A Behavioural and Neurobiological Investigation of Basic Reading Processes

The act of reading aloud is routine for skilled readers and thus our awareness of the underlying processes is quite nominal. Dating at least as far back as Cattell (1886), researchers have strived to uncover the underlying processes that are at work during normal and impaired reading (e.g., Besner & Smith, 1992; Forster & Chambers, 1973; Marshall & Newcombe, 1973; Plaut, 1999; Pugh, et al., 1996; Sandak, Mencl, Frost, & Pugh, 2004). Despite all the years of investigation, researchers are still debating the basic processes involved in the translation of print to speech.

Publications from our laboratory have suggested that two systems contribute to basic reading processing, which will be referred to as sight vocabulary (SV) and phonetic decoding (PD) throughout this dissertation (Borowsky, Cummine, Owen, Friesen, Shih, & Sarty, 2006; McDougall, Borowsky, MacKinnon, & Hymel, 2005; see also Forster & Chambers, 1973; Marshall & Newcombe, 1973).[1] The SV, or whole-word, system is involved in the processing of words via their whole-word representations. Thus, accuracy in reading letter strings to which the spelling-to-sound correspondence is atypical, such as exception words (EXCs; e.g., *pint*, given that the remainder of the _int family of words are pronounced with a short vowel) reflects processing of the SV system because these words can only be read correctly by SV processing. In contrast, the PD, or sub-word system, is involved in the processing of words via grapheme-phoneme correspondences. Letter strings are broken down into graphemes and are 'sounded out' based on our existing phonological knowledge. In this case, accuracy in reading nonwords (NWs; e.g., *bint*) reflects processing of the PD system because these words can only be read correctly by PD processing. It has been recently argued that pseudohomophones (PHs; e.g., *pynt*) might serve as a more ecologically valid measure of PD processing, given that they have a

familiar phonological lexical representation to be checked against whereas NWs do not (Borowsky et al., 2006; McDougall et al., 2005; Owen, Borowsky & Sarty, 2004). Although the role of the PD system is to translate orthography into phonology using grapheme-phoneme rules, a crucial step in reading via the PD system is to 'check' the derived pronunciation against the phonological lexical system prior to speech (e.g., consider the situation when one is decoding a word they have heard but never seen before, as is the case during reading development). While NWs are considered a measure of PD processing, PHs capture PD processing that incorporates the crucial aspect of checking one's phonological lexical system; a component of reading that is important for achieving correct pronunciation (Borowsky, Owen & Masson, 2002; Kinoshita, Lupker, & Rastle, 2004). Further, PHs may also serve as a more valid type of stimulus for activating the PD system given that NW naming accuracy is subject to the researcher's interpretation (e.g., a nonword like "gead" can rhyme with 'bead' or 'head', and the onset can be pronounced hard like 'get' or soft like 'gem'). PHs might correct for this problem by providing participants with stimuli that have unfamiliar spelling patterns but familiar phonological lexical representations. Finally, regular words (REGs; e.g., *mint*) are letter strings which have characteristics of both SV and PD processing. That is, while REGs can be read via a grapheme-phoneme mapping, such stimuli are often assumed to be read via a whole-word system (i.e., SV) if they are of high familiarity.

How these systems (i.e., SV and PD) interact during basic word recognition is still hotly debated. For example, several researchers have promoted a single-mechanism account of reading aloud (i.e., where the system that represents SV is redundant with the system that represents PD; see Figure 1A; e.g., the Parallel Distributed Processing group; Plaut, 1999; Plaut & Booth, 2000; 2006; Plaut, McClelland, Seidenberg, & Patterson, 1996; and some analogy

Models of Basic Reading Systems

Model of Redundancy:
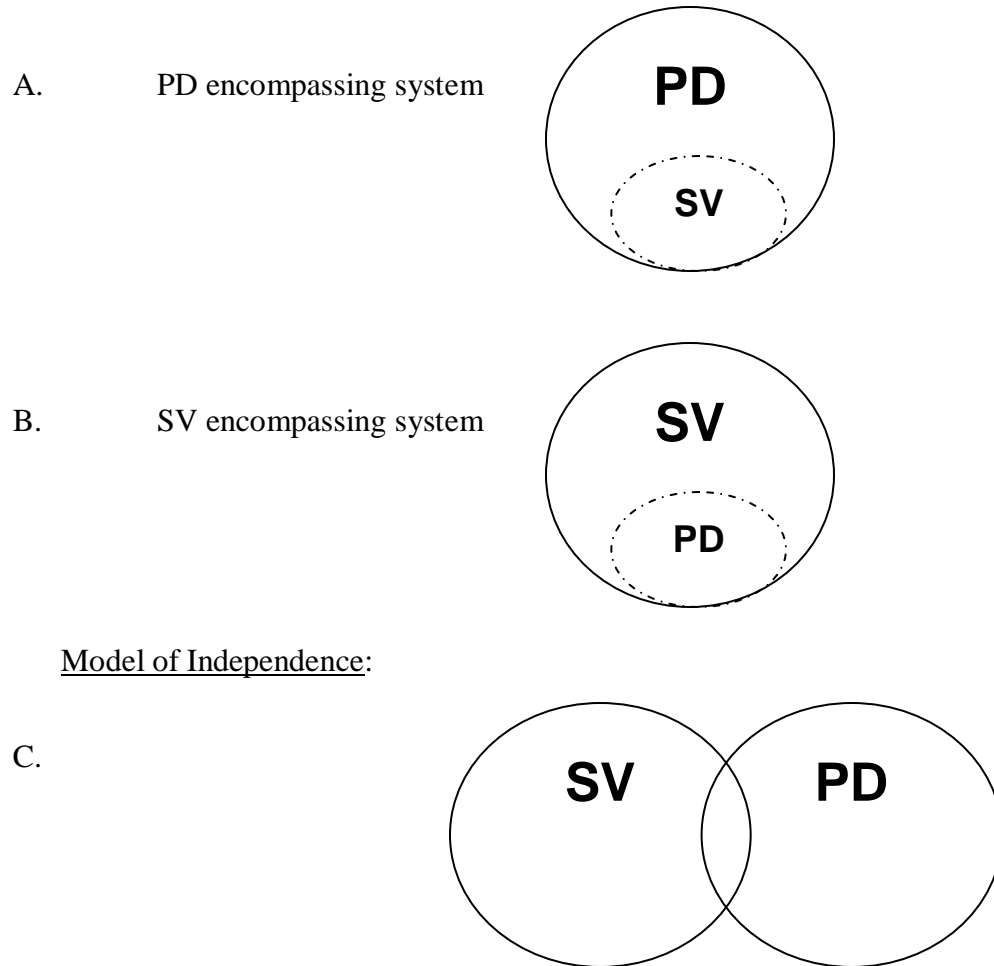
A.   PD encompassing system

PD

SV

B.   SV encompassing system

SV

PD

Model of Independence:

C.

