Mauchly's test indicated that the assumption of sphericity had been violated, $X^2(2) = 12.15$, $p < .05$; therefore a Greenhouse-Geisser correction was applied. The nonwords showed a small, but significant, main effect of prime–type, $F(1.40,32.29) = 13.83$, $p < .001$, $\eta_p^2 = .38$. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, $F(1,23) = 5.73$, $p = .03$, $\eta_p^2 = .20$, and between ORTH and UNPRIMED, $F(1,23) = 8.60$, $p = .008$, $\eta_p^2 = .27$.

3.7.2.2 Reaction Time Analyses by Items

Items analyses corroborated the findings. For real words, the results showed a significant main effect of prime–type, $F(2,218) = 52.79$, $p < .001$, $\eta_p^2 = .33$. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, $F(1,109) = 18.75$, $p < .001$, $\eta_p^2 = .15$, and between ORTH and UNPRIMED, $F(1,109) = 32.65$, $p < .001$, $\eta_p^2 = .23$.

The nonwords showed a small, but significant, main effect of prime–type, $F(2,218) = 19.49$, $p < .001$, $\eta_p^2 = .15$. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, $F(1,109) = 5.55$, $p = .02$, $\eta_p^2 = .05$, and between ORTH and UNPRIMED, $F(1,109) = 14.11$, $p < .001$, $\eta_p^2 = .12$.

In sum, word targets were responded to faster overall and showed phonological priming (PSEUD faster than ORTH) and orthographic priming (ORTH faster than UNPRIMED). Nonword trials also showed phonological priming and orthographic priming.

3.7.3 Discussion

The purpose of Experiment 3 was to explore whether a phonological priming effect could be produced for nonword targets using a reading aloud task. For nonword targets, for the first time in this series of experiments, a phonological advantage was shown for the pseudohomophone prime over and above the significant orthographic form priming effect. The effect size was small with just 7 ms between the reaction times for the pseudohomophone and the orthographic conditions. However, this difference is in line with predictions that the sublexical portion of the behavioural priming effect is between 7 and 10 ms (Forster et al., 2003). This evidence for sublexical phonological priming gives a basis for expecting phonological priming of nonwords using the same experiment in MEG.

For the word targets, a significant orthographic priming effect was shown, with a further significant advantage for phonological priming. At 15 ms, this is the largest difference between the pseudohomophone and the orthographic conditions that has been seen so far in the current series of experiments. The increase in phonological priming could relate to an additional effect of the priming of articulatory planning processes for speech output, however, the orthographic priming effect is also more than double that of Experiment 1 (9 ms and 21 ms, respectively), suggesting that other mechanisms may be involved. It could be that the process of lexical decision slows the behavioural response such that an early orthographic priming advantage is lost, though the mean reaction time for words is only 11 ms faster than for Experiment 1.

At this point, significant phonological priming has been shown for nonword targets as well as word targets in a reading aloud task. We deemed this sufficient evidence to warrant translating the experiment into an MEG task to examine when and where in the brain any differences can be shown between the phonological and orthographic conditions for both words and nonwords. The patterns of differences between words and nonwords can then be compared and contrasted to test the hypothesis that early activation of Broca’s area during visual word recognition relates to sublexical phonological processes.

3.8 Experiment 4

A question remains regarding the behavioural nonword priming effect. Will the same phonological priming effect be seen if the nonwords are presented alone? Experiment 3 used the same experimental format as Experiment 1, and therefore comprised a mix of word and nonword trials; however, there is evidence to suggest that there is a cost to processing mixed stimulus lists compared to pure blocks that separate different types of stimuli (e.g., Los, 1996). For example, Los (1999) demonstrated that when participants had to identify noise-degraded and segment-deleted digits, participants were slower to identify the digit during the mixed presentation of stimulus types compared to pure blocks of either noise-degraded or segment-deleted digits. The mixing cost was not reduced by cues to the following trial type. Therefore, Los argued that this reaction time cost during mixed presentation comes from stimulus-driven adjustments in perceptual processing on a trial-by-trial basis.

According to Los' (1996) mixing cost account, any stimuli will produce slower reaction times when mixed with other stimuli, than when presented alone. In contrast, according to Lupker et al.'s (1997) 'time criterion effect', participants set a response time criterion during a task (e.g., the time when articulation will be initiated) that is appropriate for the difficulty level of the stimuli. This response time stays relatively constant over during a block of stimuli and is set at an intermediate level when easy and difficult items are mixed together. Therefore, easier items would be responded to more slowly when mixed with more difficult items, and more difficult items might be responded to faster. Lupker et al. describe this combination of mixing costs and mixing benefits as a homogenisation pattern; demonstrated by showing that nonwords can be named faster when mixed with easier stimuli, such as high frequency words than when presented in pure blocks.

On the basis of these examples, it is difficult to predict how separating the word and nonword trials into pure blocks will affect the vocal reaction times. The aim for Experiment 4 was, therefore, to extend the priming result to separate blocks of words and nonwords and to explore any possible interaction between design type (i.e., mixed vs. blocked stimulus presentation) and priming effect. Experiment 4 was identical to Experiment 3, except that participants were presented with all of the real word trials first followed by the nonword trials or vice versa.

3.8.1 Methods

3.8.1.1 Participants

Twenty four native-English-speaking adults (8 males; M_{age} 21.08 years, *SD* 6.10) gave their informed consent to participate on a voluntary basis. All were reported to be right-handed, with normal or corrected-to-normal vision, and with no history of any reading disorder.

An additional 2 participants (2 females, M_{age} 19 years, *SD* 0) were tested, but were excluded from all analyses due to (1) having a heavy cold that resulted in mispronunciation of many of the targets, (2) an incorrect block sequence was presented.

3.8.1.2 Materials & Design

The materials and design were identical to Experiment 3.

3.8.1.3 Procedure

The procedure was identical to Experiment 3, with the exception that all words were presented first followed by all nonwords, or vice versa. The order of word and nonword presentation was determined by the participant number allocated when the experiment appointment was booked.

3.8.2 Results

Incorrect responses were first removed; the mean error rate was 5.00% (*SD* 3.09). VRTs greater or less than 3 standard deviations from the mean (by condition for each subject) were excluded from analyses. VRTs greater than 1100 ms or less than 200 ms were also excluded. The mean attrition rate after error removal, thresholding, and any trials where the participant did not respond, was 8.83% (*SD* 7.18).

There appeared to be a trend for PSEUD to be responded to fastest, followed by ORTH, with UNPRIMED being the slowest. Overall, the real word targets were responded to 52 ms faster than the nonword targets. Mean reaction times for Experiment 4 (Blocked) are shown alongside those from Experiment 3 (Mixed) in Figure 3.7.

3.8.2.1 Reaction Time Analyses by Participants

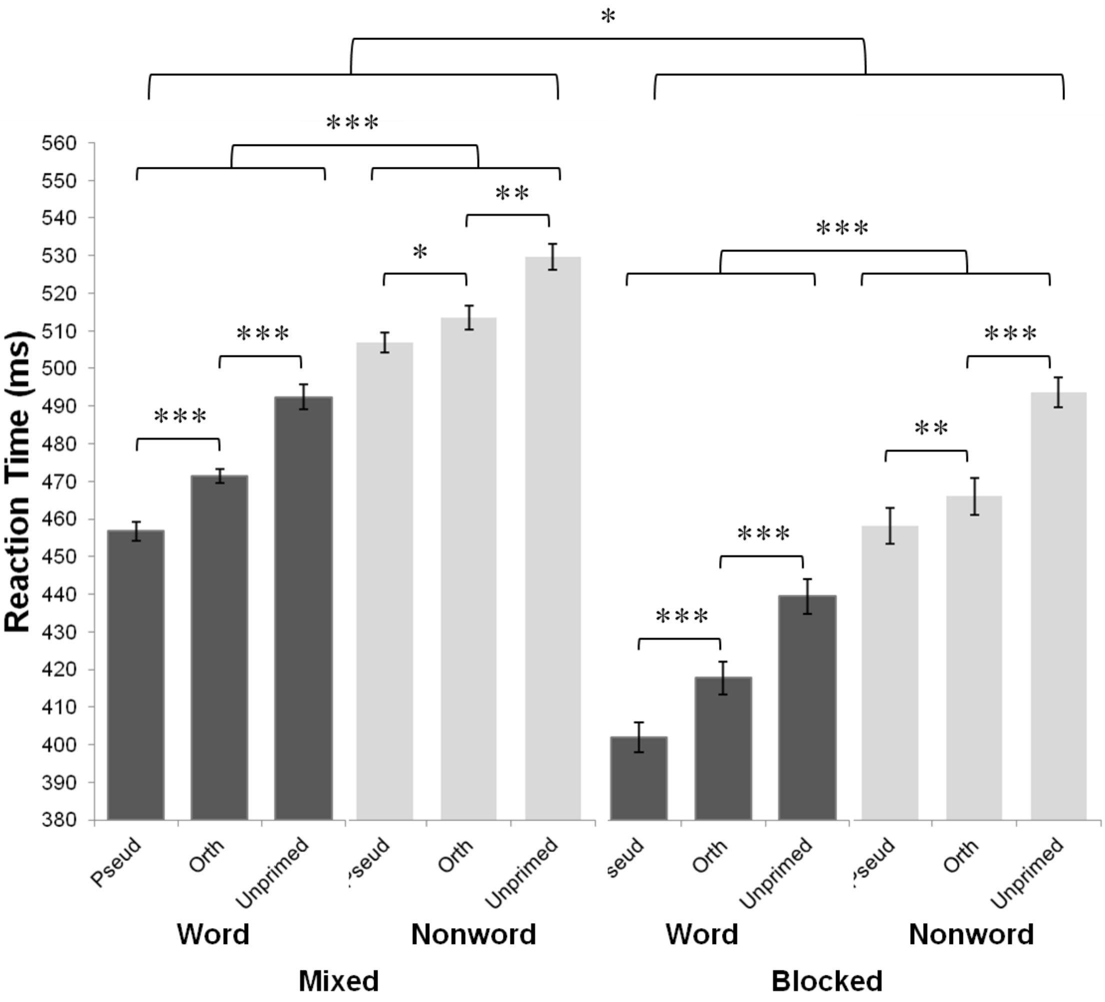


Figure 3.7 Mixed (Exp 3) and blocked (Exp 4) mean reaction times by prime–type and lexicality. Standard error bars, corrected for repeated measures.

*** *p* < .001, ** *p* < .01, * *p* < .05.

First an omnibus 2x2x3 ANOVA was conducted including the data from Experiments 3 and 4. This included the between-subjects factor of design (Mixed vs. Blocked), and the within-subjects factors of lexicality (word vs. nonword) and prime–type (PSEUD, ORTH, UNPRIMED). Mauchly’s test indicated that the assumption of sphericity had been violated for prime–type, $X^2(2) = 13.35$, $p < .05$, and lexicality*prime–type, $X^2(2) = 10.54$, $p < .05$; therefore a Greenhouse-Geisser correction was applied. The results showed a significant main effect of lexicality, $F(1,46) = 121.04$, $p < .001$, $\eta_p^2 = .73$, and of prime–type, $F(1.59,73.20) = 130.96$, $p < .001$, $\eta_p^2 = .74$ and a significant interaction between lexicality and prime–type $F(1.66,76.11) = 4.29$, $p = .02$, $\eta_p^2 = .09$. There was a significant main effect of design, *F*(1,46) = 4.18, *p* = .047, η_p^2 = .09, but no interaction with lexicality, *F*(1,46) = 1.14, *p* = .29, η_p^2 = .02, or with prime–type, *F*(1.59,73.20) = 1.67, *p* = .20, η_p^2 = .04, or with lexicality* prime–type, *F*(1.65,76.11) = 2.05, *p* = .15, η_p^2 = .04.

Next, for the Blocked data, a two-by-three repeated measures ANOVA with the within-subject factors of lexicality and prime–type was conducted. Mauchly's test indicated that the assumption of sphericity had been violated for prime–type, $X^2(2)$ = 6.52, *p* < .05; therefore a Greenhouse-Geisser correction was applied in this case. The results showed a significant main effect of lexicality, *F*(1,23) = 43.66, *p* < .001, η_p^2 = .66, and of prime–type, *F*(1.59,36.61) = 86.06, *p* < .001, η_p^2 = .79, but no significant interaction, *F*(2,46) = 2.76, *p* = .07, η_p^2 = .11.

Separate one-by-three ANOVAs were then conducted, splitting the data by lexicality. For real words, there was a significant main effect of prime–type, *F*(2,46) = 77.07, *p* < .001, η_p^2 = .77. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, *F*(1,23) = 28.65, *p* < .001, η_p^2 = .56, and between ORTH and UNPRIMED, *F*(1,23) = 53.75, *p* < .001, η_p^2 = .70.

For nonwords, Mauchly's test indicated that the assumption of sphericity had been violated, $X^2(2)$ = 8.78, *p* < .05; therefore a Greenhouse-Geisser correction was applied. The nonwords showed a significant main effect of prime–type, *F*(1.51,34.61) = 53.40, *p* < .001, η_p^2 = .70. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, *F*(1,23) = 8.94, *p* = .007, η_p^2 = .28, and between ORTH and UNPRIMED, *F*(1,23) = 62.04, *p* < .001, η_p^2 = .73.

3.8.2.2 Reaction Time Analyses by Items

Items analyses corroborated the findings. For real words, there was a significant main effect of prime–type, *F*(2,218) = 125.99, *p* < .001, η_p^2 = .54. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, *F*(1,109) = 43.75, *p* < .001, η_p^2 = .29, and between ORTH and UNPRIMED, *F*(1,109) = 78.06, *p* < .001, η_p^2 = .42.

For nonwords, the results showed a significant main effect of prime–type, *F*(2,218) = 63.87, *p* < .001, η_p^2 = .37. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, *F*(1,109) = 10.78, *p* = .001, η_p^2 = .09, and between ORTH and UNPRIMED, *F*(1,109) = 54.77, *p* < .001, η_p^2 = .33.

Table 3.2

Summary of Phonological Priming Effect for all Experiments (ms)

	Word Target			Nonword Target		
Experiment	PSEUD	ORTH	Priming	PSEUD	ORTH	Priming
1 Lex. Dec.	474	486	12	512	512	0
2 Lex. Dec.	479	487	8	530	525	-5
3 Mixed	457	471	15	507	514	7
4 Blocked	402	418	16	458	465	8

Overall, reaction times for the "blocked" experiment were 49 ms faster than for the "mixed" experiment, with a small but significant main effect of design. The blocked experiment also appeared to elicit a slightly stronger priming effect than the mixed experiment for the nonwords (as shown in Table 3.2, along with the phonological priming effects for all four experiments), with a larger effect size for this contrast for blocked than for mixed. Both words and nonwords showed phonological and orthographic priming.

3.8.3 Discussion

Experiment 4 shows that phonological and orthographic priming can also be shown in a reading aloud task when the words and nonwords are presented in separate blocks. The reaction times in this blocked experiment were significantly faster overall than the mixed experiment, and the differences between conditions were slightly larger, though there was no significant interaction between design and the other factors, indicating that the overall priming pattern remained the same over both experiments. Again, this experiment provides evidence of sublexical orthographic and phonological priming effects, due to the significant priming effects for nonword targets primed by nonwords.

The difference in reaction times between the blocked and mixed versions of the experiment cannot easily be explained in terms of Lupker et al.'s (1997) time criterion effect due to the fact that both words and nonwords were named more slowing during mixed presentation. Lupker et al. would predict a homogenisation of reaction times, meaning that nonwords (the harder stimuli) would be named faster in the presence of real words (the easier stimuli) due to a shifting response time criterion. The apparent mixing cost for both words and nonwords fits better with Los' (1996) account of a cost of switching between different processes for different types of stimuli. Though, this account does not explain the presence of homogenisation effects in the literature. Lupker, Kinoshita, Coltheart, and Taylor (2003) argued that a combination of mixing costs and homogenisation effects can account for both types of effect. Lupker et al. (2003) posited that mixing stimuli that require the same processing routine will result in homogenisation, whereas mixing stimuli that require different processing routes will result in a mixing cost for both stimuli, due to the necessity to switch between processes on a trial-by-trial basis. Lupker and colleagues also suggested that for more difficult word lists, especially those including nonwords, lexical-checking strategies may be introduced in order to check the prepared articulatory output against an output lexicon. If this were the case, this delay in response due to lexical-checking in the mixed experiment could result in a small loss of priming effect by the time the response is initiated.

3.9 General Discussion

This chapter reported four behavioural priming experiments, designed with the purpose of choosing suitable parameters and stimuli for a phonological priming experiment to use in MEG. A suitable experiment would show phonological priming effects for both word and nonword targets under equivalent priming conditions. This would then be used in MEG to explore the possibility of sublexical phonological priming effects in Broca's area.

Experiments 1 and 2 used a lexical decision task with two slightly different priming paradigms. Both experiments showed significant orthographic priming of nonword targets. However, neither experiment showed any phonological priming effect for nonwords. Although these experiments failed to show any sublexical phonological effect, they cannot be interpreted in terms of lexical level priming, as this interpretation would not predict any priming when the target is also a nonword. These experiments, therefore, demonstrate sublexical orthographic form priming of nonwords in a lexical decision task in English. Though, neither experiment resulted in a suitable paradigm for an MEG investigation of sublexical phonological priming.

Experiments 3 and 4 used a reading aloud task. Both experiments resulted in significant orthographic and phonological priming of nonwords. The priming effect appeared marginally stronger in Experiment 4, where word and nonword targets were presented in separate blocks, than in Experiment 3, where words and nonwords were mixed. For the first time in English, these experiments demonstrate behavioural phonological priming of nonword targets; further evidence against a fully lexical account of masked priming effects (e.g., Forster & Davis, 1984; Forster et al., 2003). In both cases, the real word targets showed stronger phonological priming effects. This could be due to the further contribution of lexical priming effects for real word targets, or that some of the priming advantage is lost for nonword targets due to the longer reaction times.

If the purpose of these behavioural experiments was to explore the mechanisms of behavioural masked priming then a number of limitations must be addressed. For example, Experiments 3 and 4 used a refined set of stimuli, which may have contributed to the enhanced priming effects. The word stimuli in particular were chosen on the basis of previous phonological priming effects. Therefore, in order to fully explore the phonological priming effect in lexical decision, Experiment 1 should be repeated using the refined stimulus set. The data from Experiments 1 and 2 could be reanalysed using just the refined stimulus set, however, this would not be a fair comparison, as Experiments 3 and 4 were completed by twice as many participants. Furthermore, there was an important change between the two sets of experiments that makes comparison difficult. In Experiments 1 and 2 stimuli were presented in black on a light grey background, however, in Experiments 3 and 4 this was changed to white stimuli on a black background. In hindsight, all of the experiments should have been run with white stimuli on a black background, as this is the presentation method that will be used in MEG. Experiment 2, along with the findings of Tzur and Frost (2007) and Frost et al. (2003), shows the importance of ensuring that SOA–luminance interactions are kept constant across experiments and experimental conditions. Therefore, the presentation method was changed to match the MEG constraints for Experiments 3 and 4, but unfortunately this means Experiments 1 and 2 are not directly comparable. Consequently, this series of experiments is adequate for the purpose of producing a sublexical priming test for use in MEG, but not sufficient for drawing strong conclusions about the mechanisms of masked phonological priming. On the basis of these experiments, the possibility of finding phonological priming in a lexical decision task in English has not been thoroughly investigated.

In conclusion, both Experiments 3 and 4 showed phonological priming of nonwords, and so both would be suitable for use in an MEG exploration of sublexical phonological priming. As a direction for future research, it would be interesting to explore the differences between these experiments in MEG. For the purpose of this thesis, Experiment 3 will be translated into an MEG experiment. This experiment provides an intermediate position between the blocked experiment and a lexical decision experiment, both of which should ultimately also be tested in MEG.

Chapter 4

Experiment 5: MEG

4.1 Overview

This chapter reports a phonological priming experiment in MEG on a set of participants who were selected on the basis of their performance in the behavioural experiment based on Experiment 3 of Chapter 3. The main purpose of this MEG experiment was to investigate the role of Broca’s area for phonology during visual word recognition, and the nature of any phonological representations at Broca’s area. In order to test the hypothesis that Broca’s area is involved in sublexical phonological encoding, a phonological priming task was used with nonword primes and targets. Equivalent priming effects for words and nonwords would suggest early involvement of sublexical phonological processes. Source localisation techniques allow any priming effects to be placed with good spatial resolution in the brain. Region of interest analyses further allow priming conditions to be directly compared with excellent temporal resolution. First, MEG will be introduced as an imaging method and reviewed with regard to its suitability for this experiment.

4.2 Introduction to MEG

MEG is a non-invasive method for studying neural activity, providing a direct means of looking ‘through the skull’ (Hari & Salmelin, 1997), in a way previously only achievable in animals or brain-injured patients (Lounasmaa, Hämäläinen, Hari, & Salmelin, 1996). As with any neuroimaging technique, the ultimate goal of MEG is to measure, and reconstruct as accurately as possible, neural activity. The purpose of this is to understand how neural networks interact to form the basis of perception, action, and even conscious thought (Lounasmaa, et al., 1996).

4.2.1 MEG Recording

4.2.1.1 What Are The Signals?

The neural activity measured with MEG originates mainly in the 2500 cm^2 of cerebral cortex, whose 2–4 mm thickness is highly convoluted to fit the 700 cm^2 surface of the inner skull. The human cerebral cortex contains on the order of 10^{11} neurons interconnected via approximately 10^{14} synapses (Hämäläinen, Hari, Illmoniemi, Knuutila, & Lounasmaa, 1993). Neurons communicate across synapses by releasing neurotransmitters into the extracellular space, affecting the potential of post-synaptic cells in an inhibitory or excitatory way. If a cell receives enough excitatory input, it will fire an action potential, and propagate the signal, via the release of neurotransmitters at the synapse, to neighbouring neurons. Any task involving the brain requires simultaneous activity in large populations of neurons, communicating via electrical and chemical activity. The primary signals detectable by MEG are thought to be generated by the large pyramidal neurons due to their arrangement perpendicular to the cortical surface, with approximately 10^5 pyramidal cells per mm^2 of cortex (Hämäläinen & Hari, 2002). The post-synaptic potentials produced by these neurons can last several tens of milliseconds, allowing the temporal summation of electrical currents from populations of neighbouring, parallel oriented neurons (Baillet, Mosher, & Leahy, 2001). These post-synaptic currents, like any current, produce a corresponding magnetic field, and it is these tiny net magnetic fields that MEG is tailored to detect.

The magnetic fields generated by the brain are typically around 50–500 femtoTeslas (10^{-15} Tesla) in strength. That is one part in 10^9 or 10^8 of the Earth's magnetic field at 0.5 microTeslas (Lounasmaa, et al., 1996; Vrba & Robinson, 2001). These signals are far weaker than many other environmental magnetic disturbances, such as power lines or moving vehicles, and biomagnetic fields, such as eye or muscle movements. Cardiac activity, for example, produces magnetic fields 100–1000 times larger than the signals of interest (Vrba, 2002). Therefore, for the magnetic fields to be detectable outside the head, simultaneous activity from 10^4–10^5 pyramidal cells is required (Vrba & Robinson, 2001), coming from around a 40 mm^2 area of cortex (Hämäläinen, et al., 1993). These magnetic fields pass through the scalp and intervening tissue largely undistorted (Hari & Salmelin, 1997); unlike the electrical potentials measured by the closely related EEG method. Although MEG and EEG detect signals generated by the same synchronised neural activity, the electrical potentials measured by EEG suffer from disturbances caused by, for example, the low conductivity of the skull (1/80–1/100 that of the brain; Hämäläinen & Hari, 2002).

4.2.1.2 How Are They Measured?

MEG uses an array of magnetometers placed at many locations around the head, usually in a helmet-shaped configuration. These magnetometers contain superconducting quantum interference devices (SQUIDs) and flux transformers immersed in cryogen (liquid He or N_2) within a thermally insulated and electromagnetically transparent dewar (Vrba & Robinson, 2001). SQUID magnetometers are highly sensitive to the external magnetic flux associated with current flow, such as at synapses and during action potentials. The magnetic flux is detected by the superconducting flux transformers and then magnetically coupled to the SQUID by the signal coil (Hari & Salmelin, 1997).

During MEG recording, the participant sits or lies with their head inside the dewar, which is typically situated within a magnetically shielded room (Vrba & Robinson, 2001). The protection from external magnetic disturbances provided by the magnetically shielded room is an important component of a setup designed to ensure a high signal-to-noise ratio (Hämäläinen & Hari, 2002). This setup also includes the configuration of the magnetometers (designed to be maximally sensitive to brain signals) as well as online and offline noise reduction (by monitoring the electromagnetic noise within the room) and bandpass filtering (Hämäläinen, et al., 1993). Additionally, the measurement and rejection of (or correction for) biomagnetic artefacts, such as eye movements, and averaging over a large number of trials, serve to increase the signal-to-noise ratio further (Hämäläinen, et al., 1993).

The position of the participants head within the dewar (and therefore relative to the MEG sensors) must be known, particularly for group source-space analyses (see section 4.2.3). It is recorded by the MEG system using a combination of 3D digitizing methods and small coils mounted at specific anatomical landmarks on the participant's head, such as the nasion and preauricular points (Hämäläinen & Hari, 2002; Vrba & Robinson, 2001). A current is passed through each coil so that its magnetic field can be detected by the MEG system and used to determine the position of the participant's head (Vrba & Robinson, 2001). These anatomical landmarks can also be used to co-register the MEG data with a structural MRI scan, in order to specify the shape and location of the participant's brain in relation to the MEG sensors (Vrba & Robinson, 2001).

This recording procedure results in a distribution of magnetic fields across a 2-dimensional helmet-shaped array of sensors outside of the head. However, the challenge for analysis methods is to infer how these fields were generated within the 3-dimensional volume of the brain. MEG analyses fall into two categories; sensor space approaches, which analyse data directly at the level of the sensors, and source space approaches, which aim to localise the 3D neural sources of activity. These approaches will be discussed in the next section.

4.2.2 Introduction to MEG Analysis

4.2.2.1 Preprocessing

Depending on the subsequent analyses to be performed and the software used, various preprocessing steps can be incorporated. The time-window of interest (or epoch) for a trial should be defined; for example, an epoch might span the 900 ms prior to the stimulus onset, until 1000 ms post stimulus onset. Any epochs containing magnetic artefacts, such as blinks, must be identified, by eye or using electrooculogram (EOG) data recorded during the scan. These epochs must then be removed or corrected before further analysis. Epochs may be averaged across conditions, within or between participants, in order to increase the signal-to-noise ratio.

4.2.2.2 Sensor Space Analyses

The simplest level of MEG data analysis is to plot the signal patterns recorded at the sensors without attempting to infer the neural sources responsible for these signals. One type of sensor space analysis is the event-related field (ERF or overlaid response plot) in which the magnitude of the pre-processed MEG data is plotted over time, such that a single figure represents all sensors overlaid, averaged across one condition, for one participant, for the duration of the epoch (see Figure 4.1). The magnitude and latency of the peaks can then be compared across conditions. Contour plots are another way of representing sensor space information and more commonly used than overlaid response plots. Contour plots display the distribution of activity across sensors from one participant, for one experimental condition, at one point in time (see Figure 4.2). Choosing plots that are representative of the data is difficult for this type of analysis, as it is unfeasible to present contour plots for every combination of participants, experimental conditions, and points in time. Furthermore, sensor space analyses can take into account the layout of the sensors, but do not explicitly account for the position of the participant’s head in the dewar or individual differences in head size and shape. Because a signal pattern at a particular sensor in one participant does not necessarily come from the same brain location as an identical sensor for another participant, group analyses are not usually performed in sensor space.

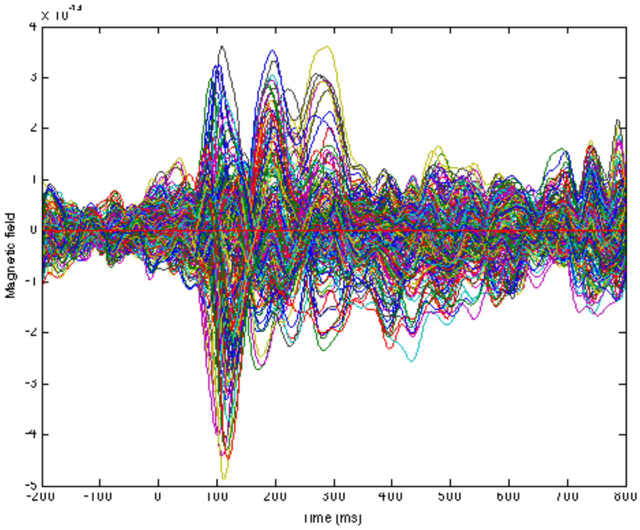


Figure 4.1 Overlaid response plot. Shows one participant, for one condition. Each coloured line represents the magnitude of the magnetic field over time for one MEG sensor.

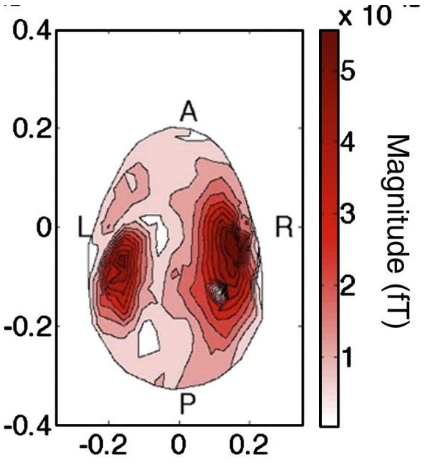


Figure 4.2 Contour plot. A single plot shows the magnetic field recorded at the sensors for one participant, for one experimental condition, at one time window.

4.2.3 Source Space Analysis

4.2.3.1 The Inverse Problem

Although sensor space analyses can compare conditions with millisecond temporal resolution, this is not sufficient for an exploration of where in the brain the activity is taking place. Source space techniques can be used to infer the locations of neural activity responsible for generating the signals recorded at the sensors. A step that is vital for testing the hypotheses of this chapter. However, there are inherent problems with this, due to attempting to work backwards from the 2D sensor space to the 3D neural sources. This difficulty is termed the ‘inverse problem’; that is, even if the magnetic field has been precisely measured outside the head, there is not a unique solution of the primary current distribution within the head (Hämäläinen & Hari, 2002; Hämäläinen et al., 1993). As Helmholtz (1853, as cited by Hämäläinen, et al., 1993) demonstrated, knowledge about the electromagnetic fields outside a spherical conductor is not sufficient to provide a unique description of the current distribution inside the conductor, owing in part to the existence of primary current distributions that are magnetically silent (e.g., radial sources, see section 4.2.4), electrically silent, or both (Hämäläinen, et al., 1993). Therefore, in order to localise successfully the source(s) of neural activity based on a two-dimensional map of magnetic field distribution, assumptions must be made which constrain the number of possibilities and render the problem soluble (Hillebrand, Singh, Holliday, Furlong, & Barnes, 2005).

Various source reconstruction techniques have been designed to cope with the inverse problem, which applies whenever one is trying to deduce the source currents from the externally measured signals, either in MEG or EEG (Hämäläinen, et al., 1993). Different source localisation techniques apply different assumptions and/or restrictions to the data, resulting in a variety of strengths and limitations across techniques. For example, analysis methods may differ in terms of spatial and temporal resolution or their abilities to detect focused or distributed sources. Nevertheless, whatever the analysis technique, the inverse problem remains vastly underdetermined, due to the restricted number of spatial measurements (in the region of 100–300) and the number of unknowns (on the order of 10^4; Baillet, et al., 2001).

4.2.3.2 Current Dipole Modelling

Current dipole modelling is an example of a source space analysis method, and as such, attempts to estimate the location, strength and orientation of neural sources from the magnetic fields measured at the sensors (Hämäläinen & Hari, 2002). In the simplest case, the single best-fitting current dipole, or equivalent current dipole, is calculated for the measured magnetic fields at any particular point in time (Hämäläinen & Hari, 2002). Multi-dipole fitting requires more complex modelling and is based on the assumption that only a small number of neural sources contributed to the measured field, often using a priori estimates of the number of sources. In either case, the optimal source parameters are found by using the least-squares criterion to minimise the difference between the measured magnetic fields and the magnetic fields predicted by the model. The result is an estimate of the orientations and locations of the dipoles, as well the strengths of the dipoles over time (Hämäläinen & Hari, 2002).

One drawback to current dipole modelling is the lack of stability of the model as more neural sources contribute to the measured magnetic field. The success of equivalent current dipole modelling may also be limited if there are competing possibilities for the neural source configuration, or if the actual distribution of the sources is not well approximated by a dipole (Hämäläinen & Hari, 2002). Furthermore, the use of a priori knowledge of expected sources is often needed to constrain the selection of the best-fitting solution, meaning that it is not necessarily suitable for exploratory analysis.

4.2.3.3 Minimum Norm Estimation

Minimum norm estimation is another source space approach, which assumes neural sources are distributed, either across the cortical surface or within the brain volume, using information from structural MRI scans to constrain the model (Hämäläinen & Hari, 2002). The aim is to produce an estimated distribution of sources that has the least energy and minimises the difference between the magnetic fields estimated from the model and the measured magnetic fields (Hillebrand et al., 2005). The assumption that the chosen solution should be the solution with the least energy results in a bias towards superficial sources and necessitates the investigator to factor in a depth bias based on previous fMRI data, Bayesian inference, or simulated data (Hillebrand et al., 2005).

Minimum norm estimation will result a blurred estimate of the neural sources, even for point-like sources (Hämäläinen & Hari, 2002); unlike dipole modelling, which will always result in focal source estimates, even if the actual neural source distribution was diffuse (Hillebrand et al., 2005). In assessing the suitability of these two methods for a study, it is therefore necessary to have some prior knowledge of the expected source distribution.

4.2.3.4 Beamforming

The chosen analysis method for the MEG data presented in this chapter is beamforming. Beamforming is a spatial filtering technique for MEG source space analysis, which uses narrowband filters to increase the sensitivity to signals from a location of interest, while attenuating signals coming from all other locations (e.g., Hillebrand et al., 2005). This selective spatial filtering is applied throughout the volume of the brain to each point of a pre-defined regular grid of points. In fact, three spatial filters, or ‘beamformers’, are applied at each grid point, one for each of three orthogonal directions. This grid can be constrained by anatomical information from a structural MRI scan, ensuring that only points from within that participant’s brain are examined. The particular beamformer applied at York Neuroimaging Centre (YNiC) is a linearly constrained minimum variance beamformer adapted from Van Veen, van Drongelen, Yuchtman, and Suzuki (1997). Optimal spatial filters are implemented across the grid by applying a set of weights to the data. These weights must satisfy a linear constraint that allows the signal to be passed from each location of interest, while the power minimisation suppresses activity originating from other brain locations (Van Veen et al., 1997). Beamforming, therefore, sidesteps the inverse problem by using this regular array of beamformers to calculate the contribution of each grid location to the measured field, rather than trying to work backwards to fit the total measured field (Hämäläinen & Hari, 2002). Beamforming can model both focal and distributed sources, including even point-like neural sources under favourable signal-to-noise ratios, down to the size of the filter grid (Huang et al., 2004). Furthermore, there is no limit to the number of neural sources that can be resolved, and the number of expected sources does not have to be defined a priori (Van Veen et al., 1997).

The signal-to-noise ratio of the data is often small, which can result in false detection or missed detection of neural sources in the resulting power map. This can be improved in two ways. First, it is important that only clean data are entered into the analyses. That is, data that are free of magnetic artefacts caused, for example, by blinks and other movements. Each “epoch” (i.e., chunk of data, such as an experimental trial) is examined either by eye or using an algorithm and then either corrected or removed prior to beamforming. Next, the resulting map of neural power is normalised by an estimate of the noise power map, aided by reference channels within the magnetically shielded room, but away from the participants head. This normalisation results in a neural activity index (NAI) map. Local maxima in the NAI are then identified as neural sources. A drawback of this approach is that any spatially distant sources that are perfectly correlated will be identified as noise and cancelled out. However, perfect correlation between two distinct sources is unlikely and Huang et al. (2004) demonstrated that beamforming is capable of resolving sources correlated as highly as 90%.

4.2.3.5 Evoked Versus Induced Responses

A significant attraction of beamforming is the ability to resolve both evoked and induced changes in oscillatory neural activity. Evoked responses are those which are tightly phase-locked to the stimulus, in other words, they generate a stereotypical wave sequence at a fixed time after a specific stimulus is presented. The averaging of evoked responses in the amplitude domain across repeated trials cancels out surrounding brain noise and sums together the systematic signal changes, similar to the ERPs of EEG analysis. However, any non-phase-locked changes, in other words any signal changes that are jittered in latency from trial to trial, will be cancelled out during averaging in the time domain (see e.g., Hillebrand, et al., 2005). These non-phase-locked changes are termed ‘induced’ and can be revealed by averaging in the frequency domain (see Figure 4.3 for an illustration). Changes in the power of this on-going non-phase-locked signal component were often overlooked by researchers using evoked averaging. However, it has been shown that these induced changes play an important role in cortical function. For example, optical imaging and simultaneous microelectrode recording in cats has shown that ongoing non-phase-locked oscillatory activity can be used to predict later evoked responses (Arieli, Sterkin, Grinvald, & Aertsen, 1996). In humans, alpha oscillations (8–13 Hz) in the visual cortex have been shown to increase in power when participants close their eyes (e.g., Chapman, Ilmoniemi, Barbanera, & Romani, 1984). Tallon-Baudry, Bertrand, Peronnet and Pernier (1998) proposed that gamma band oscillations play a role in binding together different aspects of neural processing in order to build a complete percept. Recent MEG investigations have also shown that cued spatial attention to the hand can increase the power of mu-alpha (7–14 Hz) and mu-beta (15–29 Hz) oscillations in the somatosensory hand area, which decrease when attention is cued to the foot (Jones et al., 2010). Finally, in a state of the art concurrent transcranial magnetic stimulation (TMS, discussed in more detail in Chapter 5) and EEG study, Thut et al. (2011) demonstrated that alpha oscillations could be stimulated and enhanced by TMS to the parietal cortex attention network. This alpha oscillation entrainment was due to increased phase-locking of the on-going activity. It occurred only at the intrinsic alpha frequency of each participant and interacted behaviourally with performance on visual attention tasks. This demonstrates not only a correlation between intrinsic neural oscillations and behaviours but also that stimulating and enhancing these oscillations has a measurable effect on behaviour.

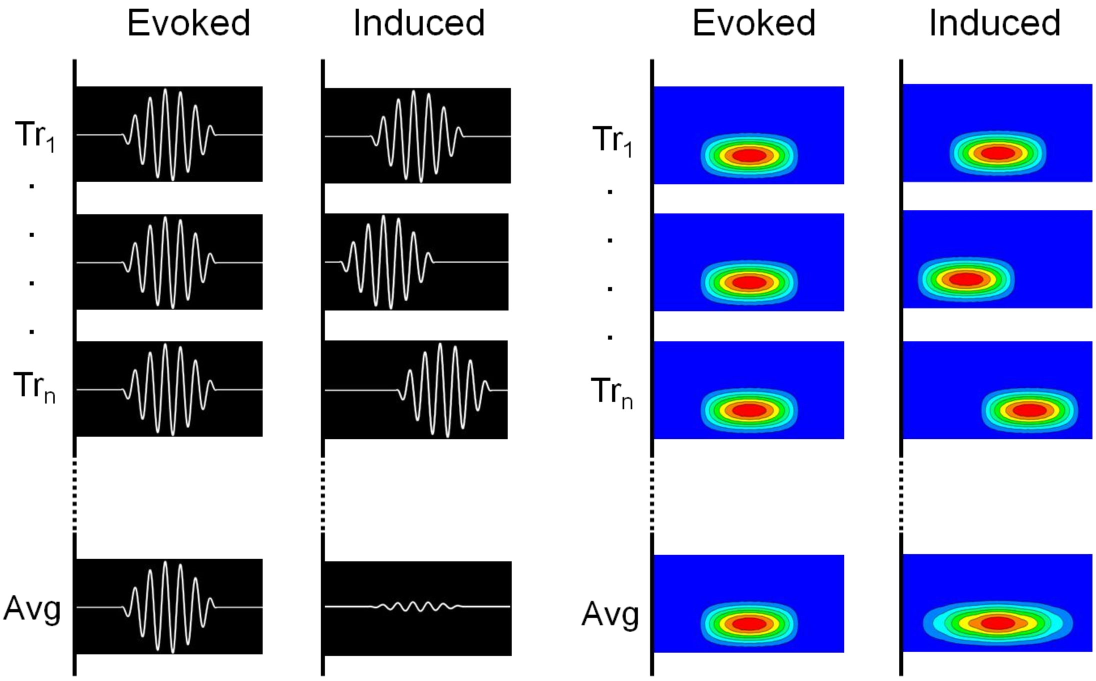


Figure 4.3 Amplitude versus frequency domain analyses. The example of the left shows responses in the amplitude domain and on the right shows the frequency domain. Where the responses are jittered in time across trials (induced), they will be cancelled out in the amplitude domain, but can be revealed in the frequency domain. Evoked responses can be revealed by both methods.

Frequency domain analysis successfully reveals both non-phase-locked (induced) and phase-locked (evoked) responses as changes in power at a particular frequency at a particular time. The role of particular frequency components with respect to visual word recognition is poorly understood, however, whatever the functions of different aspects of the signal, it is clear that there is an advantage of being able to reveal as much information about the signal as possible, and that to average over epochs in such as way as to attenuate the induced component results in a loss of available information. Furthermore, Wheat et al. (2010) showed their early phonological priming was revealed by time–frequency analyses that reveal both phase-locked and non-phase-locked changes, whereas previous ERP studies (capable of revealing only phase-locked responses) typically reveal a later involvement of phonology (e.g., Grainger et al., 2006; Mainy et al., 2008).