SV   **PD**

Figure 1. Models for the relationship between sight vocabulary (SV) and phonetic decoding (PD) systems: A. Redundancy between SV and PD (i.e., single mechanism) whereby PD is the encompassing system, B. Redundancy between SV and PD (i.e., single mechanism) whereby SV is the encompassing system, C. The model of mathematical independence between SV and PD (i.e., dual – route mechanisms) suggests that two systems (i.e., SV *and* PD) are necessary for basic reading processes. The models of redundancy suggest a single system (i.e., SV *or* PD) is necessary for basic reading processes.

theorists, see Figure 1B; e.g., Glushko 1979; Marchand & Damper, 2004; Marchand & Damper, 2000). Other researchers have argued that at least two distinct processes are required to account for reading aloud (i.e., the systems that represent SV and PD are mathematically independent, see Figure 1C; e.g., the Dual-Route theorists, Besner & Smith, 1992; Forster & Chambers, 1973; Marshall & Newcombe, 1973; Paap & Noel, 1991). [2] The following two sections provide an overview of current literature on dual-route and single-mechanism models in basic word recognition.
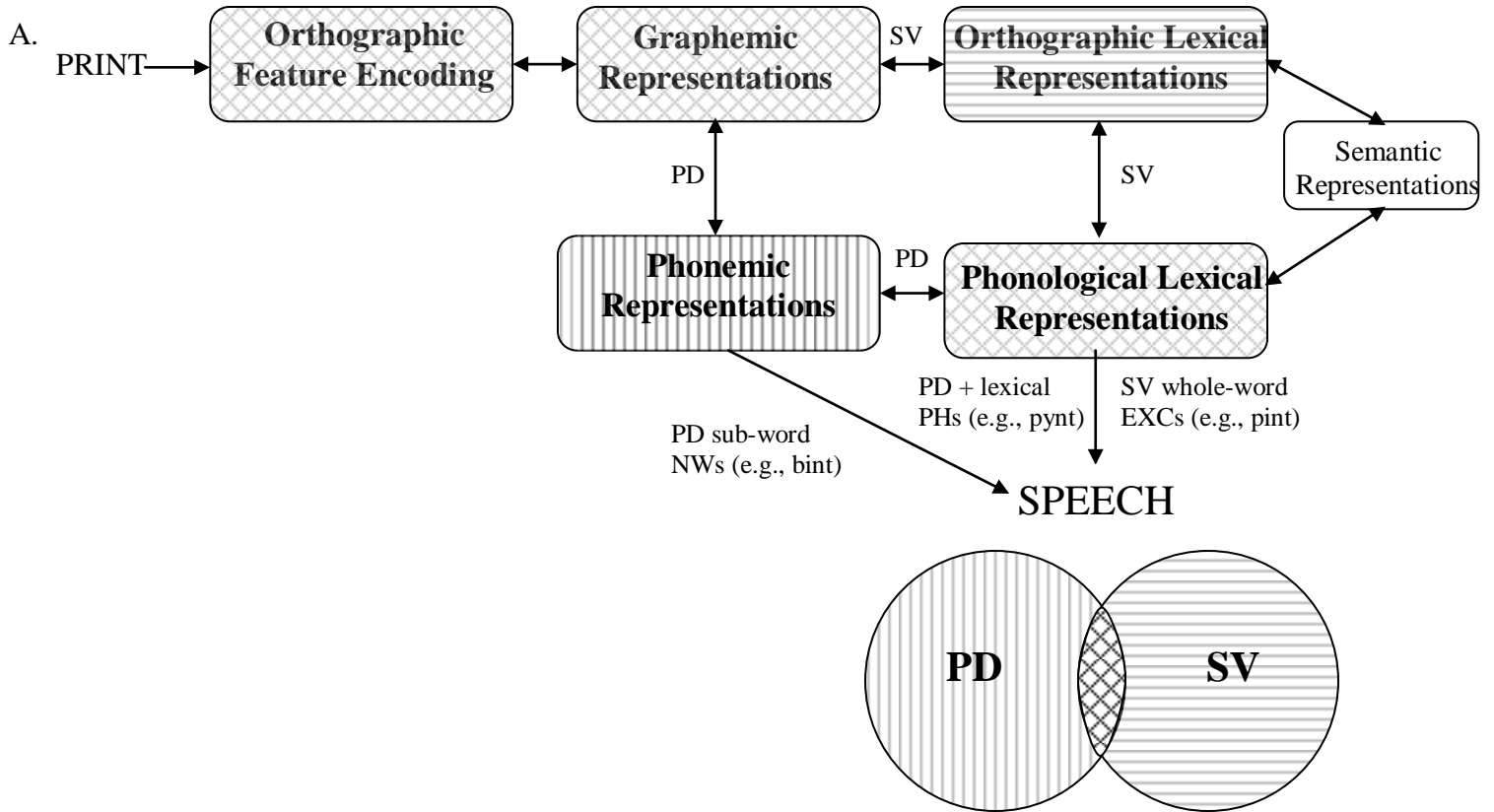
Dual-Route Model of Basic Reading Processes

The dual-route model of basic reading processes makes a major distinction between two routes referred to as lexical (i.e., SV or whole-word) and sub-lexical (i.e., PD or sub-word) systems (see Figure 2A; e.g., Besner & Smith, 1992; Coltheart et al., 2001; Forster & Chambers, 1973; Marshall & Newcombe, 1973; Paap & Noel, 1991). Although both systems begin at a level of orthographic encoding and end at a motor output system (in the case of overt naming), they contribute to correct naming independently. Similar to our representations of SV and PD processing, the lexical system specializes in processing whole-word stimuli such as EXCs and the sub-lexical system specializes in reading sub-word stimuli such as NWs or PHs (e.g., Glushko, 1979; Monsell, Graham, Hughes, Patterson & Milroy, 1992). Both of these systems can independently contribute to the correct naming of familiar REGs given that such words have both lexical representations and typical spelling-to-sound correspondences.[3]

Single-Mechanism Models

In contrast to the dual-route model of reading, several researchers have proposed a single-mechanism model of reading acquisition and suggested that only one mechanism or system is necessary to name words and develop reading skills (see Figure 2B.; Glushko, 1979; Marchand

Mathematically Independent Dual Route Model
(i.e., dual mechanisms)

A.