4.2.3.6 The Statistics of Beamforming

The beamforming procedure described above can be used to generate NAI maps for epochs of MEG data, such as experimental trials. These epochs can then be statistically compared to test the hypotheses of the experiment by dividing epochs into groups, for example, by block, experimental condition, participant group, and so on. Whole-brain analyses across a group of participants can also be used to examine the spread of activity across the brain during a trial for different experimental conditions. In order to achieve this, epochs of data (in this example, spanning a trial plus some pre-trial period) are portioned into time windows and frequency bands for each condition separately. For example, 200 ms long time windows from trial onset for the duration of interest (e.g., 0–200 ms, 100–300 ms, 200–400 ms, etc.) and 10 Hz frequency bands (e.g., 5–15 Hz, 15–25 Hz, 25–35 Hz, etc.). Each data portion from the ‘active’ period of interest (i.e., the trial part of the epoch) is then compared to an equivalent size ‘passive’ baseline period, such as a 200 ms window from the pre-trial part of the epoch. For each time–frequency portion of an epoch, for a particular condition, the null hypothesis that the ‘active’ NAI map is not significantly different from the ‘passive’ NAI map is then tested.

For the first, within-subjects, level of whole-brain analysis, a paired samples *t*-statistic is computed for every point in the grid, using the mean difference in oscillatory power, averaged across epochs, for the relevant frequency bands, between the passive and active NAI maps. In this way, a separate *t* map is generated for each participant, for each active–passive contrast, for each of the time-window and frequency-band combinations, for each experimental condition. Participant’s *t* maps are then transformed into the Montreal Neurological Institute (MNI) standard space.

The group level of analysis uses a multi-step non-parametric permutation method based on the methods of Nichols and Holmes (2004). The permutation distribution of the maximal statistic (the largest mean *t*-value, in this case) is computed (averaging across participants), by re-labelling experimental conditions (in this case active vs. passive), from the population of grid points in the standard MNI space

(Nichols & Holmes, 2004). The null hypothesis for a single grid point states that the *t* distribution would have been the same, whatever the labelling of experimental conditions (i.e., there is no difference in *t* distribution between the active and passive periods). At the level of the group whole-brain image, the omnibus hypothesis (that the hypothesis for all grid points is true) is rejected at level α if the maximal statistic for the actual labelling of the experiment was in the top 100α % of the permutation distribution for the maximal statistic. Where *N* is the number of possible relabelings and *T* is the value of the statistic for the actual labelling of the experiment, Nichols & Holmes (2004) state that

> *We reject the null hypothesis at significance level α if the p-value is less than α. Equivalently, T must be greater or equal to the 100(1−α)%ile of the permutation distribution. Thus, the critical value is the (c + 1)th largest member of the permutation distribution, where c = [αN], αN rounded down. If T exceeds this critical value then the test is significant at level α. (p. 8).*

This test has been shown to have strong control over experiment-wise Type I error, thus inherently correcting for multiple comparisons without the need to apply additional corrections (such as Bonferroni). For a formal proof see Holmes, Blair, Watson, and Ford (1996). The resulting group *t* maps can then be used to display activity that is significantly different from baseline for each of the active–passive comparisons. Changes in power in a positive direction, relative to baseline, are often termed event related synchronization (ERS), whilst negative changes are termed event related desynchronisation (ERD; Pfurtscheller & Lopes da Silva, 1999).

The same method can be used to compare one experimental condition directly with another, rather than an active–passive contrast. For example, a specific time window and frequency band of the condition A could be directly contrasted with the equivalent window of condition B, akin to contrasts in fMRI. However, a direct comparison of this kind could potentially produce false negative results if the same regions were equally active during both conditions. Furthermore, a whole brain contrast between conditions also runs the risk of producing false negative results if, for example, positive and negative power changes in different frequency bands cancelled each other out. A region of interest approach can be used to directly compare conditions, with the further advantage that the time–frequency resolution of the data is preserved.

4.2.3.7 Virtual Electrodes

One weakness of the whole-brain beamforming analyses, described above, is that the analyses are performed over long time windows (~200 ms), resulting in a loss of temporal resolution. An ROI approach can be used to retain a higher degree of temporal resolution at specific locations in the brain by using ‘virtual electrodes’. A virtual electrode is essentially the result of beamforming at a single point in 3D grid of points (computed separately from the grid defined for whole-brain analysis). As described above, for each grid point of interest, three spatial filters are applied, one for each orthogonal direction. The virtual electrode procedure results in a description of the oscillatory power over the duration of an epoch coming from the location of interest in the three directions, for each participant, for each experimental condition.

As discussed above, a particular advantage of beamforming is its ability to resolve induced changes in oscillatory power. In order to be able to do this, the time series produced by each beamformer is transformed into a time–frequency representation of the data (see, Figure 4.4). At YNiC the specific transform used is the Stockwell Transform (Stockwell, Mansinha, & Lowe, 1996), has a frequency dependent resolution, meaning that temporal resolution is better at higher frequencies and frequency resolution is better at lower frequencies. This has implications for the interpretation of virtual electrode results, which will be discussed in more detail below.

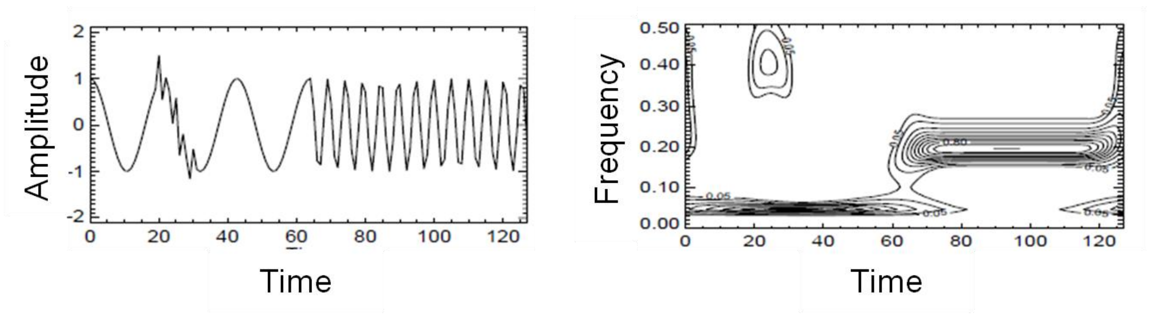


Figure 4.4 Transform from amplitude domain to frequency domain. The transform shown is the Stockwell Transform. Adapted from Stockwell et al. (1996).

The Stockwell Transform results in time–frequency plots of total (non-phase-locked plus phase-locked) and evoked (phase-locked) power, for each virtual electrode (separate plots for each direction, participant and condition). Plots can then be averaged over direction and participants to make statistical comparisons between the group-level time–frequency plots for different conditions by, for example, computing a difference or a percentage signal change between conditions. Statistical comparisons between plots must take into account spatial covariance. That is, due to the nature of the plots, the power in one time–frequency pixel is more likely to be similar to a neighbouring pixel than it is to a pixel further away. The virtual electrode method of beamforming allows the potential for millisecond temporal resolution inherent in the data to be retained, and does not require the data to be partitioned into time-windows and frequency-bands.

4.2.4 Limitations of MEG

The major limitation of MEG lies in the ability to accurately and precisely reconstruct the spatial locations of neural sources. There are inherent inhomogeneities in the achievable spatial resolution across the brain; in particular, deep sources cause difficulties because the magnitudes of the magnetic fields fall off rapidly with the square of distance from the source of electrical activity (Hillebrand & Barnes, 2002). Hillebrand and Barnes (2002) demonstrated a ~90% detection rate for MEG signals from the upper cortical surface (such as the inferior frontal, precentral, and middle occipital gyri) while signals from the underside of the brain were poorly detected. For example, detection probability fell to ~50% for the medial portion of the middle and anterior fusiform gyrus (the territory of so-called VWFA, see section 2.3.3.1).

Further difficulties come from detecting radially oriented sources, that is, those sources oriented perpendicular to the surface of the scalp (see Figure 4.5). Perfectly radially oriented sources are magnetically silent as the magnetic field generated does not penetrate the scalp, unlike tangential sources. This means that any number of radial sources could be present, without any effect on the signal recorded at the sensors. However, Hillebrand & Barnes (2002) noted that, although radial sources (defined as having 0–15° angle with radius) have a low detection probability, they comprise less than 5% of the cortical surface, and are situated in very thin (~2 mm) strips at the crests of gyri.

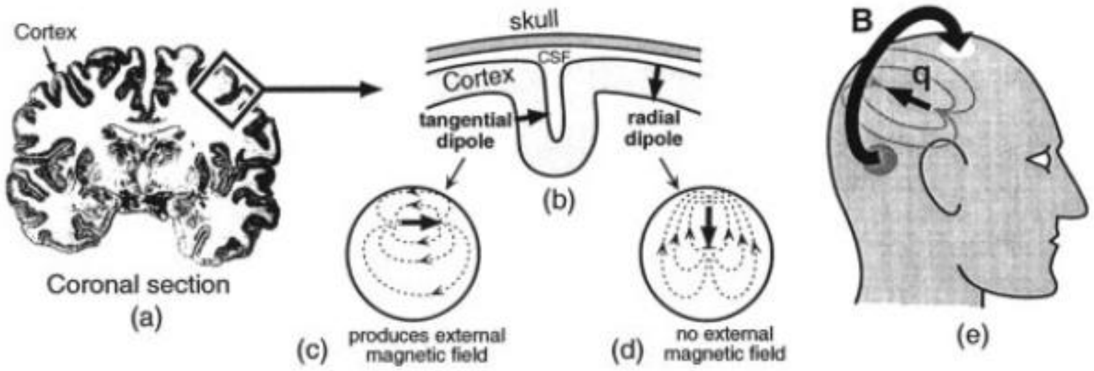


Figure 4.5 Tangential and radial sources. (a) Coronal section of a brain, showing the cortex in grey. (b) The convoluted cortical surface and perpendicular orientation of pyramidal neurons result in radial and tangential currents. (c) Tangential currents will result in an external magnetic field. (d) No external magnetic field will be observed from perfectly radially oriented sources. (e) Magnetic fields from tangential sources will exit and enter the scalp. From Vrba & Robinson (2001).

Finally, with regard to the spatial resolution achievable with beamforming analyses in MEG, Barnes, Hillebrand, Fawcett, and Singh (2004) conducted a beamforming analysis of MEG responses to a flickering checker board stimulus, reversing at 17 Hz, presented visually for 15 s blocks separated by 15 s fixation. Data were divided into 1 s epochs of active (checkerboard) and passive (fixation) stimulation. Barnes et al. analysed the data with a virtual electrode grid spacing of 1 mm and calculated the smoothness of the activation patterns across voxels in terms of the full-width half-maximum (FWHM) of an equivalent Gaussian point spread function. They found that ~85% of voxels had a FWHM of 10 mm or less. For spatial sampling at k mm intervals, the smallest FWHM it is possible to estimate is 2k mm (Friston, Holmes, Poline, Price, & Frith, 1996). As per the Nyquist sampling theorem, any portions of the image less smooth than 2k mm FWHM will be under sampled or, equivalently, the resolution in the image for those voxels will be determined by the sampling interval. In the experiment reported in this chapter, for reasons of computational resources, 5 mm grid spacing was used rendering 5 mm^3 voxels. Therefore, based on the data from Barnes et al. it is estimated that ~85% of the voxels in the data reported here would have been under sampled. Hence the resolution in individual participants' images was most likely constrained by the 5 mm sampling grid, and not by the smoothness of the data.

For reference, ~95% of voxels in Barnes et al. had a FWHM of 12 mm or less, and this is equivalent to a grid spacing of 6 mm. Therefore, it is possible to calculate that cortical responses in the studies reported in this thesis could be localized to within 6 mm with a $p = .05$. However, the achievable spatial resolution here may be disadvantaged compared to Barnes et al. Visual word recognition has many transient and physically distributed components and, here, each stimulus is presented for only a few 100 ms. In contrast, Barnes et al. analysed long time windows where the visual system is expected to fall into a steady state. This is likely to result in a much higher signal-to-noise ratio for the experiments presented by Barnes et al. compared to the experiment presented in this chapter: Although, any loss of local spatial resolution in the current experiment will be compensated for by the fact that there are likely to be several centimetres separating the active nodes of the reading network.

4.2.5 Advantages Over Other Neuroimaging Methods

The spatial resolution of MEG is limited compared to techniques such as fMRI and PET, both by the small number of spatial measurements (generally 100–300) and by the inherent ambiguity in reconstructing the underlying sources from the measured signals (the inverse problem; Baillet et al., 2001). However, there are many advantages of using MEG over other imaging methods for the type of experiment presented in this chapter.

4.2.5.1 Hemodynamic Imaging Methods

Hemodynamic imaging techniques, such as fMRI and PET, are so called because they rely on signals relating to blood flow in order to infer the underlying neural activity from the metabolic activity of the brain. fMRI takes advantage of the lack of local energy stores in the brain, the high demand for energy by active neurons, and therefore the need for increased blood flow to active areas (Huettel, Song, & McCarthy, 2008). The blood oxygen level dependent (BOLD) signal is measured from this blood flow, and results from the differing concentrations of oxygenated and deoxygenated haemoglobin depending on the metabolic activity of the neurons. The degree of deoxygenation of the haemoglobin affects the susceptibility of the blood to the field of the MRI magnet; the more highly oxygenated the blood, the stronger the MR signal (Huettel, et al., 2008).

Although fMRI and PET provide excellent spatial resolution, they have poor temporal resolution (typically on the order of seconds for fMRI and tens of seconds for

PET (Hämäläinen, et al., 1993). PET has the further disadvantage of requiring an injection of a radiolabelled tracer, making it a highly invasive technique and limiting the number of times a person can be scanned (Palmer, Brown, Petersen, & Schlaggar, 2004). The invasiveness of PET, combined with its particularly low temporal resolution, rules it out as a potential technique for this experiment. While MRI is unsuitable for patients and participants with metal in their bodies including implants such as pace makers or shunts, it is relatively non-invasive. However, the temporal resolution of MRI is limited, not just by the inherent temporal resolution of blood flow, but also by the acquisition parameters. A single brain slice can be acquired very quickly; however, it typically takes around 2–3 seconds to scan a whole brain volume using standard parameters. The averaging procedures needed to ensure a good signal-to-noise ration then blur the temporal resolution further. For the purposes of this experiment, temporal resolution is critical. In order to compare the processing of real words and nonwords, they must be examined in space and time. It is possible to predict (based on behavioural results) that nonwords would be processed via the same regions, but lag behind the real words in processing speed. This would not necessarily be revealed by MRI analyses. In fact, due to the summing of data over large time windows, MRI might not reveal activity in all of the early basic word recognition regions that are of interest to this thesis as activity has been shown to spread and evolve rapidly after word onset (e.g., Hauk et al., 2006).

4.2.5.2 Electroencephalography

As mentioned above, EEG detects signals generated by the same neural activity as MEG, but the actual signals detected are different. Whereas MEG measures magnetic field, EEG measures the electrical potentials that pass through the skull. Because the conductivity of the skull is low the electrical signals can become distorted, decreasing the ability of EEG analysis to spatially localise the neural activity (Hämäläinen & Hari, 2002). Furthermore, analysis of EEG is often limited to ERPs which, due to the averaging procedures, only reveal the evoked (phase-locked) component of the signal. Cognitive tasks in particular might not be expected to generate strictly phase-locked responses, and therefore may benefit from the ability of MEG to resolve both evoked and induced (non-phase-locked) components. As discussed in Chapter 2, ERP studies have typically revealed phonological processes from around 250 ms after target word onset (e.g., Carreiras et al., 2009; Grainger et al., 2006; Holcomb & Grainger, 2006; Holcomb & Grainger, 2007; Mainy et al., 2008; Newman & Connelly, 2004; Sahin et al., 2009). However, Wheat et al. (2010) showed their early phonological effects (~100 ms) were in the induced component, and argued that this may be why ERP studies have generally failed to show such an early phonological effect. Therefore, for the purposes of investigating early phonological processes MEG is able to reveal non-phase-locked responses that cannot be seen using ERPs, and further able to localise these with better spatial resolution than EEG.

4.2.5.3 Optimal Spatial and Temporal Resolution

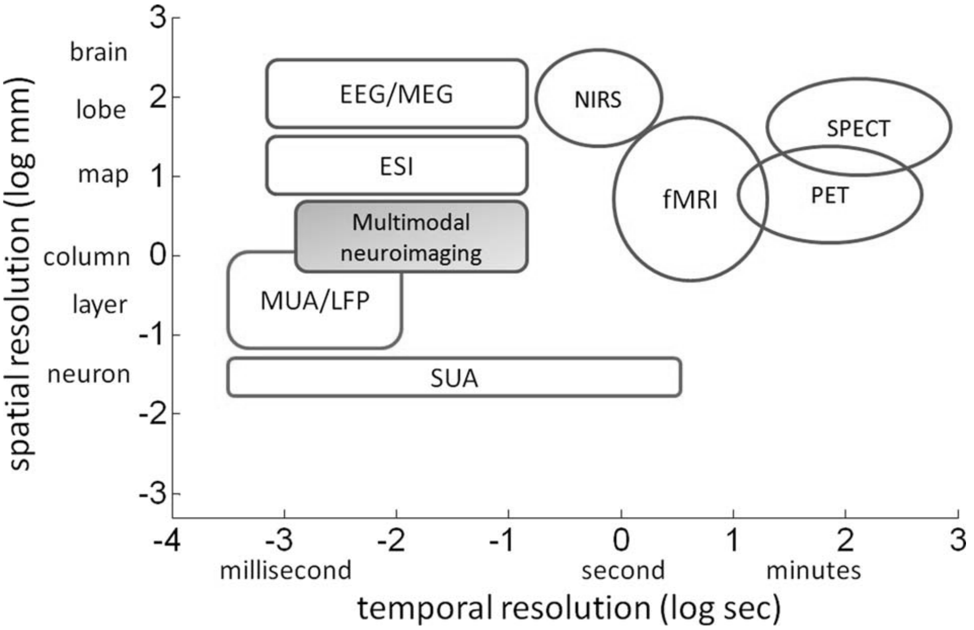


Figure 4.6 Multimodal imaging offers improved combined spatial and temporal resolution compared to EEG/MEG or fMRI alone. From He, Yang, Wilke, and Yuan (2011).

NIRS, near-infrared spectroscopy; SPECT, single-photon emission computed tomography; ESI, electrospray ionisation; MUA/LFP, multi-unit neuronal activity/local field potential; SUA, single-unit activity.

The optimal spatial and temporal localisation of neural activity comes from multimodal studies that are able to take advantage of the strengths of different imaging techniques to compensate for the weakness inherent in other techniques (see Figure 4.6). For example, in a multimodal fMRI/EEG/MEG study, Ou et al. (2010) acquired concurrent EEG and MEG (E/MEG) data during somatosensory and auditory tasks and (separately) fMRI scans of the same participants performing the same somatosensory and auditory tasks. Ou et al.'s "fMRI-informed regional estimation" is similar to the minimum norm procedure, but a set of weights is computed from both the E/MEG and the fMRI data. These weights are applied to a dense grid of source locations (independently for each location), taking advantage of the spatial alignment of neural and hemodynamic activity, but allowing for their inherent differences. In this way, the inherent ambiguity in the spatial resolution of minimum norm estimates (due to the inverse problem and magnetically silent sources, see above) is reduced by the superior spatial resolution of fMRI, whilst retaining temporal resolution that could not be achieved by hemodynamic methods (for a review see He, Yang, Wilke, & Yuan, 2011).

4.2.6 Summary

In sum, the aim of this section was to introduce MEG as the appropriate imaging technique for the study presented in this chapter, and has shown that:

- Whist MEG and EEG detect signals generated by the same synchronised neural activity, the magnetic fields recorded by MEG pass freely through the skull, unlike the electrical potentials detected by EEG.
- A challenge for MEG is in inferring the 3D neural sources from a 2D map of the magnetic field. This 'inverse problem' has no unique solution, but there are many source space techniques that aim to overcome this.
- Current dipole modelling and minimum norm estimation are suitable for detecting focal and distributed sources, respectively, requiring a prior assumption about the expected distribution of sources.
- Beamforming does not aim to solve the inverse problem and therefore requires fewer prior assumptions. However, it does assume that sources are not perfectly correlated, and requires averaging over time windows of ~200 ms and frequency bands of ~10 Hz.
- Beamforming can be used in a virtual electrode approach, allowing the full time–frequency range of the data to be seen. MEG is capable of very high temporal resolution, with a sampling frequency range of 678.17–4069.01 Hz.
- Whereas ERPs can only reveal phase-locked (evoked) responses, MEG beamforming analyses can also reveal non-phase-locked (induced) changes in

oscillatory activity. This has previously been argued to be important for uncovering early phonological processes (Wheat et al., 2010).

- Although the spatial resolution of MEG is lower (~6 mm) than fMRI (~1 mm), this trade off in spatial resolution is not a critical as the difference in temporal resolution. The millisecond temporal resolution of MEG will essential for probing the earliest processes of visual word recognition.

In conclusion, like any neuroimaging technique, there are limits to the capabilities of MEG. However, MEG combines the properties of excellent temporal resolution, good spatial resolution, and the ability to resolve both evoked and induced neural responses. Thus, MEG provides the opportunity to study the fine grained rapid temporal evolution of cortical activity as well as accurately reconstruct the location of the neural sources and resolve both the phase-locked and the non-phase-locked components of the response.

4.3 Experiment 5

Following on from the experiments in Chapter 3, here an MEG translation of a behavioural phonological priming task will be presented. The aim is to test the hypothesis that Broca’s area, specifically the pars opercularis of left IFG and neighbouring precentral gyrus (LIFGpo/PCG), is involved in rapid phonological access during visual word recognition. It is also hypothesised that these early phonological representations at LIFGpo/PCG will be sublexical. This experiment, therefore, aims to replicate and extend the findings of Wheat et al. (2010).

Wheat et al. (2010) used masked phonological priming of silent reading in MEG to demonstrate that LIFGpo/PCG activity could be modulated by the phonological relationship between prime and target. The response was stronger at LIFGpo/PCG for primes and targets with complete phonological overlap (e.g., *brein–BRAIN*) than for primes and targets with only partial phonological overlap (e.g., *broin–BRAIN*). Crucially, the orthographic overlap between the two conditions was the same. Furthermore, this difference in activity was seen within 100 ms of a target word being presented. This timing is much earlier than might have been predicted from previous EEG (e.g., Grainger et al., 2006; Mainy et al., 2008) studies. However, early activation of this region is in line with previous MEG studies of visual word recognition (e.g., Cornelissen et al., 2009; Pammer et al., 2004) and some EEG studies (Ashby, 2010;

Ashby et al., 2009). This region has previously been linked to articulatory speech-motor processes, supporting the interpretation of this activity as prelexical phonological access via an articulatory code. Alternative interpretations include the conflict resolution processes described, for example, by January et al. (2009; see section 2.3.3.4).

Although, Wheat et al. (2010) were able to strongly link LIFGpo/PCG activity to phonological processes using a masked priming task, a question still remains about the nature of any phonological representations. As discussed in Chapter 3, this experiment will extend the findings of Wheat et al. by including nonword targets, as well as word targets, in a silent reading task. Extension of the result to nonword targets will imply a sublexical basis for the phonological priming result, as nonwords would not be expected to produce lexical level priming. Replication of the original finding for real word targets is also important. This will show generalisation of the effect to a different set of stimuli and participants. Moreover, the nonword activity at LIFGpo/PCG should be equivalent to the word activity, both in this experiment and of Wheat et al., in order to infer that this sublexical access is an automatic part of normal word reading, and not a specific artefact of nonword decoding.

As shown in Chapter 3, it was important to start this experiment with a strong phonological priming effect. Once behavioural phonological priming has been achieved, MEG allows us to view when and where in the brain phonologically relevant activity can be seen. There is often individual variability in priming effects; for example, Appendix C shows the priming effects for the participants of Experiment 3 (mixed naming; see also Holyk & Pexman, 2004). This demonstrates that while most participants (22/24 for words; 15/24 for nonwords) showed a positive priming effect (i.e., phonological condition faster), nevertheless, a minority of participants (2/24 for words; 7/24 for nonwords) showed a negative effect (i.e., orthographic condition faster) or no priming effect (2/24 for nonwords). Therefore, in the unselected population of Experiment 3 (mixed naming) positive priming was shown to be the norm. Here, in order to maximise the signal-to-noise ratio for investigating the neural correlates of priming in MEG, participants were pre-screened for their ability to be phonologically primed. Participants were only invited to take part in MEG only if they showed phonological priming of words. No participant selection was made on the basis of the nonword effect.

4.3.1 Methods

4.3.1.1 Participants

Participants were 30 native-English-speaking adults (9 males; M_{age} 21.7 years, *SD* 3.12) who gave their informed consent to participate on a voluntary basis. The study conformed to ethical approval, granted by the Research Ethics Committee, York Neuroimaging Centre. All scored strongly right-handed (Annett, 1970), and had normal or corrected-to-normal vision, with no history of any reading disorder. Reading proficiency was verified using the Test of Word Reading Efficiency (TOWRE; Torgesen, Wagner, & Rashotte, 1999) and the Test of Irregular Word Reading Efficiency (TIWRE; Reynolds & Kamphaus, 2007).

Of these, 24 participants attended an MEG scan. Data from four MEG participants were excluded due to a high artefact rejection rate (87%), falling asleep during the scan, a large change in head position during the scan (*M* 1.95 cm; *SD* 1.32 cm), or poor performance on the behavioural task (10% targets detected). The final group of MEG participants were 20 native-English-speaking adults (7 males; M_{age} 22.10 years, *SD* 3.61), who passed the selection criteria.

4.3.1.2 Behavioural: Materials, Design & Procedure

The materials, design and procedure were identical to Experiment 3. Participants were presented with word and nonword targets in a pseudorandom order and asked to read them out loud as quickly and accurately as possible. After completing the experiment, the TOWRE and TIWRE were administered, in that order.

4.3.1.3 MEG: Materials, Design & Procedure

The materials, design & procedure was identical to Experiment 3 with the following exceptions. The experiment was performed in a completely dark, magnetically shielded room. At a viewing distance of ~75 cm stimuli subtended ~1° vertical and, on average, ~5° horizontal. All participants saw all stimuli from four experimental conditions (PSEUD–WORD, ORTH–WORD, PSEUD–NONWORD, and ORTH–NONWORD); the unprimed conditions were not included in order to shorten the duration of the experiment. A longer duration makes it more likely that a participant will become uncomfortable, resulting in more movement, including head movement.

The experiment was performed with the projector brightness set to 0 and with the addition of a 50% neutral density filter. The filter reduced the glare halo created by light from the projector being scattered by the projector screen. This extra light seen without the filter made the stimuli difficult to view comfortably. With the filter, pilot testing showed that the stimuli could be seen clearly without any extra glare. These were also the settings used by Wheat et al. (2010). These settings minimise the transient contrast changes when stimuli appear and disappear, which in turn helps to reduce the transient responses seen in MEG which may otherwise dominate the response pattern. The addition of nonius lines above and below the stimuli as a fixation indicator also removed unnecessary transients relating to the fixation cross appearing and disappearing. Instead, the nonius lines remained on screen throughout the experiment, but were dimmed to indicate the intertrial interval.

Participants were instructed to read each real word or nonsense word silently in their head. They were also asked to press a button whenever they saw an animal name. These catch trials were created by inserting an animal name into the position of the prime or the target. Catch trials in the target position allowed online monitoring of whether the participant was attending to the experiment. Prime position catch trials allowed online monitoring of whether the participant was consciously aware of, and able to report, the prime identity. Responses were made with the forefinger (word) and middle finger (nonword) of the left hand.

The mean delay between the behavioural session and the subsequent MEG session was 37 days (Range 8–166).

4.3.1.4 MEG: Data Acquisition

MEG data were collected at YNiC using a 4D Neuroimaging Magnes 3600 Whole Head, 248 Channel system, with SQUIDs arranged in a helmet shaped array. Data were sampled with an anti-alias filter at 200 Hz and a sample rate of 678.17 Hz. Prior to scanning, a 3-D digitizer (Polhemus Fastrak) was used to record the shape of the participant's head and the relative position of the five head coils for co-registration with the MRI scan. All participants underwent an MRI scan at YNiC to obtain a high resolution T1 weighted anatomical volume with 1 mm isotropic resolution, using GE 3.0T Signa Excite HDx. MEG and MRI data were co-registered using an in-house technique adapted from Kozinska, Carducci, and Nowinski (2001).

4.3.1.5 MEG: Data Analysis

After data acquisition, the continuously acquired MEG data were segmented into epochs of 1490 ms, which spanned from 790 ms before target onset to 700 ms after; any epochs containing artefacts, such as blinks, swallows and other movements, were rejected manually (e.g., see Appendix D).

A minimum variance beamforming technique, which was developed and coded at YNiC, and which is adapted from Van Veen, van Drongelen, Yuchtman, and Suzuki, (1997) was used for source reconstruction. For each participant's brain, a regular 3D lattice of points, spaced 5 mm apart was defined. At each grid point in the lattice, for each participant, three beamformers were applied to reconstruct current flow in the brain in three orthogonal directions, separately for each experimental condition. Next (for purposes of whole brain frequency domain analysis), at each of these points, comparisons of the power at particular frequency bands were made between a 200 ms passive time window and a sequence of 200 ms active windows. We defined the passive window as -790 to -590 ms (target onset = 0 ms) during a period of blank screen prior to the forward mask near the start of a trial (see Figure 4.7). See Appendix E for a discussion of the placement of the passive period.

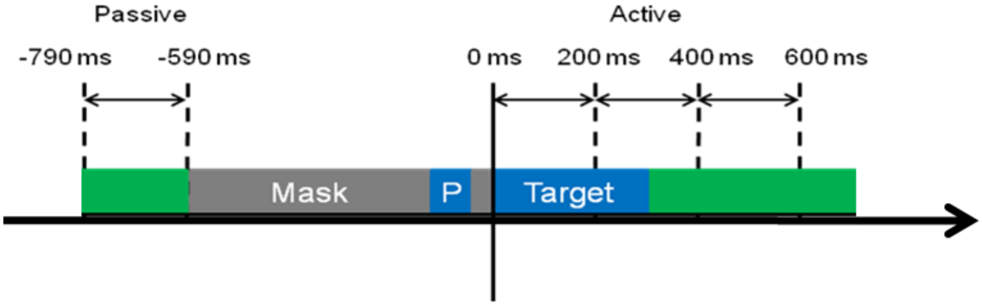


Figure 4.7 Epoch segmentation. One 1490 ms epoch, showing the position of the passive window and active windows. The trial sequence is *mask–prime–mask–target*. The inter-trial blank screen is shown in green.

Nonparametric permutation tests were used to derive whole brain real *t*-statistical maps for each participant (see e.g., Nichols & Holmes, 2001). Finally, the individual *t*-maps were transformed into MNI space to permit group analysis, again using non-parametric statistics. Separate group statistical maps were plotted for "alpha" (5-15 Hz), "beta" (15-25 Hz) and "low gamma" (25-35 Hz) frequency bands for each condition. For a review of beamforming methodologies see Huang et al. (2004).

For the virtual electrode analysis, regions of interest were chosen from the whole-brain beamforming results. The corresponding individual slice number coordinates were then computed for all participants from their structural MRI data and beamformers applied to the equivalent grid point in each participant. A Stockwell Transform was performed (using Matlab, MathWorks, Natick, MA) on the resulting time series for each direction, for each participant, for each condition. These time–frequency representations were then averaged over participants and directions, in order to make statistical comparisons between conditions. The statistics will be discussed below.

4.3.1.6 Behavioural: Data Analysis

Responses were recorded using a digital microphone positioned directly in front of the participant. Sound level was calibrated individually prior to recording. Timings of voice key responses were logged by Presentation (Neurobehavioral Systems, Inc., Albany, NY) and sound files of responses were recorded for offline analysis. All incorrect responses and voice key triggers other than verbal responses (such as coughs and hesitations) were removed prior to VRT analysis. VRTs outside 3 standard deviations of the mean (by condition for each subject) were treated as outlying data points and were excluded from further analysis.

Prior to inclusion in the group analyses, all participants' data were plotted individually (after error removal and thresholding) and excluded if the mean reaction time for PSEUD–WORD was not faster than for ORTH–WORD (i.e., test for phonological priming of words). Four participants were excluded on this basis. A further two participants dropped out of the study at this stage and four participants were excluded after participating in MEG. One participant previously participated in Experiment 3 and was not re-tested prior to participating in the MEG study. Reported behavioural data are, therefore, based on 19 of the 20 participants who successfully completed the MEG scan.

4.3.2 Results

4.3.2.1 Behavioural Pretesting

Incorrect responses were removed; the mean error rate was 2.41% (SD 1.85). The mean attrition rate after error removal, thresholding, and any trials where the participant did not respond, was 3.84% (SD 2.78). As shown in Figure 4.8, there appeared to be a trend for targets primed by pseudohomophones to be responded to fastest, followed by orthographic controls, and unprimed targets responded to slowest. Overall, the real word targets were responded to 47 ms faster than the nonword targets.

A two-by-three repeated measures ANOVA with the within-subject factors of Lexicality and Prime-Type was conducted. Mauchly's test indicated that the assumption of sphericity had been violated for Prime Type, $X^2(2) = 7.17$, $p < .05$; therefore a Greenhouse-Geisser correction was applied. The results showed a significant main effect of Lexicality, $F(1,18) = 168.32$, $p < .001$, $\eta_p^2 = .90$, and of Prime Type, $F(1.49,46.36) = 33.15$, $p < .001$, $\eta_p^2 = .65$, and a significant interaction, $F(2,36) = 15.15$, $p < .001$, $\eta_p^2 = .46$.

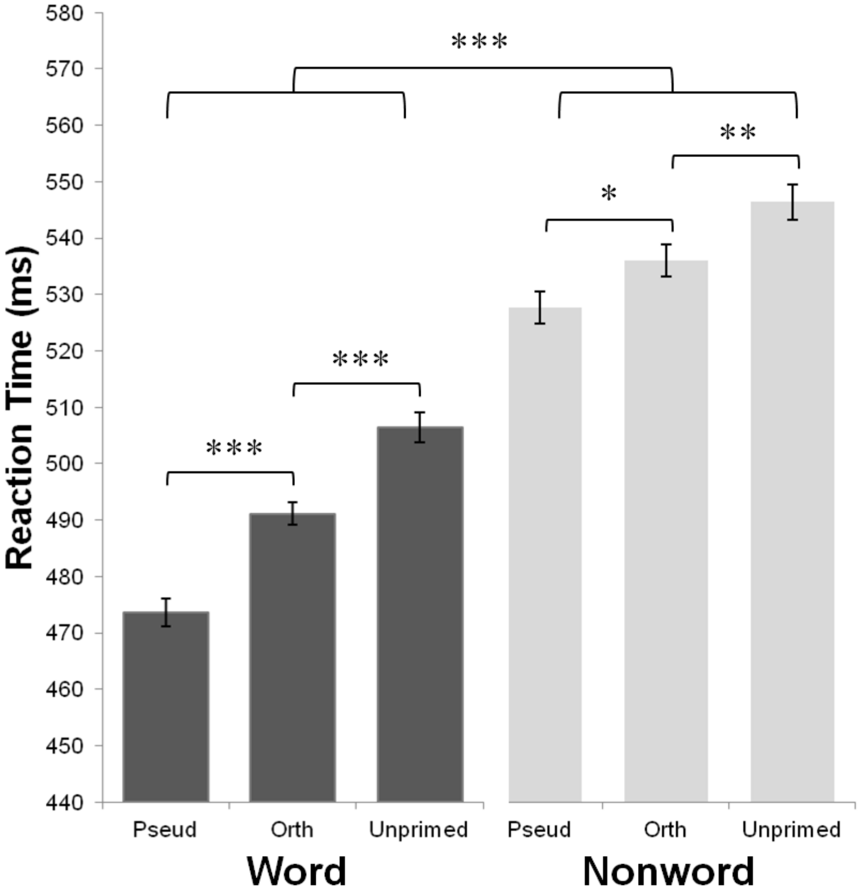


Figure 4.8 Mean reaction times by prime–type and lexicality. Standard error bars, corrected for repeated measures.

*** $p < .001$, ** $p < .01$, * $p < .05$.

Separate one-by-three ANOVAs were then conducted, splitting the data by Lexicality. For real words, Mauchly's test indicated that the assumption of sphericity had been violated, $X^2(2) = 6.05$, $p < .05$; therefore a Greenhouse-Geisser correction was applied. There was a significant main effect of Prime Type, $F(1.54,27.70) = 71.41$, $p < .001$, $\eta_p^2 = .80$. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, $F(1,18) = 88.15$, $p < .001$, $\eta_p^2 = .83$, and between ORTH and UNPRIMED, $F(1,18) = 66.57$, $p < .001$, $\eta_p^2 = .59$.

For nonwords, there was a significant main effect of Prime Type, $F(2,36) = 11.04$, $p < .001$, $\eta_p^2 = .38$. Planned repeated contrasts revealed significant differences between PSEUD and ORTH, $F(1,18) = 8.98$, $p = .008$, $\eta_p^2 = .33$, and between ORTH and UNPRIMED, $F(1,18) = 6.05$, $p = .024$, $\eta_p^2 = .25$.

4.3.2.2 MEG: Preprocessing and Catch Trial Responses

Data from four participants were not included in any analyses. The remaining 20 participants had a mean artefact rejection rate of 21% (*SD* 19%) and a mean head movement of 0.41 cm (*SD* 0.17 cm). The head movement score for each participant was computed by averaging over the movement values for the five head coils.

Signal detection analysis of catch trial responses revealed a .12 probability of correctly identifying an animal word in the prime position, resulting in a mean *d’* of 1.04 (*SD* 0.60), indicating a low level of visibility. For animals in the target position, there was a .87 probability of correct identification, resulting in a mean *d’* of 3.78 (*SD* 0.68), indicating participants were successfully attending to the task.

4.3.2.3 MEG: Whole-Brain Beamforming

As shown in Figure 4.9, whole-brain beamforming revealed significant activity in the region of LIFGpo/PCG within the first 200 ms when the target word was a real word and the prime was a pseudohomophone. This is an isolated region of left frontal activity in this first time window, with a concurrent spread of activity across the occipital lobe and ventrally towards the left middle temporal region. Within the first 400 ms, activity continues to spread from the occipital pole ventrally, towards the left temporal pole, and dorsally, to encompass inferior parietal regions. The frontal region of activity also spreads to cover most of the inferior frontal gyrus and the inferior portion of precentral gyrus. Activity in the right hemisphere and underside of the brain can be seen in Appendix F.

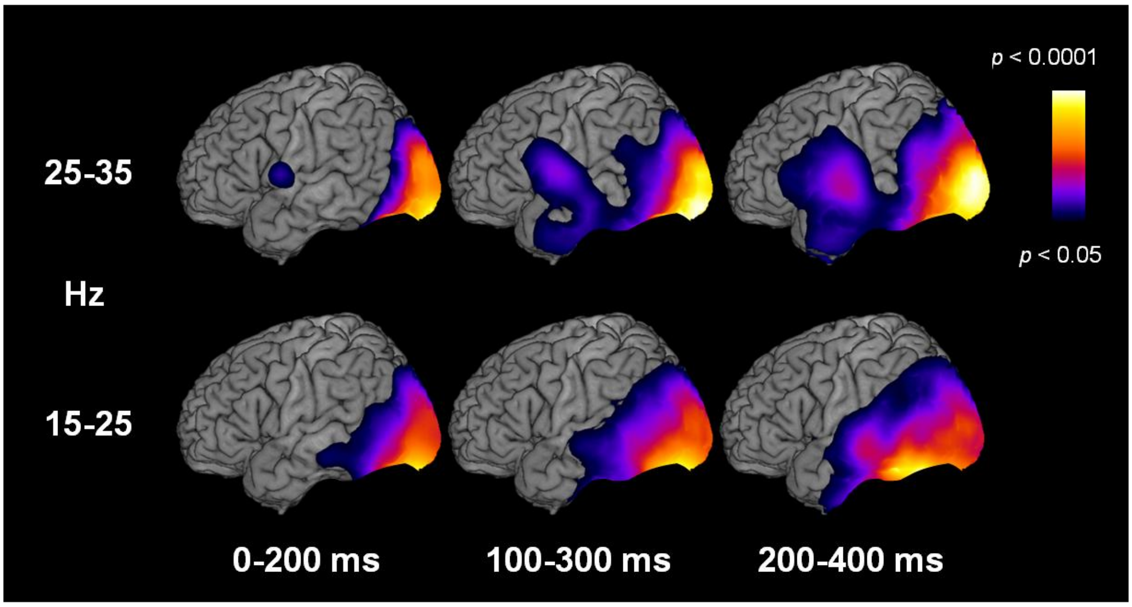


Figure 4.9 Beamforming for PSEUD–WORD. Three-dimensional rendered cortical representations showing significant activity above baseline in the left hemisphere for PSEUD–WORD, in the frequency range 15–25 Hz, from 0–400 ms from target word onset. *t*-Maps are thresholded at $p < .05$ (corrected).

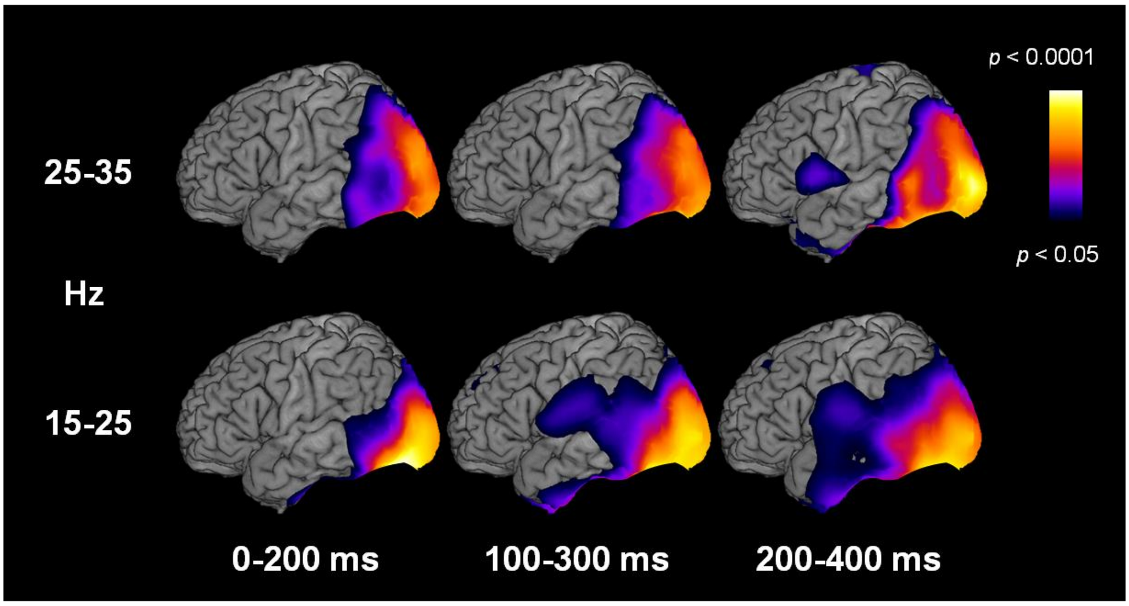


Figure 4.10 Beamforming for ORTH–WORD. Three-dimensional rendered cortical representations showing significant activity above baseline in the left hemisphere for ORTH–WORD, in the frequency range 15–25 Hz, from 0–400 ms from target word onset. *t*-Maps are thresholded at $p < .05$ (corrected).

In the orthographically primed condition for real words (shown in Figure 4.10) LIFGpo/PCG activity is not apparent until the 100–300 ms time window. Again, activity spreads from the occipital pole ventrally towards the temporal pole and dorsally towards the parietal lobe within the first 400 ms. Activity in the inferior frontal gyrus is restricted to the pars opercularis within this time and frequency range. All activations were in the ERD direction, meaning that the passive period has more power than the active period. No differences were found in the other direction for any active period.

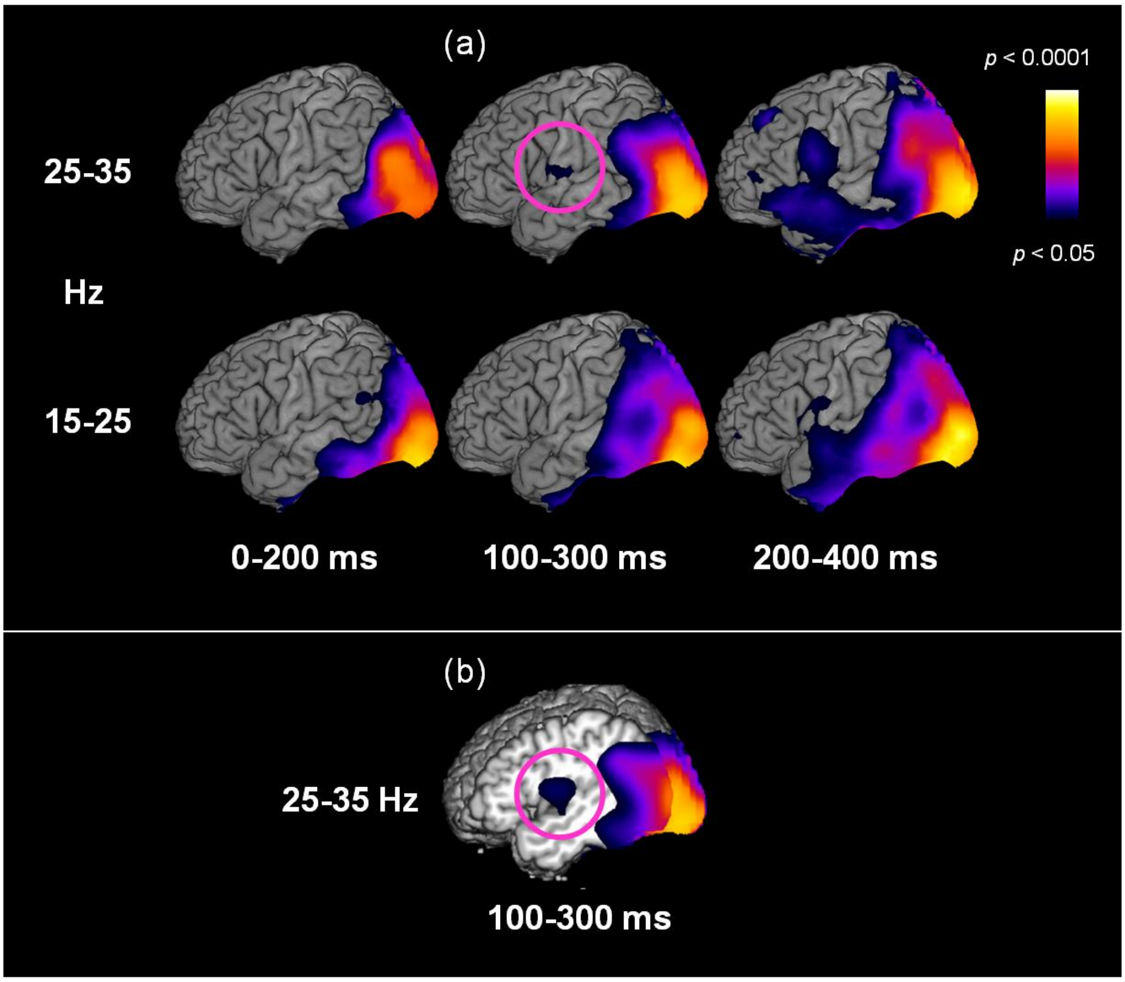


Figure 4.11 Beamforming for PSEUD–NONWORD. Three-dimensional rendered cortical representations showing significant activity above baseline in the left hemisphere for PSEUD–NONWORD, in the frequency range 15–25 Hz, from 0–400 ms from target nonword onset. *t*-Maps are thresholded at $p < .05$ (corrected). (a) Shows the earliest occurrence of LIFGpo/PCG activity (b) shows a sagittal section into this activity.

For the nonword targets, activity in the phonologically primed condition shows a similar pattern of activation to both the real word conditions. As shown in Figure 4.11, there is a similar spread of left hemisphere ventral and dorsal activations, evolving across the first 400 ms from target nonword onset. Here an isolated region of frontal activity is seen at LIFGpo/PCG by 100–300 ms with no frontal activations within the first 200 ms time window. The cutaway in Figure 4.11(b) shows that this region of activity is larger than it appears from the surface. No other time windows (in any condition) showed activity hidden just under the surface. By 200–400 ms, there is widespread left temporal and frontal activation. Right hemisphere and underside activations can be seen in Appendix F. In contrast, for the orthographically primed nonwords, there is no LIFGpo/PCG activity that is significantly different from baseline activity within the first 400 ms from target nonword onset (see Figure 4.12). Orthographically primed nonwords show a similar ventral and dorsal spread of activity, but to a lesser extent than seen in the other three conditions, and with no frontal component.

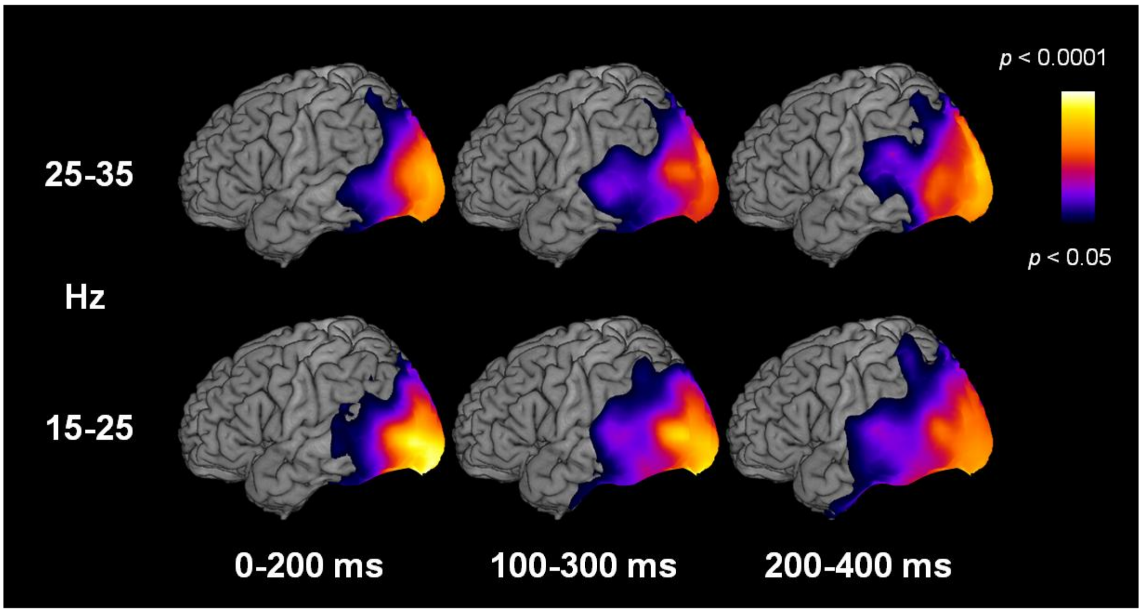


Figure 4.12 Beamforming for ORTH–NONWORD. Three-dimensional rendered cortical representations showing significant activity above baseline in the left hemisphere for ORTH–NONWORD, in the frequency range 15–25 Hz, from 0–400 ms from target nonword onset. *t*-Maps are thresholded at $p <$ .05 (corrected).

In sum, on the basis of whole-brain beamforming results, there appears to be a difference between the phonologically primed and the orthographically primed conditions for both real words and nonwords. For the PSEUD–WORD condition, LIFGpo/PCG appears to be active earlier than for the ORTH–WORD condition in comparison to the passive baseline period. For the PSEUD–NONWORD condition activation includes LIFGpo/PCG, in contrast to the ORTH–NONWORD condition, which shows no LIFGpo/PCG activity that is significantly different from baseline. Therefore, both words and nonwords show and advantage of phonological priming at LIFGpo/PCG. However, the precise time and frequency range of the activations cannot be seen through whole-brain methods. Furthermore, these results represent active–passive contrasts, which may mask any brain regions that are equally active throughout the epoch, including the chosen passive period. These whole-brain methods also do not allow statistical comparisons between conditions. Thus, ROIs will be chosen for more detailed analyses.

4.3.2.4 MEG: Virtual Electrodes

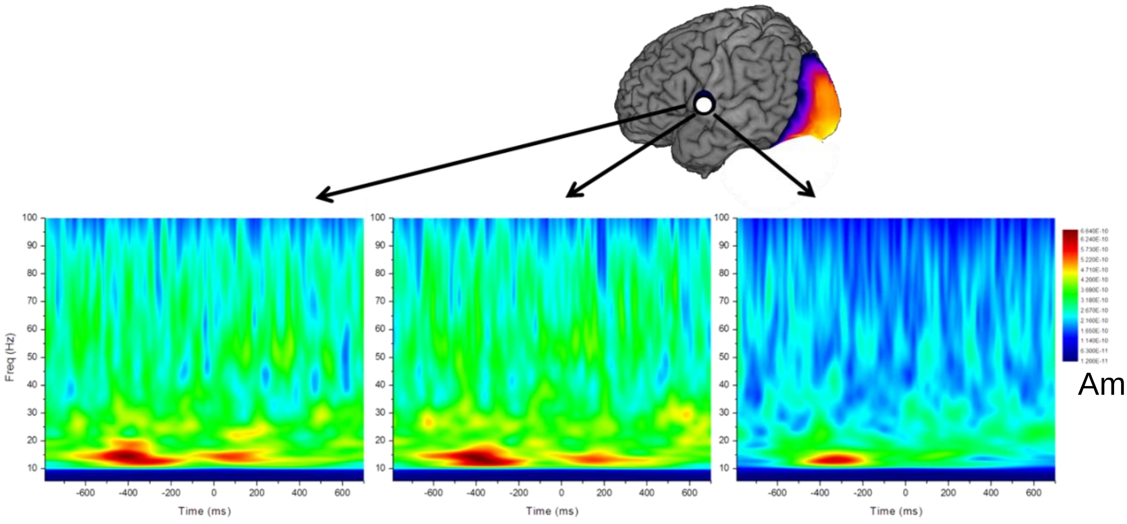


Figure 4.13 Evoked time–frequency plots for three directions at LIFGpo/PCG, MNI -44, 20, -8. Separate plots showing the averaged X Y and Z directions for the evoked response to PSEUD–WORD across the full epoch (-790–700 ms) and frequency range (5–100 Hz).

In order to compare activity at LIFGpo/PCG across the conditions, a region of interest was chosen based on the only area of frontal activity during the first 200 ms. The area of this activity from the PSEUD–WORD condition was centred on MNI coordinates -44, 20, -8 (see Figure 4.13). The virtual electrode analyses shown here will focus on time–frequency analyses that allow the total power change to be seen. This includes the non-phase-locked (induced), as well as the phase-locked (evoked) response. However, the first example will step through the analysis path for the evoked response, as the nature of the evoked response makes it more easily identifiable. The evoked signal is revealed by computing the average signal in the time domain, for each participant, for each direction separately. A Stockwell transform is then computed for this time domain average for each participant and direction. Conversely, to retain the total signal, the Stockwell transform is computed for each individual trial, for every participant and direction, without any prior averaging in the time domain. The average Stockwell is then computed for each participant, for each direction separately. Thus, both cases result in 3 average Stockwells (one per direction) for each of 20 participants, the difference being that the evoked data are pre-averaged across trials in the time domain, whereas the total data are only averaged after transforming to the frequency domain.

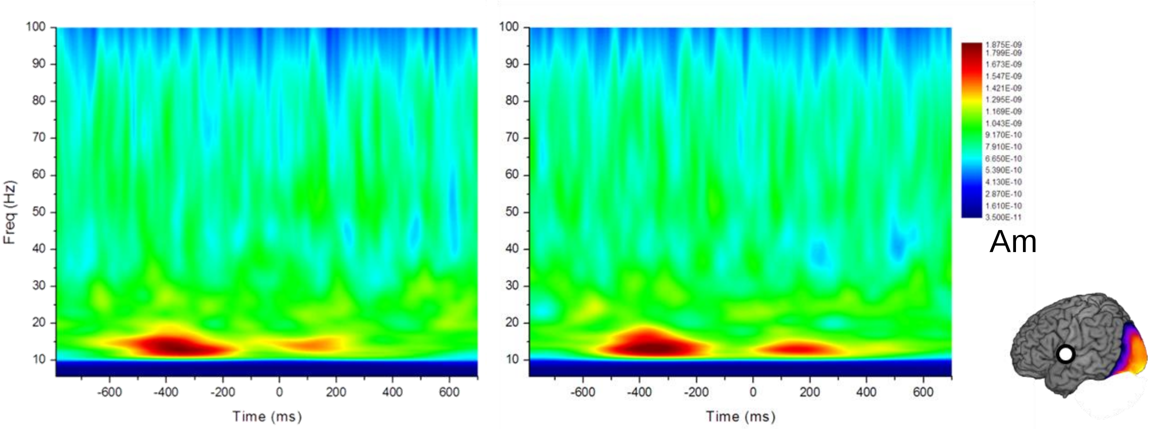


Figure 4.14 Evoked grand averages for PSEUD–WORD and ORTH–WORD at LIFGpo/PCG, MNI -44, 20, -8. The evoked response for PSEUD–WORD (left) and ORTH–WORD (right) after summing across the three directions for the full epoch (-790–700 ms) and frequency range (5–100 Hz).

For both evoked and total analyses, the first step was to average the time–frequency representation of power of the 20 participants, for each direction separately; examples of the averaged time–frequency plots for the PSEUD–WORD condition for the evoked response are shown in Figure 4.13. The three directions are then summed and averaged across participants (G. G. R. Green & W. Woods, personal communication, 2008) to compute a grand average for each condition. Figure 4.14 shows the results of this averaging for PSEUD–WORD and ORTH–WORD for the evoked response. Statistical comparisons can then be made across the two plots to directly compare the two conditions for differences in power at LIFGpo/PCG for the duration and frequency range of interest. Differences between conditions before 0 ms will not be examined, as this is when the target is presented and a priming response cannot occur prior to this. However, as shown in Figure 4.14, there is a large response prior to 0 ms. The premask started at -590 ms, followed by the prime at -90ms, and the post mask at -20 ms. The timing of the pretarget response therefore coincides with the mask and may relate, for example, to the expectation of an upcoming target word.

In order to statistically compare the grand average time–frequency plots between conditions, it is important to consider problem of spatial covariance; that is, time–frequency tiles that are closer together are more likely to have similar values for the outcome variable between conditions than tiles that are further apart from each other (see Figure 4.15 for an illustration). The Proc Mixed analysis in SAS (SAS Institute Inc., North Carolina, US) is able to estimate the spatial covariance in the time–frequency space, in order that corrected estimates of the significance of the least squared mean of the outcome variable in each time–frequency tile can be reported, and spatial covariance thereby accounted for.

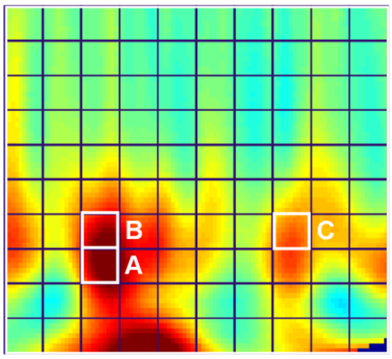


Figure 4.15 Spatial covariance. In a time–frequency plot, tiles that are closer are more likely to be similar to each other than distant tiles. For example, the magnitudes of the outcome variable in Tile A and Tile B are more likely to be similar to each other due to their proximity, where as they are less likely to be similar to Tile C. Statistical comparisons of plots must take this into account.

4.3.2.5 MEG: Evoked Power Virtual Electrodes

The result of PSEUD–WORD minus ORTH–WORD evoked response is shown in Figure 4.16(a). This is the raw difference between the two grand average plots, showing regions of time–frequency where the power in one condition is greater or less than the other. Note that the difference plots show just the time–frequency period of specific interest, where as the previous raw plots have shown the full time–frequency range. Figure 4.16(b) then shows the p distribution of the results of Proc Mixed, highlighting regions where $p < .05$. Plot (b) shows significant differences in either direction, therefore, comparison with (a) is necessary to understand the direction of a difference.

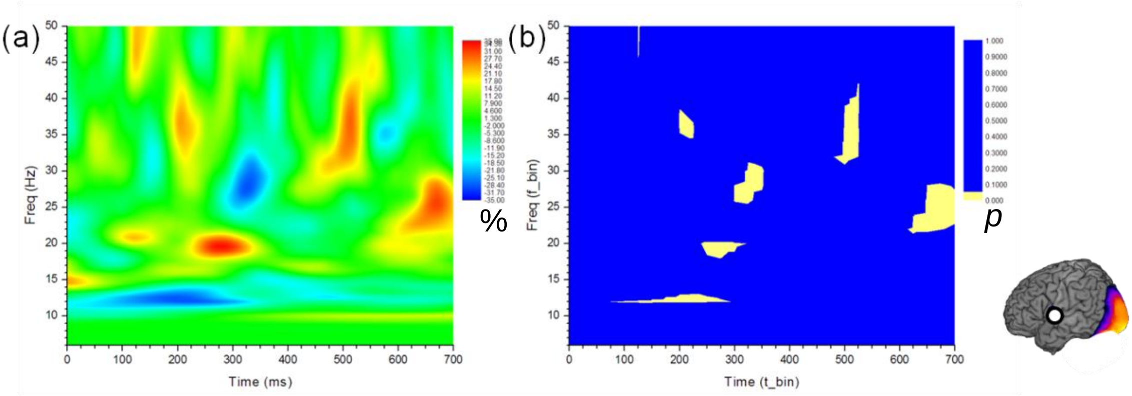


Figure 4.16 Evoked difference between PSEUD–WORD and ORTH–WORD at LIFGpo/PCG, MNI -44, 20, -8. (a) shows the raw difference between the two conditions (red PSEUD>ORTH, blue ORTH>PSEUD) for the duration of the trial (0–700 ms) for 5–50 Hz, (b) shows the *p* values for the *t*-tests of least squared means at each tile in the time–frequency plot. Light yellow represents regions of significant change between PSEUD–WORD and ORTH–WORD, $p < .05$.

This evoked response for PSEUD–WORD minus ORTH–WORD at LIFGpo/PCG shows both phonological and orthographic priming in different frequency bands (as indicated by the significant regions of both red and blue) within around 200 ms of word onset. The ~13 Hz evoked response is likely to occur around 200 ms, although it appears to start around 100 ms due to the lower temporal resolution of lower frequencies in the Stockwell transform. Next the total power analysis path with be illustrated.

4.3.2.6 MEG: Total Power Virtual Electrodes

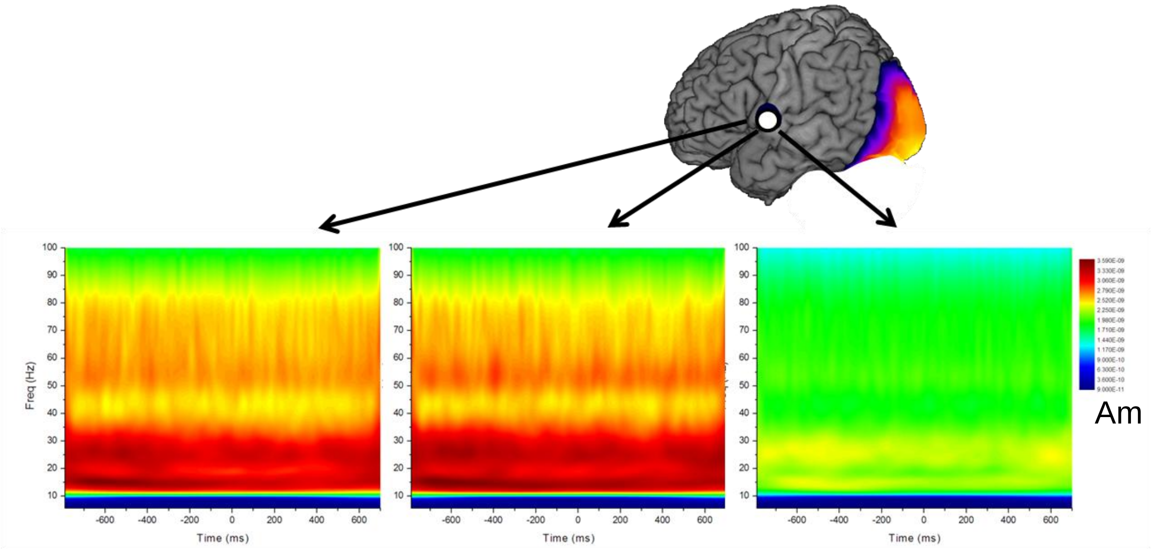


Figure 4.17 Total time–frequency plots for three directions at LIFGpo/PCG, MNI -44, 20, -8. Separate plots showing the X Y and Z directions for the total power of PSEUD–WORD across the full epoch (-790–700 ms) and frequency range (5–100 Hz).

For grand average of total power for each condition, first the time–frequency representation of power was averaged over the 20 participants, for each direction separately; examples of the averaged time–frequency plots for the PSEUD–WORD condition for the total response are shown in Figure 4.17. The three directions are then summed and averaged across participants (G. G. R. Green & W. Woods, personal communication, 2008) to compute a grand average for each condition (see Figure 4.18). However, unlike the evoked component, no clear areas of response in relation to stimulus onset can be seen. This is because there are large global changes in the power spectrum from the alpha band, through the frequency ranges, up to the gamma band and beyond. The power range for a typical time–frequency plot of total power, averaged across time, is shown in Figure 4.19(a). It shows an order of magnitude difference in mean power between the highest and lowest frequencies. Attempting to capture such a large range of power on one colour scale means that the relatively small changes of power within a frequency band will be difficult to resolve visually because they will be embedded within such a small range of the colour scale.

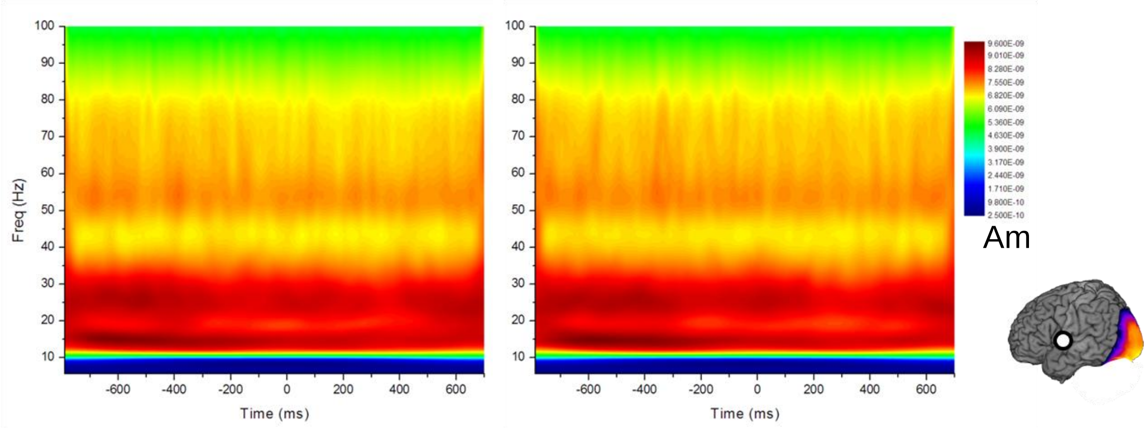


Figure 4.18 Total grand averages for PSEUD–WORD and ORTH–WORD at LIFGpo/PCG, MNI -44, 20, -8. The total power of PSEUD–WORD (left) and ORTH–WORD (right) after summing across the three directions for the full epoch (-790–700 ms) and frequency range (5–100 Hz).

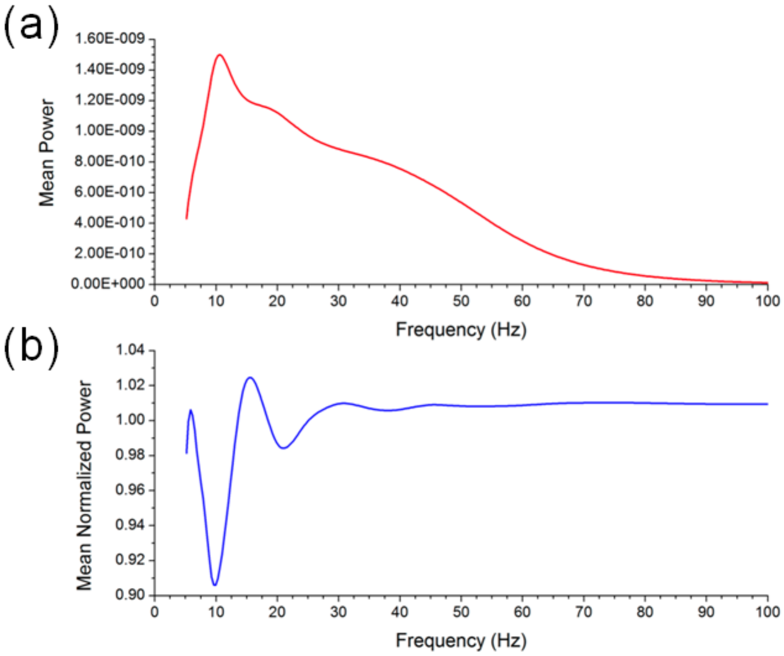


Figure 4.19 Mean power per frequency. Plot (a) shows a large difference in mean power per frequency from the lowest to the highest frequencies. After normalisation (b), mean power is almost flat from ~15 Hz upwards.

In this thesis, two methods have, therefore, been used to allow the relatively small changes in total power within and between conditions to be visualised. First, the grand average time–frequency plots for each condition have been normalised per frequency bin with respect to the same baseline as is used for the whole-brain beamforming analyses. To do this, first average total power is computed for each frequency bin over the passive period -790–-590 ms. Then, total power at each time point in the time–frequency plot is normalised with respect to that frequency bin by computing the percentage signal change, that is,

$$\left(\left(\frac{\text{total power at freq } x}{\text{mean baseline power at freq } x}\right) - 1\right) * 100$$

(see Figure 4.20 for an illustration). As can be seen by comparing the axes of Figure 4.19 (a) and (b), the range of power across frequency bins is much smaller after normalisation. The steep drop in power as a function of frequency is almost flattened out; meaning changes in power within frequency bands within relatively narrow frequency bands are easily resolved by the colour scale as a result. To generate grand averaged time–frequency plots which illustrate the difference between conditions, we simply compute a percentage signal change between two conditions directly, much the same as is done when computing a contrast in fMRI.

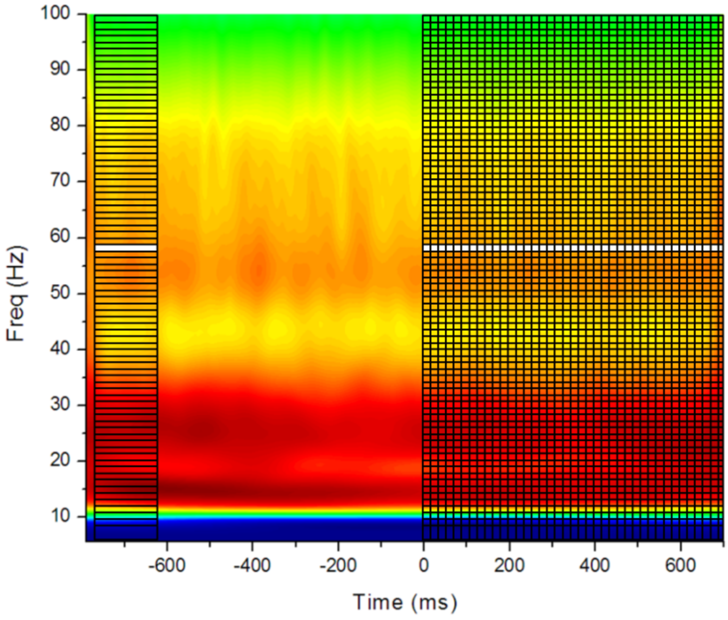


Figure 4.20 An illustration of the normalisation procedure. The average power for each frequency bin in the passive period is used to calculate the percentage signal change per frequency between baseline and each time–frequency tile in the period of interest.

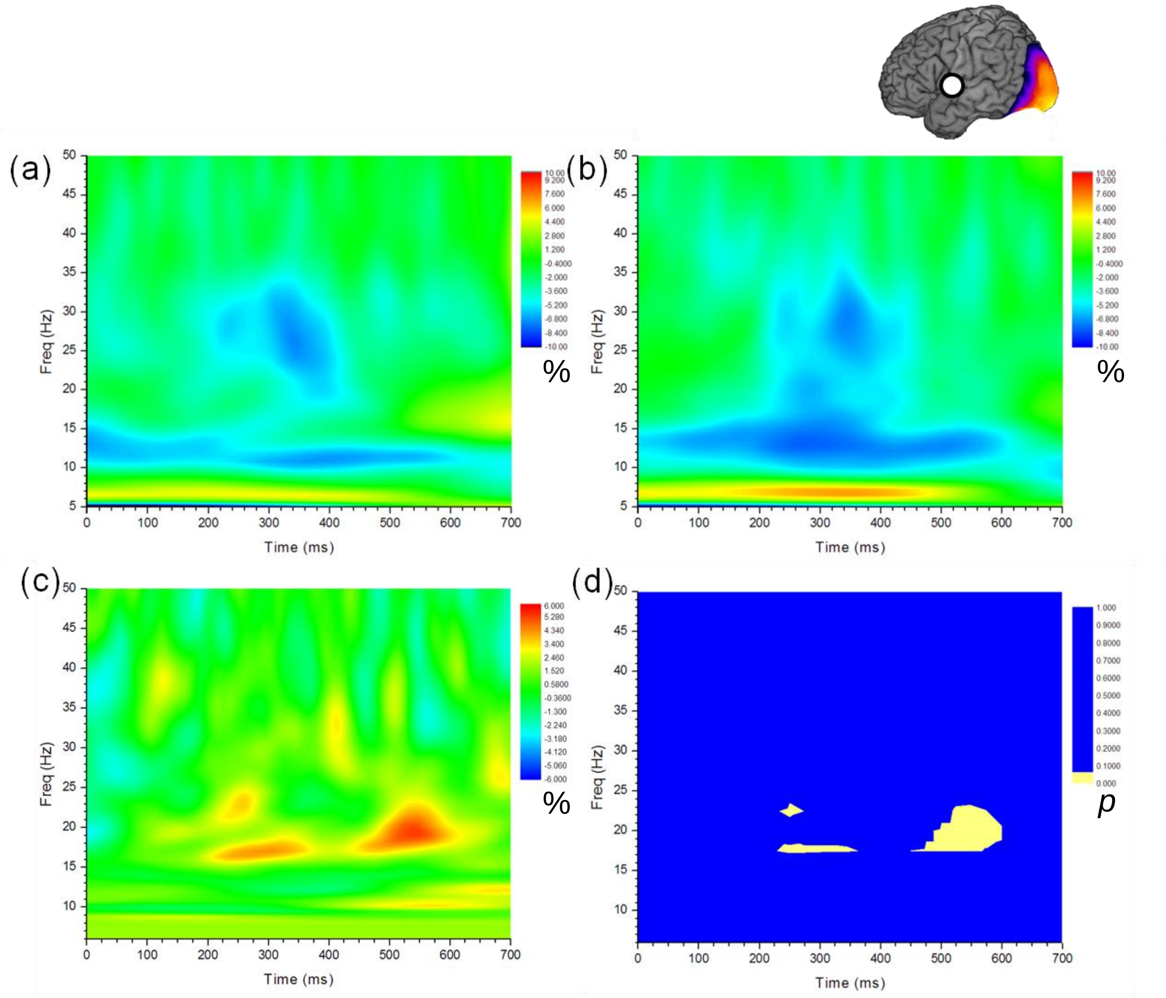


Figure 4.21 Total percentage signal change between PSEUD–WORD and ORTH–WORD at LIFGpo/PCG, MNI -44, 20, -8. (a) and (b) show the normalised grand averages for PSEUD–WORD and ORTH–WORD, respectively; (c) shows the % signal change between the two conditions (red PSEUD>ORTH, blue ORTH>PSEUD) for the duration of the trial (0–700 ms) for 5–50 Hz; and (d) shows the *p* values for the *t*-tests of least squared means at each tile in the time–frequency plot. Light yellow represents regions of significant change between PSEUD–WORD and ORTH–WORD, $p < .05$.

First, the total power for the word conditions is examined. Figure 4.21 shows the results of the normalisation of PSEUD–WORD and ORTH–WORD. Figure 4.21(c) the shows the raw percentage signal change; Figure 4.21(d) shows, for each time–frequency tile, whether the percentage signal change between the two conditions is significantly different from 0, computed using Proc Mixed controlling for spatial covariance. Regions shown in light yellow indicate regions where PSEUD–WORD is stronger than

ORTH–WORD at LIFGpo/PCG, indicating phonological priming (red) within ~250 ms from word onset, but no orthographic priming (blue).

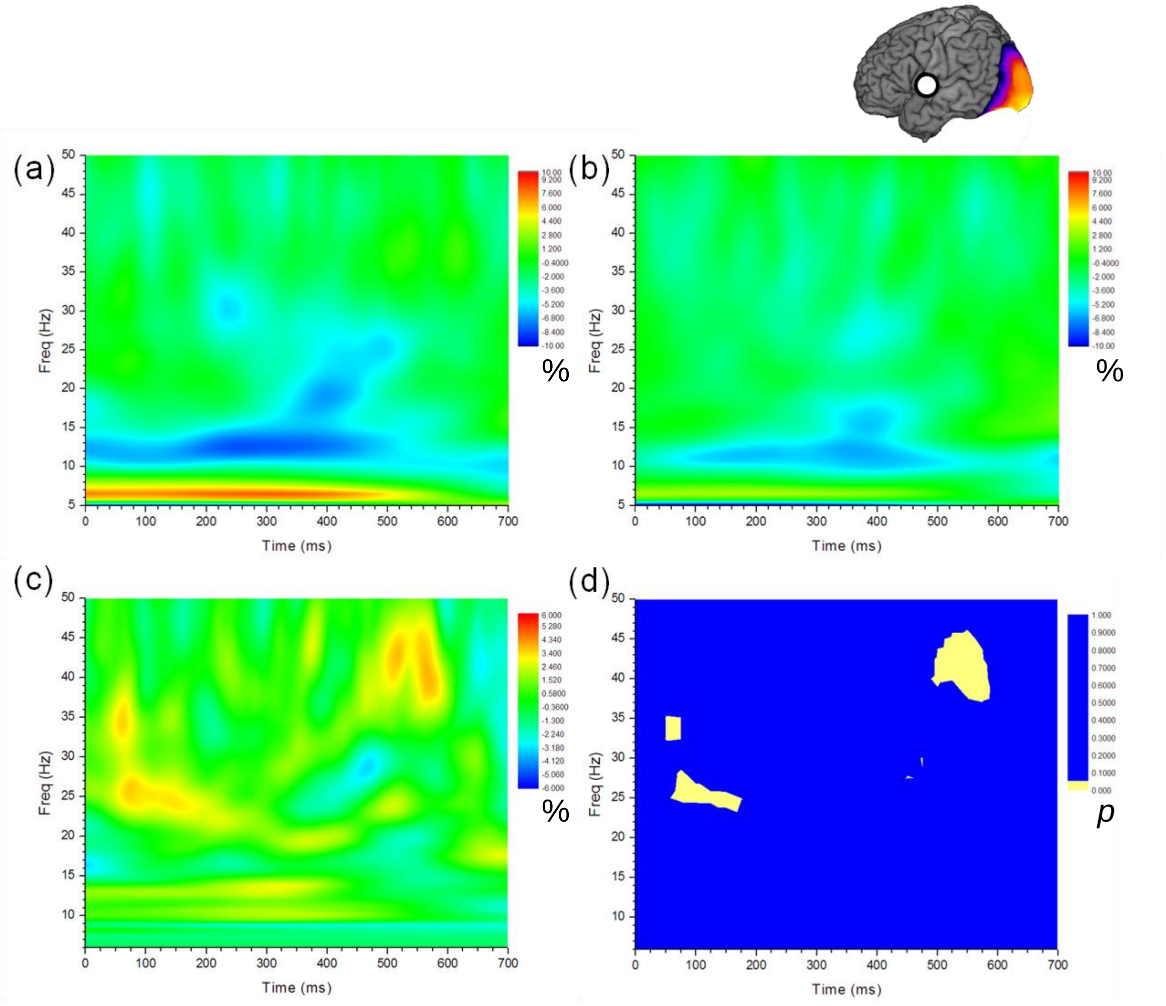


Figure 4.22 Total percentage signal change between PSEUD–NONWORD and ORTH–NONWORD at LIFGpo/PCG, MNI -44, 20, -8. (a) and (b) show the normalised grand averages for PSEUD–NONWORD and ORTH–NONWORD, respectively; (c) shows the % signal change between the two conditions (red PSEUD>ORTH, blue ORTH>PSEUD) for the duration of the trial (0–700 ms) for 5–50 Hz; and (d) shows the *p* values for the *t*-tests of least squared means at each tile in the time–frequency plot. Light yellow represents regions of significant change between PSEUD–NONWORD and ORTH–NONWORD, $p < .05$.

Next, the same analysis path was used to explore the total response at LIFGpo/PCG for nonword targets. Figure 4.22 shows the normalised grand average total response for PSEUD–NONWORD and ORTH–NONWORD, with the raw percentage signal change, and the plot of *p* values indicating whether this percentage signal change is significantly different from 0. Here, phonological priming can be seen at around 50–150 ms and again at 500–600 ms, with no advantage for the orthographically primed nonwords.

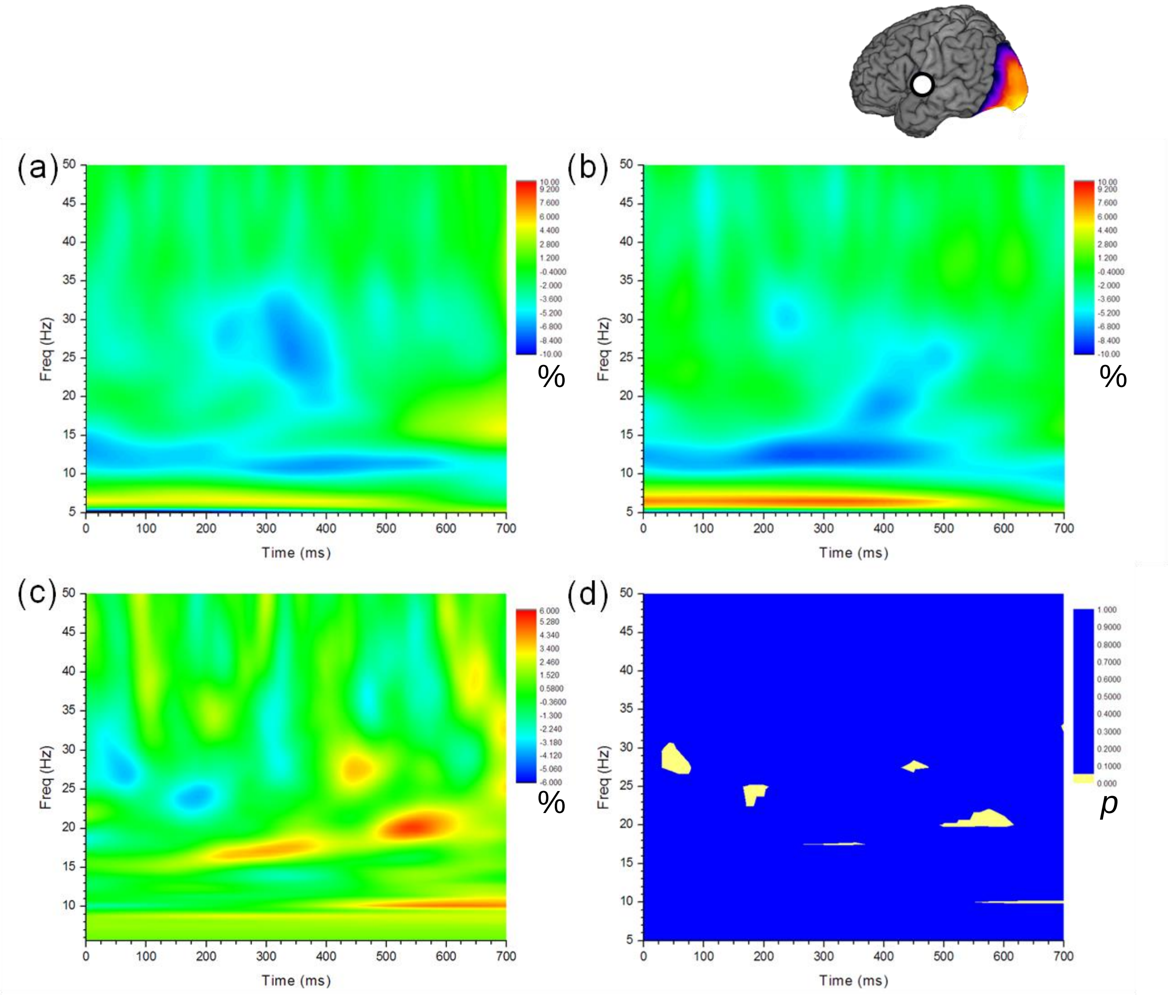


Figure 4.23 Total percentage signal change between PSEUD–WORD and PSEUD–NONWORD at LIFGpo/PCG, MNI -44, 20, -8. (a) and (b) show the normalised grand averages for PSEUD–WORD and PSEUD–NONWORD, respectively; (c) shows the % signal change between the two conditions (red WORD>NONWORD, blue NONWORD>WORD) for the duration of the trial (0–700 ms) for 5–50 Hz; and (d) shows the *p* values for the *t*-tests of least squared means at each tile in the time–frequency plot. Light yellow represents regions of significant change between PSEUD–WORD and PSEUD–NONWORD, $p < .05$.