PRINT → **Orthographic Feature Encoding** ↔ **Graphemic Representations** —SV→ **Orthographic Lexical Representations**

Semantic Representations

PD (Graphemic ↔ Phonemic)

SV (Orthographic Lexical ↔ Phonological Lexical)

Phonemic Representations —PD→ **Phonological Lexical Representations**

PD + lexical PHs (e.g., pynt)   SV whole-word EXCs (e.g., pint)

PD sub-word NWs (e.g., bint)

SPEECH

PD   SV

Redundant Single Route Model
(i.e., single mechanism)

B.

PRINT → **Orthographic Representations** ↔ Semantic Representations

↕

Phonological Representations ↔
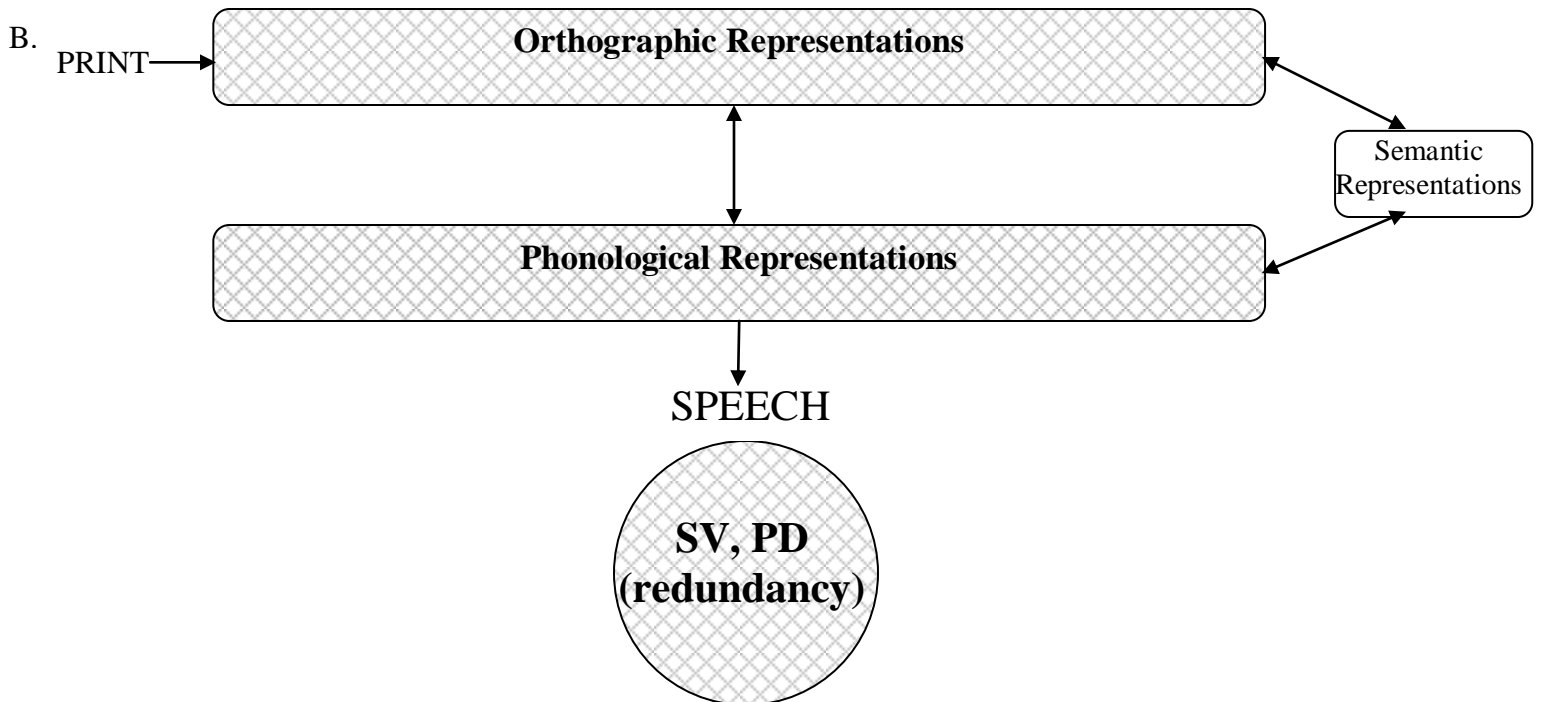
SPEECH

SV, PD (redundancy)

5

Figure 2. Depiction of the relationship between sight vocabulary and phonetic decoding in a dual-route model. A representation of the pathways involved in the translation of print to speech using nonwords (NWs), pseudohomophones (PHs) and exception words (EXCs); regular words (REGs; e.g., hint) can be read by either or both routes.

& Damper, 2000; 2004; Plaut et al., 1996; Plaut, 1999). Often single mechanism models suggest that the need for a separate rule-based mechanism is unnecessary and overcomplicates the interpretations of simple word reading findings (i.e., Glushko, 1979; Marchand & Damper, 2000; Plaut, 1999). Instead, general stored information about letter strings, letter features and spelling-to-sound correspondences of subparts of the letter strings are accessed from a single system to pronounce words and novel words (Glushko, 1979). The underlying principles outlined by Glushko (1979) have been applied to several single mechanism models in the current literature. Two such models are described in more detail below.

The architecture of the single mechanism model proposed by Plaut et al. (1996) involves a distributed representation of phonemes in which units correspond to phonetic features. These representations are part of a larger network in which all of the phonetic feature units are connected to each other and to a set of phonological cleanup units. Plaut (1999; see also Plaut et al., 1996) emphasizes the cooperative division of labor using input from all parts of the processing system (i.e., orthographic representations and phonological representations) and explicitly contrasts his model with the dual-route model that involves two distinct and different pathways to translate print to speech.

Marchand and Damper (2000; 2004) who suggest basic reading processes are carried out via lexical analogy propose another single-mechanism model. Words (both known and novel ones) are presented to the input system and their spelling patterns are evaluated. The incoming stimulus is then matched against all orthographic entries in the lexicon. Processing continues in a feed-forward fashion whereby information about substrings having common letters to the incoming stimulus is continually evaluated until an appropriate pronunciation is composed. Thus, it is the phonological knowledge and corresponding pronunciation of words, which is

implicitly contained in one's lexicon that is utilized to name words and novel words (Marchand & Friedman, 2005).

Although neither Plaut's (1999) nor Marchand and Damper's (2000; 2004) model is explicit in their claims to whether a mechanism of SV or PD is the encompassing system at work during word naming, such a clarification is not necessary. The critical point is that there are competing theories in the literature regarding whether successful word naming requires single or multiple routes. Our work assesses both possible models of redundancy with SV as the encompassing system and with PD as the encompassing system (and with two measures of PD) in an attempt to maximize what single mechanism models might encapsulate. The incorporation and evaluation of such models allows us to assess whether a representation of reading that relies solely on PD processing or one that relies solely on SV processing can adequately characterize behavioural and functional measures from basic naming studies.