The last virtual electrode comparisons at LIFGpo/PCG are directly between the word and nonword conditions. Figure 4.23 shows the percentage signal change between total power for PSEUD–WORD and PSEUD–NONWORD, indicating a stronger response to phonologically primed nonwords than phonologically primed words prior to 100 ms and at 150–200 ms. Conversely, there are only marginally significant differences between the orthographically primed word and nonword conditions (see Figure 4.24).

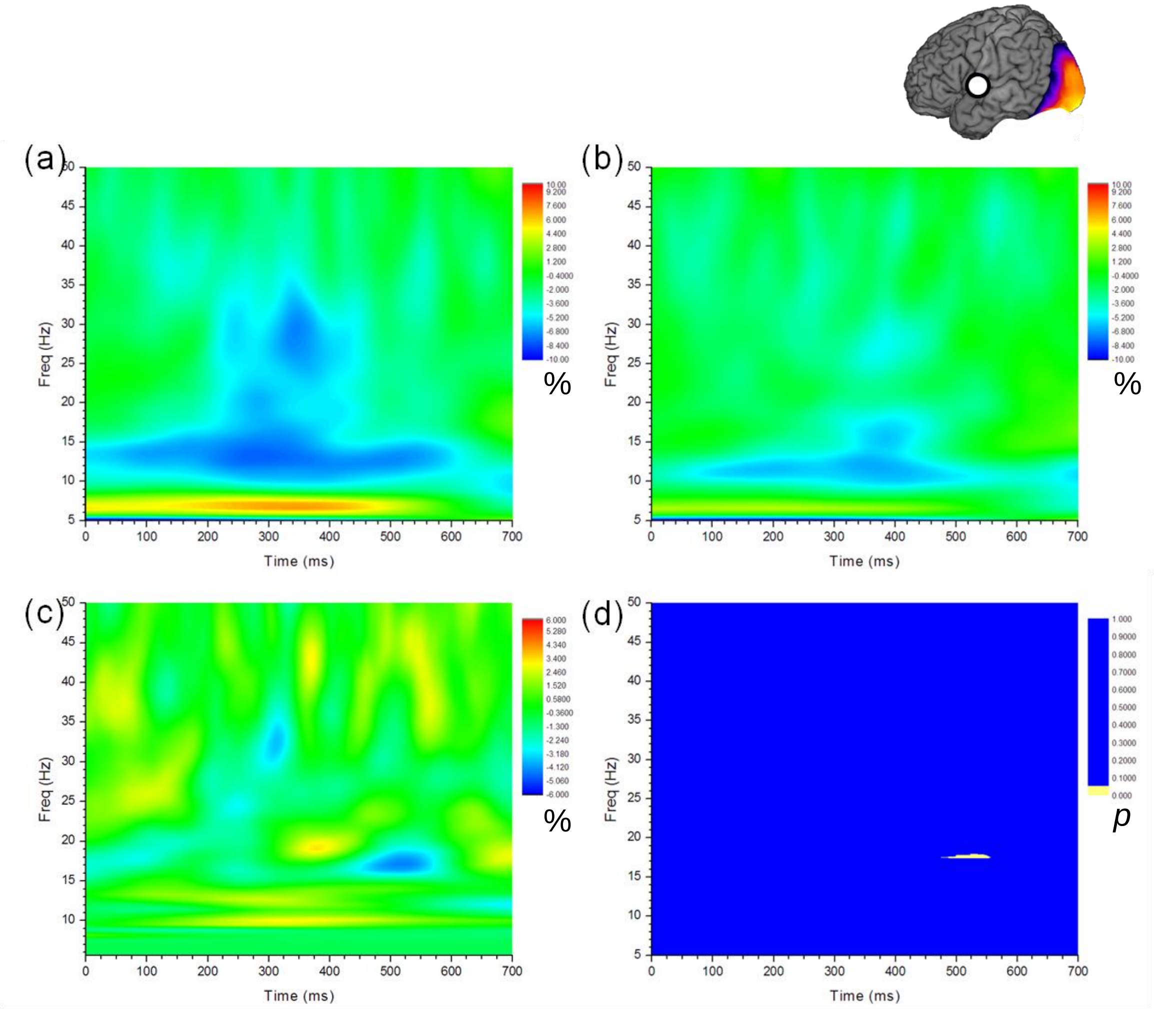


Figure 4.24 Total percentage signal change between ORTH–WORD and ORTH–NONWORD at LIFGpo/PCG, MNI -44, 20, -8. (a) and (b) show the normalised grand averages for ORTH–WORD and ORTH–NONWORD, respectively; (c) shows the % signal change between the two conditions (red WORD>NONWORD, blue NONWORD>WORD) for the duration of the trial (0–700 ms) for 5–50 Hz; and (d) shows the *p* values for the *t*-tests of least squared means at each tile in the time–frequency plot. Light yellow represents regions of significant change between ORTH–WORD and ORTH–NONWORD, $p < .05$.

Finally, a control virtual electrode was placed at left middle occipital gyrus (LMOG). The site was chosen based on the same beamforming comparison used to place the LIFGpo/PCG virtual electrode; the first 200 ms window of the PSEUD–WORD beamforming. The LMOG virtual electrode was placed at MNI -18, -98, -2, which is the peak of the occipital activity and the only other significant peak of activity during the first 200 ms. Figure 4.25 shows the percentage signal change between PSEUD and ORTH for words and nonwords at this site. As can be seen in parts (b) and (d), there are only marginal regions of significant difference for both comparisons.

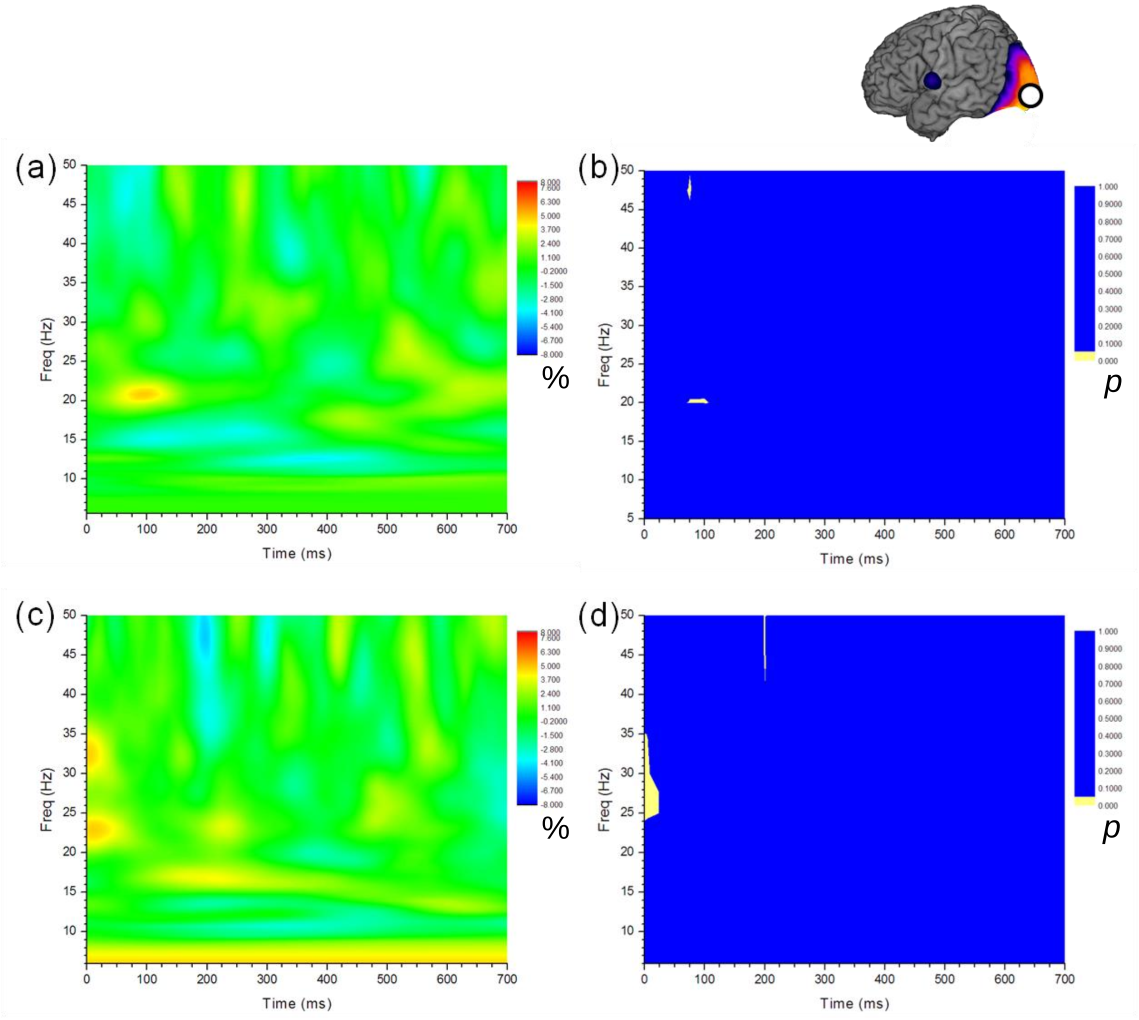


Figure 4.25 Left middle occipital gyrus control virtual electrode at MNI -18, -98, -2. (a) and (b) show the percentage signal change and *p* values between PSEUD–WORD and ORTH–WORD; (c) and (d) show the percentage signal change and *p* values between PSEUD–NONWORD and ORTH–NONWORD. $p < .05$ shown in light yellow.

4.3.3 Discussion

The aim of this experiment was to test the hypothesis that Broca’s area is involved in rapid phonological access during visual word recognition, in a replication of Wheat et al.’s (2010) finding. In an extension of Wheat et al.’s study, it was also hypothesised that any early phonological representation would be sublexical in nature, as tested by the addition of nonword targets to the experiment.

The suitability of the participants to take part in the MEG study was verified by ensuring all participants showed a phonological priming effect for words, as this has been shown to be variable across individuals in previous experiments (see e.g., Appendix C; Holyk & Pexman, 2004). Although participants were not selected on the basis of nonword priming, there was a significant effect of both phonological and orthographic priming for nonwords. This sublexical behavioural priming result confirmed the potential of the experimental design and stimuli for investigating sublexical effects.

The whole-brain beamforming results show a replication of early Broca’s area involvement in phonological processing of words within the first 200 ms of target word onset. As in Wheat et al.’s (2010) study, this Broca’s area activity for phonologically primed words (as compared to baseline) peaked around the border of LIFGpo/PCG. This activity did not become apparent for orthographically primed words until 100–300 ms, demonstrating an early advantage of phonological priming at LIFGpo/PCG. A direct comparison of PSEUD–WORD and ORTH–WORD using virtual electrodes showed significant differences between the two conditions from around 200 ms; later than would have been predicted based on Wheat et al. For nonwords, again, whole-brain beamforming results indicated that LIFGpo/PCG activity for PSEUD–NONWORD was stronger than baseline by around 100–300 ms, with a large spread of activity around Broca’s area by 200–400 ms. Conversely, ORTH–NONWORD showed no LIFGpo/PCG activity that was significantly greater than baseline within the first 400 ms. Interestingly, a direct virtual electrode comparison between PSEUD–NONWORD and ORTH–NONWORD, indicated early differences between the conditions. Phonologically primed nonwords showed significantly stronger activity at LIFGpo/PCG prior to 100 ms from target nonword onset.

One particularly interesting finding is an early significant difference between phonologically primed words and phonologically primed nonwords at LIFGpo/PCG prior to ~75 ms. This finding shows a stronger response at LIFGpo/PCG to phonologically primed nonwords than words. However, there is only marginal difference between orthographically primed words and nonwords. These comparisons suggest that the phonological priming advantage is significantly stronger or earlier for nonwords than words, and that this difference is specific to phonological priming and not a general lexicality effect. A general lexicality effect would be apparent in both phonological and orthographic word-versus-nonword comparisons. It can be inferred from this finding that LIFGpo/PCG is particularly involved in phonological processing of nonwords and that perhaps there are other lexical processing mechanisms involved in reading the real words, lessening the advantage of phonological priming at LIFGpo/PCG. Another possible interpretation is based on the timing of the word and nonword response, and will be discussed below.

Another feature of these virtual electrode comparisons is a late (400–600 ms) phonological advantage for both words and nonwords. This later difference may relate to an articulatory planning response in preparation for a spoken response, or the effects of withholding that response during silent reading. LIFGpo/PCG gained the name *Broca's area* due to its link to speech disorder (as in Broca's aphasia; Broca 1861a) and has since been strongly related to speech output processes (e.g., Brown et al., 2008; Greenlee et al., 2004; Pulvermüller et al., 2006). This suggests a dual role for LIFGpo/PCG during reading aloud in both phonological input processes, and articulatory output processes. This possibility of "many-to-one" mappings of function to structure has been discussed, for example, by Price and Devlin (2003), McIntosh (2000), and Friston and Price (2011).

Finally, with regard to the LIFGpo/PCG results, the timing of the real word phonological advantage appears later than predicted on the basis of Wheat et al. (2010). This result can be explained by the mixing cost account of Los (1996). If the reading network responds flexibly on a trial-by-trial basis, then there will be a reaction time cost when different types of stimuli, that require different types of processes, are mixed together. This reaction time cost was shown between Experiments 3 and 4 in Chapter 3. When words and nonwords were mixed together, vocal reaction times were slower than when words and nonwords were in separate blocks. As Wheat et al. did not use nonwords, the words were necessarily presented in pure blocks. The later timings of the priming result for words in the current experiment could, therefore, relate to this mixing cost. Surprisingly, there does not appear to be a mixing cost for nonwords, due to the earlier priming effect for nonwords than words. Furthermore, this earlier effect for nonwords than words is in contrast to reaction time data, where words are consistently named faster than nonwords, as shown in Chapter 3 (see also, e.g., Coltheart et al., 2001; McCann & Besner, 1987). However, looking at the direct comparison between PSEUD–WORD and PSEUD–NONWORD, it appears that, while the early (~100 ms) priming effect favours the nonword targets, there is a significant advantage in the later aspect (400–600 ms) for real word targets. If this later aspect relates to articulatory planning, this might explain the reaction time advantage for real words over nonwords. This interpretation is suggestive of a highly complex interactive network that is flexible based on the needs of the task and stimuli (Friston & Price, 2011) and perhaps shows that within the same stimuli both mixing costs and mixing benefits occur, similar to Lupker et al.’s (2003) suggestions.

In sum, both word and nonword targets showed evidence of phonological priming at LIFGpo/PCG. Phonological priming of real words replicates the findings of Wheat et al. (2010), providing further evidence of a phonological role for LIFGpo/PCG during visual word recognition. Though, for real words the priming effect appears slightly later than shown by Wheat et al. Activation of LIFGpo/PCG during silent naming of nonwords shows that this region is not solely involved in lexical level processes. Furthermore, phonological priming of nonwords demonstrates that this region is sensitive to the sublexical phonological relationship between nonword primes and targets. The specificity of this phonological priming to LIFGpo/PCG is further supported by the near lack of differences between the equivalent comparisons at LMOG for a peak chosen from the same beamforming result. There do appear to be slight differences between the phonological and orthographically primed conditions at this site, however, these differences are small and only marginally significant.

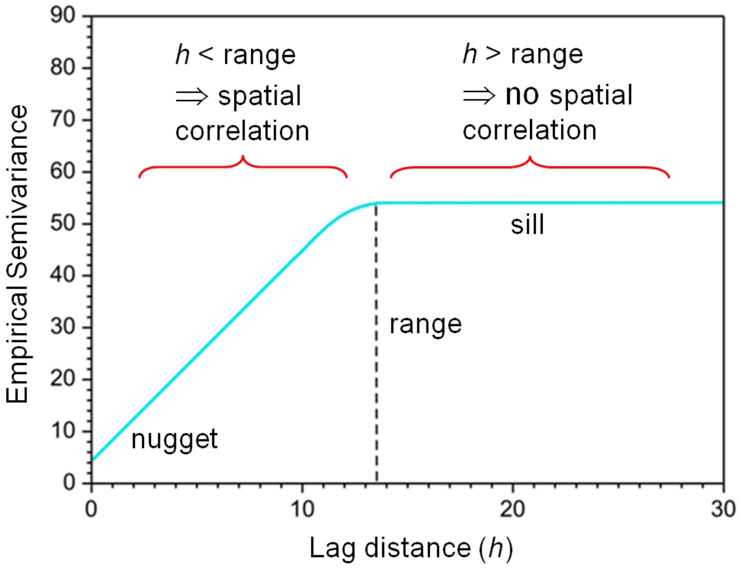


Figure 4.26 An illustrative semivariogram. The blue line indicates the value of empirical semivariance as a function of the separation *h* between pairs of points in the time–frequency plot. The line begins at the “nugget”, indicating the empirical semivariance of pairs for which *h* = 0. Spatial correlation decreases (i.e., empirical semivariance increases) until the “range” is reached, after which there is no further change in spatial correlation, the “sill”.

There is a limitation in the current analysis pathway that should be borne in mind when interpreting the virtual electrode results. Spatial covariance can be estimated from a variogram, or plot of empirical semivariance (γ), which is calculated from the formula

$$\gamma(h) = \frac{1}{2m}\sum(y_i - y_j)^2$$

where *m* is the number of pairs of observations; *h* is the distance apart of a given pair of observations y_i and y_j in the time–frequency plot; and y_i is the *i*th value of percentage signal change (in the current case) which is *h* distance away from the *j*th value of signal change, y_j. Thus, for every distance *h*, empirical semivariance is equal to the sum of the squared differences between all pairs of points (at distance *h*), multiplied by 1 over twice the number of pairs (Littell, Milliken, Stroup, Wolfinger, & Schabenberger, 2006). A semivariogram can then be plotted as illustrated in Figure 4.26. The critical values of this plot (i.e., the nugget, range, and sill) can be estimated for a given dataset and entered as parameters into the mixed model specified in Proc Mixed, in order to control for spatial covariance, as has been done for the data described in this chapter. An example of the variogram for real data is shown in Figure 4.27 and clearly demonstrates the existence of spatial covariance in these data.

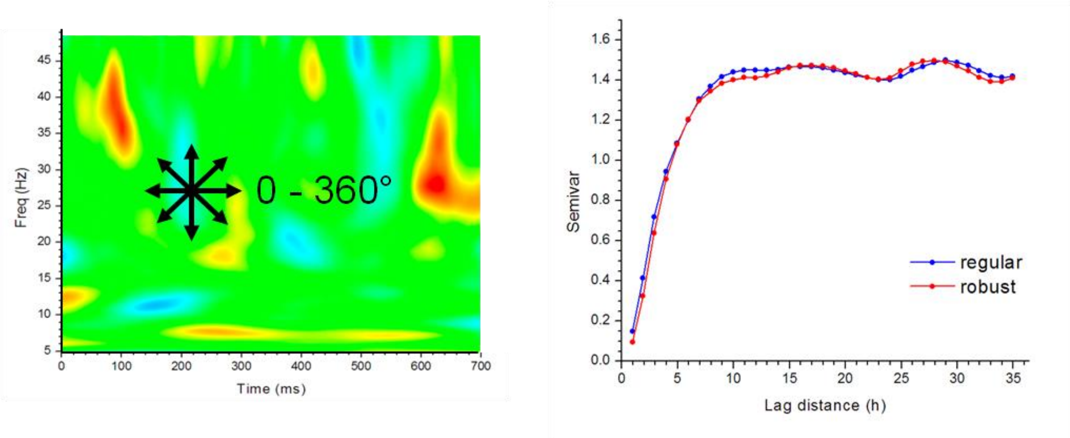


Figure 4.27 Empirical semivariance. The empirical semivariance (right) computed from a representative MEG dataset (left), plotted as a function of *h* for all directions.

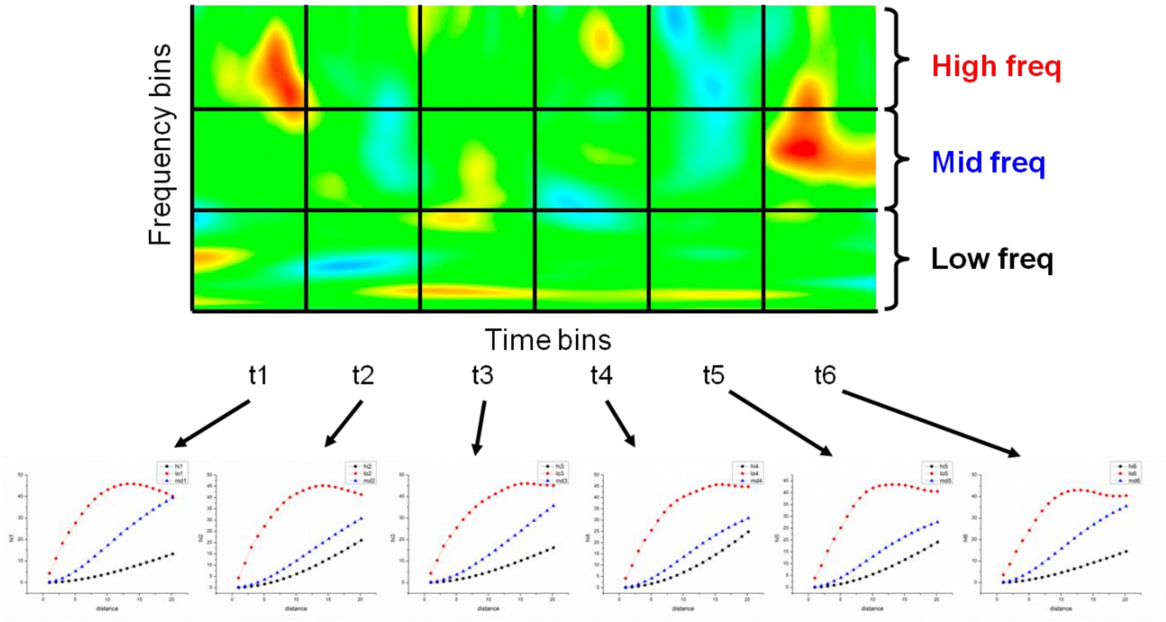


Figure 4.28 Irregularities in the subsetted variograms. The six small plots show empirical variance within a time–frequency tile, for each of the six time bins, with each line representing one frequency bin. Empirical semivariance is therefore not regular across the plot, due to the inherent time–frequency inhomogeneity of the Stockwell transform.

Returning to the limitation alluded to above; the problem arises from the inherent time–frequency inhomogeneity of the Stockwell transform. As mentioned above, the Stockwell transform results in a time–frequency distribution that has better temporal resolution at higher frequencies, and better frequency resolution at lower frequencies. Figure 4.28 illustrates the problem. In this figure, the time–frequency plot has been split into equally sized time–frequency tiles for six time bins and 3 frequency bins. If empirical semivariance is computed and plotted separately for each tile, we can see that the slope, range, and sill values depend of the frequency range in each tile. This inhomogeneity is not ideal because, as currently implemented in SAS, Proc Mixed assumes that the smoothing function used to estimate spatial covariance should maintain a constant shape and scale across the sampled space (here the time–frequency plot). Currently, as implemented in SAS 9.2, it is not adaptive.

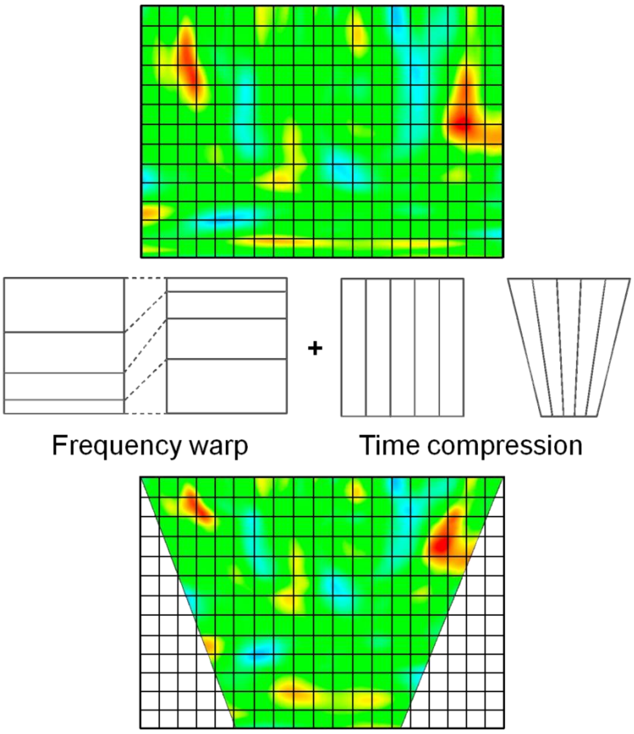


Figure 4.29 The time–frequency resolution of the Stockwell transform and Proc Mixed. The regular time–frequency tiles of Proc Mixed are not a good match for the time–frequency resolution of the Stockwell transform. However, a frequency warp and time compression could be applied to the plot in order to match the time–frequency resolution to Proc Mixed.

Therefore, one possible solution might be to apply a transform to regularise the time–frequency resolution (but more importantly, the spatial covariance) of the plots before performing any statistical comparisons, thereby bypassing the problem. See Figure 4.29 for an illustration of such a transform. This procedure should be investigated for future analyses of this type.

Other directions for future research include a comparison of the mixed design (as presented here) with the blocked design experiment (as shown in section 3.8). A within-participants investigation of the apparent mixing cost would be particularly important for relating the later phonological priming effect for words shown here with the earlier effect shown by Wheat et al. (2010). Furthermore, a blocked design experiment would allow interpretation of the difference in timing between real word and nonword targets shown here. The mixed versus blocked design would highlight whether these differences relate to intrinsic differences in the timings of word and nonword processes, or to differences attributable to the mixing costs and mixing benefits of the different stimuli.

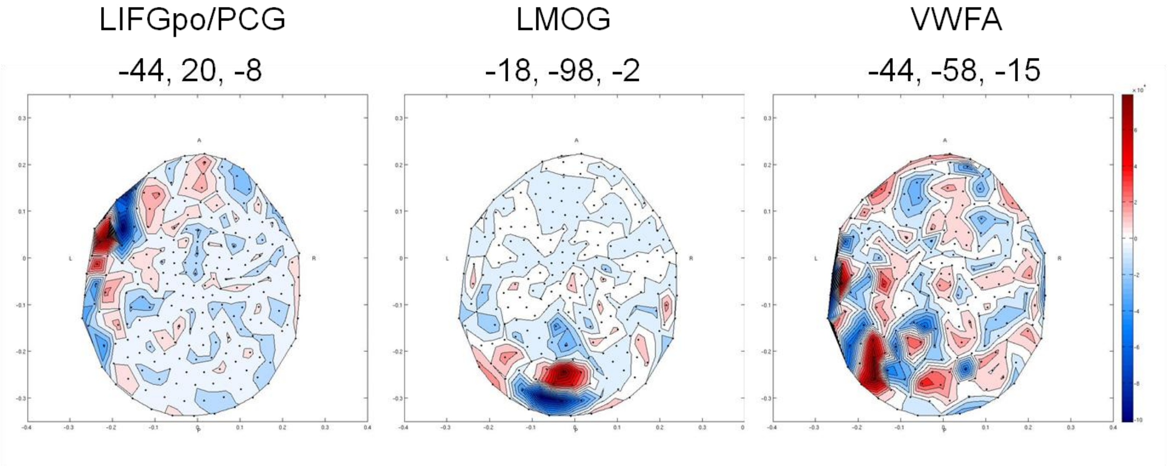


Figure 4.30 Comparison of virtual electrode locations. The spatial filters of LIFGpo/PCG and LMOG (left and centre) appear more focused than for VWFA (right).

Additionally, future research may wish to include other likely visual word recognition nodes, such as other regions implicated in phonological processing (e.g., inferior parietal areas; Vigneau et al., 2006), regions associated with semantics (e.g., angular gyrus, inferior temporal gyrus; Binder et al., 2009), and regions implicated in orthographic processing (e.g., vOT; Dehaene et al., 2002), as well as investigating the right hemisphere homologues of these sites. While the two ROIs displayed here address many of the questions posed in this thesis, they do not represent a full exploratory analysis of the data. However, an important caveat when choosing virtual electrode locations is that the spatial filter for any one beamformer needs to be relatively well focused. While this requirement is well met for superior virtual electrodes, the spatial filters for sites further away from the sensors, such as vOT, are increasingly less focused, meaning that virtual electrodes placed in these regions would not be as anatomically specific as for more superior regions. While vOT/VWFA is a region of great interest for many researchers investigating visual word recognition, ROIs in the ventral occipital/mid fusiform territory may not be directly comparable with more superior sites, such as the LIFGpo/PCG ROI used here. For example, Figure 4.30 shows the spatial filters weightings of the group beamformers (in one direction) applied to the LIFGpo/PCG and LMOG virtual electrode sites, compared to a similar plot for published fMRI coordinates of VWFA (MNI -44, -58, -15; Jobard et al., 2003). These plots show that the LIFGpo/PCG and LMOG sites appear more focused than the VWFA site. However, as yet, there is no way to quantify the apparent differences between these plots.

Finally, the data presented here—whilst in favour of a role for LIFGpo/PCG in sublexical phonological input processes—do not necessarily rule out alternative interpretations. For example, phonologically related activity could indicate a persistent neural association between orthography and phonology that is left over from learning to read (such as when using letter–sound knowledge to sound out a new word) but that no longer plays a part in visual word recognition (Whitney & Cornelissen, 2005). Many studies have shown the predictive value of phonological awareness on learning to read (e.g., Bradley & Bryant, 1983). However, it has also been shown that—while poor phonological awareness continues to be associated with reading disability in later life—high reading proficiency can be associated with surprisingly low scores on measures of phonological awareness (e.g., Scarborough, Ehri, Olson, & Fowler, 1998). This may indicate that skilled readers have less need to rely on phonological skills than beginning readers. Alternatively, LIFGpo/PCG activity could relate to conflict resolution mechanisms such as those described by January et al. (2009; see section 2.3.3.4). This would be particularly relevant for phonological priming, where there is a potential conflict to resolve between different orthographic representations activating the same phonological representation (e.g., *brein–BRAIN*) versus two different orthographic and phonological representations (e.g., *broin–BRAIN*). Further support for this region in conflict resolution comes from Novick, Kan, Trueswell, and Thompson-Schill (2010) who suggested, from a case study of a Broca's aphasic, that the typical deficits of Broca's aphasia could be explained by a general top-down cognitive control mechanism involved in selecting between competing alternatives. In contrast, Fedorenko, Bher, and Kanwisher (2011) recently showed in their fMRI data that posterior LIFG was not activated by cognitive control or conflict resolution type tasks. Fedorenko et al. did show an overlap between written language processing and verbal working memory tasks in this region, and inferred that previous cognitive control and conflict resolution tasks activate LIFG due to a necessary role of verbal working memory during demanding cognitive tasks. Fedorenko et al. ultimately proposed that posterior LIFG is a linguistically specialised brain region, rather than a region that supports language via more general functions.

These alternatives cannot be conclusively ruled out on the basis of the current MEG results. However, first, it is difficult to explain how verbal working memory might differentially be affected by phonological and orthographic primes, and secondly, if LIFGpo/PCG activity related to conflict control mechanisms then the question arises of when and where the phonological representations are formed that are then resolved at LIFGpo/PCG by ~100 ms. In order to rule out LIFGpo/PCG as activating sublexical phonological representations that are no longer necessary for successful reading, Chapter 5 will present a TMS investigation of this region.

4.4 Summary

The key findings from Experiment 5 were

- A significant phonological priming advantage at LIFGpo/PCG for both words and nonwords.
- Phonological priming for words was evident by ~250 ms from word target onset.
- Phonological priming for nonwords was evident by ~75 ms from nonword target onset.
- Nonwords showed an earlier or stronger phonological priming effect than words at LIFGpo/PCG.

- A late (500–600 ms) phonological advantage was also shown for words and nonwords, implicating LIFGpo/PCG in articulatory output processes.
- The specificity of the priming effect to LIFGpo/PCG was shown by a null result for equivalent contrasts at LMOG.

In conclusion, a phonological priming effect was localised to LIFGpo/PCG, indicating a role for this region in phonological processes during visual word recognition. The earliest effects were shown with around 75 ms of target onset, demonstrating a likely role in input processes. A later (500–600 ms) phonological advantage suggests a complex and interactive role of LIFGpo/PCG in word reading and naming. Ultimately, it appears that LIFGpo/PCG is significant for phonological input and output processes, however, these results should be viewed in light of the important caveat that MEG data are inherently correlational. Therefore, it is not possible to infer from these results that LIFGpo/PCG performs a functionally necessary role during visual word recognition, as will be discussed in Chapter 5.

Chapter 5

Experiment 6: fMRI-Guided TMS

5.1 Overview

This chapter presents an fMRI-guided transcranial magnetic stimulation (TMS) study conducted in Dutch with native Dutch speakers. The main purpose of this study was to investigate whether Broca's area performs a necessary function during visual word recognition. This was tested by stimulating individually fMRI-defined left IFG and comparing performance during word reading and picture naming. Single pulse TMS was used to chart the functional involvement of this region to the two tasks.

5.2 Introduction to Transcranial Magnetic Stimulation

When studying visual word recognition, it is important to consider not just the input to and output from the reading system, but also to understand what is happening inside the black box. Neuroimaging methods such as fMRI, MEG and EEG allow us to investigate the internal workings of the system by measuring correlations between input stimulus, overt behaviour and signals from cortical and subcortical structures with varying degrees of spatial and temporal resolution. A well accepted limitation of this approach, however, is that an observed correlation does not necessarily indicate that the measured signals are causally related to the behavioural task under consideration (Pascual-Leone et al., 2000). For example, it is difficult to control for strategic behaviours used by participants that are not necessary for a behavioural outcome per se, but which may nevertheless produce misleading correlations between behaviour and brain activity (Pascual-Leone, 1999; Pascual-Leone et al., 2000). While careful experimental design can minimize effects like these, thereby bolstering the evidence for causality, nevertheless, neuroimaging methods alone can never be sufficient to make the case: they are inherently correlational. However, by disrupting normal brain function, TMS can create a transient “virtual brain lesion” (Pascual-Leone, 1999; Walsh & Rushworth, 1999). Therefore, by delivering TMS pulses appropriately in space and time (Walsh & Rushworth, 1999), and comparing the consequences of the induced temporary lesions to appropriate controls (de Graaf & Sack, 2011), researchers can infer whether activity in specific brain regions is indeed necessary for a given task (Pascual-Leone et al., 1999).

When a current is passed through a coil of wire, a magnetic field is induced. During TMS, this magnetic field—induced in a coil—is placed close to the scalp, resulting in an electric field perpendicular to the magnetic field. This electric field will cause current to flow parallel to the plane of the coil, activating populations of neurons via synaptic inputs (see e.g., Hallet, 2000). In contrast to the diffuse and irreversible brain lesions studied in neuropsychology (see Chapter 2) TMS can induce relatively spatially specific lesions, with a spatial resolution in the region of 0.5–1.5 cm (Walsh & Rushworth, 1999). Furthermore, Pascual-Leone, Bartres-Faz, and Keenan (1999) detailed a number of advantages TMS has over lesion deficit studies, for example: TMS can be conducted in normal participants, avoiding any potential confounds of additional lesions or health problems; TMS lesions can be studied immediately, lessening the possible confounds that arise as a result of functional reorganisation in patients; TMS can be repeated within and between participants, allowing experiments to be conducted on groups of participants, as compared to the serendipity of lesion location in different patients; and dissociations between closely spatially related brain regions can be studied by creating relatively focal lesions.

The magnetic pulses delivered during TMS can be applied in a number of different ways, with different behavioural outcomes (see e.g., Hallet, 2007). Effects can be either inhibitory or excitatory, for example, stimulation of visual cortex can result in scotomas (inhibitory) or phosphenes (excitatory), depending on the type of TMS delivery (O’Shea & Walsh, 2007). In single pulse TMS just one pulse is delivered per trial. Using this method, the contribution of an area to a function can be charted chronometrically by varying the time of pulse delivery and measuring a behavioural outcome. In order to have a stronger and longer lasting effect, multiple pulses can be delivered per trial, such as the triple pulse design of Schuhmann, Schiller, Goebel, and Sack (2009). Schuhmann et al. used triplets at a frequency of 40 Hz (i.e., three pulses delivered over 50 ms) to measure the chronometric functional contribution of Broca's area to picture naming. In repetitive TMS, low or high frequency trains of pulses are delivered for a period of time prior to a task. The effects of repetitive TMS can last beyond the stimulation time, with 1 Hz or less pulse delivery often leading to inhibitory effects, but greater than 5 Hz stimulation leading to facilitatory aftereffects (Hoogendam, Ramakers, & Lazzaro, 2010). Furthermore, longer stimulation durations lead to longer lasting aftereffects (Hoogendam et al., 2010). Single pulse TMS therefore has the highest temporal resolution both with respect to the shorter time taken to deliver the TMS pulse (or train of pulses) and the shorter duration of any TMS-induced effect. On the other hand, because single pulse TMS is temporally transient, when exactly the pulse is delivered with respect to the stimulus may be more critical for finding an effect, especially when the neural process to be disrupted is also brief, representing a possible temporal disadvantage for some studies.

5.3 Experiment 6

5.3.1 Motivation

In Chapter 4 of this thesis (see also Ashby, 2010; Ashby et al., 2009; Cornelissen et al., 2009; Pammer et al., 2004, Wheat et al., 2010), evidence was presented for sublexical phonological representations at LIFGpo/PCG within ~75 ms of target onset. The fact that Broca's area activation can be seen within the first ~75–100 ms of viewing a word and that this can be modulated by phonological relationship provides support for the idea that the activity seen relates to fast phonological access. Moreover, phonological priming of LIFGpo/PCG is not likely to be due to any strategic behaviour because the participants were not aware of the primes and therefore could not modify their behaviour based on predictions about prime–target relationship. However, although there is a strong case for fast phonological access that is necessary for encoding, because MEG and EEG cannot demonstrate a causal relationship between brain signals and behaviour not all alternatives can be discounted. For example, in the previous chapter (p. 145) conflict resolution mechanisms (e.g., January et al., 2009; Novick et al., 2010), verbal working memory (e.g., Fedorenko et al., 2011), and redundant phonological representations, were presented as possible alternative interpretations for early LIFGpo/PCG activity. Here, TMS will be used to create focal and transient virtual lesions to LIFGpo/PCG in a chronometric design in order to test the hypothesis that the putative early sublexical phonological representations seen at LIFGpo/PCG are functionally necessary for visual word recognition.

5.3.2 Background

In order to demonstrate that TMS has had an effect on visual word recognition at all, it is necessary to show a change in an appropriate behavioural measure, such as VRT. However, a change in VRT in response to a written word, when a TMS pulse is delivered at a certain time to a specific stimulation site, would not necessarily show that the site was involved in word identification or encoding at that time. This is because an effect on VRT could equally be caused by a disruption to the speech output processes that are also necessary for successful reading aloud but that are not specifically related to the early encoding processes of word identification. It is therefore important to have an appropriate control condition that allows us to make the distinction between the putative encoding processes that lead to successful visual word recognition versus any speech output components that lead to successful naming and so will also have an effect on the vocal reaction time.

Picture naming offers a useful control condition for comparison with reading aloud. The processes we are particularly interested in disrupting with TMS are the early encoding processes, such as the mapping of orthographic to phonological representations, which may occur at LIFGpo/PCG within the first 100 ms. This type of phonological access may be required for visual word recognition, but, arguably, would not be required for picture recognition. However, in an overt naming task, both reading aloud and picture naming would require articulatory–motor representations for speech output. For example, based on a meta-analysis of 82 neuroimaging studies of word production, Indefrey and Levelt (2004) described the process of “syllabification” as being the point in the word reading and picture naming where the two processing streams converge. Syllabification is defined by Indefrey and Levelt as an abstract segmental phonological representation that takes place prior to the activation of phonetic/articulatory motor representations that are required for speech output, and occurs by around 330 ms after viewing a picture in their model.

In Indefrey and Levelt’s (2004) model, activations flow from posterior to anterior sites, with no (or very little) feedback. This suggestion was supported by MEG findings from Vihla, Laine, and Salmelin (2006) during naming and categorisation of object pictures. Vihla et al. showed a similar posterior to anterior progression, with activity peaking in frontal sites (in the region of posterior IFG and PCG) at ~330–600 ms. Furthermore, Vihla et al. demonstrated that this frontal activity was stronger when participants named the pictures or performed a phonological judgement than when they performed semantic or visual judgements, supporting Indefrey and Levelt's prediction that abstract phonological processes occur around this time.