Overview

The present work evaluated basic reading processes from two methodological perspectives (i.e., behavioural and neurobiological) and from two research perspectives (i.e., basic and applied). Chapter 1 evaluates evidence for whether single versus multiple routes are involved in the translation of print to speech via equations that predict mathematical independence or redundancy between SV and PD processes. Both behavioural and functional measures are examined and the extent to which reading performance can be accurately accounted for is assessed. Chapter 2 evaluates evidence for single versus multiple routes via functional data that provides critical information about the pathways involved during basic reading processes. In Chapter 3, behavioural and functional measures are compared to evaluate the extent to which such data can be integrated to provide more information about specific sub-systems within SV

and PD routes and the contribution of particular brain regions to reading particular stimuli. Chapter 4 evaluates overt naming with respect to motion artefacts that emerge when NW stimuli are read and provides critical information regarding methodological considerations that should be taken into account when conducting behavioural and functional research on basic reading processes. Finally, in Chapter 5 basic and applied areas of research involving SV and PD processes are compared to help inform and develop models of impaired reading.

Chapter 1: The Relationship Between Sight Vocabulary and Phonetic Decoding

Summary

Both behavioral (naming accuracy and reaction time) and neurobiological (fMRI measures) evidence for the relationship between SV and PD was evaluated. Importantly, behavioral research has not yet compared all existing models of basic reading (i.e., independence and redundancy) within a single study, and has not yet investigated the extent to which mathematical independence is found in behavioural measures other than accuracy. In addition, an evaluation of mathematical independence has yet to be applied to measures extracted from neurobiological research. Such an investigation is important for assessing the relationship between SV and PD. Overall, we provide strong support for a mathematically independent model of basic reading processes, both behaviorally and neurobiologically.

Experiment 1 replicated and extended previous behavioural findings of mathematical independence between SV and PD with naming accuracy. More specifically, we examined basic reading in a skilled population and provided a more thorough examination of several possible theoretical models of basic reading.   The application of equations derived for predicting REG reading accuracy that assume mathematical independence between SV and PD systems (i.e., dual-route models) or redundancy between these systems (i.e., single mechanism models) were evaluated.   Multiple regression analyses were conducted that assessed whether actual REG reading performance was best accounted for with a model of independence or redundancy. Our results provide support for mathematical independence between SV and PD on behavioural naming accuracy.

Experiment 2, (published in **Cummine, J.**, Borowsky, R., Vakorin, V., Bird, J, & Sarty, G. (2008). *Magnetic Resonance Imaging*, *26*, 824-834) examined the extent to which

mathematical independence would be evident in other measures, namely behavioural response time and the Blood Oxygenation Level Dependent (BOLD) response width, intensity, time to peak, volume and initial slope when participants named aloud REGs, EXCs, NWs and PHs while in an fMRI experiment. Regression analyses were conducted to examine the extent to which obtained REG naming measures could be predicted given equations derived to reflect various models. Our results provide support for mathematical independence between SV and PD on behavioural response time and BOLD width, intensity and time to peak.

Introduction

Experiment 1

One way to conceptualize the dual-route and single mechanism theories of reading can be represented by models of independence and redundancy, respectively (see Figure 1). The model of independence suggests that two systems exist for processing letter strings (Figure 1C and Figure 2A). Although these systems overlap and thus share in some aspects of processing (e.g., early visual analysis or orthographic encoding and later articulatory phonetics or motor output) both systems are necessary to allow for the correct reading of all types of letter strings. As previously mentioned, the SV system correctly reads EXCs and the PD system correctly reads novel words (e.g., NWs and PHs). Both systems can contribute to the correct naming of REGs. As a demonstration of this mathematical independence between the SV and PD systems, McDougall et al. (2005; see also Castles, Bates & Coltheart, 2006) developed an equation to predict REG reading accuracy given SV and PD processing:

$$A_{REG} = SV + PD - (SV * PD) \tag{1.1}$$

This can be expressed as,

$$A_{REG} = A_{EXC} + A_{NW} - (A_{EXC}A_{NW}) \tag{1.2}$$

or

$$A_{REG} = A_{EXC} + A_{PH} - (A_{EXC}A_{PH}). \tag{1.3}$$

Where A_{REG} represents accuracy in REG naming, A_{EXC} represents accuracy in EXC naming, A_{NW} represents accuracy in NW naming and A_{PH} represents accuracy in PH naming. A_{EXC} serves as a measure of performance of the SV system and A_{NW} and A_{PH} are measures of the performance of the PD system.

The models that assume redundancy suggest that only one system or a single mechanism is necessary for basic word processing (Figure 1A and 1B). Any other level of representation (i.e., sub-levels) must be assumed to be redundant within the encompassing system. The models of redundancy can be further broken down into two types. The first model is representative of a theory that suggests all words are read via analogy to our lexicon. Such a model would predict REG accuracy by the following equation:

$$A_{REG} = A_{EXC} \qquad (1.4)$$

Given that EXC reading accuracy reflects processing of the SV system, it can be suggested that accuracy in naming EXCs would be an accurate predictor of accuracy in naming REGs. The second redundancy model would represent a theory that suggests all words are read via their phonological representations. This model is represented by the following equation:

$$A_{REG} = A_{NW} \qquad (1.5)$$

or

$$A_{REG} = A_{PH} \qquad (1.6)$$

Given that NW or PH reading accuracy both reflect processing of the PD system it can be suggested that accuracy in naming NWs or PHs would be an accurate predictor of accuracy in naming REGs.

Research regarding the prediction of REG reading accuracy from EXC and NW reading accuracy and the independent relationship between SV and PD systems has primarily focused on children, although the dual-route theory from which such equations are based is clearly able to generalize to skilled readers (Castles et al., 2006; Coltheart et al., 2001; McDougall et al., 2005). Thus, an examination of the dual-route theory and derived equations with a skilled population allowed us to determine the robustness of these claims.

The goal of Experiment 1 was to replicate and extend the findings of McDougall et al. (2005; see also Castles et al., 2006) by examining the extent to which SV and PD systems display a mathematically independent relationship in skilled adult readers. We considered behavioural evidence by comparing *obtained* to *predicted* REG word reading accuracy given the equations previously outlined.

Methods

Participants

Undergraduate students (N=64; mean age = 19.67) performed the naming tasks, for credit in their Introductory Psychology course. Inclusion criteria consisted of normal or corrected normal vision, and English as a first language. The experiment was performed in compliance with the relevant laws and institutional guidelines, and was approved by the University of Saskatchewan Behavioral Sciences Ethics Committee (see Appendix A).