Schuhmann et al. (2009) used TMS to show that Broca's area is functionally involved in picture naming at around 300 ms after a target was presented. Dutch participants were shown pictures of monosyllabic Dutch nouns and asked to name them aloud. Using an online event-related triple-pulse TMS paradigm, these authors applied 40 Hz TMS triplets to posterior Broca's area at five time points (150/175/200 ms, 225/250/275 ms, 300/325/350 ms, 400/425/450 ms, and 525/550/575 ms) following picture presentation. VRTs were slowest for pulses delivered around 300 ms. Schuhmann et al. interpret this as a disruption to syllabification in line with the model of speech production presented by Indefrey and Levelt (2004). However, Schuhmann, Schiller, Goebel, and Sack (2011) recently published data that contradict parts of Indefrey and Levelt's (2004) model. In a similar triple-pulse TMS design, Schuhmann et al. (2011) stimulated the posterior part of left superior temporal gyrus (Wernicke's area), posterior Broca's area (in the region of pars opercularis), and the midsection of the left middle temporal gyrus. Triple-pulse TMS stimulation of each site (in separate sessions) between 150 and 575 ms following picture presentation replicated the finding that Broca's area is critical for picture naming at around 300 ms. Stimulation to Wernicke's area disrupted picture naming for pulses delivered around 400 ms. Surprisingly, based on Indefrey and Levelt's model, stimulation of middle temporal gyrus produced significantly shower VRTs when pulses were delivered at around 225 ms and again at around 400 ms. This finding suggests a complex network for picture naming, including both feedforward and feedback processes. In contrast, Indefrey and Levelt's model predicts only feedforward processes, including the opposite prediction that Wernicke's area will be active prior to Broca's area. No part of Indefrey and Levelt's model can account for the later reactivation of middle temporal gyrus.

Thus, there is converging evidence that posterior Broca's area is functionally relevant for picture naming at around 300 ms, although it is not yet clear precisely what function this region performs. Furthermore, on the basis of Schuhmann et al (2009;

2011) and Vihla et al. (2006), it was not expected that this region would be involved in picture naming prior to ~300 ms. Though it should be noted that Schuhmann et al.'s (2009; 2011) earliest pulse trains started at 150 ms after stimulus onset, meaning that Broca's involvement prior to 150 ms cannot be ruled out for these studies.

Here, the naming paradigm of Schuhmann et al. (2009) was extended to include written words as well as pictures. One further change from Schuhmann et al.'s experiment was that they defined the stimulation target region anatomically whereas here it was defined functionally. In Schuhmann et al.'s study, LIFGpo was specified in each participant individually based on their structural anatomy, revealed by MRI. While this does take account of the anatomical variation between participants, it does not take into account the known functional variation of this region (e.g., Derrfuss, Brass, von Cramon, Lohmann, & Amunts, 2009). Therefore, in the current study, an fMRI localiser was used to identify a phonologically relevant peak of activity in LIFGpo/PCG for each participant in order to stimulate this site precisely. fMRI-guided TMS was shown by Sack et al. (2009) to be a more powerful localisation technique than using structural MRI data alone.

In sum, by comparing the effect of TMS to LIFGpo/PCG on picture naming and single word reading, we can dissociate the early encoding processes, hypothesised to occur only for word reading, from the later speech output processes, hypothesised to be common to reading and naming. Individually defined LIFGpo/PCG target sites were stimulated during word reading and picture naming, using VRTs as a measure of successful task performance. Slowed reaction times would be expected if the stimulation site is necessary for the current task at the time of pulse delivery. Therefore, for picture naming we expected to replicate slowed reaction times for pulse delivery at 300 ms (Schuhmann et al., 2009; 2011) and to show no effect of TMS pulses earlier than 300 ms. For word reading, in line with the findings of Chapter 4 (and previous findings for written English, e.g., Ashby et al., 2009; Cornelissen et al., 2009; Pammer et al., 2004; Wheat et al., 2010) slowed VRTs were expected at ~100 ms, and again at ~300 ms. This later reactivation of LIFGpo/PCG would mirror the virtual electrode findings of the previous chapter and coincide with the convergence of word reading and picture naming during preparatory output processes described by Indefrey and Levelt (2004).

5.3.3 Methods

5.3.3.1 Participants

Participants were 12 right-handed, native Dutch speakers, with no history of reading disorder, 2 of whom were male (M_{age} = 21.22; *SD* = 1.72). Of these participants, 10 (2 male) subsequently underwent TMS (M_{age} = 20.85; *SD* = 1.46). All had normal or corrected-to-normal vision and had no history of neurological or psychiatric disorders. They received medical approval for participation and gave their written informed consent in accordance with the Medical Ethical Commission of Maastricht University. They were compensated with vouchers worth €40 on completion of the study. Due to the possibly of discomfort during TMS, all participants who scheduled and attended a TMS session were eligible for full compensation without the need to complete the study. This was explained to the participants at the first TMS session.

5.3.3.2 Materials

For both experiments, Presentation (version 14) was used to control stimulus presentation and record participants' responses.

Table 5.1

Means and Standard Deviations of Stimulus Properties

Type	Mean String Length	Mean Frequency per Million (CELEX INL)	Mean Horizontal Visual Angle
Dutch word	3.8 (0.71)	69.30 (105.98)	2.2°
Pseudoword	3.8 (0.71)	-	2.2°
Line drawing	-	69.30 (105.98)	2.6°
Checkerboard	-	-	2.6°

Stimuli for the TMS experiment consisted of 30 high frequency, monosyllabic Dutch nouns (CELEX INL corpus) and 30 line drawings of the objects that the same Dutch nouns represent (adapted from Snodgrass & Vanderwart, 1980). For the fMRI experiment, two additional stimulus categories were 30 pseudowords created from the real Dutch words by replacing one or two letters, and a black and white square checkerboard stimulus. The properties of these stimuli are given in Table 5.1 and examples in Figure 5.1. The full stimulus list of pseudowords, Dutch words, and

English translations can be seen in Appendix G. Stimuli were always presented as white on a black background.

Figure 5.1 Stimulus examples. The Dutch word *vlag* (*flag*) was transformed into the nonword *vlog* for the pseudoword condition.

Pulses were applied using the MagProX100 stimulator (Medtronic Functional Diagnostics A/S, Sklovunde, Denmark) and a figure-of-eight coil (MC-B70, inner radius 10 mm, outer radius 50 mm). The maximum output of this coil and stimulator combination is approximately 1.9 Tesla and 150 A/µS. During sham stimulation, a specific figure-of-eight placebo coil (MC-P-B70) was used to reproduce the same acoustic stimulation as the active coil without inducing a magnetic field.

5.3.3.3 fMRI Design and Procedure

A blocked design was employed for the fMRI localiser. This ensured maximum power to localise activity related to each target category. A total of 240 trials, 60 per condition, were assigned to 3 functional acquisition runs containing 8 target blocks each. The 8 blocks, presented in a pseudorandom order, each consisted of 10 trials of a particular category. A trial comprised 600 ms blank screen followed by 1000 ms target, resulting in 16 s blocks. Target blocks were separated by a 16 s fixation screen. Each run started with visual instruction followed by fixation. The duration of a run was 4.5 min, resulting in a total duration of 13.5 min. Participants were instructed to attend the fixation cross and to silently read or name the stimuli. Participants viewed all picture stimuli twice before the scan. They were instructed to read the stimuli out loud on the first presentation, in order to learn them, and to practise silent naming without any lips movements on the second presentation. The checkerboard was trained with the name “patroon” (pattern).

5.3.3.4 TMS Design and Procedure

An event-related single-pulse TMS design was employed in order to give the maximum temporal resolution (in terms of pulse delivery duration and duration of the effect). The experiment consisted of two sessions, one using real TMS, and one using the sham coil. Session order was counterbalanced across participants. The mean delay between the first and second session was 3 days (Range 2–7). Across participants it was also counterbalanced as to whether all words or all pictures were presented first. The randomised word and picture stimulus lists were each chunked into 6 mini-blocks to allow participants sufficient rest breaks. The (on average) 35 trials per mini-block had durations between 6850 and 8850 ms, resulting in mini-block lengths of ~5 min and session lengths of around 1 hour. Trial timings are depicted in Figure 5.2. Pulses (1 per trial) were applied at 75, 100, 125, 225, 300, or 500 ms post target onset. The cluster of pulses around 100 ms was chosen in order to maximise the chances of capturing an early effect. The 300 ms pulse was chosen based on Schuhmann et al.’s (2009; 2011) finding and the 225 ms and 500 ms pulses were expected to show a return to baseline VRTs. Thus, this irregular pulse spacing potentially allows the double peak of disruption and return to baseline to be captured with fewer pulses than if they were regularly spaced. Online control trials where no pulse was delivered were also included. All stimuli appeared once under each pulse time (i.e., 7 times). Trials were presented in a new random order for each participant.

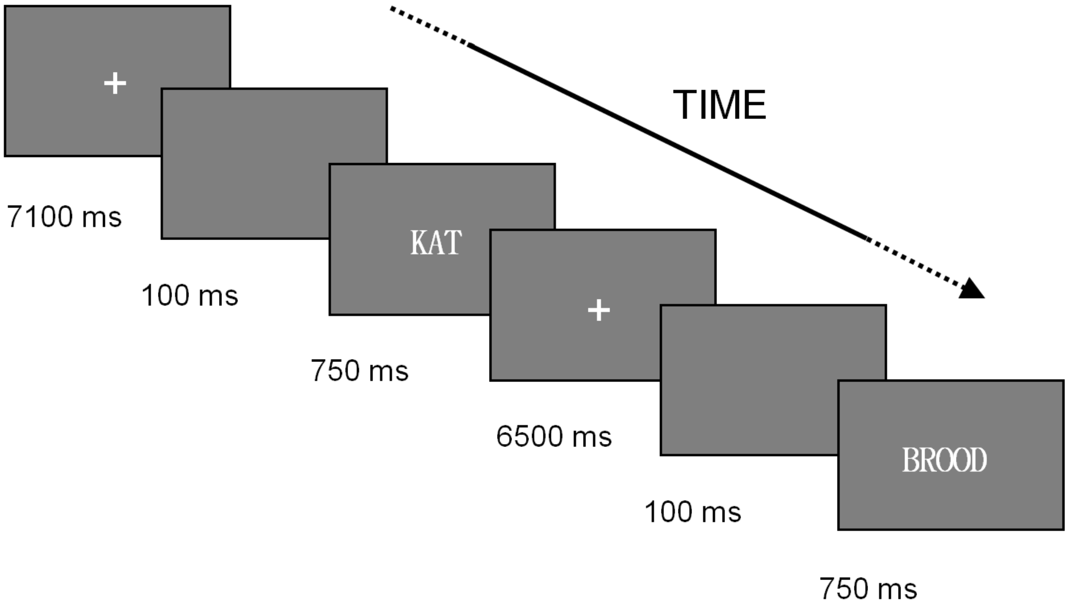


Figure 5.2 TMS trial timings. Two typical trials starting with a fixation cross randomly jittered between 6000 and 8000 ms duration in steps of 100 ms. Trials looped continuously.

Participants were instructed to read the stimuli aloud as quickly and accurately as possible. Responses were recorded using a digital microphone. TMS was applied with the coil manually held tangentially to the skull with the coil handle oriented perpendicular to the opercular part of the inferior frontal gyrus.

The target site was chosen based on each individual's fMRI data, by identifying a peak of frontal activity (for each individual separately) that fell within the approximate anatomical territory of pars opercularis of LIFG. At the start of each TMS session, participants were coregistered to their structural brain imaging data using the BrainVoyager TMS Neuronavigator (Brain Innovation BV, Maastricht, the Netherlands). This allows for continuous online coil navigation to a target point on the cortical surface pre-defined based on the fMRI data. During the sessions, the proximity of the coil to the target point was continuously monitored and the coil position adjusted between trials when necessary.

Stimulation intensity was determined by finding each participant's resting motor threshold (RMT) prior to the experiment. RMT provides a measure of sensitivity to stimulation and is used to ensure an equivalent stimulation level for each participant that is proportionate to his or her cortical excitability at rest (see e.g., Stewart, Walsh, & Rothwell, 2001). RMT was deemed a suitable estimate for excitability of LIFGpo/PCG due to its proximity to motor cortex. When stimulating visual cortex, a similar thresholding procedure with visual phosphenes is used (Stewart et al., 2001). Here, RMT was determined by observing physical movements, though measurement of motor evoked potential can also be used. RMT was defined as the stimulation level at which a hand twitch occurred on 50% trials (i.e., a stimulation level half-way between no observable motor stimulation and full motor stimulation), by placing the coil over the hand area of right motor cortex and gradually increasing the stimulation intensity. The experimental stimulation level was then determined from this threshold (up to a maximum of 200% RMT), however, the level of facial muscle reactions generated by stimulating LIFGpo/PCG limited the level of stimulation that could be applied in most cases. The average stimulation level was 150% RMT (Range = 119–190%).

5.3.3.5 MRI Data Acquisition

During each of the three functional runs, 150 functional volumes were acquired with a T2* weighted echo-planar imaging (EPI) sequence (TE – echo time, 30 ms, TR – repetition time, 2000 ms, FA – flip angle, 90°, 32 slices with a thickness of 3.5 mm, 224 mm FOV – field of view, with a 64 x 64 matrix resulting in 3.5 x 3.5 mm in plane resolution). These were followed with a high-resolution anatomical image, acquired using a magnetisation-prepared rapid acquisition gradient echo (MPRAGE) sequence with a 1 mm isotropic resolution. This sequence consisted of 192 1 mm sagittal slices with a matrix of 256 by 256 voxels (TR = 2250 ms, TE = 2.6 ms, FA = 9°). All MRI data were acquired in a 3-T magnetic resonance scanner (Siemens Allegra MR Tomograph; Siemens AG, Erlangen, Germany) with a volume head coil at the Faculty of Psychology and Neuroscience, Maastricht University, the Netherlands. Stimuli were displayed onto a frosted screen at the head end of the scanner bore, using an LCD projector (PLC-XT11-16, Sanyo North America Corporation, San Diego, CA). Subjects viewed the screen via an adjustable mirror mounted on the head coil.

5.3.3.6 MRI Analysis

MRI data were analysed offline using BrainVoyager QX 2.0 (BrainInnovation, Maastricht, the Netherlands). The first 4 volumes of each functional run were excluded to allow for T_1 saturation, permitting the T_2-weighted MR signal to stabilize. Preprocessing of the functional data consisted of slice scan time correction using cubic spline interpolation, 3D motion correction involving trilinear/sinc interpolation, and linear trend removal. Functional runs were visually inspected to examine whether any subject moved excessively during data recording, which was not the case. The 2D functional runs were transformed into 3D volume time courses, aligned to the high-resolution anatomical volume. The high-resolution volumes were used for surface reconstruction of the left hemisphere of each participant. The surface reconstruction was performed in order to recover the exact spatial structure of the cortical sheet in order to improve the visualisation of the functional data in relation to the anatomy of each participant. This allowed for precise localisation of TMS stimulation using Neuronavigation.

For the group analyses, anatomical and functional data from each participant were transformed into Talairach standard space (Talairach & Tournoux, 1988). Each participant’s cortical surface (in Talairach space) was then aligned to create an average group surface reconstruction. Functional analyses were then performed using a random effects general linear model (RFX GLM) and the results overlaid on the group average surface reconstruction. The RFX GLM allows the generalization of the group statistical inferences to the population level.

For the individual analyses, anatomical and functional data from each participant were aligned to AC-PC space (rotating the cerebrum into the anterior commissure - posterior commissure plane) without performing any spatial transformation. Functional analyses were performed for each participant separately using a fixed effects GLM and overlaid on their own surface reconstruction.

For both the RFX and fixed effects GLM, the fixation periods were entered into the model as the baseline. The predictor time courses in the model (for words, pseudowords, pictures and checkerboards) were adjusted to account for the delay in the hemodynamic response by convolution with a hemodynamic response function.

5.3.3.7 TMS Response Time Analysis

Responses were recorded using a microphone positioned directly in front of the participant. Sound level was calibrated individually prior to recording. Timings of voice key responses were logged by Presentation and sound files of responses were recorded for offline analysis. All incorrect responses and voice key triggers other than verbal responses (such as coughs, hesitations and TMS pulse clicks) were removed prior to VRT analysis (see Appendix B for a discussion of voice key efficacy). VRTs outside 4 standard deviations of the mean for a participant by type (word/picture), pulse time, and stimulation (TMS/Sham) were treated as outlying data points and were excluded from further analysis.

5.3.4 Results

5.3.4.1 fMRI

RFX GLM group results shows regions of activity ($p < .001$) for each condition as compared to the passive baseline fixation condition. For all blocks other than fixation, participants were asked to name the stimuli silently in their head. As shown in Figure 5.3, words, pseudowords and pictures show a peak of activity at the junction of the inferior frontal sulcus (IFS) and precentral sulcus (PCS), in other words, the border of LIFGpo and PCG. At a lower threshold the pattern of BOLD responses can be seen to include cortical areas commonly activated by reading and visual word recognition tasks (Dehaene et al., 2005; Jobard et al., 2003; Vigneau, et al., 2005).

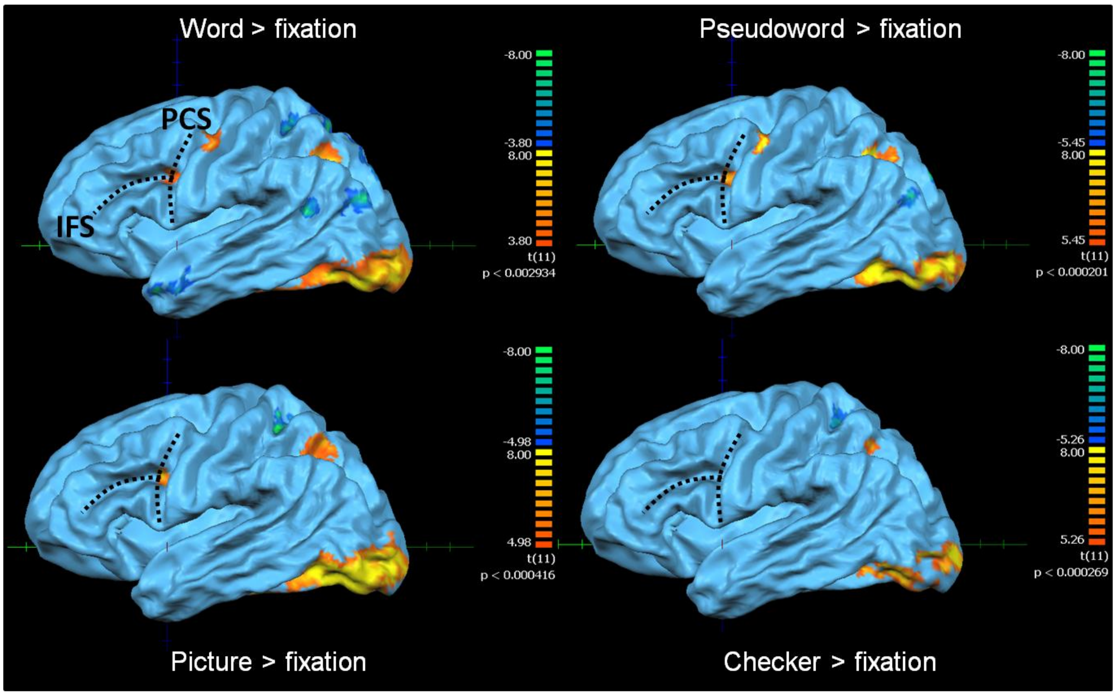


Figure 5.3 RFX GLM results. Activity shown at junction of inferior frontal sulcus (IFS) and precentral sulcus (PCS; dotted black lines) for all but the checkerboard condition (*p* < .001). Results are displayed on an average of the cortical surface reconstructions of the 12 participants.

The contrast pseudowords > words was expected to strongly localise LIFGpo/PCG, based on an fMRI study by Wimmer et al. (2010) in German participants. In Wimmer et al.'s study, participants were asked to make phonological lexical decisions to words, pseudohomophones, and nonwords. For example, *taxi* and *taksi* would require a *yes* response, while *tazi* would require a *no* response. Normal readers showed significantly stronger LIFGpo activity for nonwords, followed by pseudohomophones, then real words. Wimmer et al. suggested that this LIFGpo activity might relate to the access of sublexical phonological segments and phonological productive processes, due to the greater need to piece together phonological segments for pseudowords than words (in a dual-route framework). German is a highly regular language, as is Dutch and it was important for this study that a contrast was chosen to localise phonology within the confines of such a transparent orthography. Similar research in English would not necessarily have provided a reliable basis for use here due to the opacity of English orthography (e.g., the highly irregular spelling-to-sound correspondence in *yacht*). Here, this contrast was therefore expected to localise phonologically relevant areas of LIFGpo/PCG for each individual. As shown in Figure 5.4, this group contrast revealed significantly greater activation for pseudowords over real words along PCS, bordering LIFGpo and PCG. Figure 5.5a shows the results of the contrast pseudowords > words using a Fixed Effects GLM for one representative participant.

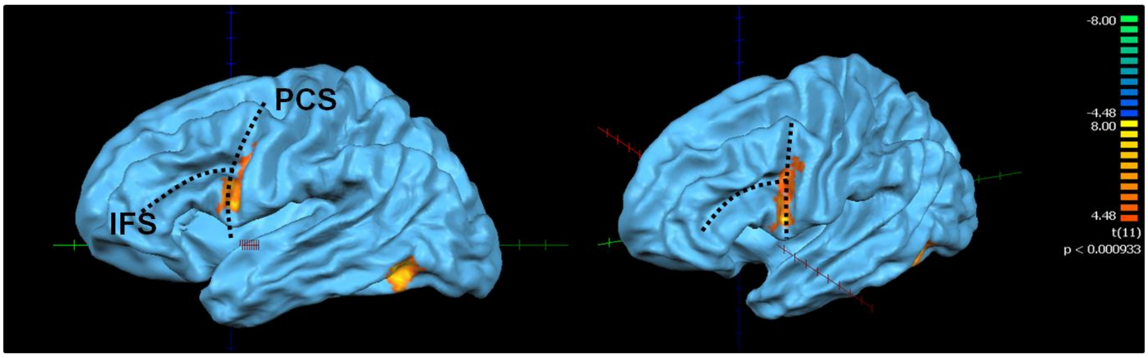


Figure 5.4 RFX GLM contrast. Activity shown at junction of inferior frontal sulcus (IFS) and precentral sulcus (PCS; dotted black lines) where pseudoword > word (*p* < .001). Results are displayed on an average of the cortical surface reconstructions of the 12 participants.

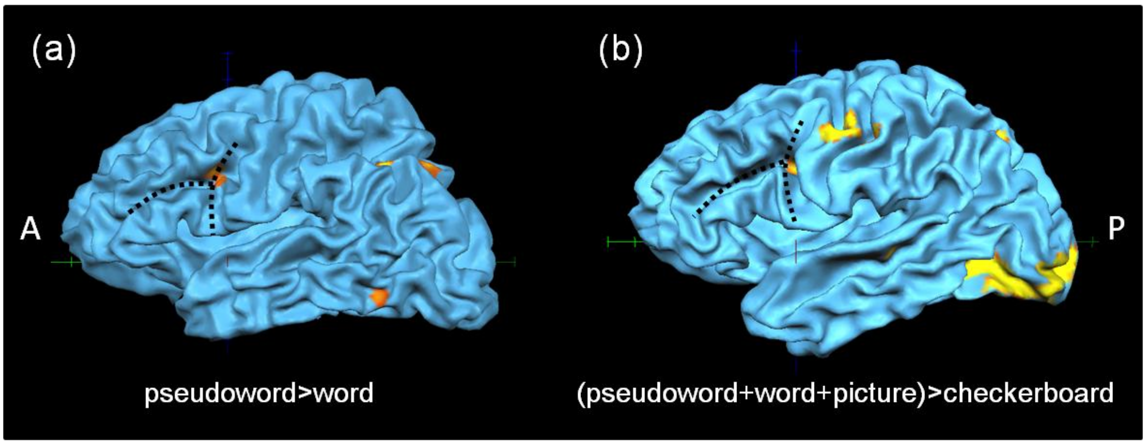


Figure 5.5 Fixed effects GLM. Activity shown at junction of inferior frontal sulcus (IFS) and precentral sulcus (PCS; dotted black lines) for two participants (*p* < .001). Results are displayed on the cortical surface reconstructions of two individual participants.

Significantly stronger activation for pseudowords than words, relating to sublexical phonological access in LIFGpo/PCG, was observed in 7/10 participants. For the remaining three participants, the contrast (words + pseudowords + pictures) > checkerboards was used to define an equivalent response in the LIFGpo/PCG region (Figure 5.5b). Closely corresponding activity was found for all participants; the peak of this activity for each individual was then marked as the target point for TMS neuronavigation. The peak of this activity fell close to the site stimulated by Schuhmann et al. (2011), which they located "superior to the apex of the vertical ascending ramus" (p. 3), at the division of pars opercularis and pars triangularis.

5.3.4.2 TMS Induced Changes in Accuracy

All incorrect, nonverbal and outlier responses were removed and data from one participant excluded from all analyses due to the high number of missing or rejected trials.

The mean error rates (including missed trials due to hesitation) were calculated for each pulse time for both the real TMS and sham stimulation, for words and pictures separately. The mean error rates were: TMS pictures = 4.5% (SD 0.9); TMS words = 0.5% (SD 0.6); Sham pictures = 3.1% (SD 0.7); Sham words = 0.8% (SD 0.7).

A three-factor, repeated-measures ANOVA of number of errors was computed in SPSS. The within-subjects factors of TMS–sham (TMS vs. sham stimulation type), stimulus (word vs. picture stimuli), and pulse time (six levels) were entered into the model. The results showed a significant main effect of stimulus, $F(1,8) = 23.77$, $p = .001$, $\eta_p^2 = .75$, and a significant interaction between stimulus and TMS–sham, $F(1,8) = 7.56$, $p = .03$, $\eta_p^2 = .49$. No other effects were significant ($F < 1.7$, $p > .17$). These results demonstrate that participants made significantly more errors to the picture stimuli, and that this difference was significantly greater under real TMS stimulation.

5.3.4.3 TMS Induced Changes in VRT

Mean VRTs were calculated for each pulse time for both stimulation and stimulus types. The means are plotted in Figure 5.6. This figure shows a large difference between the sham and TMS VRTs for the no-pulse trials for words and pictures (34 ms and 21 ms difference, respectively). Due to these large differences, the no-pulse trials are excluded from all analyses. See below for a discussion.

A three-factor, repeated-measures ANOVA of VRTs was computed in SPSS. The within-subjects factors of TMS–sham (TMS vs. sham stimulation type), stimulus (word vs. picture stimuli), and pulse time (six levels) were entered into the model. The results showed significant main effects of stimulus, $F(1,8) = 91.19$, $p < .001$, $\eta_p^2 = .92$, and pulse time, $F(5,40) = 4.83$, $p = .002$, $\eta_p^2 = .38$, but not of TMS–sham, $F(1,8) = 1.45$, $p = .26$, $\eta_p^2 = .15$. There was also a significant TMS–sham*pulse time interaction, $F(5,40) = 2.69$, $p = .04$, $\eta_p^2 = .25$. No other interactions were significant ($F < 1.5$, $p > .26$). These results show that pictures were named significantly slower than words, that the timing of pulse delivery affected VRTs, and that this was modulated by the type of stimulation applied (real vs. sham).

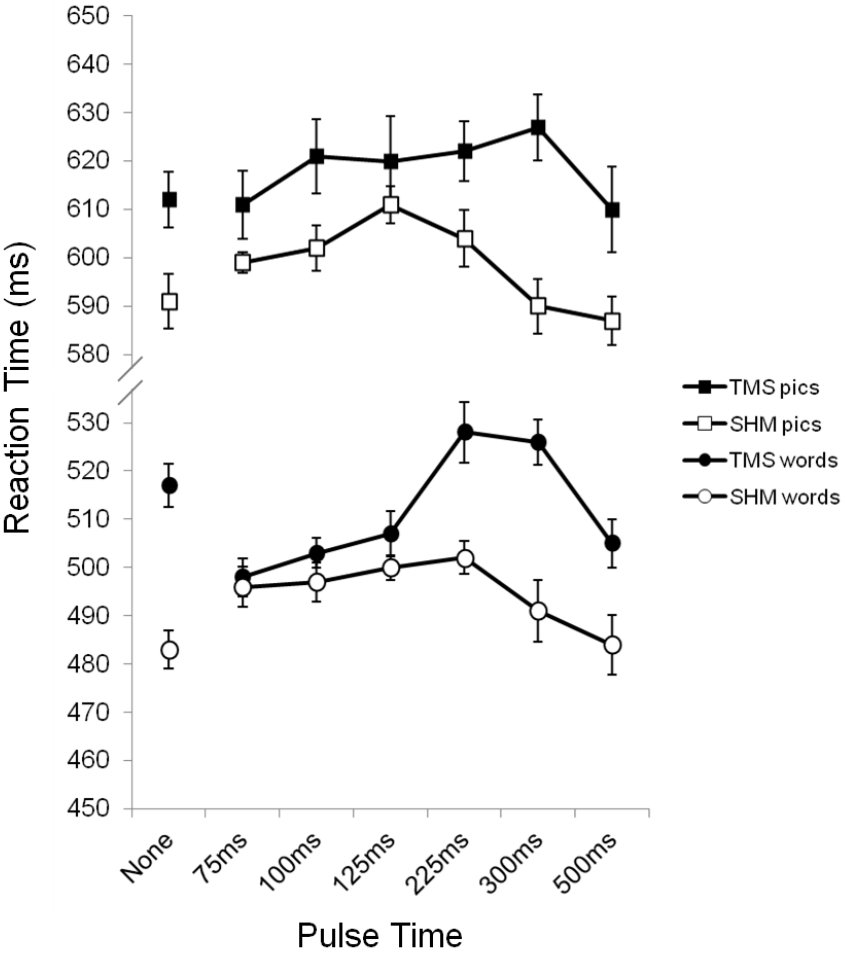


Figure 5.6 Mean VRTs for both TMS and sham conditions. Separate lines for TMS–pictures, sham–pictures, TMS–words, and sham–words. Standard errors.

A separate two-factor, repeated-measures ANOVA of VRTs for TMS stimulation was computed for the factors stimulus and pulse time. The results showed a main effect of stimulus, $F(1,8) = 75.98$, $p < .001$, $\eta_p^2 = .91$, and of pulse time, $F(5,40) = 3.36$, $p = .01$, $\eta_p^2 = .30$, but no interaction, $F(5,40) = 0.78$, $p = .57$, $\eta_p^2 = .09$. This lack of interaction suggests that words and pictures are equivalently affected by TMS pulse delivered at different times. Planned polynomial contrasts revealed a significant quadratic effect of pulse time, $F(1,8)$, $p = .008$, $\eta_p^2 = .61$. Significant pairwise comparisons are indicated in Figure 5.7 (corrected for multiple comparisons with Least Significant Difference, however, these comparisons did not survive the stricter Bonferroni correction).

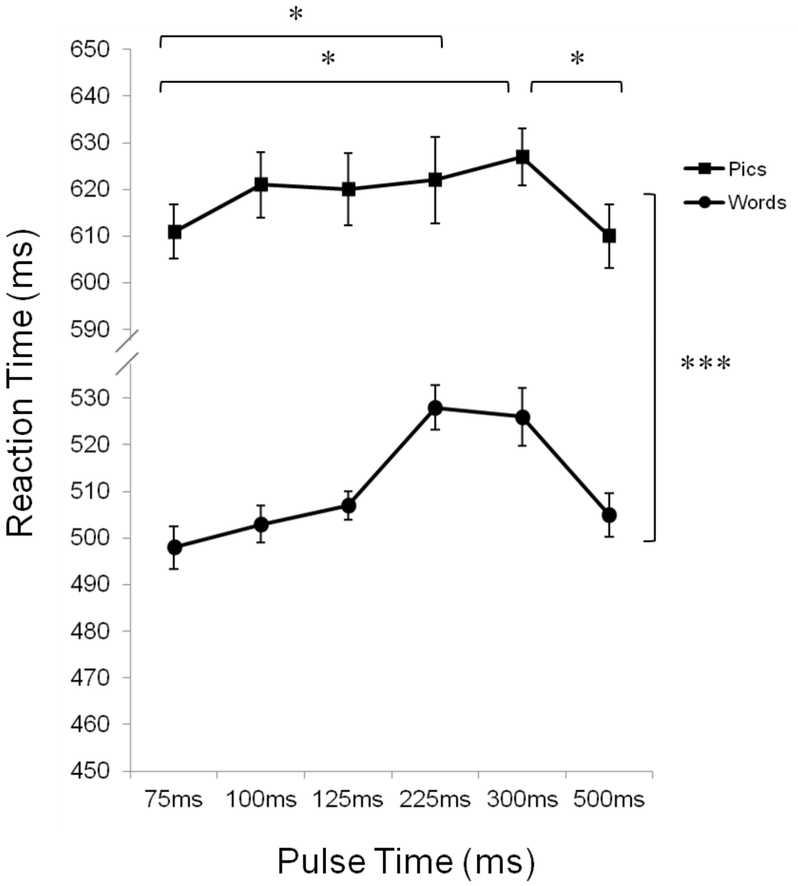


Figure 5.7 Significant pairwise comparisons for TMS words and pictures. No other comparisons were significant.

* $p < .05$, *** $p < .001$

A similar two-factor, repeated-measures ANOVA for sham stimulation was computed for the factors stimulus and pulse time. The results showed a main effect of stimulus, $F(1,8) = 60.36$, $p < .001$, $\eta_p^2 = .88$, and of pulse time, $F(2.91,23.29) = 3.96$, $p = .02$, $\eta_p^2 = .33$ [corrected for a violation of sphericity, $\chi^2(14) = 26.49$, $p < .05$], but no interaction, $F(5,40) = 0.37$, $p = .87$, $\eta_p^2 = .04$. Planned polynomial contrasts showed a small significant linear trend, $F(1,8) = 5.42$, $p = .048$, $\eta_p^2 = .40$.

5.3.5 Discussion

This study was designed to address whether LIFGpo/PCG activity observed within ~100 ms of viewing a word (Ashby et al., 2009; Ashby, 2010; Cornelissen et al., 2009; Pammer et al., 2004; Wheat et al., 2010) is necessary for successful single word reading. In native Dutch speakers, TMS was applied to LIFGpo/PCG over a range of time delays with respect to stimulus onset and compared the impact of the TMS at each time delay on the vocal reaction times for word reading and picture naming. It was predicted that for picture naming, pulse delivery at 300 ms would result in slower VRTs (Schuhmann et al., 2009; 2011). For word reading, slower VRTs were predicted for TMS pulses delivered at around 100 ms as well as at 300 ms.

As predicted, VRTs were slowest for picture naming when TMS pulses were delivered at 300 ms after viewing the picture. In addition, reaction times were slowed for pulse delivery at 225 ms. Word reading was also disrupted by pulses delivered at 225 to 300 ms after word presentation. Contrary to expectations, there was no disruption to word reading for pulses delivered prior to 225 ms. Pulses delivered between 75 and 125 ms produced no significant change to VRT or accuracy for words or for pictures. The lack of significant interaction between stimulus type and pulse time shows that the TMS effects were equivalent for both stimulus types.

The sham results showed a main effect of stimulus type, owing to the consistently faster reaction times to words than to pictures. However, the sham condition also showed a small linear effect of pulse time, relating to the slightly faster VRTs for later pulse times. This is a surprising result, as the sham condition would be expected to show no change in VRT across pulse times. This result does detract slightly from the result for real TMS stimulation, as the sham condition should be used to demonstrate that there are no non-TMS-specific effects of different pulse times due to, for example, the clicking noise of the coil when a pulse is sent. On the other hand, the shapes of the sham and TMS effects are different, suggesting that any effects during the sham condition cannot explain away the whole effect seen during the TMS condition. The sham effect will be discussed in more detail below.

The group fMRI results confirmed that LIFGpo/PCG is activated during silent reading and silent naming of the stimuli used in the TMS task. Furthermore, all participants showed activity at a closely corresponding site on the LIFGpo/PCG border, demonstrating the suitability of the stimulation site for the TMS task in all participants. However, as discussed previously, the fMRI results do not give an indication of the timing of LIFGpo/PCG involvement in word or picture recognition, and cannot be used to determine that LIFGpo/PCG is functionally necessary for the task.

The results of the current study replicate the slower VRTs of Schuhmann et al. (2009; 2011) when TMS is administered to Broca's area at ~300 ms during picture naming. This is consistent with the interpretation that Broca's area is critically involved in picture naming at ~300 ms following stimulus presentation. This study extends the work of Schuhmann et al. (2009; 2011) by showing that Broca's area activation at ~225–300 ms is also necessary for successful single word reading. In addition, the current study improved on Schuhmann et al.'s (2009; 2011) TMS target site selection procedure by using a prior fMRI task to locate the peak of phonologically related activity within the LIFGpo/PCG border for each participant.

Indefrey and Levelt's (2004) account of speech production suggests that abstract syllabification processes occur by around 330 ms after viewing either a picture or a written word. This would coincide with the slower reaction times seen here after TMS pulses were delivered at ~300 ms. Although this finding fits with Indefrey and Levelt's account of speech production, neither their model, nor the results presented here, explain how written words and pictures can activate syllabification processes at equivalent times, but then produce ~100 ms slower reaction times for pictures than for words. These findings show the slowest mean response for picture naming at 300 ms and the slowest mean response for word reading at 225 ms, though overall, VRTs at 225 and 300 ms are not significantly different from each other. It may be that pulses delivered just prior to 225 ms would have been even more effective at disrupting words, or pulses delivered just after 300 ms would have been more effective at disrupting pictures, thereby revealing a greater dissociation between the two processes, and relating more to the ~100 ms difference in VRT. Indefrey (2011) recently updated the timing estimates for word production processes, including integrating Schuhmann et al.'s (2009) finding. Indefrey (2011) now suggests that abstract phonological syllabification processes do not take place until 355–455 ms, but suggest that due to the short stimuli and short naming latencies of Schuhmann et al. (2009), syllabification might be expected to occur earlier in this case. Indefrey (2011) also concedes (contrary to Indefrey & Levelt, 2004) that subregions of IFG may have distinct roles for word production, including articulatory-motor planning aspects, rather than just abstract syllabification processes as previously argued.

The results presented in this chapter do not support the hypothesis that successful single word reading requires the involvement of LIFGpo/PCG within ~100 ms of word presentation. Following from this, three interesting theoretical interpretations will be discussed. (1) LIFGpo/PCG is not necessary for reading aloud before 225 ms at all. It may be that previously seen early LIFGpo/PCG activation, although associated with viewing written words, is not a necessary component of successful reading aloud. For example, Whitney and Cornelissen (2005) proposed that when children are learning to read, they are engaged in explicitly mapping between orthography and phonology when sounding out a new word. Hence sequential phonological representations of words are rehearsed during reading development and become strongly associated with their corresponding lexical representations. With experience and exposure to print, readers later become more able to make use of direct orthographic-to-lexical representations, removing the necessity for orthography-to-phonology mapping during successful word identification. Although no longer necessary, the strong orthography-to-phonology connections may remain, resulting in an automatic activation of a phonological representation that does not directly contribute to task performance. Alternatively, LIFGpo/PCG may indicate verbal memory activations that, although consistently activated by written stimuli (e.g., Fedorenko et al., 2011) are not necessary for the basic process of reading aloud. They may instead form the foundations of later processes, such as integrating words into sentences. For example, Nixon, Lazarova, Hodinott-Hill, Gough, and Passingham (2004) demonstrated a facilitatory effect on phonological verbal working memory using repetitive TMS to posterior LIFG. Though, their study does not rule out that these facilitations were, in fact, related to the initial encoding of the written stimuli rather than to a memory aspect. (2) LIFGpo/PCG is not necessary prior to 225 ms for reading aloud in native Dutch speakers, but is still required for readers of English. Wheat et al. (2010) and Chapter 4 demonstrated the phonological relevance of LIFGpo/PCG at ~75–100 ms during silent reading in native English speakers, but due to differences in the transparency of orthography between English and Dutch, it may be that LIFGpo/PCG is not useful for phonological access in Dutch and so is not necessary for reading until the later output processes occurring around 225–300 ms. For example, Ziegler et al. (2010) showed that in more opaque orthographies, such as English, French, and Portuguese (based on measures of orthographic entropy; Borgwaldt, Hellwig, & De Groot, 2005), phonological awareness has a greater impact on reading performance than in relatively transparent orthographies, such as Dutch, Hungarian, and Finnish. Due to the opaque orthography of English, it may also be true that conflict resolution processes are more important for English readers than for Dutch. January et al. (2009) demonstrated that LIFG is active during conflict resolution of Stroop stimuli and during resolution of syntactically ambiguous sentences in English participants. However, studies of native Dutch normal and dyslexic readers have shown no anterior activity during passive observation of incongruent letter–speech sound pairs (Blau, Van Atteveldt, Ekkebus, Goebel, & Blomert, 2009; Blau et al., 2010; Van Atteveldt, Formisano, Blomert, & Goebel, 2007). Therefore, the irregular letter–sound correspondence in English may require a more complex process in order to resolve phonological ambiguities. There are many instances in English where the same graphemes can be pronounced many ways (e.g., *hint* vs. *pint*) or where the same pronunciation arises from many spellings (e.g., *through* vs. *threw*). This may involve many simultaneous representations along a dorsal and ventral route, which are then resolved at LIFGpo/PCG. Although, if this were the case, it would call into question where and when the phonological representations are formed that are then resolved at LIFGpo/PCG. (3) LIFGpo/PCG is not necessary for reading aloud in this case where native Dutch speakers are reading high frequency words that are viewed many times. The high frequency and therefore familiar nature of the targets, combined with transparent Dutch orthography may create a situation where rapid phonological access (as hypothesised to occur at LIFGpo/PCG) may simply not be required for successful lexical access and word identification. If the word identity is solvable via an orthographic–lexical route, such as described by Coltheart et al. (2001), then successful word reading may take place in this case without early LIFGpo/PCG involvement. This option suggests possible differences in processing between English and Dutch readers, or possible variable recruitment of the reading network depending on the task constraints. Evidence for differences in language processing between Dutch and English native speakers can be found, for example, in two studies on the effects of orthography on speech production (Damian & Bowers, 2003; Roelofs, 2006). In both studies, participants learned sets of prompt–response pairs of words and were asked to produce the appropriate spoken response when presented with the written prompt. The orthographic and phonological relationship between the initial phonemes of prompt–response pairs in a block was manipulated; such pairs shared initial phoneme and letter, or just phoneme, or just letter. Damian and Bowers (2003) showed evidence of a mandatory activation of an orthographic code during speech production in English speakers. This was true even when computing orthography was not relevant, and in fact disruptive, for the task. This was demonstrated by a reaction time cost for items sharing initial phoneme but mismatched on letter (e.g., camel–kidney) In contrast, Roelofs (2006) showed that in a comparable experiment Dutch speakers did not show a disruptive effect of orthography during speech production on tasks where the orthography is not relevant. On the other hand, Brysbaert (2001) showed—using masked pseudohomophone priming—that native Dutch speakers automatically access sublexical phonology, suggesting that sublexical processes may, in fact, take place even when a word can be identified using orthographic–lexical mechanisms.