Stimuli

The stimuli consisted of REGs, EXCs, PHs, and NWs. There were 55 letter strings in each category for a total of 220 letter strings (see Appendix B for complete lists). Where applicable, stimuli were matched for onset phoneme, length and word frequency (McDougall et al., 2005).

Materials

Stimuli were presented on a PC computer running EPrime software (Psychology Software Tools, Inc., Pittsburgh, PA, 2003). The experimenter used a button response (i.e., mouse key) to code accuracy.

Procedure

Participants came to a lab where they were seated in front of a computer. The letter strings were presented in four pure blocks, stimuli were selected randomly for presentation within each block and instructions were given prior to each block. After giving written consent, participants were instructed to read each letter string aloud as quickly and accurately as possible. Letter strings were presented one at a time at the top of the computer screen in 18 point font. Participants had 1800ms to name the letter string. If naming was made before 250ms or after 1800ms, the response was coded as an error. The presentation of the letter string blocks was randomized using a Latin Square design to minimize any effects due to presentation order.

Results

Individual predicted accuracy scores were derived for each model (i.e., independence and redundancy) and for each participant using the equation outlined by McDougall et al., (2005; Equation 1.1) and the subsequently derived equations. Overall mean accuracy for each stimulus type was: Mean REG accuracy = .97, Mean EXC accuracy = .91, Mean NW accuracy = .83, and Mean PH accuracy = .84. Pearson correlation analyses were run to assess the relationships between accuracy scores for each class of stimuli (see Table 1) and between the independent variables (i.e., predicted REG accuracy) with the dependent variable (i.e., actual REG reading accuracy; see Table 2). Multiple linear regression analyses were conducted to evaluate the prediction of actual REG reading accuracy from the different models together (see Table 3). The dependent variable for the regression analyses was actual REG reading accuracy. The independent variables included predicted REG reading accuracy as derived from the model equations (i.e., independence and redundancy) computed two ways: either with NW or PH naming accuracy as the measure of PD proficiency.

Table 1. Pearson Correlation Matrix Values of Naming Accuracy for each Stimulus Type

	Exception Words	Nonwords	Pseudohomophones
Regular Words	.346*	.371*	.375*
Exception Words		.416*	.462*
Nonwords			.630*

*.*p*<.005

Table 2. Pearson Correlation Matrix Values of Actual Regular Word Naming Accuracy with the

Derived Models

	IND(nw)	IND(ph)	RED(exc)	RED(nw)	RED(ph)
ActualREG	.477*	.456*	.346*	.371*	.375*

*. *p*<.005

Abbreviations:

ActualREG = Actual regular word reading accuracy

Type of Stimuli: NW = Nonwords; PH = Pseudohomophones; EXC = Exception Words

E.g., IND(nw) = Predicted REG reading accuracy as derived from the independence model with EXC Accuracy

and NW Accuracy.

RED(exc) = Predicted REG reading accuracy as derived from the redundancy model with EXC Accuracy.

Independence vs. Redundancy

     Using NWs to measure PD. A multiple regression analysis was conducted to evaluate how well the predicted REG accuracy from the independence model ($A_{REG} = A_{EXC} + A_{NW} -$ ($A_{EXC}*A_{NW}$)) and the first redundancy model ($A_{REG} = A_{NW}$) could account for actual REG reading accuracy. As shown in Table 3, the overall regression model was significant. The predicted REG accuracy from the independence equation was significant within the overall model whereas the predicted REG accuracy from the redundancy equation was not. A partial regression plot was generated to depict the unique contribution of the independence model to actual REG reading accuracy after partialling out the contribution of the redundancy model with NWs from both variables (see Figure 3).

     Next, the predicted REG accuracy from the independence model and the second redundancy model ($A_{REG} = A_{EXC}$) were used to account for actual REG reading accuracy. The overall model was significant (Table 3). The predicted REG accuracy derived from the independence equation was significant within the overall model whereas the predicted REG accuracy from the redundancy equation was not. A partial regression plot was generated to depict the unique contribution of predicted REG reading accuracy as derived from the independence model to actual REG reading accuracy after partialling out the contribution of the redundancy model with EXCs from both variables (see Figure 4).

     Using PHs to measure PD. A multiple regression analysis was conducted to evaluate how well predicted REG reading accuracy from the independence model ($A_{REG} = A_{EXC} + A_{PH} -$ ($A_{EXC}*A_{PH}$)) and the first redundancy model ($A_{REG} = A_{PH}$) could account for actual REG reading accuracy. As shown in Table 3, the overall regression model was significant. In this analysis,

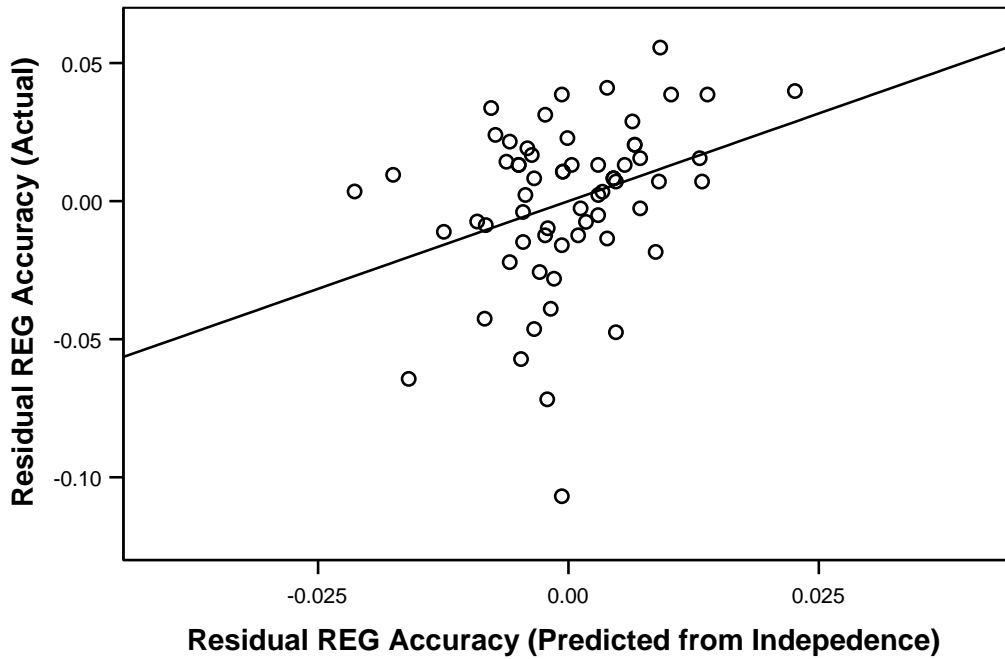Independence using (using NWs) vs. Redundancy (using NWs)