There are some methodological aspects that should be considered when interpreting the results. The single pulse TMS paradigm allows precise temporal stimulation of a specific target site. While we can be confident (based on the fMRI-guided neuronavigation) that the target site was selected appropriately, we cannot rule out the possibility that reading relevant processes were indeed taking place at the target site that were not influenced by the particular choices for pulse sequence, strength and timing. Here, a cluster of TMS pulse times around 100 ms was used in order to minimise the possibility that the processes of interest would take place at a short duration falling between our pulse times, however, it is still feasible that this has occurred. Future studies aiming to explore an early encoding role of LIFGpo/PCG could use even more pulses delivered within the early period of interest, or use double- or triple-pulse paradigms with overlapping pulse delivery times. However, choice of pulse strength and sequence may be limited due to the fact that increasing pulse strength and number of pulses applied over LIFGpo/PCG will increase the strength of the facial muscle reactions experienced by participants (Wasserman, 1998). These muscle reactions may cause discomfort, and may also make it more difficult for participants to produce a vocal response and therefore have confounding effects on VRT.

Further limitations include the difference in mean VRT across the no-pulse conditions. The purpose of the online no-pulse condition is to monitor baseline performance to the task in order to account for any nonspecific session effects, such as general fatigue. In order for this to be a useful control, the mean VRT across the TMS and sham sessions would be expected to be very similar. However, VRT appeared much slower to no-pulse trials during real TMS than during sham. This suggests an oddball-like deviation from expectation when no pulse is delivered (see also de Graaf, Herring, & Sack, 2011, for a similar occurrence), therefore making these trials an inappropriate control. The second control condition was the sham stimulation. The sham condition was expected to produce no change in VRTs over time, demonstrating that there are no disruptive effects of the TMS clicking noise or other non-TMS-specific effects. However, this was not the case, as there was a significant effect of pulse time for sham stimulation. This finding is difficult to explain but, unfortunately, may be a consequence of the small sample size of this study. Examining the individual responses to the sham conditions (see Appendix H), there does not appear to be a strong trend in sham VRTs across pulse times. Therefore, it is possible that small deviations across participants have undue influence on the sample mean. Again, this also calls into question the results from the real TMS condition. The individual results for real TMS appear more strongly disrupted across pulse time, but this effect does not appear consistent across participants. The results of Schuhmann et al. (2009; 2011) help to support the findings of the current experiment by corroborating the role of LIFGpo/PCG for naming at around 300 ms post-target. However, in general, the results of the current experiment should be viewed with caution and as a preliminary experiment of a larger study. Replication with a larger sample size would be the first necessary step to allowing stronger inferences to be made.

More speculative interpretations and opportunities for future directions include the possibility of right hemisphere compensation during TMS stimulation. For example, Hartwigsen et al. (2010) showed that four-pulse trains of 10 Hz TMS to both right and left posterior IFG disrupted phonological decisions to visually and auditorily presented words (see also Hartwigsen & Siebner, 2011, for a review). Furthermore, in the right-hemisphere hypothesis of deep dyslexia (characterised by an inability to read nonwords but preserved high-frequency word recognition) it is suggested that deep dyslexics translate print into meaning in the right hemisphere and output speech using the left hemisphere (e.g., Coltheart, 1980; Coltheart, 2000). Such an allocation of resources during the current TMS experiment would explain the lack of an early LIFGpo/PCG disruption for written words, due to the ability of a right hemisphere language system to read high frequency concrete words, along with a significant late disruption relating to speech output by the left hemisphere.

Finally, another speculative consideration is the type of neural activity that can be disrupted by TMS. Wheat et al. (2010) showed that the early LIFGpo/PCG activity reveal by MEG is induced oscillatory activity (see section 4.2.3.5). This is as opposed to the evoked responses revealed by ERP analysis, which has shown LIFGpo/PCG occurring later, at around 300 ms (e.g., Grainger et al., 2006). The timing of this evoked response fits well with the timing of the LIFGpo/PCG revealed by TMS in the current experiment. Therefore, if TMS were better suited to disrupting evoked rather than induced oscillatory responses, this might account for the lack of early effect shown here. The hypothetical interaction between TMS and the on-going evoked neural activity would be along the lines of a destructive interference between the stereotypical wave of the evoked response and a similar wave created by the TMS pulse; analogous to the interaction between two sets of ripples in a pond. For induced activity, however, there is no stereotypical wave, rather these is an increase or decrease in the power of on-going oscillatory activity. The predictable phase pattern of TMS may therefore have less effect on this non-phase-locked activity. An underlying assumption of this speculation is that TMS pulses produce a wave, rather than other noisy disruption. Evidence for this is currently sparse, however, Paus, Sipila, and Strafella (2001) administered single pulse TMS to left primary motor cortex during concurrent EEG recording. Paus et al. showed that TMS elicited a series of evoked potentials with a positive peak at 30 ms, and negative peaks at 45 and 100 ms following a single pulse. This P30/N45/N100 waveform was then followed by highly synchronised oscillatory activity in the beta frequency range and lasting for several hundred milliseconds. TMS delivered at the appropriate time may therefore interfere with similar phase-locked evoked neural responses. However, any non-phase-locked induced component may not be predictably affected by a single TMS pulse due to an inconsistent response pattern across participants and trials.

5.4 Summary

The key findings of Experiment 6 were

- Consistent LIFGpo/PCG activity to pseudowords greater than words for all participants in fMRI
- Significant disruption to vocal reaction times for both pictures and words for TMS pulses delivered between 225 and 300 ms
- No significant disruption to word reading prior to 225 ms, contrary to predictions
- No significant disruption to picture naming prior to 225 ms, in line with predictions

In conclusion, this experiment replicated the findings of Schuhmann et al. (2009) that Broca’s area is functionally relevant for picture naming from 225 to 300 ms after stimulus presentation and extending this finding to word reading. This experiment failed to show evidence for a necessary functional role of LIFGpo/PCG for word reading before 225 ms in Dutch speakers, contrary to predictions from MEG in English speakers. Further work is needed to confirm the validity of the findings from this preliminary experiment and many possibilities for future directions have arisen. Thorough investigation of the choice of TMS pulse sequence and strength and the possibility of differential effects on evoked and induced neural activity should be carried out. Following this, assuming the current pattern of results holds, further experiments are needed to tease apart the possible theoretical interpretations. Any future experiments should also be replicated in native English speakers.

Chapter 6

Summary and General Discussion

6.1 Overview

This chapter summarises and discusses the main findings from the experiments presented in this thesis. Theoretical implications of the findings are discussed and future directions are proposed.

6.2 Research Aims

Based on the evidence presented in Chapter 2, it was concluded that the specific nature of phonology representations during visual word recognition and when and where they are activated are yet to be defined in the literature. Evidence was presented in favour of a rapid (~100 ms) activation of sublexical phonology during visual word recognition at Broca's area, however, many alternative roles for Broca's area during visual word recognition have also been proposed. Therefore, the aims of this thesis were to test the hypotheses (1) that Broca's area is involved in rapid phonological access during visual word recognition, (2) that Broca's area represents sublexical phonological information, and (3) that these sublexical phonological representations play a necessary functional role in word recognition.

6.3 Summary of Research Findings

6.3.1 Chapter 3

In Chapter 3, four behavioural masked priming experiments were presented. Experiments 1 and 2 used a lexical decision task to investigate the possibility of finding sublexical phonological priming of nonword targets by homophonic nonword primes. Neither experiment found evidence for sublexical phonological priming; however, both experiments showed significant orthographic priming of nonwords, suggesting that it is possible to find some sublexical masked priming effects in English. As the intention was to investigate sublexical phonological priming in MEG, further experiments were carried out with the aim of extending this finding to phonological effects.

In Experiments 3 and 4, the task was changed to reading aloud, along with some refinements to the experimental stimuli and procedure. Both of these experiments showed significant sublexical phonological priming effects, as well as orthographic effects. The priming effect was smaller for nonwords than for words, in line with predictions by Forster et al. (2003). The difference between Experiments 3 and 4 was that in Experiment 3 word and nonword targets were presented in a mixed list, whereas in Experiment 4 word and nonword targets were presented in separate blocks. This difference resulted in significantly faster reaction times to the blocked version of the experiment, in line with the predictions of Lupker et al. (2003) and Los (1999).

6.3.2 Chapter 4

In Chapter 4 an MEG masked phonological priming experiment was presented. The significant behavioural sublexical phonological effect of Experiment 3 (mixed naming) was used as a basis for the silent reading task used in this experiment. Furthermore, all participants were pre-screened for behavioural phonological priming. This provided a strong basis for localising sublexical phonological effects using MEG. The key findings of Chapter 4 were

- A significant phonological priming advantage at LIFGpo/PCG for both words and nonwords.
- Phonological priming for words was evident by ~250 ms from word target onset.
- Phonological priming for nonwords was evident by ~75 ms from nonword target onset.
- Nonwords showed an earlier or stronger phonological priming effect than words at LIFGpo/PCG.
- A late (500–600 ms) phonological advantage was also shown for words and nonwords, implicating LIFGpo/PCG in articulatory output processes.
- The specificity of the priming effect to LIFGpo/PCG was shown by a null result for equivalent contrasts at LMOG.

6.3.3 Chapter 5

Chapter 5 presented a chronometric fMRI-guided TMS investigation of the functional relevance of LIFGpo/PCG during visual word recognition, in comparison with picture naming. The key findings of Chapter 5 were

- Consistent LIFGpo/PCG activity for all participants in the fMRI localiser task.
- Significant disruption to VRTs for both pictures and words for TMS pulses delivered at around 225–300 ms.
- No significant disruption to word reading prior to 225 ms, contrary to predictions of functional relevance of LIFGpo/PCG to visual word recognition at ~100 ms.
- No significant disruption to picture naming prior to 225 ms, in line with predictions.

6.4 General Discussion

Overall, the findings of this thesis support a role for posterior Broca's area in rapid phonological access during visual word recognition. The MEG results showed significant phonological priming at LIFGpo/PCG within ~75–200 ms in a silent reading task. This task was shown behaviourally to produce phonological priming effects, as shown by the contrast *pseudohomophone condition minus orthographic condition.* Using the same contrasts in MEG, significantly greater activity for phonological priming was found at LIFGpo/PCG within ~200 ms for real words and within ~75 ms for nonwords. This differential LIFGpo/PCG activity based on the phonological relationship between the prime and target provides evidence of the role for posterior Broca's area in rapid phonological access. No such priming was found at the LMOG control site, which was based on the only other peak of activity apparent within the 0–200 ms beamforming window.

Moreover, that a phonological advantage was shown for nonword targets indicates that the putative phonological representations at LIFGpo/PCG are sublexical in nature. The earlier advantage for nonword phonological priming than word phonological priming further suggests that LIFGpo/PCG may be particularly specialised for nonword identification via grapheme-to-phoneme mapping, and that other lexical mechanisms may contribute to the recognition of real words.

However, no evidence presented in this thesis can strongly support a necessary functional role of LIFGpo/PCG during visual word recognition. Although this region appears sensitive to phonological relationships, particularly for nonwords, MEG data are inherently correlational and therefore cannot conclusively rule out other possible functions of this activation. For example, LIFGpo/PCG has been implicated in conflict resolution (e.g., January et al., 2009; Novick et al., 2010) and verbal working memory (e.g., Fedorenko et al., 2011). Alternatively, although phonological representations may be activated in this region, they may be redundant for visual word recognition. The TMS study did not indicate a functional role for LIFGpo/PCG prior to ~225 ms, due to the lack of disruption to VRTs during reading aloud for TMS pulses delivered prior to this time. Therefore, these alternative interpretations of the MEG data cannot be ruled out.

6.5 Future Research

It is clear from the findings presented in this thesis that LIFGpo/PCG is sensitive to the phonology of written words within a very early timeframe. Other studies have shown activation within a similar brain region at similarly early timings for real words (Ashby, 2010; Ashby et al., 2009; Cornelissen et al., 2009; Pammer et al., 2004, Wheat et al., 2010). The evidence presented here now also suggests that this sensitivity is modulated by lexicality; showing a preferential response to the phonology of nonwords. However, despite this mounting evidence, what is still not clear is the functional significance of this activation.

There are a number of investigations that, based on the findings of this thesis, appear critical to understanding the role of LIFGpo/PCG, prior to ~200 ms, during visual word recognition. First, the possibility of differences between native Dutch and native English readers must be investigated. The MEG paradigm presented here must be replicated in Dutch and the TMS study must be replicated in English before strong theoretical interpretations of the data can be proposed. For example, whether or not the early LIFGpo/PCG response is apparent in MEG during visual word recognition in Dutch has implications for whether TMS of this region in Dutch could be expected to influence behaviour. Similarly, whether or not the TMS finding can be replicated in English is important before the possibility of a functional role of LIFGpo/PCG can be ruled out with more confidence. There are a number of possible combinations of outcomes from this line of investigation, as outlined in Table 6.1. The following discussion of these possibilities assumes that sufficient improvements have been made to the TMS experiment so that the results can be relied upon with reasonable confidence. For example, as discussed in Chapter 5, the choice of pulse timing and sequence could be changed to cover the entire period of interest with overlapping pulse trains, in an extension of the triple-pulse TMS design used by Schuhmann et al. (2009; 2011). Furthermore, as the current line of investigation is particularly interested in visual word recognition, rather than picture naming, future experiments might replace the picture condition with a nonword reading condition. The inclusion of a nonword reading condition might improve the chances of disrupting processes at LIFGpo/PCG that are necessary for nonword reading but that can be bypassed by high frequency real words. The chronometric investigation of picture naming has been thoroughly investigated by Schuhmann and colleagues and it would make the experiment unfeasibly large to use words, nonwords, and pictures. Therefore the picture condition would not need to be replicated. However, if any early disruption was found for words or nonwords, post-hoc confirmation that similar disruption could not be achieved for pictures under identical conditions would be prudent.

6.5.1 Outcome A: Replication in Both Languages

Outcome A in Table 6.1 refers to the simplest outcome, and the most beneficial for the hypotheses of this thesis. This outcome would be that Dutch participants show a similar early phonological priming pattern in MEG that is localised to LIFGpo/PCG for words and nonwords. In this case, it would be predicted that Dutch and English participants would behave similarly in TMS. Therefore, it would be hypothesised that both English and Dutch participants would show an early (<200 ms) behavioural disruption to reading aloud in line with the hypotheses of this thesis. The TMS experiment presented in Chapter 5 has not yet ruled out this possibility, due to the limitations discussed previously (e.g., small sample size, choice of pulse sequence). Finding this TMS disruption in both Dutch and English participants would be strong support for a necessary role for LIFGpo/PCG during the early stages of visual word recognition.

Table 6.1

Outcomes of MEG and TMS Replication in Dutch and English

	DUTCH			
ENGLISH	MEG = yes*		MEG = no*	
MEG = yes	TMS = yes[†]	TMS = no[†]	TMS = yes[†]	TMS = no[†]
TMS = yes[†]	A Functionally necessary in Dutch and English	B Functionally necessary in English only	C	D Present and functionally necessary in English only
TMS = no[†]	E	F Never functionally necessary for encoding **or** not disruptable with TMS	G	H Present in English only but not functionally necessary

*MEG = yes / no refers to the presence of absence of phonological priming at LIFGpo/PCG prior to 200 ms

[†] TMS = yes / no refers to the presence or absence of disruption to VRTs prior to 200 ms during reading aloud

6.5.2 Outcome B: Same MEG but Different TMS

The interpretation becomes more complicated under the possibility that Dutch and English participants show similar MEG priming, but deviate with respect to their TMS results. In other words, this possibility takes into account that the current TMS results may hold for Dutch participants, but investigations in English may reveal an early word reading disruption. This outcome would imply that although LIFGpo/PCG is universally sensitive to sublexical phonology, English, but not Dutch, readers require this information for visual word recognition. Differences in the orthographic opacity of the two languages might result in this difference. Due to the presence of many heterographic homophones (e.g., *through* vs. *threw*) and homographic heteronyms (e.g., to *close* the door vs. come *close* to me), English may require a more complex visual word recognition process that relies on the information provided by LIFGpo/PCG in order to settle on the appropriate pronunciation for a word, whereas the more regular orthography of Dutch may mean other mechanisms are able to compensate for the loss of phonological information from LIFGpo/PCG.

6.5.3 Outcome D: Different MEG and Different TMS

It may happen that no LIFGpo/PCG activity is found for Dutch participants in MEG and the current pattern of TMS results hold in Dutch. In this case, if an early disruption were found for English participants a functional role of LIFGpo/PCG in English would be apparent that does not occur in Dutch. An interpretation based on the difference in opacity of Dutch and English orthography would be likely in this case, similar to Outcome B, above. This outcome would open up a research line comparing various levels of orthographic opacity in MEG and TMS and would have significant implications for models of visual word recognition. In this case, models of reading based on English data could not necessarily be considered applicable to languages with a more transparent orthography.

6.5.4 Outcome F: Same MEG, Same TMS

This outcome considers the possibility that, even though the MEG results are replicated in Dutch, neither Dutch nor English participants show any early disruption during TMS. The two general interpretations for this would be, firstly, that LIFGpo/PCG is not necessary for reading aloud in either language, or secondly, that LIFGpo/PCG is not disruptable with TMS. This outcome would require in depth investigation of the possible interpretations discussed in Chapter 5. For example, the first step would be to investigate whether induced oscillatory activity, of the kind seen in the MEG experiment, could be disrupted with TMS. If this could be established, a line of research would open up to ascertain whether early LIFGpo/PCG activity might contribute to any task, such as those with a strong conflict resolution or verbal working memory component. The phonological masked priming task might also be performed under TMS in order to verify that early LIFGpo/PCG activity does, in fact, result in the behavioural phonological advantage seen during overt naming.

6.5.5 Outcome H: Different MEG but same TMS

This outcome considers the possibility that Dutch participants may not show LIFGpo/PCG activity in MEG, and neither language may show an early TMS disruption. In this case, a likely interpretation would be along the lines of redundant LIFGpo/PCG activity in English due to the nature of learning to read a language with a more opaque orthography. On the other hand, as in Outcome F, it would need to be established that early LIFGpo/PCG activity does not contribute significantly to conflict resolution or verbal working memory tasks. A difference in the disruption of these tasks in Dutch would then need to be verified. However, this would call into question where these types of activities took place in Dutch, or why they were less relevant for reading in Dutch.

6.5.6 Outcomes C, E, and G

It is considered unlikely that replication of the TMS experiment using an improved design and a larger sample would reveal early disruption to visual word recognition in Dutch that cannot then be replicated in a native English sample (Outcomes E and G). It would be very difficult to interpret such results if they arose. Multi-region TMS to the networks of Dutch and English readers would be necessary to investigate divergence and convergence of the two reading systems.

Outcome C, that Dutch and English readers would show the opposite pattern of TMS and MEG results, is also considered unlikely. In other words, if Dutch participants show no early LIFGpo/PCG in MEG, then it is not predicted that Dutch readers would show an early TMS effect at this region, but English readers would not.

6.5.7 Summary

Many interesting interpretations arise from the possible combinations of outcomes that would be predicted for a replication of the MEG and TMS experiments described in this thesis in a native Dutch and native English sample. All of these outcomes would result in further lines of research into the possible behaviour of the underlying reading system of the brain.

6.6 Implications

6.6.1 Connectivity of the Visual Word Recognition Network

Notwithstanding the need for further investigations into the replicability of these results within and across languages, the implications of the current results will be considered. The current pattern of results is suggestive of a highly complex and interactive network. For example, LIFGpo/PCG appears to be sensitive to the sublexical phonology of written words as early as ~75 ms after stimulus presentation. Furthermore, it appears that the reading system differentially processes words and nonwords within this rapid timeframe. This suggests possible feedforward and feedback connections operating rapidly to shape the network for the appropriate type of processing. Revealing this rapid connectivity may be beyond the scope of whole-brain MEG analyses (as revealed by the limited spread of activation averaged across the first 200 ms in Chapter 4). However, recent investigations using time sensitive effective connectivity measures, suggest that it may be possible to reveal early parallelisation of the visual word recognition network within the first 100 ms of viewing a word. For example Lobier et al. (2011; also, Munding, 2011; Quinn, 2011) reported an MEG experiment where single word reading was used with a one-back repetition identification task. Here, partial directed coherence (PDC; Baccalá & Sameshima, 2001) was used as a measure of Granger causality in order to investigate the partial influence of brain regions on other brain regions. The results suggest that within 100 ms, changes in PDC are already evident between many putative nodes of the reading network. Notably, PDC also increases from LMOG to LIFG by around 200 ms, with no increase in connectivity in the other direction, though the results are unable to rule out the influence of a third node on both these regions that might account for this apparent connectivity.

Further, evidence for this possible early interactivity of the reading network comes, for example, from Penolazzi, Hauk, and Pulvermüller (2007), who used highly probable and less probable pairs of words in sentences to show an effect of word frequency and of context probability in parallel at around 120 ms from target word onset. The authors suggested that this near-simultaneous lexical access and context integration shows evidence for parallel rather than sequential stages of visual word recognition. Pulvermüller, Shytrov, & Hauk (2009) also demonstrated using EEG data that phonological, lexical and semantic features of words are extracted and integrated with the semantic and syntactic context in parallel processes occurring within 100 and 200 ms of viewing a word. Pulvermüller et al. (2009) suggested that from around 200 ms, second-order cognitive processes then take place, such as semantic reanalysis.

Interactivity is also apparent in fMRI evidence of top-down modulation of activity at vOT. For example, Twomey, Duncan, Price, and Devlin (2011) showed that vOT activity during lexical decision could be modulated by the type of task (orthographic vs. phonological lexical decisions) and the type of stimuli (words, pseudowords, and pseudohomophones), with a significant task*stimuli interaction that is difficult to explain in terms of a purely feedforward account of visual word recognition. Semantic modulation (Devlin et al., 2006) and phonological modulation

(Hellyer et al., 2011) of vOT activity also support this account of interactivity, despite the inherent lack of temporal information in these fMRI data.

The interactivity and parallelisation of the visual word recognition network does not relate well to feedforward modular cognitive models (e.g., DRC; Coltheart et al., 2001), but is indicative of the type of cortical organisation suggested by interactive or dynamical system models. According to this approach, the dynamics of word recognition are characterised by a connectionist network; such as the PDP or triangle family of models (introduced in section 2.2.2 ; e.g., Harm & Seidenberg, 2004; Plaut et al., 1996; Seidenberg & McClelland, 1989). Here, two phases of processing occur in response to seeing a word; first, changes in the pattern of activation between nodes of the network settle into an "attractor state" that represents the properties of the word, distributed across the network; secondly, and at a slower timescale, the strengths of connections between nodes are adjusted via a learning process (Rueckl, 2002). This self-organising pattern of learning via exposure can occur both on a long and short timescale, with the shortest timescale accounting for priming effects due to the adjustment of the weightings of recently activated connections, so that on subsequent activations the system is able to respond faster and more accurately (Rueckl, 2002).

Investigations into this possible parallelisation of the reading network, in particular the choice of signal processing methods (such as PDC), should take into account the physiology of neuronal communication: Averaging MEG and EEG data over windows even as small as 100 ms may result in a loss of information that can only be revealed by methods such as single- and multi-unit recording and local field potentials. For example, Liu, Agam, Madsen, and Kreiman (2009) recorded intracranial field potentials from 912 electrodes, distributed across the occipital, temporal, frontal, and parietal lobes of 11 patients (implanted for the purpose of surgical evaluation of severe epilepsy). Patients viewed pictures of objects from different categories while intracranial field potentials were recorded. Of the 111 (12%) of electrodes that showed a selective category response, the majority were found in ventral occipitotemporal cortex. A classifier was then able to decode the object category viewed on a single trial as early as 100 ms after stimulus presentation. The results of Liu et al. demonstrate two important principles; first, that within 100 ms in the human brain sufficient processing has already taken place that can allow the category of an object to be revealed, and secondly, that intracranial recording can reveal patterns of activation specific to an individual trial. Information from individual trials is not usually examined with MEG or

EEG due to the much lower signal-to-noise ratio (though, various methods have been used to examine single-trial ERPs, e.g., Quiroga & Garcia, 2003). Physiological methods with a much higher local spatial and temporal resolution should therefore also be used to inform theories of visual word recognition that tend to be based on the more general view of the system provided by fMRI, EEG, and MEG. Similarly, theories regarding the pattern of spatial communication between areas should relate to the viable anatomical connectivity between these regions, such as evidence from diffusion tensor imaging (DTI) and diffusion spectrum imaging (DSI). For example, Friederici (2009) reviewed the white matter fibre tracts (as revealed by DTI and DSI) connecting language-implicated regions of the temporal and frontal cortices; in particular, suggesting that a connection between posterior Broca’s area and posterior superior temporal gyrus is crucial for human language ability. This was supported by the finding that primates which are unable to process hierarchically structured sequences do not possess this connection (Friederici, 2009).

6.6.2 The Nature of Phonological Representation at LIFGpo/PCG

The final issue to be considered is the way in which this putative sublexical phonology at LIFGpo/PCG might be represented. Wheat et al. (2010) argued that these representations are formed via a sublexical articulatory code, citing evidence from electrical stimulation tract tracing in patients (Greenlee et al., 2004). Greenlee et al. recorded evoked responses in the orofacial representation of PCG in response to electrical stimulation of LIFG, demonstrating functional connectivity between these two regions. Brown et al. (2008) also demonstrated activity of this region during articulatory movements in fMRI. Two lines of evidence then stem from the known articulatory role of LIFGpo/PCG territory, in support of a sublexical articulatory phonological representation of visually presented words.

The first line of evidence comes from theories of embodied cognition. The central viewpoint of embodied cognition asserts that cognitive processes are rooted in the body’s interactions with the world (Wilson, 2002). One general principle of embodied cognitive theory is that the purpose of cognition, in evolutionary terms, is action (Wilson, 2002). For example, visual perception of an object seen in a particular orientation facilitates subsequent performance on a grasping task when the two objects match in orientation (Craighero, Fadiga, Umiltà, & Rizzolatti, 1996). In other words, the visual input primes the motor system for activation. Single unit recording in macaque monkeys has shown that motor neurons that respond during grasping movements also respond when a monkey looks at a graspable object, even when no action is performed (Rizzolatti et al., 1988). Furthermore, so-called “mirror-neurons” have been observed which are active both when monkeys make goal directed movements and when monkeys observe these movements being performed (Rizzolatti et al., 1996). The implication is a hard wired shared representational network for action and perception, stemming from the observation and imitation of the behaviour of others (Meltzoff & Decety, 2003). When observing both lexical and nonlexical lip movements, in PET, participants show activity in LIFG that is greater for lexical lip movements (Paulesu et al., 2003). Taken together, these studies start to form the picture that the representation and understanding of observed actions takes place via the neurons used to perform those actions, and that this theory might extend to speech. The motor theory of speech perception thus postulates that the motor cortex is involved in processing the auditory information from speech (Liberman & Mattingly, 1985; see also, Pulvermüller et al., 2006); in other words, that speech sounds are mapped onto their corresponding motor (i.e., articulatory) representations. Although, more moderate views emphasise auditory processing in speech perception, whilst accepting that speech perception and production are linked, especially during language development (see e.g., Scott & Johnsrude, 2003) and evidence from aphasia shows a dissociation between deficits of speech comprehension and deficits of speech production (see e.g., Scott, McGettigan, & Eisner, 2009).

The second line of evidence then comes from the idea that reading and speech production may be intricately linked via the process of learning to read, by sounding out words and by reading aloud to an adult (Kujala et al., 2007). Furthermore, Dehaene and Cohen (2011) discussed the idea of a “neuronal recycling” process, whereby existing cortical systems are reused and reorganised in order to represent written words. Therefore, returning to the suggestion of an articulatory-motor representation of sublexical phonology during visual word recognition, these existing speech-motor representations, used in both producing and understanding speech (due to learning via the imitation of others), are then recycled during the process of learning to read, resulting in an articulatory-motor representation of what (in alphabetic writing systems) is, essentially, written speech.

6.7 Conclusion

The results presented in this thesis indicate an early sensitivity to sublexical phonological information at LIFGpo/PCG during silent reading of English. The present experiments have failed to demonstrate that this region is functionally necessary for reading aloud prior to 200 ms in Dutch. The combination of these findings leads to many possible interpretations, which cannot be ruled in or out without further investigation. As yet, the functional significance of this activation, therefore, remains unclear.

Appendix A

Full Behavioural Stimulus List

WORD	Pseud	Orth	NONW	Pseud	Orth
ABOUT	abowt	abopt	AHAIN	ahayn	ahaln
ABSENT	abcent	abrent	AHEED	aheid	ahend
ACID	asid	apid	AITER	aeter	anter
ACTOR	aktor	astor	ALIM	alym	alam
ADORE	adorr	adork	ANGEW	angeu	anged
AFFECT	affekt	affest	BANTS	bantz	banty
AGILE	ajile	anile	BOCUS	bokus	bofus
AIRWAY	aerway	aurway	CABON	kabon	sabon
ARENA	arina	arona	CAINK	cainc	cainp
BAIL	bayl	barl	CALLO	kallo	mallo
BEIGE	baige	boige	CANOL	kanol	panol
BIRCH	burch	borch	CAREET	kareet	nareet
BLEAK	bleik	blerk	CEIFY	seify	heify
BLOW	bloe	blop	CILD	sild	hild
BLOWN	bloan	bloin	CIVEN	siven	biven
BRAIN	brayn	brarn	CIVIB	sivib	vivib
BREW	bruw	braw	CLAFF	klaff	plaff
BRIBE	brybe	brobe	CLAINK	clainc	clainp
BRIEF	breef	broef	CLYMP	climp	clemp
BURST	berst	barst	COIG	coyg	corg
BURY	bery	bory	COPST	copzt	copat
CADET	kadet	madet	COUNKY	cownky	colnky
CAMEO	kameo	bameo	COUPOX	coopox	colpox
CANAL	kanal	hanal	CROOG	kroog	proog
CASUAL	cazual	caqual	CUNIC	cunik	cunie
CENTRE	sentre	rentre	DIMPER	dymper	domper

CEREAL	cireal	coreal	DINIM	dynim	dunim
CHEEK	cheak	cheuk	DORIN	doryn	dormn
CHIVE	chyve	cheve	DRIVEG	dryveg	draveg
CIRCUS	cercus	corcus	DUAF	dwaf	diaf
CITRUS	sitrus	hitrus	EANCE	eanse	eange
CIVIL	sivil	bivil	FACEM	fasem	fadem
CLEAN	klean	plean	FEEPLY	feaply	femply
CLEAR	cleer	cleur	FEVY	fevi	fevo
CLEFT	kleft	sleft	FEYTER	fayter	foyter
CLUNG	klung	plung	FICKY	fikky	firky
COLUMN	columm	colump	FIECE	feece	frece
COMET	komet	fomet	FLAIG	flayg	flarg
COOKIE	cookiy	cookip	FLEACH	fleech	fleych
COUCH	cowch	corch	FLOAK	floac	floam
CRISP	krisp	trisp	FOGRY	fogri	fogre
CROOK	krook	frook	FRENK	frenc	frene
CROWD	croud	crond	FRIT	fryt	frut
CRUST	krust	grust	GANIC	ganik	ganim
CURSE	kurse	lurse	GASLY	gazly	gaply
DEAF	deff	deif	GECTO	gekto	geito
DECADE	dekade	deyade	GEPTIC	geptik	geptil
DECAY	dekay	denay	GIEBE	geebe	gnebe
DISMAL	dysmal	dosmal	GIECA	gieka	giela
DIVERT	divurt	divart	GLACK	glakk	glask
DOUBT	douwt	doust	GLEAF	gleef	gleff
DRINK	drynk	dronk	GLING	glyng	glong
DROWN	droun	dromn	GOISE	goize	goime
DWARF	dwarv	dwarn	GROOS	grooz	grook
EDIT	edyt	edat	GUIRE	gwire	gaire
ELBOW	elboe	elbox	GUOL	gwol	geol
EMPTY	empti	empth	HANTY	hanti	hanth
ENGINE	enginn	engino	HEASH	heesh	helsh
EPIC	epik	epin	HEASY	heazy	heaby
EQUIP	eqwip	eqsip	HERGE	herje	herme

ERASE	eraze	erale	HODGY	hodjy	hodzy
EXACT	exakt	exast	HOGGY	hoggi	hogga
EXCEPT	ekcept	elcept	HOYLE	hoile	hoole
FANCY	fansy	fangy	HYCKLE	hickle	hockle
FENCE	fense	fende	ICORN	ikorn	idorn
FILM	fylm	falm	INCER	inser	inger
FLICK	flyck	fluck	INKO	inco	inlo
FLOUR	flowr	floar	IRIM	irym	irom
FOIL	foyl	forl	JALM	jarm	jaum
FRAUD	frawd	fraed	JEEDS	jeads	jends
FREE	frea	frem	KANCE	kanse	kanke
FROWN	froun	frozn	KEANS	keens	kelns
FRUIT	fruut	frunt	KINIS	kynis	kanis
FUDGE	fudje	fudle	KOLP	colp	solp
GARLIC	garlyc	garloc	KORIC	korik	korit
GLUE	gluw	gluf	KOSSY	cossy	nossy
GREW	gruw	graw	KROLP	crolp	srolp
HAIL	hayl	haal	LAINY	laini	laind
HEAVY	hevvy	hervy	LAULT	lawlt	lailt
HEDGE	hedje	hedre	LAYMAT	laimat	lammat
INCOME	inkome	inrome	LEACY	leecy	lebcy
JAUNT	jawnt	jasnt	LENIAL	leniel	lenirl
JOUST	jowst	jorst	LOEGS	loegz	loegy
KNEEL	kneal	knetl	LOKELY	lokeli	lokelt
KNEW	gnew	enew	MACLY	macli	macle
KNIFE	knyfe	knafe	MANTS	mantz	manty
LEASH	leesh	leosh	MASEL	mazel	manel
LEGEND	lejend	lebend	MASPIE	mazpie	madpie
LILAC	lilak	lilag	MASUAL	mazual	macual
LIMB	limm	limy	MEVY	mevi	meva
LIST	lisd	lisk	MINTEL	myntel	muntel
LOCAL	lokal	lopal	MITTY	mitti	mitta
LOCATE	lokate	lomate	MODGE	modje	modse
LOCUS	lokus	lowus	MUGIC	mujic	muxic

LOGIC	logyc	logac	MURIST	muryst	murost
LOGIC	lojic	loxic	MYRAL	miral	maral
LOUNGE	lownge	loinge	NAITER	nayter	nalter
MASCOT	maskot	masoot	NAIZE	naise	naibe
MERGE	merje	merne	NEAF	neif	necf
MILK	mylk	malk	NEEF	neaf	nelf
MIMED	mymed	momed	NERM	nirm	narm
MINT	mynt	mant	NERTEX	nirtex	nortex
MOCHA	mocka	mocua	NOFFEE	noffie	noffle
MOIST	moyst	monst	NOSAL	nozal	nopal
NASAL	nazal	nalal	NULSE	nulce	nulle
NOUN	nown	nomn	OLOK	oloc	olop
NUDGE	nudje	nudue	OPINY	opyny	opuny
OBJECT	objekt	objest	ORDI	ordy	ordo
OLIVE	olyve	olove	ORLOE	orlow	orlod
OUTER	owter	oster	OUNCH	ownch	olnch
OVEN	uven	yven	PABSE	pabze	pable
PALM	parm	paim	PAILOR	paylor	paslor
PAUSE	pauze	paure	PAREA	paria	parga
PEANUT	peenut	pernut	PASMA	pazma	pamma
PENCIL	pensil	penoil	PASMY	pazmy	paimy
PIANO	pyano	phano	PEVIL	pevyl	pevol
PINK	pynk	ponk	PHEEM	pheam	phelm
POINT	poynt	poant	PHEN	fhen	shen
POSER	pozer	poger	PIAM	pyam	pham
POUCH	powch	polch	PIEF	peef	pref
POUND	pownd	polnd	PINEW	pineu	pinex
PRIDE	pryde	prade	PINKON	pincon	pindon
PURSE	perse	porse	PISMIL	pizmil	piamil
QUARTZ	quarts	quarty	PLICE	plyce	pluce
QUASH	kuash	duash	PLUR	pler	plar
QUASH	qwash	qiash	POUNK	pownk	polnk
QUEEN	quean	quern	PREK	prec	pren
QUIZ	cuiz	luiz	PRUNCE	prunse	prunle

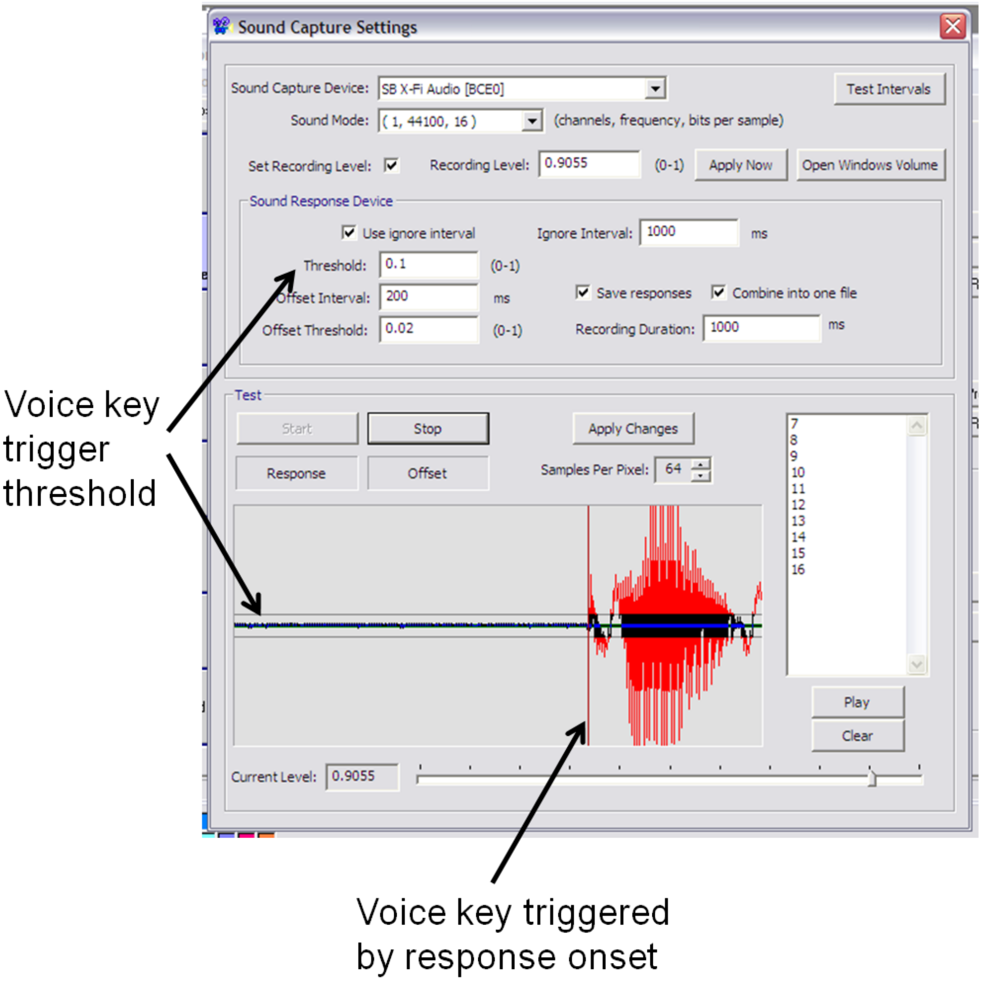
REALM	rellm	reulm	PRYSH	prish	prash
RECORD	rekord	relord	PUNPY	punpi	punph
RESIN	rezin	remin	PURSAR	persar	porsar
RHYME	rhime	rhome	PUSIL	pusyl	pusol
RINSE	rince	ringe	QUAIM	cuaim	buaim
RISK	risc	riss	QUENT	cuent	puent
ROSE	roze	rore	QUERM	quirm	quorm
SAUCE	sawce	samce	QUMID	cumid	numid
SAUNA	sawna	sarna	RARKLY	rarkli	rarkld
SCARF	skarf	starf	RAVIL	ravyl	ravol
SCOPE	skope	spope	REASH	reesh	rensh
SCRAP	skrap	sprap	RESULE	rezule	regule
SCRAWL	skrawl	shrawl	RHISH	rhysh	rhosh
SCREW	skrew	sprew	RISET	rizet	riget
SENSE	sence	senge	RITAL	rytal	retal
SHEEN	shean	sheon	RUCKY	rukky	rulky
SHOE	shoo	shox	RURD	rerd	rard
SILK	silc	sila	SAIRG	saerg	saurg
SILVER	sylver	salver	SCARO	skaro	sharo
SING	syng	seng	SCRAD	skrad	shrad
SLEEP	sleap	slenp	SHUET	shwet	shret
SLEET	sleat	sleut	SHUNKY	shunki	shunkt
SLICE	slyce	sloce	SHYME	shime	shume
SMALL	smaul	smail	SIPRIN	ciprin	viprin
SMIRK	smerk	smark	SKIRB	skerb	skarb
SNEAK	sneek	sneck	SLASM	slazm	slarm
SOAK	sowk	solk	SLINT	slynt	slont
SONIC	sonyc	sonac	SNEAF	sneef	snelf
SOUND	sownd	soind	SNING	snyng	snung
SPICE	spise	spige	SOULE	soole	sorle
SPIKE	spyke	spuke	SOUST	sowst	sonst
SPILT	spylt	spolt	SPEE	spea	spem
SPOUT	spowt	spoct	SPRIN	spryn	spran
SQUAD	squod	squed	STRECT	strekt	strert

STEAK	steyk	stenk	SWOUT	swowt	swont
SWAMP	swomp	swimp	TEWL	teul	terl
SWILL	swyll	swall	TEWSE	teuse	telse
SWIRL	swurl	swarl	THAFT	thafd	thafe
SWITCH	swytch	swetch	THAWK	thauk	thask
SYRUP	sirup	sorup	THITE	thyte	thate
TACTIC	tactyc	tactac	TISAL	tizal	tigal
TAUNT	tawnt	tarnt	TOUSH	toosh	tonsh
TEACH	teech	terch	TRAIX	trayx	tralx
TEASE	teaze	teape	TRASK	trasc	trasm
TENSE	tence	tenge	TRISK	trisc	trism
THINK	thynk	thonk	TUINT	twint	thint
THINK	thinc	thinn	TWIFT	twyft	twuft
THIRST	therst	thorst	TWIK	twyk	twak
THRIFT	thryft	throft	UNCE	unse	unle
TONIC	tonik	tonif	UNKY	unki	unkt
TOXIC	toxik	toxie	UREAM	ureem	urelm
TRIP	tryp	trop	URIME	uryme	urome
TRUCE	truse	truve	UTCER	utser	uteer
TUNIC	tunik	tunil	VEARER	veerer	verrer
TURBO	tirbo	tarbo	VERK	virk	vark
TWIST	twyst	twost	VERKY	virky	vorky
TYPE	tipe	tope	VIGIT	vigyt	vigot
ULCER	ulser	ulver	VIRTY	verty	vorty
URGENT	urjent	urment	VORCE	vorse	vorle
VACANT	vakant	vagant	VORRY	vorri	vorro
VICAR	vikar	vifar	VOUP	voop	voip
VIDEO	vidio	vidoo	VUNISH	vunysh	vunosh
VIEW	viuw	viow	WACKLE	wakkle	warkle
VISIT	vizit	vigit	WECS	wecx	wech
WHISK	whisc	whism	WIMER	wymer	womer
WISE	wize	wime	YARSE	yarze	yarte
WORTH	wirth	warth	YAUNA	yawna	yalna
WOUND	woond	wornd	YEARY	yeery	yemry

WRIST	wryst	wrast	YISK	yisc	yish
YELLOW	yelloh	yellok	ZEEK	zeak	zeck
YIELD	yeeld	yueld	ZENE	xene	yene
YOUTH	yooth	yonth	ZIABLE	zyable	zoable

Appendix B

Voice Recording



Sound Capture Device: SB X-Fi Audio [BCE0]

Sound Mode: (1, 44100, 16) (channels, frequency, bits per sample)

Set Recording Level: ☑ Recording Level: 0.9055 (0-1)

Sound Response Device

☑ Use ignore interval Ignore Interval: 1000 ms

Threshold: 0.1 (0-1)

Offset Interval: 200 ms

Offset Threshold: 0.02 (0-1)

☑ Save responses ☑ Combine into one file

Recording Duration: 1000 ms

Samples Per Pixel: 64

Current Level: 0.9055

Voice key trigger threshold

Voice key triggered by response onset

Figure B.1 Screenshot of voice key calibration procedure. Each participant was given a list of words to speak aloud while the input volume was adjusted until the onset of each word consistently triggered the voice key. If necessary, the voice key trigger threshold was also adjusted to make it more or less sensitive. There will have been variation in the effectiveness of the voice key for stimuli with liquid or fricative onsets; however, this will have been a constant source of variability across the conditions, due to the repetition of targets across conditions. In other words, no condition contained targets that would have set off the voice key less effectively than for another condition.