Figure 3. Partial regression plot of the residuals of actual REG reading accuracy as a function of the residuals of predicted REG reading accuracy as derived from the independence model with NWs after partialling out the unique contribution of the redundancy model with NWs from both variables. (Abbreviations: REG- regular word, NW- nonword)

Table 3. Regression Analyses of *Actual* Regular Naming Accuracy as a function of the Derived

Models

Multiple Regressions (for models)	Independent Variables	Adj.R^2	Semi-Partial	Coefficient	Standardized Coefficient	F	t	p
ActualREG = C + IND(nw) + RED(nw)		.21				9.19		<.001
	IND(nw) = EXC + NW − (EXC*NW)		.31	1.27	.58		2.73	.01
	RED(nw) = NW		-.06	-.04	-.12		-.57	.57
ActualREG = C + IND(nw) + RED(exc)		.21				9.03		<.001
	IND(nw) = EXC + NW − (EXC*NW)		.33	1.13	.51		2.94	.005
	RED(exc) = EXC		-.03	-.04	-.05		-.27	.79

	R²				t/F	p
ActualREG = C + IND(ph) + RED(ph)	.18				8.07	.001
IND(ph) = EXC + PH − (EXC*PH)		.26	1.31	.52	2.30	.03
RED(ph) = PH		-.04	-.03	-.08	-.34	.73
ActualREG = C + IND(ph) + RED(exc)	.18				8.02	.001
IND(ph) = EXC + PH − (EXC*PH)		.30	1.22	.49	2.62	.01
RED(exc) = EXC		-.02	-.03	-.04	-.21	.84
ActualREG = C + IND(nw) + IND(ph)	.21				9.44	<.001
IND(nw) = EXC + NW −		.17	.71	.32	1.51	.14

(EXC*NW)					
IND(ph) = EXC	.09	.45	.18	.84	.41
+ PH −					
(EXC*PH)					

Abbreviations:

ActualREG = Actual regular word reading accuracy; C = Constant

Type of Stimuli: NW = Nonword Accuracy; PH = Pseudohomophone Accuracy; EXC = Exception Word Accuracy

E.g., IND(nw) = Predicted REG reading accuracy as derived from the independence model with EXC Accuracy

and NW Accuracy.

   RED(exc) = Predicted REG reading accuracy as derived from the redundancy model with EXC Accuracy.

Independence using (using NWs) vs. Redundancy (using EXCs)
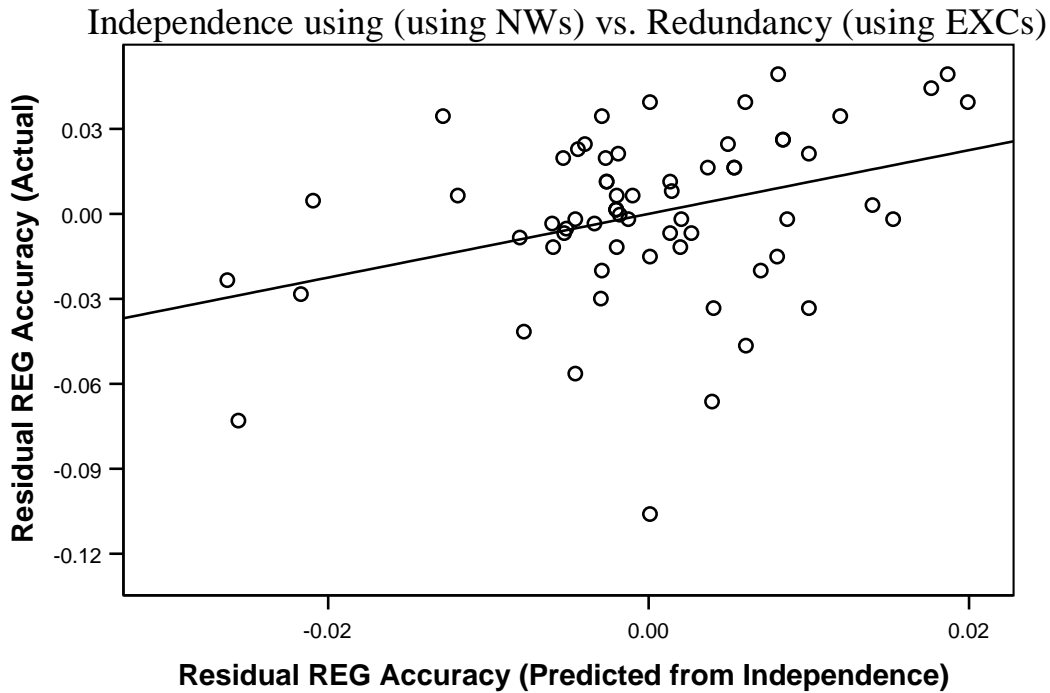
Figure 4. Partial regression plot of the residuals of actual REG reading accuracy as a function of the residuals of predicted REG reading accuracy as derived from the independence model with NWs after partialling out the unique contribution of the redundancy model with EXCs from both variables. (Abbreviations: REG- regular word, NW- nonword, EXC – exception word)

the predicted REG reading accuracy as derived from the independence equation accounted for significant unique variance in actual REG reading whereas the predicted REG reading accuracy as derived from the redundancy model did not. A partial regression plot was generated to depict the unique contribution of predicted REG reading accuracy from the independence model to actual REG reading accuracy after partialling out the contribution of the redundancy model with PHs from both variables (see Figure 5).

Finally, predicted REG reading accuracy from the independence model and the second redundancy model ($A_{REG} = A_{EXC}$) were used to account for actual REG reading accuracy. As seen in Table 3, the overall model was significant and only predicted REG reading accuracy as derived from the independence model accounted for unique variance in actual REG reading. A partial regression plot was generated to depict the unique contribution of predicted REG reading accuracy from the independence model to actual REG reading accuracy after partialling out the contribution of the redundancy model with EXCs from both variables (see Figure 6).

Using NWs and PHs to measure PD. A multiple regression analysis was conducted to evaluate how well predicted REG reading accuracy as derived from both independence equations (i.e., NWs and PHs) could account for actual REG reading accuracy. The overall regression model was significant (Table 3). However, given the amount of overlap in variance accounted for by the two variables, neither independence equation contributed any significant unique variance to REG reading accuracy within the overall model. [4]

Discussion

Results of Experiment 1 support the assumption of mathematical independence between SV and PD processes. When we compared REG reading accuracy predicted from the equations of independence and redundancy, a larger portion of variance in actual REG reading accuracy
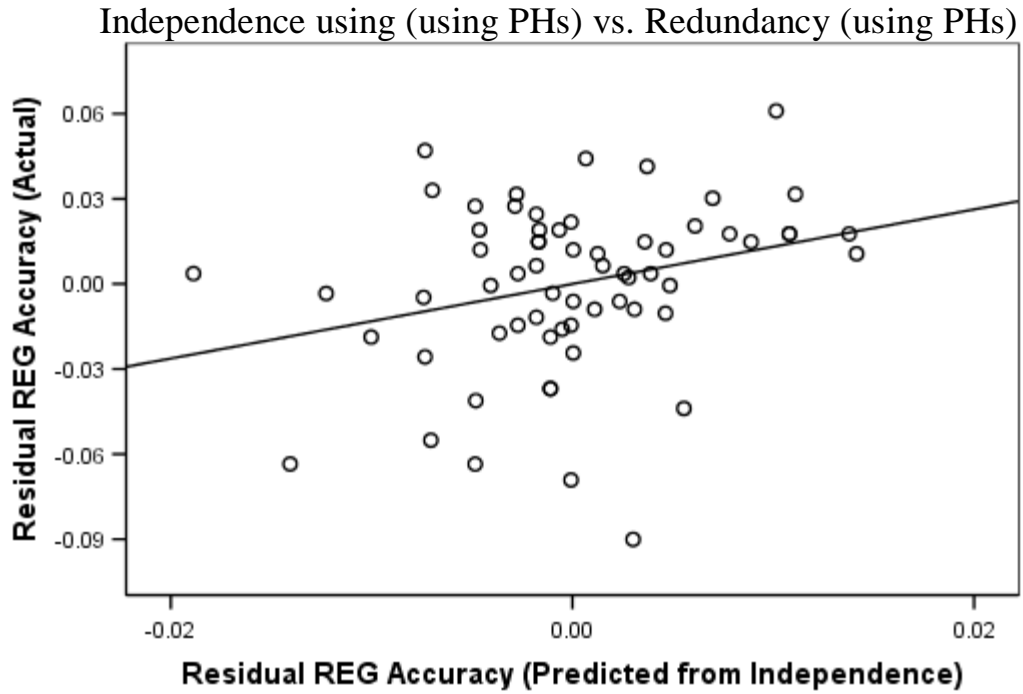
Independence using (using PHs) vs. Redundancy (using PHs)

Figure 5. Partial regression plot of the residuals of actual REG reading accuracy as a function of the residuals of predicted REG reading accuracy as derived from the independence model with PHs after partialling out the unique contribution of the redundancy model with PHs from both variables. (Abbreviations: REG- regular word, PH- pseudohomophone)
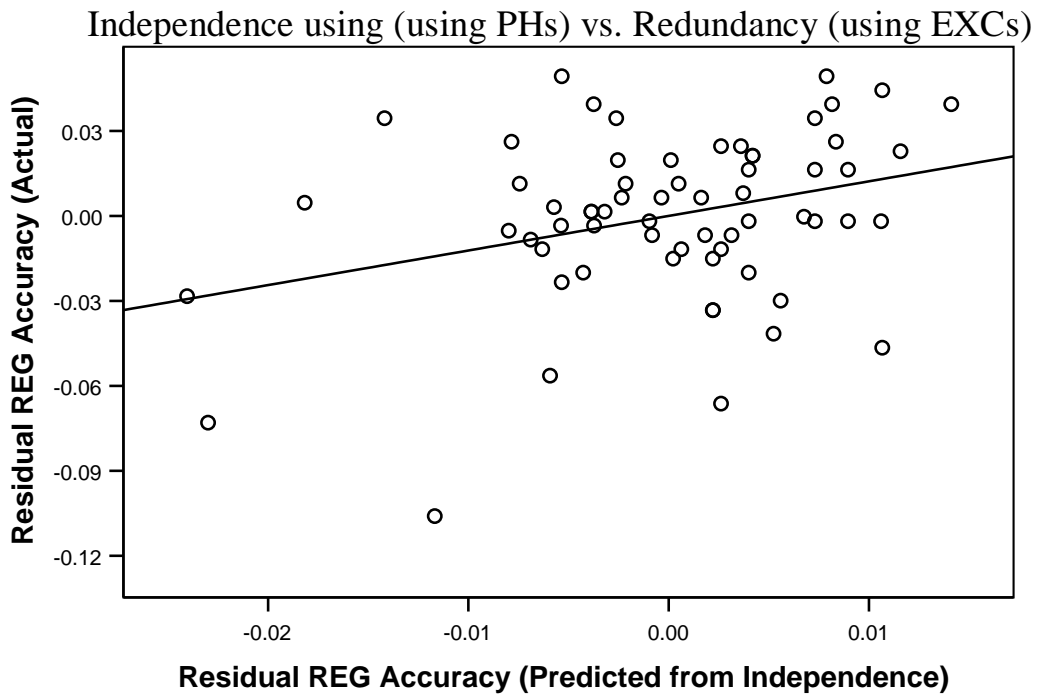
Independence using (using PHs) vs. Redundancy (using EXCs)

Figure 6. Partial regression plot of the residuals of actual REG reading accuracy as a function of the residuals of predicted REG reading accuracy as derived from the independence model with PHs after partialling out the unique contribution of the redundancy model with EXCs from both variables. (Abbreviations: REG- regular word, PH – pseudohomophone, EXC – exception word)

was accounted for by the predicted REG reading accuracy as derived from the independence equations than the redundancy equations. Furthermore, these results showed that a measure of PD based on PH naming accuracy produced similar results as found with PD based on NW naming accuracy. Given these results, it is suggested that PH reading accuracy not only has ecological validity, but also appears to capture similar PD processing as NWs in the independence equations.

Our work provides evidence for the extension of mathematically independent equations of naming accuracy to skilled readers under conditions of pure block presentation and speeded naming instructions. Specifically, predicted REG reading accuracy as derived from the independence equation with NW and PH naming accuracy as measures of PD processing and EXC naming accuracy as a measure of SV processing, accurately and consistently predicted performance of actual REG naming. The present experiment provided a more thorough examination of the different cognitive models of basic reading by incorporating two types of independence models (one with NWs and the other with PHs as measures of PD) and comparing them to several forms of redundancy models. The data also provides strong evidence against single-mechanism models (e.g., Marchand & Damper, 2000; Plaut, 1999). The three redundancy models tested in these experiments did not account for any unique variance in actual REG reading accuracy. Accordingly, neither a PD nor SV driven single mechanism model can adequately account for REG reading accuracy. The present experiment is, to our knowledge, the first to directly compare SV and PD models of independence with models of redundancy within the same study.