Appendix C

Individual Variability of Exp. 3

	Word			Nonword		
Participant	Pseud	Orth	**Priming**	Pseud	Orth	**Priming**
1[‡]	409	432	**23**	478	472	**-6**
2	359	371	**12**	390	395	**5**
3	380	405	**25**	442	454	**12**
4	286	298	**12**	315	330	**14**
5	356	375	**19**	405	416	**11**
6	383	400	**17**	401	425	**24**
7	645	672	**26**	726	727	**1**
8	348	361	**13**	381	394	**12**
9[‡]	477	487	**10**	541	520	**-21**
10	444	458	**14**	523	535	**13**
11	400	439	**39**	450	472	**21**
12[†]	567	555	**-12**	603	626	**23**
13[‡]	737	767	**30**	788	783	**-5**
14	466	479	**13**	512	522	**10**
15	393	409	**16**	473	482	**9**
16[¥]	488	492	**4**	515	515	**0**
17[†‡]	558	547	**-10**	615	604	**-11**
18[¥]	519	531	**12**	571	571	**0**
19[‡]	445	463	**18**	471	468	**-4**
20	412	430	**18**	449	468	**20**
21[‡]	450	466	**16**	518	507	**-11**
22	382	392	**10**	423	447	**24**
23	479	505	**26**	565	598	**33**
24[‡]	579	581	**1**	608	595	**-12**

[†] Negative priming words, [‡] Negative priming nonwords, [¥] No priming nonwords

Appendix D

Artefact Rejection

The first stage of artefact rejection is an overview of all epochs for one participant. In this view, any epochs with unusually large amplitudes can be removed. For example, in Figure D.1, epochs 171 and 172 have been highlighted for removal. These epochs are contaminated by a large artefact such as a car moving close to the building. After any particularly large artefacts have been removed, the next stage is to examine each remaining epoch individually. Figure D.2 shows the view of all channels for a typical epoch, with target onset at time 0. This epoch has been contaminated by blinking as shown by a stereotypical crossover shape (circled) that is particularly strong in the anterior channels. This trial would be rejected. Finally, Figure D.3 (left) shows a portion of typical clean data, compared to data that have been contaminated by muscle movement in Figure D.3 (right). In the case of Figure D.3 (right), this artefact appears to have the stereotypical shape of a swallow.

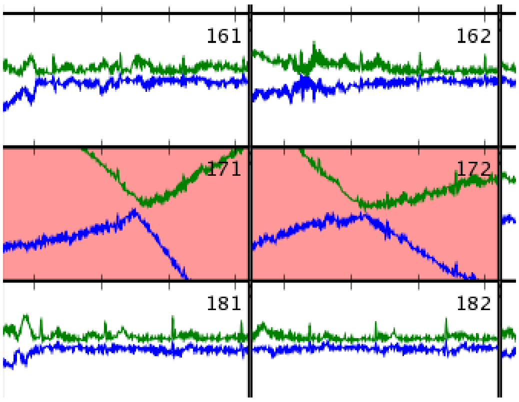


Figure D.1 First pass artefact rejection. Any particularly large artefacts are removed during this first stage.

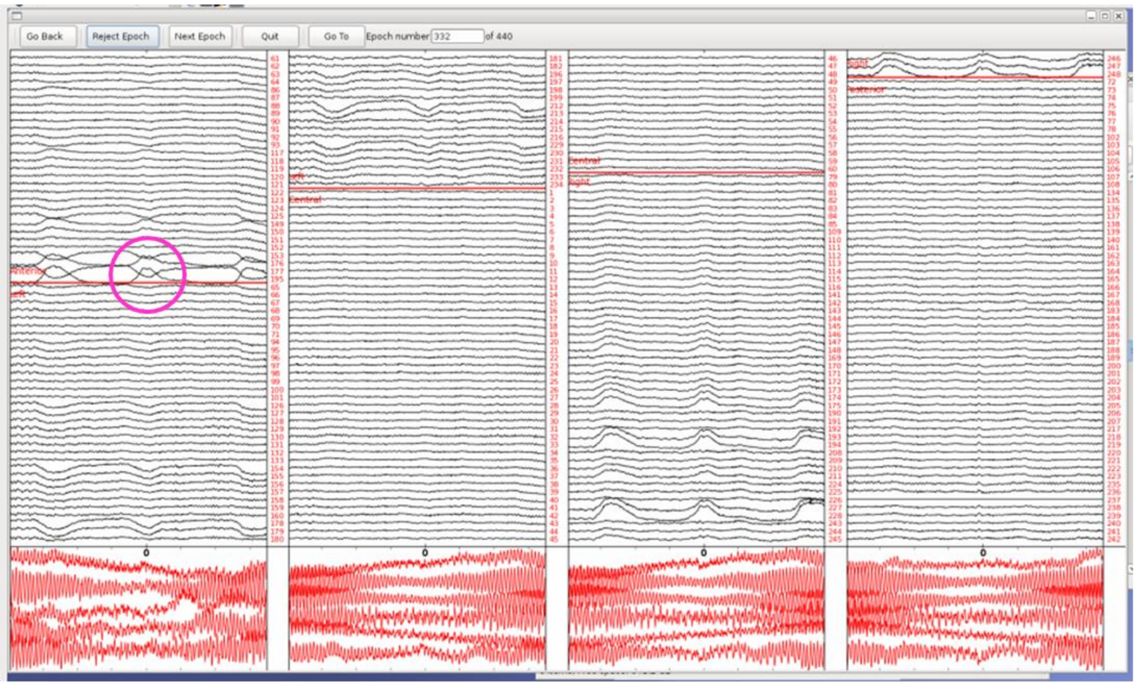


Figure D.2 Screenshot of the second pass artefact rejection window. This view shows one epoch of data across all channels. Here a stereotypical blink is highlighted. On this basis, this epoch would be rejected.

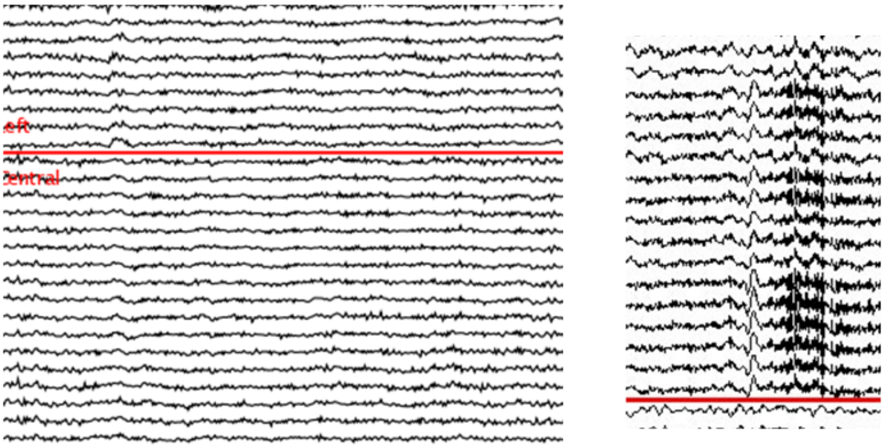


Figure D.3 Screenshot of clean and contaminated data. On the left a typical portion of data that free of artefacts can be seen. In comparison, the portion of data on the right shows a stereotypical swallow movement.

Appendix E

Passive Period Selection

In the current experiment, there are few (if any) viable alternatives for the placement of the passive period. The passive window should be selected from the period prior to the trial, as selection from the post-trial period is likely to cause systematic effects in the passive period of each condition, due to the nature of the preceding trial. In other words, a post-trial passive window will always be preceded by the same condition, whereas pre-trial passive windows should be preceded by a roughly equal proportion of trials from different conditions. Here, the target is preceded by a rapid sequence of masks and prime, and it does not make sense to place the passive period within this sequence. Placing the passive period too far in advance of the trial shortens the available intertrial interval for the participant to blink and swallow. Therefore, the passive was placed immediately prior to the onset of the first mask.

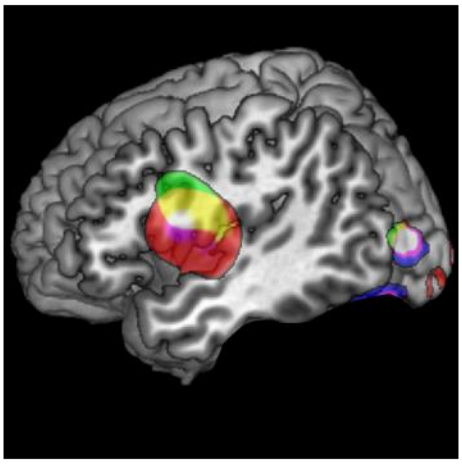


Figure E.1 Passive period examples. Three different passive periods used in an active minus passive contrast for one participant in one frequency band. White indicates overlap of all three contrasts at the LIFGpo/PCG border.

The question remains whether alternative passive windows may have considerably affected the results. Figure E.1 shows the effect of moving the passive period on LIFG activation, in a similar MEG visual word recognition paradigm at YNiC

(Lobier, Hansen, Wheat, Valdois, & Cornelissen, 2011). Three passive periods were chosen prior to target onset at 0 ms (-800–-600ms, -600–-400 ms, and -400–-200 ms). A clear overlap between the three different passive periods can be seen in white, for one participant and frequency band, using the same active time window. This indicates that there is considerable agreement in the results regardless of the choice of passive window. It should be noted that this result is below statistical threshold as there is not enough power in single subject data to reveal significant results.

Appendix F

Beamforming Figures

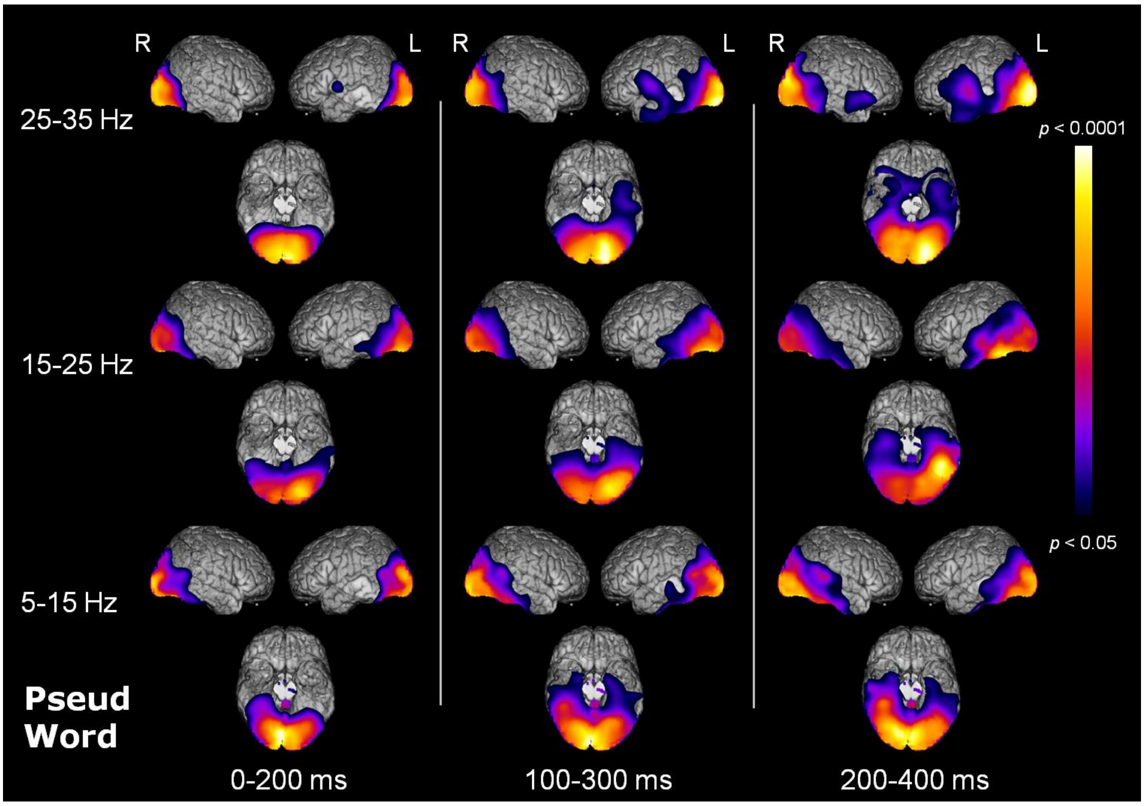


Figure F.1 Beamforming for Pseud–Word. Three-dimensional rendered cortical representations showing significant activity above baseline for PSEUD–WORD at three frequency bands and three overlapping time windows. *t*-Maps are thresholded at $p < .05$ (corrected).

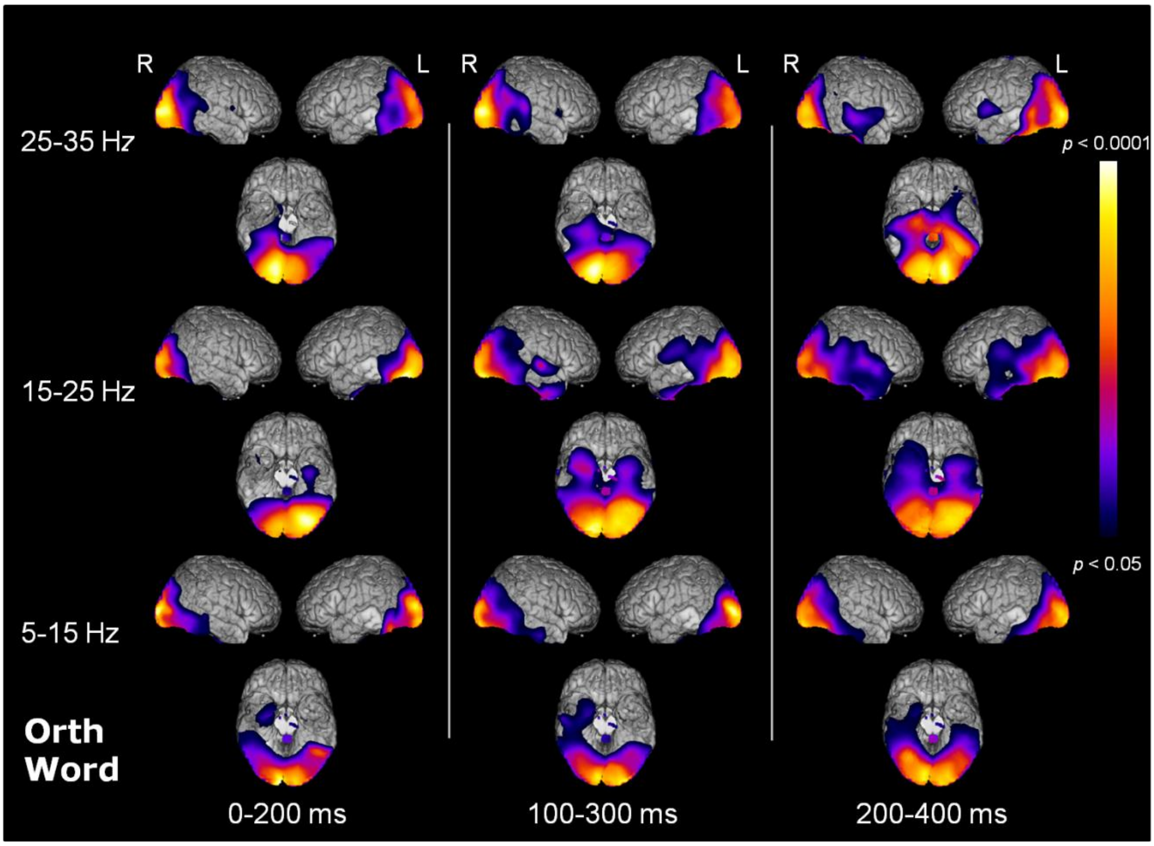


Figure F.2 Beamforming for Orth–Word. Three-dimensional rendered cortical representations showing significant activity above baseline for PSEUD–WORD at three frequency bands and three overlapping time windows. *t*-Maps are thresholded at $p < .05$ (corrected).

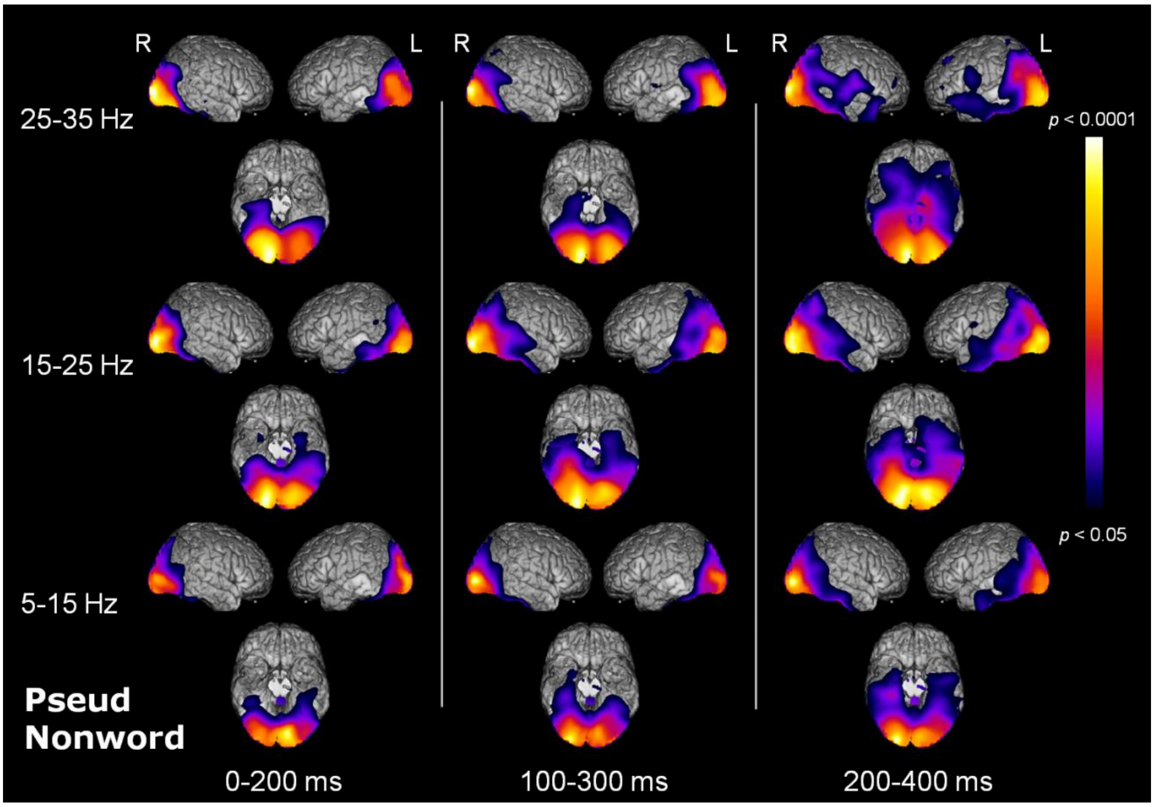


Figure F.3 Beamforming for Pseud–Nonword. Three-dimensional rendered cortical representations showing significant activity above baseline for PSEUD–WORD at three frequency bands and three overlapping time windows. *t*-Maps are thresholded at $p < .05$ (corrected).

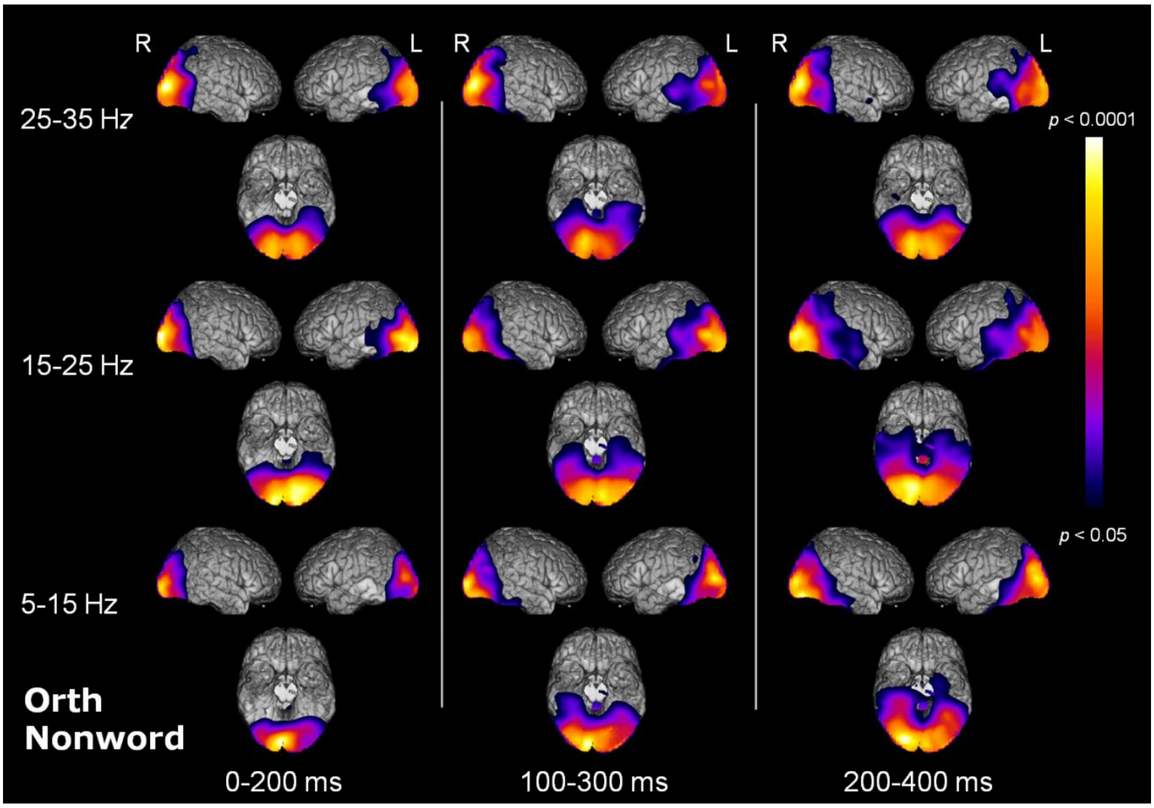


Figure F.4 Beamforming for Orth–Nonword. Three-dimensional rendered cortical representations showing significant activity above baseline for PSEUD–WORD at three frequency bands and three overlapping time windows. *t*-Maps are thresholded at $p < .05$ (corrected).

Appendix G

TMS Stimuli

Dutch Word Stimuli with Matching Pseudowords and English Translations

Dutch Word	Pseudoword	English Translation
Arm	Orm	Arm
Bal	Lal	Ball
Bed	Bam	Bed
Beer	Beur	Bear
Bel	Bem	Bell
Blad	Blod	Leaf
Boom	Bool	Tree
Bril	Bral	Glasses
Brood	Broot	Bread
Eend	Uund	Duck
Glas	Glos	Glass
Huis	Heis	House
Kat	Kot	Cat
Kip	Kep	Chicken
Klok	Klek	Clock
Kroon	Kroin	Crown
Lamp	Lamt	Lamp
Maan	Maun	Moon
Mes	Mas	Knife
Neus	Nuis	Nose
Oog	Eog	Eye
Oor	Oer	Ear
Riem	Reum	Belt
Ring	Rong	Ring
Rok	Rik	Skirt
Slang	Slong	Snake
Trein	Truan	Train
Vis	Ves	Fish
Vlag	Vlog	Flag
Vork	Virk	Fork

Appendix H

Individual TMS Results

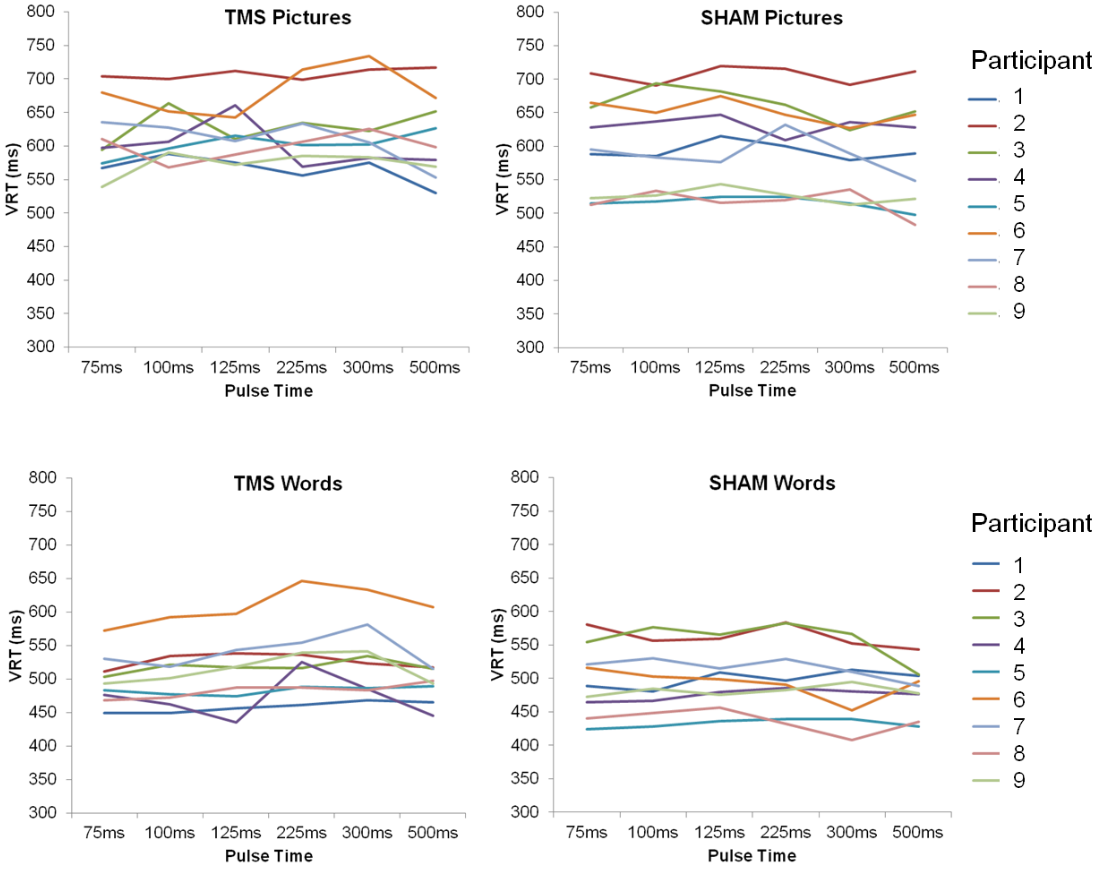


Figure H.1 Individual TMS results. Separate lines for each participant across each of the four conditions.

Glossary

AC-PC	anterior commissure-posterior commissure
BA	Brodmann area
BIAM	bi-modal interactive activation model
BOLD	blood oxygen level dependent
DRC	dual route cascaded
DSI	diffusion spectrum imaging
DTI	diffusion tensor imaging
EEG	electroencephalography
E/MEG	concurrent electro- and magneto-encephalography
EOG	electrooculogram
EPI	echo-planar imaging
ERD	event related desynchronisation
ERF	event related field
ERP	event related potential
ERS	event related synchronisation
FA	flip angle
fMRI	functional magnetic resonance imaging
FOV	field of view
FWHM	full-width half-maximum
IFG	inferior frontal gyrus
IFS	inferior frontal sulcus
LIFGpo/PCG	pars opercularis of left inferior frontal gyrus/precentral gyrus
LMOG	left middle occipital gyrus
MEG	magnetoencephalography
MNI	Montreal Neurological Institute
MPRAGE	magnetisation-prepared rapid acquisition gradient echo
NAI	neural activity index
ORTH	orthographic prime

PCG	precentral gyrus
PCS	precentral sulcus
PDC	partial directed coherence
PDP	parallel distributed processing
PET	positron emission tomography
PSEUD	pseudohomophone prime
RFX GLM	random effects general linear model
RMT	resting motor threshold
ROI	region of interest
RT	reaction time
SOA	stimulus onset asynchrony
SQUID	superconducting quantum interference devices
TE	echo time
TIWRE	test of irregular word reading efficiency
TMS	transcranial magnetic stimulation
TOWRE	test of word reading efficiency
TR	repetition time
vOT	ventral occipitotemporal cortex
VRT	vocal reaction time
VWFA	visual word form area
YNiC	York Neuroimaging Centre

References

Abramson, M., & Goldinger, S. D. (1997). What the reader’s eye tells the mind’s ear: Silent reading activates inner speech. *Perception and Psychophysics, 59,* 1059-1068.

Alexander, M. P., Naeser, M. A., & Palumbo, C. (1990). Broca’s area aphasias: Aphasia after lesions including the frontal operculum. *Neurology, 40,* 353-62.

Allport, A. (1977). On knowing the meaning of words we are unable to report: the effects of visual masking. In S. Dornic, (Ed.) *Attention and performance VI* (pp. 505-533). Hillsdale NJ: Erlbaum Press.

Annett, M. (1970). A classification of hand preferences by association analysis. *British Journal of Psychology, 61*, 303-321.

Arieli, A., Sterkin, A., Grinvald, A., & Aertsen, A. (1996). Dynamics of ongoing activity: Explanation of the large variability in evoked cortical responses. *Science, 273,* 1868-1871.

Ashby, J. (2010). Phonology is fundamental in skilled reading: Evidence from ERPs. *Psychonomic Bulletin and Review, 17,* 95-100.

Ashby, J., Sanders, L. D., & Kingston, J. (2009). Skilled readers begin processing sub-phonemic features by 80 ms during visual word recognition: Evidence from ERPs. *Biological Psychology, 80,* 84-94.

Baccalá, L. A., & Sameshima, K. (2001). Partial directed coherence: A new concept in neural structure determination. *Biological Cybernetics, 84,* 463-474.

Baillet, S., Mosher, J. C., & Leahy, R. M. (2001). Electromagnetic brain mapping. *Signal Processing Magazine IEEE, 18,* 14-30.

Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proceedings of the National Academy of Sciences, 104*, 9087-9092.

Balota, D. A., & Abrams, R. A. (1995). Mental chronometry: beyond onset latencies in the lexical decision task. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21,* 1289-302.

Balota, D. A., & Chumbley, J. I. (1984). Are lexical decisions a good measure of lexical access? The role of word frequency in the neglected decision stage. *Journal of Experimental Psychology: Human Perception and Performance, 10,* 340-57.

Barnes, G. R., Hillebrand, A., Fawcett, I. P., & Singh, K. D. (2004). Realistic spatial sampling for MEG beamformer images. *Human Brain Mapping, 23*, 120-7.

Berent, I. (1997). Phonological priming in the lexical decision task: Regularity effects are not necessary evidence for assembly. *Journal of Experimental Psychology: Human Perception and Performance, 23*, 1727-1742.

Berent, I., & Perfetti, C. A. (1995). A Rose Is a REEZ: The two-cycles model of phonology assembly in reading English. *Psychological Review, 102,* 146-184.

Berndt, R. S., & Caramazza, A. (1980). A redefinition of the syndrome of Broca's aphasia: Implications for a neuropsychological model of language. *Applied Psycholinguistics, 1*, 225-278.

Ben-Shachar, M., Dougherty, R. F., Deutsch, G. K., & Wandell, B. A. (2011). The development of cortical sensitivity to visual word forms. *Journal of Cognitive Neuroscience, 23*, 2387-2399.

Benson, D. F. (1977). The third alexia. *Archives of Neurology, 34,* 327-331.

Besner, D., Coltheart, M., & Davelaar, E. (1984). Basic processes in reading: Computation of abstract letter identities. *Canadian Journal of Psychology/Revue Canadienne de Psychologie, 38,* 126.

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the Semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex, 19*, 2767-2796.

Binkofski, F., Amunts, K., Stephan, K. M., Posse, S., Schormann, T., Freund, H. J., … Seitz, R. J. (2000). Broca's region subserves imagery of motion: A combined cytoarchitectonic and fMRI study. *Human Brain Mapping, 11*, 273-285.

Binkofski, F., Buccino, G., Stephan, K. M., Rizzolatti, G., Seitz, R. J., & Freund, H. J. (1999) A parieto-premotor network for object manipulation: Evidence from neuroimaging. *Experimental Brain Research, 128,* 210-213.

Blau, V., Reithler, J., Van Atteveldt, N., Seitz, J., Gerretsen, P., Goebel, R., & Blomert, L. (2010). Deviant processing of letters and speech sounds as proximate cause of reading failure: A functional magnetic resonance imaging study of dyslexic children. *Brain, 133,* 868-879.

Blau, V., Van Atteveldt, N., Ekkebus, M., Goebel, R., & Blomert, L. (2009). Reduced neural integration of letters and speech sounds links phonological and reading deficits in adult dyslexia. *Current Biology, 19,* 503-508.

Blomert, L. (2011). The neural signature of orthographic–phonological binding in successful and failing reading development. *NeuroImage*, *57,* 695-703.

Boccardi, E., Bruzzone, M., & Vignolo, L. (1984). Alexia in recent and late Broca's aphasia. *Neuropsychologia*, *22,* 745-754.

Bodner, G. E., & Masson, M. E. J. (1997). Masked repetition priming of words and nonwords: Evidence for a nonlexical basis for priming. *Journal of Memory and Language*, *37*, 268-293.

Bookheimer, S. (2002). Functional MRI of language: New Approaches to understanding the cortical organization of semantic processing. *Annual*

Review of Neuroscience, 25, 151-188.

Borgwaldt, S. R., Hellwig, F. M., & Groot, A. M. B. D. (2005). Onset entropy matters-Letter-to-phoneme mappings in seven languages. *Reading and Writing, 18,* 211-229.

Braber, N., Patterson, K., Ellis, K., & Lambon Ralph, M. A. (2005). The relationship between phonological and morphological deficits in Broca's aphasia: Further evidence from errors in verb inflection. *Brain and Language, 92*, 278-287.

Bradley, L., & Bryant, P. E. (1983). Categorizing sounds and learning to read: A causal connection. *Nature, 301*, 419-421.

Broca, P. (1861a). Nouvelle observation aphémie produite par un lésion de la moité postérieure des deuxième et troisième circonvolutions frontales. *Bulletins de la Société Anatomique, 6,* 398-407.

Broca, P. (1861b). Remarques sur le siége de la faculté du langage articulé, suivies d'une observatoin d'aphémie (Perte de la Parole). *Bulletin de la Société Anatomique de Paris, 6*, 330-357.

Broca, P. (1863). Localisation des fonctions cérébrales. Siège du langage articulé. *Bulletins de la Société d'Anthropologie, 4*, 200-204.

Broca, P. (1865). Sur le siège de la faculté du langage articule. *Bulletins de la Société d'Anthropologie, 6,* 377-393.

Brown, S., Ngan, E., & Liotti, M. (2008). A larynx area in the human motor cortex. *Cerebral Cortex, 28,* 837-845.

Brysbaert, M. (2001). Prelexical phonological coding of visual words in Dutch: Automatic after all. *Memory & Cognition, 29,* 765-773.

Brysbaert, M., & Praet, C. (1992). Reading isolated words: No evidence for automatic incorporation of the phonetic code. *Psychological Research*, *54,* 91-102.

Büchel, C., Price, C., & Friston, K. (1998). A multimodal language region in the ventral visual pathway. *Nature*, *394*, 274–277.

Burton, M. W., LoCasto, P. C., Krebs-Noble, D., & Gullapalli, R. P. (2005). A systematic investigation of the functional neuroanatomy of auditory and visual phonological processing. *NeuroImage, 26,* 647-661.

Carreiras, M., Perea, M., Vergara, M., & Pollatsek, A. (2009). The time course of orthography and phonology: ERP correlates of masked priming effects in Spanish. *Psychophysiology, 46*, 1113-1122.

Chapman, R. M., Ilmoniemi, R., Barbanera, S., & Romani, G. (1984). Selective localization of alpha brain activity with neuromagnetic measurements. *Electroencephalography and Clinical Neurophysiology, 58,* 569-572.

Cohen, L., Dehaene, S., Naccache, L., Lehéricy, S., Dehaene-Lambertz, G., Hénaff, M. A., & Michel, F. (2000). The visual word form area. *Brain*, *123*, 291-307.

Coltheart, M. (1978). Lexical access in simple reading tasks. In G. Underwood (Ed.), *Strategies of information processing* (pp. 151-216). London: Academic Press.

Coltheart, M. (1980). Reading, phonological recoding and deep dyslexia. In M. Coltheart, K. E. Patterson, & J.C. Marshall, (Eds.), *Deep dyslexia* (pp. 197-226) London: Routledge.

Coltheart, M. (2000). Deep dyslexia is right-hemisphere reading. *Brain and Language, 71,* 299-309.

Coltheart, M., Davelaar, E., Jonasson, T., & Besner, D. (1977). Access to the internal lexicon. In S. Dornic (Ed.), *Attention and Performance VI* (pp. 64-85). Hillsdale, NJ: Erlbaum.

Coltheart, M., Rastle, K., Perry, C., Ziegler, J., & Langdon, R. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review*, *108*, 204-256.

Cornelissen, P. L., Kringelbach, M. L., Ellis, A. W., Whitney, C., Holliday, I. E., & Hansen, P. C. (2009). Activation of the left inferior frontal gyrus in the first 200 ms of reading: Evidence from magnetoencephalography (MEG). *PLoS ONE, 4*, e5359.

Craighero, L., Fadiga, L., Umiltà, C. A., & Rizzolatti, G. (1996). Evidence for visuomotor priming effect. *NeuroReport*, *8*, 347.

Damian, M. F., & Bowers, J. S. (2003). Effects of orthography on speech production in a form-preparation paradigm. *Journal of Memory and Language, 49,* 119-132.

Davies, M. (2010). Double Dissociation: Understanding its Role in Cognitive Neuropsychology. *Mind and Language*, *25*, 500-540.

Davis, C., Kleinman, J. T., Newhart, M., Gingis, L., Pawlak, M., & Hillis, A. E. (2008). Speech and language functions that require a functioning Broca’s area. *Brain and Language*, *105*, 50-58.

De Graaf, T. A., Herring, J., & Sack, A. T. (2011). A chronometric exploration of high-resolution “sensitive TMS masking” effects on subjective and objective measures of vision. *Experimental Brain Research*, *209*, 19-27.

De Graaf, T. A., & Sack, A. T. (2011). Null results in TMS: From absence of evidence to evidence of absence. *Neuroscience and Biobehavioral Reviews*, *35*, 871-877.

DeFrancis, J. (1989) *Visible speech: The diverse oneness of writing systems*. Honolulu, HI: University of Hawaii Press.

Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences, 15,* 254-262.

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences, 9*, 335-341.

Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J. B., Le Bihan, D., & Cohen, L. (2004). Letter binding and invariant recognition of masked words. *Psychological Science*, *15,* 307-313.

Dehaene, S., Le Clec’H, G., Poline, J.-B, Bihan, D. L., & Cohen, L. (2002). The visual word form area: A prelexical representation of visual words in the fusiform gyrus. *NeuroReport, 13,* 321-325.

Dehaene, S., Naccache, L., Cohen, L., Bihan, D. L., Mangin, J.-F, Poline, J.-B, & Rivière, D. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience, 4*, 752-758.

Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Filho, G. N., Jobert, A., … Cohen, L. (2010). How learning to read changes the cortical networks for vision and language. *Science, 330,* 1359-1364.

Démonet, J-F, Thierry, G., & Cardebat, D. (2005). Renewal of the neurophysiology of language: Functional neuroimaging. *Physiological Reviews, 85,* 49-95.

Dennis, I., & Newstead, S. E. (1981). Is phonological recoding under strategic control? *Memory and Cognition, 9,* 472-477.

Derrfuss, J., Brass, M., von Cramon, D. Y., Lohmann, G., & Amunts, K. (2009). Neural activations at the junction of the inferior frontal sulcus and the inferior precentral sulcus: Interindividual variability, reliability, and association with sulcal morphology. *Human Brain Mapping, 30,* 299-311.

Devlin, J. T., Jamison, H. L., Gonnerman, L. M., & Matthews, P. M. (2006). The role of the posterior fusiform gyrus in reading. *Journal of Cognitive Neuroscience, 18,* 911-22.

Diependaele, K., Ziegler, J. C., & Grainger, J. (2010). Fast phonology and the Bimodal Interactive Activation Model. *European Journal of Cognitive Psychology, 22,* 764-778.

Dunn, J. C., & Kirsner, K. (2003). What can we infer from double dissociations? *Cortex, 39*, 1-7.

Duyck, W., Desmet, T., Verbeke, L. P. C., & Brysbaert, M. (2004). WordGen: A tool for word selection and nonword generation in Dutch, English, German, and French. *Behavior Research Methods, Instruments, & Computers, 36,* 488-499.

Evett, L. J., & Humphreys, G. W. (1981). The use of abstract graphemic information in lexical access. *The Quarterly Journal of Experimental Psychology*, *33,* 325-350.

Fedorenko, E., Behr, M. K., & Kanwisher, N. (2011). Functional specificity for high-level linguistic processing in the human brain. *Proceedings of the National Academy of Sciences, 108*, 16428-16433.

Ferrand, L., & Grainger, J. (1992). Phonology and orthography in visual word recognition: Evidence from masked non-word priming. *The Quarterly Journal of Experimental Psychology, 45A,* 353-372.

Ferrand, L., & Grainger, J. (1993). The time course of orthographic and phonological code activation in the early phases of visual word recognition. *Bulletin of the Psychnomic Society, 31*, 119-122.

Ferrand, L., & Grainger, J. (1994). Effects of orthography are independent of phonology in masked priming. *The Quarterly Journal of Experimental Psychology, 47A,* 365-382.

Fiez, J. A., & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences, 95*, 914.

Fincham, J. M., Carter, C. S., van Veen, V., Stenger, V. A., & Anderson, J. R. (2002). Neural mechanisms of planning: A computational analysis using event-related fMRI. *Procedings of the National Acadamy of Science USA, 99*, 3346-3351.

Forbach, G. B., Stanners, R. F., & Hochhaus, L. (1974). Repetition and practice effects in a lexical decision task. *Memory & Cognition*, *2,* 337-339.

Forster, K. I. (1998). The pros and cons of masked priming. *Journal of Psycholinguistic Research*, *27*, 203-233.

Forster, K. I., & Davis, C. (1984). Repetition priming and frequency attenuation in lexical access. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *10,* 680.

Forster, K. I., & Davis, C. (1991). The Density Constraint on Form-Priming in the Naming Task: Interference Effects from a Masked Prime. *Journal of Memory and Language*, *30*, 1-25.

Forster, K. I., Davis, C., Schoknecht, C., & Carter, R. (1987). Masked priming with graphemically related forms: Repetition or partial activation? *The Quarterly Journal of Experimental Psychology*, *39*, 211-251.

Forster, K. I., Mohan, K., & Hector, J. (2003). The mechanics of masked priming. In S. Kinoshita & S. J. Lupker (Eds.), *Masked priming: The state of the art* (pp. 3-37). New York and Hove: Psychology Press.

Fowler, C. A., Wolford, G., Slade, R., & Tassinary, L. (1981). Lexical access with and without awareness. *Journal of Experimental Psychology: General*, *110*, 341-362.

Friederici, A. D. (2009). Pathways to language: Fiber tracts in the human brain. *Trends in Cognitive Sciences*, *13*, 175-181.

Friston, K. J., Holmes, A., Poline, J. B., Price, C. J., & Frith, C. D. (1996) Detecting activations in PET and fMRI: levels of inference and power. *NeuroImage*, *4*, 223-235.

Friston, K. J., & Price, C. J. (2011). Modules and brain mapping. *Cognitive Neuropsychology*, *28*, 241-250.

Frost, R. (1998). Toward a strong phonological theory of visual word recognition: True issues and false trails. *Psychological Bulletin*, *123*, 71-99.

Frost, R., Ahissar, M., Gotesman, R., & Tayeb, S. (2003). Are phonological effects fragile? The effect of luminance and exposure duration on form priming and phonological priming. *Journal of Memory and Language*, *48*, 346-378.

Gerardin, E., Sirigu, A., Lehericy, S., Poline, J. B., Gaymard, B., Marsault, C., … Le Bihan, D. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex, 10*, 1093-1104.

Glezer, L. S., Jiang, X., & Riesenhuber, M. (2009). Evidence for highly selective neuronal tuning to whole words in the "visual word form area." *Neuron*, *62,* 199-204.

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

Grainger, J., Diependaele, K., Spinelli, E., Ferrand, L., & Farioli, F. (2003). Masked repetition and phonological priming within and across modalities. *Journal of Experimental Psychology: Learning, Memory and Cognition*, *29*, 1256-1269.

Grainger, J., & Ferrand, L. (1994). Phonology and orthography in visual word recognition: effects of masked homophone primes. *Journal of Memory and Language, 33*, 218-233.

Grainger, J., & Ferrand, L. (1996). Masked orthographic and phonological priming in visual word recognition and naming: Cross-task comparisons. *Journal of Memory and Language, 35*, 623-647.

Grainger, J., & Jacobs, A. M. (1996). Orthographic processing in visual word recognition: A multiple read-out model. *Psychological review*, *103*, 518-565.

Grainger, J., Kiyonaga, K., & Holcomb, P. J. (2006). The time course of orthographic and phonological code activation. *Psychological Science*, *17*, 1021-1026.

Grainger, J., Muneaux, M., Farioli, F., & Ziegler, J. C. (2005). Effects of phonological and orthographic neighbourhood density interact in visual word recognition. *The Quarterly Journal of Experimental Psychology Section A*, *58*, 981-998.

Greenlee, J. D. W., Oya, H., Kawasaki, H., Volkov, I. O., Kaufman, O. P., Kovach, C., … Brugge, J.F. (2004). A functional connection between inferior frontal gyrus and orofacial motor cortex in human. *Journal of Neurophysiology, 92*, 1153-1164.

Grodzinsky, Y., & Amunts, K. (2006). *Broca's region*. New York, NY: Oxford University Press.

Hagoort, P. (2005). On Broca, brain, and binding: a new framework. *Trends in Cognitive Sciences*, *9*, 416-423.

Haist, F., Song, A. W., Wild, K., Faber, T. L., Popp, C. A., & Morris, R. D. (2001). Linking sight and sound: fMRI evidence of primary auditory cortex activation during visual word recognition. *Brain and Language*, *76*, 340-350.

Hallett, M. (2000). Transcranial magnetic stimulation and the human brain. *Nature, 406*, 147-150.

Hallett, M. (2007). Transcranial magnetic stimulation: A primer. *Neuron*, *55*, 187–199.

Hämäläinen, M., & Hari, R. (2002). Magnetoencephalographic (MEG) characterization of dynamic brain activation. In A.W. Toga, & J.C. Mazziotta (Eds.), *Brain mapping: The methods (2nd ed.).* (227-255). San Diego: Elsvier.

Hämäläinen, M., Hari, R., Illmoniemi, R. J., Knuutila, J., & Lounasmaa, O. V. (1993). Magnetoencephalography - theory, instrumentation, and applications to noninvasive studies of the working human brain. *Review of Modern Physics, 65*, 413-497.

Hari, R., & Salmelin, R. (1997). Human cortical oscillations: A neuromagnetic view through the skull. *Science*, *20*, 44-49.

Harm, M. W., & Seidenberg, M. S. (1999). Phonology, Reading Acquisition, and Dyslexia: Insights from Connectionist Models. *Psychological Review*, *106*, 491-528.

Harm, M. W., & Seidenberg, M. S. (2004). Computing the Meanings of Words in Reading: Cooperative Division of Labour Between Visual and Phonological Processes. *Psychological Review*, *111*, 662-720.

Hartwigsen, G., Price, C. J., Baumgaertner, A., Geiss, G., Koehnke, M., Ulmer, S., & Siebner, H. R. (2010). The right posterior inferior frontal gyrus contributes to phonological word decisions in the healthy brain: Evidence from dual-site TMS. *Neuropsychologia*, *48*, 3155-3163.

Hartwigsen, G., & Siebner, H. R. (2011). Probing the involvement of the right hemisphere in language processing with online transcranial magnetic stimulation in healthy volunteers. *Aphasiology*. Advance online publication. doi:10.1080/02687038.2011.590573

Hauk, O., Davis, M. H., Ford, M., Pulvermüller, F., & Marslen-Wilson, W. D. (2006). The time course of visual word recognition as revealed by linear regression analysis of ERP data. *NeuroImage*, *30*, 1383-1400.

He, B., Yang, L., Wilke, C., & Yuan, H. (2011). Electrophysiological imaging of brain activity and connectivity—Challenges and opportunities. *IEEE Transactions on Biomedical Engineering*, *58*, 1918-1931.

Hellyer, P. J., Woodhead, Z. V. J., Leech, R., & Wise, R. J. S. (2011). An investigation of twenty/20 vision in reading. *The Journal of Neuroscience*, *31*, 14631-14638.

Henson, R. N. A. (2003). Neuroimaging studies of priming. *Progress in Neurobiology*, *70*, 53-81.

Hillebrand, A., & Barnes, G. R. (2002). A quantitative assessment of the sensitivity of whole-head meg to activity in the adult human cortex. *NeuroImage*, *16*, 638-650.

Hillebrand, A., Singh, K. D., Holliday, I. E., Furlong, P. L., & Barnes, G. R. (2005). A new approach to neuroimaging with magnetoencephalography. *Human Brain Mapping*, *25*, 199 -211.

Holcomb, P. J., & Grainger, J. (2006). On the time course of visual word recognition: An event-related potential investigation using masked repetition priming. *Journal of Cognitive Neuroscience*, *18*, 1631-1643.

Holcomb, P. J., & Grainger, J. (2007). Exploring the temporal dynamics of visual word recognition in the masked repetition priming paradigm using event-related potentials. *Brain Research*, *1180*, 39-58.

Holmes, A.P., Blair, R.C., Watson, G., & Ford, I. (1996). Nonparametric analysis of statistic images from functional mapping experiments. *Journal of Cerebral Blood Flow & Metabolism*, *16***,** 7-22.

Holyk, G. G., & Pexman, P. M. (2004). The elusive nature of early phonological priming effects: Are there individual differences? *Brain and Language*, *90*, 353-367.

Hood, D. C., & Finkelstein, M. A. (1986) Sensitivity to light. In K. Boff, L. Kaufman, & J. Thomas (Eds.), *Handbook of perception and human performance* (Vol. 1, pp. 5.1-5.66). New York: Wiley-Interscience.

Hoogendam, J. M., Ramakers, G. M. J., & Di Lazzaro, V. (2010). Physiology of repetitive transcranial magnetic stimulation of the human brain. *Brain Stimulation, 3,* 95-118.

Horemans, I., & Schiller, N. O. (2004). Form-priming effects in nonword naming. *Brain and Language, 90*, 465-469.

Huang, M., Shih, J., Lee, R., Harrington, D., Thoma, R., Weisend, M., … Canive J. M. (2004). Commonalities and differences among vectorized beamformers in electromagnetic source imaging. *Brain Topography, 16,* 139-158.

Huettel, S. A., Song, A. W., & McCarthy, G. (2008). F*unctional magnetic resonance imaging (2nd ed.).* Sunderland, MA: Sinauer Associates.

Humphreys, G. W., Besner, D., & Quinlan, P. T. (1988). Event perception and the word repetition effect. *Journal of Experimental Psychology: General, 117,* 51-67.

Humphreys, G. W., Evett, L. J., & Taylor, D. E. (1982). Automatic phonological priming in visual word recognition. *Memory & Cognition, 10*, 576-590.

Indefrey, P. (2011). Frontiers: The spatial and temporal signatures of word production components: A critical update. *Frontiers in Language Sciences*. Advance online publication. doi: 10.3389/fpsyg.2011.00255

Indefrey, P., & Levelt, W. J. M. (2004). The spatial and temporal signatures of word production components. *Cognition, 92*, 101-144.

Jacobs, A. M., & Grainger, J. (1994). Models of visual word recognition: Sampling the state of the art. *Journal of Experimental Psychology: Human Perception and Performance, 20*, 1311-1334.

Jacobs, A. M., Rey, A., Ziegler, J. C., & Grainger, J. (1998). MROM-P: An interactive activation, multiple read-out model of orthographic and phonological processes in visual word recognition. In J. Grainger, & A. M. Jacobs (Eds.), *Localist connectionist approaches to human cognition*, (pp. 147-187). Mahwah, NJ: Lawrence Erlbaum Associates, Inc.

January, D., Trueswell, J. C., & Thompson-Schill, S. L. (2009). Co-localization of stroop and syntactic ambiguity resolution in broca’s area: Implications for the neural basis of sentence processing. *Journal of Cognitive Neuroscience, 21,* 2434-2444.

Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual-route theory of reading: A metanalysis of 35 neuroimaging studies. *NeuroImage, 20*, 693-712.

Johnston, M. B., & Castles, A. (2003). Dissociating automatic orthographic and phonological codes in lexical access and lexical acquisition. In S. Kinoshita & S. J. Lupker, *Masked priming: The state of the art* (pp. 193-222). New York and Hove: Psychology Press.

Jones, S. R., Kerr, C. E., Wan, Q., Pritchett, D. L., Hämäläinen, M., & Moore, C. I. (2010). Cued spatial attention drives functionally relevant modulation of the mu rhythm in primary somatosensory cortex. *Journal of Neuroscience, 30*, 13760–13765.

Judaš, M., & Cepanec, M. (2007). Adult structure and development of the human fronto-opercular cerebral cortex (Broca's region). *Clinical Linguistics & Phonetics*, *21*, 975-989.

Juola, P., & Plunkett, K. (2000). Why double dissociations don't mean much. In G. Cohen, R. A. Johnston, & K. Plunkett (Eds.), *Exploring cognition: Damaged brains and neural networks: Readings in cognitive neuropsychology and connectionist modelling* (pp. 319-327) Hove, England: Psychology Press.

Just, M. A., & Carpenter, P. A. (1980). A theory of reading: From eye fixations to comprehension. *Psychological Review*, *87*, 329-354.

Kahneman, D. (1968). Method, findings, and theory in studies of visual masking. *Psychological Bulletin*, *70*, 404-425.

Keller, S. S., Crow, T., Foundas, A., Amunts, K., & Roberts, N. (2009). Broca's area: nomenclature, anatomy, typology and asymmetry. *Brain and Language*, *109*, 29-48.

Kim, J., & Davis, C. (2003). Task effects in masked cross-script translation and phonological priming. *Journal of Memory and Language*, *49*, 484-499.

Kim, S.-G., Richter, W., & Uğurbil, K. (1997). Limitations of temporal resolution in functional MRI. *Magnetic Resonance in Medicine, 37*, 631-636.

Kozinska, D., Carducci, F., & Nowinski, K. (2001). Automatic alignment of EEG/MEG and MRI data sets. *Clinical Neurophysiology*, *112*, 1553-1561.

Krams, M., Rushworth, M. F., Deiber, M. P., Frackowiak, R. S., & Passingham, R. E. (1998). The preparation, execution and suppression of copied movements in the human brain. *Experimental Brain Research*, *120*, 386-398.

Kronbichler, M., Hutzler, F., Wimmer, H., Mair, A., Staffen, W., & Ladurner, G. (2004). The visual word form area and the frequency with which words are encountered: Evidence from a parametric fMRI study. *NeuroImage*, *21*, 946-953.

Kujala, J., Pammer, K., Cornelissen, P., Roebroeck, A., Formisano, E., & Salmelin, R. (2007). Phase coupling in a cerebro-cerebellar network at 8–13 Hz during reading. *Cerebral Cortex*, *17*, 1476-1485.

Liakakis, G., Nickel, J., & Seitz, R. J. (2011). Diversity of the inferior frontal gyrus: A meta-analysis of neuroimaging studies. *Behavioural Brain Research*, *225*, 341-347.

Liberman, A. M., & Mattingly, I. G. (1985). The motor theory of speech perception revised. *Cognition*, *21*, 1-36.

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D., & Schabenberger, O. (2006). *SAS for mixed models* (2nd Ed.). Cary NC; SAS Intitute Inc.

Liu, H., Agam, Y., Madsen, J. R., & Kreiman, G. (2009). Timing, timing, timing: Fast decoding of object information from intracranial field potentials in human visual cortex. *Neuron, 62,* 281-290.

Lobier, M., Hansen, P. C., Wheat, K. L., Valdois, S., & Cornelissen, P. L. (2011). [Visual word recognition in MEG]. Unpublished raw data.

Lobier, M., Hansen, P. C., Wheat, K. L., Valdois, S., & Cornelissen, P. L. (2011, November). *The first 250 ms in visual word recognition: Who is talking to whom?* Poster session presented at the Annual Meeting of the Society for Neuroscience, Washington DC, USA.

Los, S. A. (1996). On the origin of mixing costs: Exploring information processing in pure and mixed blocks of trials. *Acta Psychologica, 94,* 145-188.

Los, S. A. (1999). Identifying stimuli of different perceptual categories in pure and mixed blocks of trials: Evidence for stimulus-driven switch costs. *Acta Psychologica, 103,* 173-205.

Lounasmaa, O. V., Hämäläinen, M., Hari, R., & Salmelin, R. (1996). Information processing in the human brain: Magnetoencephalographic approach. *Proceedings of the National Academy of Sciences, 93,* 8809-8815.

Lukatela, G., & Turvey, M. T. (1993). Similar attentional, frequency, and associative effects for pseudohomophones and words. *Journal of Experimental Psychology: Human Perception and Performance, 19,* 166-178.

Lukatela, G., & Turvey, M. T. (2000). An evaluation of the two-cycles model of phonology assembly. *Journal of Memory and Language, 42,* 183-207.

Lukatela, G., Eaton, T., Lee, C., & Turvey, M. T. (2001). Does visual word identification involve a sub-phonemic level? *Cognition, 78,* B41-B52.

Lukatela, G., Eaton, T., Sabadini, L., & Turvey, M. T. (2004). Vowel duration affects visual word identification: Evidence that the mediating phonology is phonetically informed. *Perception, 30,* 151-162.

Lukatela, G., Frost, S. J., & Turvey, M. T. (1998). Phonological priming by masked nonword primes in the lexical decision task. *Human Development, 683,* 666 - 683.

Lukatela, G., Frost, S. J., & Turvey, M. T. (1999). Identity priming in english in compromised by phonological ambiguity. *Journal of Experimental Psychology: Human Perception and Performance, 25,* 755-790.

Lupker, S. J., Brown, P., & Colombo, L. (1997). Strategic control in a naming task: Changing routes or changing deadlines? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 23,* 570.

Lupker, S. J., Kinoshita, S., Coltheart, M., & Taylor, T. E. (2003). Mixing costs and mixing benefits in naming words, pictures, and sums. *Journal of Memory and Language, 49,* 556-575.

Mainy, N., Jung, J., Baciu, M., Kahane, P., Schoendorff, B., Minotti, L., … Lachaux, J. P. (2008). Cortical Dynamics of Word Recognition. *Human Brain Mapping, 29,* 1215-1230.

Marshall, J., & Newcombe, F. (1973). Patterns of paralexia: A psycholinguistic approach. *Journal of Psycholinguistic Research, 2,* 175.

Masson, M. E., & Isaak, M. I. (1999). Masked priming of words and nonwords in a naming task: further evidence for a nonlexical basis for priming. *Memory & Cognition, 27,* 399-412.

McCann, R. S., & Besner, D. (1987). Reading pseudohomophones: Implications for models of pronunciation assembly and the locus of word-frequency effects in naming. *Journal of Experimental Psychology: Human Perception and Performance, 13,* 14-24.

McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: I. An account of basic findings. *Psychological Review, 88,* 375-407.

McIntosh, A. (2000). Towards a network theory of cognition. *Neural Networks, 13,* 861-870.

Mechelli, A., Josephs, O., Lambon Ralph, M. A., McClelland, J. L., & Price, C. J. (2007). Dissociating stimulus-driven semantic and phonological effects during reading and naming. *Human Brain Mapping, 28,* 205-217.

Meltzoff, A. N., & Decety, J. (2003) What imitation tells us about social cognition: A rapprochement between developmental psychology and cognitive neuroscience. *Philosophical Transactions of the Royal Society B: Biological Sciences, 358,* 491-500.

Meyer, D. E., Schvaneveldt, R. W., & Rudy, M. G. (1974). Functions of graphemic and phonemic codes in visual word recognition. *Memory and Cognition, 2,* 309-321.

Meyer, D., Schvaneveldt, R., & Ruddy, M. (1972). *Activation of lexical memory*. Paper presented at the Meeting of the Psychonomic Society, St. Louis, Missouri.

Millard, A. R. (1986). The infancy of the alphabet. *World Archaeology, 17,* 390-398.

Miller, J. (1991). Short report: Reaction time analysis with outlier exclusion: Bias varies with sample size. *The Quarterly Journal of Experimental Psychology, 43,* 907-912.

Moore, C. J., & Price, C. J. (1999). Three distinct ventral occipitotemporal regions for reading and object naming. *Neuroimage, 10,* 181-192.

Munding, D. H., (2011). *Temporal dynamics of the reading network: An MEG connectivity study* (Unpublished master's dissertation). University of York, York, UK.

Naish, P. (1980). The effects of graphemic and phonemic similarity between targets and masks in a backward visual masking paradigm. *The Quarterly Journal of Experimental Psychology, 32,* 57-68.

Neely, J. H. (1977). Semantic priming and retrieval from lexical memory: Roles of inhibitionless spreading activation and limited-capacity attention. *Journal of Experimental Psychology: General, 106,* 226.

Newman, R. L., & Connolly, J. F. (2004). Determining the role of phonology in silent reading using event-related brain potentials. *Cognitive Brain Research*, *21,* 94-105.

Nichols, T. E., & Holmes, A. P. (2004). Nonparametric permutation tests for functional neuroimaging. In R. S. J. Frackowiak, K. J. Friston, C. D. Frith, & R. J. Dolan, (Eds.) *Human brain function (2nd ed.).* (pp. 887-910). London: Elsevier.

Nishitani, N. (2005). Broca's region: From action to language. *Physiology, 20*, 60-69.

Nixon, P., Lazarova, J., Hodinott-Hill, I., Gough, P., & Passingham, R. (2004). The inferior frontal gyrus and phonological processing: An investigation using rTMS. *Journal of Cognitive Neuroscience, 16,* 289-300.

Novick, J. M., Kan, I. P., Trueswell, J. C., & Thompson-Schill, S. L. (2009). A case for conflict across multiple domains: Memory and language impairments following damage to ventrolateral prefrontal cortex. *Cognitive Neuropsychology*, *26,* 527-567.

O'Shea, J., & Walsh, V. (2007). Transcranial magnetic stimulation. *Current Biology, 17,* R196-R199.

Ou, W., Nummenmaa, A., Ahveninen, J., Belliveau, J. W., Hämäläinen, M. S., & Golland, P. (2010). Multimodal functional imaging using fMRI-informed regional EEG/MEG source estimation. *Neuroimage*, *52,* 97-108.

Palmer, E. D., Brown, T. T., Petersen, S. E., & Schlaggar, B. L. (2004). Investigation of the functional neuroanatomy of single word reading and its development. *Scientific Studies of Reading, 8*, 203-223.

Pammer, K., Hansen, P. C., Kringelbach, M. L., Holliday, I., Barnes, G., Hillebrand, A., Singh, K., & Cornelissen, P. L. (2004). Visual word recognition: The first half second. *NeuroImage, 22*, 1819-1825.

Pascual-Leone, A. (1999). Transcranial magnetic stimulation: Studying the brain-behaviour relationship by induction of "virtual lesions." *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 354*, 1229-1238.

Pascual-Leone, A., Bartres-Faz, D., & Keenan, J. (1999). Transcranial magnetic stimulation: Studying the brain-behaviour relationship by induction of 'virtual lesions'. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *354,* 1229-1238.

Pascual-Leone, A., Walsh, V., & Rothwell, J. (2000). Transcranial magnetic stimulation in cognitive neuroscience-virtual lesion, chronometry, and functional connectivity. *Current Opinion in Neurobiology, 10,* 232-237.

Patterson, K. E. (1981). Neuropsychological approaches to the study of reading. *British Journal of Psychology*, *72*, 151-174.

Patterson, K., & Plaut, D. C. (2009). "Shallow draughts intoxicate the brain": Lessons from cognitive science for cognitive neuropsychology. *Topics in Cognitive Science*, *1,* 39-58.

Paulesu, E., Perani, D., Blasi, V., Silani, G., Borghese, N., De Giovanni, U., … Fazio,

F. (2003). A functional-anatomical model for lipreading. *Journal of Neurophysiology, 90*, 2005-2013.

Paus, T., Sipila, P., & Strafella, A. (2001). Synchronization of neuronal activity in the human primary motor cortex by transcranial magnetic stimulation: An EEG study. *Journal of Neurophysiology, 86*, 1983-1990.

Penolazzi, B., Hauk, O., & Pulvermuller, F. (2007). Early semantic context integration and lexical access as revealed by event-related brain potentials. *Biological Psychology, 74,* 374-388.

Perea, M., & Lupker, S. J. (2003). Does jugde activate COURT? Transposed-letter similarity effects in masked associative priming. *Memory & Cognition, 31,* 829-841.

Perea, M., Gómez, P., & Fraga, I. (2010). Masked nonword repetition effects in yes/no and go/no-go lexical decision: A test of the evidence accumulation and deadline accounts. *Psychonomic Bulletin & Review, 17,* 369-374.

Perfetti, C. A., Bell, L. C., & Delaney, S. M. (1988). Automatic (prelexical) phonetic activation in silent word reading: Evidence from backward masking. *Journal of Memory and Language, 27,* 59-70.

Perfetti, C., & Bolger, D. (2004). The brain might read that way. *Scientific Studies of Reading, 8*, 293-304.

Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical Neurophysiology, 110,* 1842-57.

Plaut, D. C. (1995). Double dissociation without modularity: Evidence from connectionist neuropsychology. *Journal of Clinical and Experimental Neuropsychology, 17,* 291-321.

Plaut, D. C., McClelland, J. L., Seidenberg, M. S., & Patterson, K. (1996). Understanding normal and impaired word reading: Computational principles in quasi-regular domains. *Psychological Review, 103,* 56.

Poldrack, R. A., Temple, E., Protopapas, A., Nagarajan, S., Tallal, P., Merzenich, M., & Gabrieli, J. D. (2001). Relations between the neural bases of dynamic auditory processing and phonological processing: Evidence from fMRI. *Journal of Cognitive Neuroscience, 13*, 687-697.

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

Price, C. J., & Devlin, J. T. (2003). The myth of the visual word form area. *NeuroImage, 19*, 473-481.

Price, C., Winterburn, D., Giraud, A., Moore, C., & Noppeney, U. (2003). Cortical localisation of the visual and auditory word form areas: a reconsideration of the evidence. *Brain and Language, 86,* 272-286.

Pugh, K. R., Shaywitz, B. A., Shaywitz, S. E., Constable, R. T., Skudlarski, P., Fulbright, R. K., … Gore, J. C. (1996). Cerebral organization of component processes in reading. *Brain, 119*, 1221-1238.

Pulvermüller, F., Huss, M., Kherif, F., del Prado Martin, F. M., Hauk, O., & Shtyrov, Y. (2006). Motor cortex maps articulatory features of speech sounds. *Proceedings of the National Accademy of Science, 103*, 7865-7870.

Pulvermüller, F., Kherif, F., Hauk, O., Mohr, B., & Nimmo-Smith, I. (2009). Distributed cell assemblies for general lexical and category-specific semantic processing as revealed by fMRI cluster analysis. *Human Brain Mapping, 30,* 3837-3850.

Pulvermüller, F., Shtyrov, Y., & Hauk, O. (2009). Understanding in an instant: Neurophysiological evidence for mechanistic language circuits in the brain. *Brain and Language, 110*, 81-94.

Quinn, A. (2011). *Towards a Dynamic Architecture for the Reading Network; Insights from Time-Variant, Effective Connectivity* (Unpublished master's dissertation). University of York, York, UK.

Quiroga, R. Q., & Garcia, H. (2003). Single-trial event-related potentials with wavelet denoising. *Clinical Neurophysiology, 114*, 376-390.

Raab, D. H. (1963). Backward masking. *Psychological Bulletin, 60,* 118-129.

Rapp, B., Folk, J., & Tainturier, M.-J. (2001). Word Reading. *The handbook of cognitive neuropsychology,* (pp. 233-262). Philadelphia: Psychology Press.

Rastle, K., & Brysbaert, M. (2006). Masked phonological priming effects in English: Are they real? Do they matter? *Cognitive Psychology*, *53*, 97-145.

Rastle, K., & Coltheart, M. (1999). Lexical and nonlexical phonological priming in reading aloud. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 461-481.

Rayner, K. (1998). Eye movements in reading and information processing: 20 years of research. *Psychological Bulletin*, *124,* 372.

Rayner, K., Foorman, B. R., Perfetti, C. A., Pesetsky, D., & Seidenberg, M. S. (2001). How psychological science informs the teaching of reading. *Psychological Science in the Public Interest, 2,* 31-74.

Reinke, K., Fernandes, M., Schwindt, G., O'Craven, K., & Grady, C. L. (2008). Functional specificity of the visual word form area: General activation for words and symbols but specific network activation for words. *Brain and Language*, *104*, 180-189.

Reynolds, C., & Kamphaus, R. (2007). *Test of Irregular Word Reading Efficiency*. Austin, TX: Pro-Ed.

Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G., & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkely. II. Area F5 and the control of distal movements. *Experimental Brain Research, 71,* 491-507.

Rizzolatti, G. & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscieince, 27,* 169-192.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, *3,* 131-141.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience, 2*, 661-670.

Rizzolatti, G., Fogassi, L., & Gallese, V. (2002). Motor and cognitive functions of the ventral premotor cortex. *Current Opinions in Neurobiology, 12*, 149-154.

Roelofs, A. (2006). The influence of spelling on phonological encoding in word reading, object naming, and word generation. Psychonomic bulletin & review, 13, 33-37.

Rubenstein, H., Lewis, S. S., & Rubenstein, M. A. (1971). Evidence for phonemic recoding in visual word recognition. *Journal of Verbal Learning & Verbal Behavior*, *10*, 645-657.

Rueckl, J. G. (2002). The dynamics of visual word recognition. *Ecological Psychology, 14*, 5-19.

Rushworth, M. F., Krams, M., & Passingham, R. E. (2001). The attentional role of the left parietal cortex: The distinct lateralization and localization of motor attention in the human brain. *Journal of Cognitive Neuroscience, 13,* 698-710.

Sack, A. T., Kadosh, R. C., Schuhmann, T., Moerel, M., Walsh, V., & Goebel, R. (2009). Optimizing functional accuracy of TMS in cognitive studies: A comparison of methods. *Journal of Cognitive Neuroscience, 21*, 207-221.

Sahin, N. T., Pinker, S., Cash, S. S., Schomer, D., & Halgren, E. (2009). Sequential Processing of Lexical, Grammatical, and Phonological Information Within Broca’s Area. *Science, 326*, 445-449.

Saur, D., Lange, R., Baumgaertner, A., Schraknepper, V., Willmes, K., Rijntjes, M., & Weiller, C. (2006). Dynamics of language reorganization after stroke. *Brain, 129*, 1371-1384.

Scarborough, H. S., Ehri, L. C., Olson, R. K., & Fowler, A. E. (1998). The fate of phonemic awareness beyond the elementary school years. *Scientific Studies of Reading, 2*, 115-142.

Schuhmann, T., Schiller, N. O., Goebel, R., & Sack A. T. (2009). The temporal characteristics of functional activation in Broca's area during overt picture naming. *Cortex, 45*, 1111-1116

Schuhmann, T., Schiller, N. O., Goebel, R., & Sack A. T. (2011). Speaking of which: Dissecting the neurocognitive network of language production in picture naming. *Cerebral Cortex.* Advance online publication. doi:10.1093/cercor/bhr155

Scott, S. K., & Johnsrude, I. S. (2003). The neuroanatomical and functional organization of speech perception. *Trends in Neurosciences, 26,* 100-107.

Scott, S. K., McGettigan, C., & Eisner, F. (2009). A little more conversation, a little less action—candidate roles for the motor cortex in speech perception. *Nature Reviews Neuroscience, 10,* 295-302.

Seidenberg, M. S. (2005). Connectionist models of word reading. *Society, 14*, 238-242.

Seidenberg, M. S., & McClelland, J. L. (1989). A distributed, developmental model of word recognition and naming. *Psychological Review*, *96*, 523-568.

Sereno, S. C., & Rayner, K. (2000). The When and Where of Reading in the Brain. *Brain and Cognition*, *81*, 78-81.

Shallice, T. (1979). Case study approach in neuropsychological research. *Journal of Clinical and Experimental Neuropsychology*, *1*, 183-211.

Shallice, T. (1988). *From neuropsychology to mental structure.* New York, NY: Cambridge University Press.

Shaywitz, S. E., Escobar, M. D., Shaywitz, B. A., Fletcher, J. M., & Makuch, R. (1992). Evidence that dyslexia may represent the lower tail of a normal distribution of reading ability. *New England Journal of Medicine*, *326*, 145-150.

Snodgrass, J. G. & Vanderwart, M. (1980). A standardised set of 260 pictures: Norms for name agreement, image agreement, familiarity, and visual complexity. *Journal of Experimental Psychology: Human Learning and Memory*, *6*, 174-215.

Spencer, T. J., & Shuntich, R. (1970). Evidence for an interruption theory of backward masking. *Journal of Experimental Psychology*, *85*, 198-203.

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

Stewart, L., Walsh, V., & Rothwell, J. (2001). Motor and phosphene thresholds: A transcranial magnetic stimulation correlation study. *Neuropsychologia*, *39*, 415-419.

Stockwell, R.G., Mansinha, L., & Lowe, R.P. (1996) Localization of the complex spectrum: The S transform. *IEEE Transactions of Signal Processing, 44,* 998-1001.

Talairach, J. & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain. 3-dimensional proportional system: An approach to cerebral imaging*. New York: Thieme Medical Publishers.

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences, 3,* 151-162.

Tallon-Baudry, C., Bertrand, O., Peronnet, F., & Pernier, J. (1998). Induced gamma-band activity during the delay of a visual short-term memory task in humans. *Journal of Neuroscience, 18,* 4244-4254.

Thompson-Schill, S. L., Aguirre, G.K., D'Esposito, M., & Farah, M. J. (1999). A neural basis for category and modality specificity of semantic knowledge. *Neuropsychologia*, *37,* 671-676.

Thut, G., Veniero, D., Romei, V., Miniussi, C., Schyns, P., & Gross, J. (2011). Rhythmic TMS causes local entrainment of natural oscillatory signatures. *Current Biology*, *21,* 1176-1185.

Torgersen, J.K., Wagner, R.K., & Rashotte, C.A., (1999). *Test of Word Reading*

Efficiency. Austin TX: Pro-Ed.

Turkeltaub, P. E, Eden, G. F., Jones, K. M., & Zeffiro, T. A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: Method and validation. *NeuroImage, 16,* 765-780.

Twomey, T., Duncan, K. J. K., Price, C. J., & Devlin, J. T. (2011). Top-down modulation of ventral occipito-temporal responses during visual word recognition. *NeuroImage*, *55*, 1242-1251.

Tzelgov, J., Henik, A., Sneg, R., & Baruch, O. (1996). Unintentional word reading via the phonological route: The Stroop effect with cross-script homophones. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *22*, 336-349.

Tzur, B., & Frost, R. (2007). SOA does not reveal the absolute time course of cognitive processing in fast priming experiments. *Journal of memory and language*, *56*, 321-335.

Van Atteveldt, N. M., Formisano, E., Blomert, L., & Goebel, R. (2007). The effect of temporal asynchrony on the multisensory integration of letters and speech sounds. *Cerebral Cortex*, *17*, 962-974.

Van Orden, G. C. (1987). A ROWS is a ROSE: Spelling, sound, and reading. *Memory & Cognition*, *15*, 181-198.

Van Orden, G. C., Johnston, J. C., & Hale, B. L. (1988). Word identification in reading proceeds from spelling to sound to meaning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *14,* 371-386.

Van Orden, G. C., Pennington, B. F., & Stone, G. O. (1990). Word identification in reading and the promise of subsymbolic psycholinguistics. *Psychological Review*, *97*, 488-522.

Van Veen, B., van Drongelen, W., Yuchtman, M., & Suzuki, A. (1997). Localization of brain electrical activity via linearly constrained minimum variance spatial filtering. *IEEE Transactions on Biomedical Engineering*, *44*, 867-880.

Vellutino, F. R., Fletcher, J. M., Snowling, M. J., & Scanlon, D. M. (2004). Specific reading disability (dyslexia): What have we learned in the past four decades? *Journal of Child Psychology and Psychiatry*, *45*, 2-40.

Verstaen, A., Humphreys, G. W., & Olson, A. (1995). Are phonemic effects in backward masking evidence for automatic prelexical phonemic activation in visual word recognition? *Journal of Memory and Language, 34,* 335-356.

Vigneau, M., Beaucousin, V., Herve, P., Duffau, H., Crivello, F., Houde, O., … Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing. *NeuroImage, 30,* 1414-1432.

Vigneau, M., Jobard, G., Mazoyer, B., & Tzourio-Mazoyer, N. (2005). Word and nonword reading: What role for the visual word form area? NeuroImage, 27, 694-705.

Vihla, M., Laine, M., & Salmelin, R. (2006). Cortical dynamics of visual/semantic vs. phonological analysis in picture confrontation. *Neuroimage*, *33*, 732-738.

Visser, M., Jefferies, E., & Lambon Ralph, M. (2010). Semantic processing in the anterior temporal lobes: a meta-analysis of the functional neuroimaging literature. *Journal of Cognitive Neuroscience*, *22,* 1083-1094.

Vogel, S. A., & Holt, J. K. (2003). A comparative study of adults with and without self-reported learning disabilities in six English-speaking populations: What have we learned? *Dyslexia*, *9,* 193-228.

Vrba, J. (2002). Magnetoencephalography: The art of finding a needle in a haystack. *Physica C: Superconductivity, 368,* 1-9.

Vrba, J., & Robinson, S. E. (2001). Signal processing in magnetoencephalography. *Methods, 25*, 249-71.

Walsh, V., & Rushworth, M. (1999). A primer of magnetic stimulation as a tool for neuropsychology. *Neuropsychologia, 37,* 125-136.

Wassermann, E. M. (1998). Risk and safety of repetitive transcranial magnetic stimulation: report and suggested guidelines from the International Workshop on the Safety of Repetitive Transcranial Magnetic Stimulation, June 5-7, 1996. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section, 108,* 1-16.

Wernicke, C. (1874). *Der aphasiche symptomenkomplex.* Breslau Poland: Cohen and Weigert.

Wheat, K. L., Cornelissen, P. L., Frost, S. J., & Hansen, P. C. (2010). During visual word recognition phonology is accessed within 100 ms and may be mediated by a speech production code: Evidence from MEG. *Journal of Neuroscience, 30*, 5229-5233.

Whitney, C. S., & Cornelissen, P. L. (2005). Letter-position encoding and dyslexia. *Journal of Research in Reading, 28*, 274-301.

Willems, R. M., Özyürek, A., & Hagoort, P. (2007). When language meets action: The neural integration of gesture and speech. *Cerebral Cortex*, *17,* 2322-2333.

Wilson, L. B., Tregellas, J. R., Slason, E., Pasko, B. E., & Rojas, D. C. (2010). Implicit phonological priming during visual word recognition. *NeuroImage*. *55*, 724-731.

Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, *9*, 625-636.

Wimmer, H., Schurz, M., Sturm, D., Richlan, F., Klackl, J., Kronbichler, M., & Ladurner, G. (2010). A dual-route perspective on poor reading in a regular orthography: An fMRI study. *Cortex, 46*, 1284-1298.

Woodhead, Z. V. J., Brownsett, S. L. E., Dhanjal, N. S., Beckmann, C., & Wise, R. J. S. (2011). The visual word form system in context. *The Journal of Neuroscience, 31*, 193-199.

Zevin, J. D., & Seidenberg, M. S. (2006). Simulating consistency effects and individual differences in nonword naming: A comparison of current models. *Journal of Memory and Language*, *54*, 145-160.

Ziegler, J. C., & Jacobs, A. M. (1995). Phonological information provides early sources of constraint in the processing of letter strings. *Journal of Memory and Language*, *34*, 567-593.

Ziegler, J. C., Bertrand, D., Toth, D., Csepe, V., Reis, A., Faisca, L., … Blomert, L. (2010). Orthographic Depth and Its Impact on Universal Predictors of Reading: A Cross-Language Investigation. *Psychological Science, 21*, 551-559.

Ziegler, J. C., Muneaux, M., & Grainger, J. (2003). Neighborhood effects in auditory word recognition: Phonological competition and orthographic facilitation. *Journal of Memory and Language*, *48*, 779-793.

Zimmerman, D. W. (1994). A note on the influence of outliers on parametric and nonparametric tests. *The Journal of General Psychology, 121*, 391-401.