The data lends support for the cognitive dual-route model whereby basic reading processes (i.e., SV and PD) are independent systems (Besner & Smith, 1992; McDougall et al.,

2005; Paap & Noel, 1991). The present experiment provided a generalization to McDougall et al.'s (2005) work on the dual-route model of basic reading by incorporating redundancy models, using normal skilled participants and including different testing procedures (i.e., pure blocks and speeded naming). The fact that the independence model with PHs or NWs consistently accounted for unique variance of obtained REG reading accuracy adds further support for the dual-route model of basic reading processes.

The data provides strong evidence that PH naming accuracy serves to reflect processing of the PD system. Furthermore, PHs allow for a check of the phonological lexical system, unlike NWs. We argue that this combination of systems represents the key components of what is referred to as *PD* in actual reading development. In the present experiment, predicted REG reading accuracy from the equation with PHs consistently accounted for unique variance in obtained REG reading accuracy.

Experiment 2

Given the current findings that REG naming accuracy can be accounted for by predicted REG accuracy using independence equations with EXC naming accuracy and NW or PH naming accuracy as the independent variables, it is of interest to determine whether such relationships can be extended to other behavioural and functional measures that reflect SV and PD processing. Advancements in imaging, in particular fMRI, have become critical in our current understanding of reading, and innovative techniques that combine functional imaging with behavioural research have proven to be useful in the continuing investigations of basic reading processes.

Of particular interest to researchers who study basic reading processes is the underlying mental chronometry. Mental chronometry is the temporal aspect of the decomposition of brain activity into processing stages during tasks (Binder & Price, 2001; Richter, Ugurbil,

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Georgopoulos & Kim, 1997). Often, behavioural measures such as reaction time are used to draw inferences indirectly about the underlying processes at work during the cognitive task at hand. For example, the typical Semantic Context (where a target word is preceded by either a related or unrelated context word) X Stimulus Quality (intact or degraded targets) interaction is often taken as evidence for a common stage of processing that these two variables affect (Besner & Smith, 1992; Borowksy & Besner, 1991; 1993). However, such behavioural measures do not allow researchers to make inferences about underlying neural activity or the pathways in which such stimuli are named. Developments in fMRI have led to the extraction of measures and information about the BOLD response function during such cognitive tasks. The subsequent combination of behavioural measures with functional measures has extended the investigation of mental chronometry to the underlying brain activity and allowed researchers to broaden the previous behavioural notions to particular regions within the brain (Liu, Liao, Fang, Chu, & Tan, 2004; Richter et al., 1997).

In order to extend the development of mathematically-based models of reading behaviour, we tested whether a dual-route model of mathematical independence between SV and PD systems and the relationship of equations (1.2) or (1.3) could be applied to behavioural reaction times and functional BOLD response measures. We predict that the mathematically independent relationship between SV and PD systems seen on behavioural naming accuracy should also be present when examining behavioural naming reaction time and should also follow for functional BOLD response measures.

Methods

Participants

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University graduate students (N=10; mean age = 25; 9 right handed), performed REG, EXC, NW and PH naming tasks. Inclusion criteria and ethical approval was identical to Experiment 1.

Stimuli

The stimuli were identical to those used in Experiment 1 (Appendix B).

Materials

All imaging was conducted using a 1.5T Siemens Symphony magnetic resonance imager (Erlangen, Germany). For each stimulus type (i.e., REGs, EXCs, NWs and PHs), 100 data volumes of 12 slice axial single-shot fat saturated echo-planar images (EPI) were obtained (T_R (repetition time) = 3700ms, with a 1850 ms gap of no image acquisition in each T_R, T_E (echo time) = 55ms, 64 x 64 acquisition matrix, 128 x 128 reconstruction matrix). EPI slice thickness was 8 mm (which has been argued to represent an optimal trade-off between signal-to-noise and localization; Sarty, 2006), with a 2 mm separation between slices, and a field of view of 250mm. The first 5 volumes were used to achieve a steady state of image contrast and were discarded prior to analysis. The remaining volumes were organized into 5 blocks of 19 volumes each. Each block consisted of 11 volumes of task followed by 8 volumes of rest. A computer running EPrime software (Psychology Software Tools, Inc., Pittsburgh, PA, 2003) was used to trigger each image acquisition in synchrony with the presentation of visual stimuli. Responses were monitored over the MRI intercom during the gaps in image acquisition (since there was no noise interference from the MRI) and the naming offset (i.e., completion of the naming response) was coded via a button press by the experimenter. We have found this "gap" paradigm to be particularly effective for avoiding any consistent motion artefacts due to vocalization, and participants find it easy to learn to make their vocalization within the constraints of the gap in

image acquisition (Borowsky, Owen, Wile, Friesen, Martin, & Sarty, 2005; Borowsky et al., 2006). The stimuli were presented using a data projector (interfaced with the EPrime computer) and a back-projection screen that was visible to the participant through a mirror attached to the MRI head coil. In order to capture a full-cortex volume of images for each participant, either the third or fourth inferior-most slice was centered on the posterior commissure, depending on distance between the posterior commissure and the top of the brain for each participant. T_1-weighted high-resolution spin warp spin-echo anatomical images (T_R= 400ms, T_E= 12ms, 256 x 256 acquisition and reconstruction matrix) were acquired in axial, sagittal, and coronal orientations for the purpose of overlaying the activation maps. Slice thickness was 8mm with a 2mm separation between slices. The position of the T_1 axial images matched the echo-planar images.

After giving written consent, participants were familiarized with the MRI before the experiment. Participants were instructed to read each letter string aloud as quickly and accurately as possible. A within-subjects design was used, and participants responded vocally during the regular, periodic gap in the image acquisition (Borowsky et al., 2005; 2006; Borowsky, Loehr, Friesen, Kraushaar, Kingstone, & Sarty, 2005). Specifically, following the offset of a volume of image acquisition a letter string was presented during a temporal gap in which the participant named the letter string aloud. Letter string presentation was counterbalanced in accordance to a partial Latin square design and stimuli were presented one a time to the top-center portion of the projection screen for the full duration of the gap (i.e., 1850ms). The presentation of items in pure blocks and instructing the participants as to the nature of the item they were about to see enabled the apriori knowing of which stimulus type was being presented. The motivation for pure block presentation stems from our examination of basic

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reading processes using fMRI where several stimuli must be presented in pure block format to allow for a robust BOLD function to occur. Pure block presentation also ensures that PHs be named via the PD route with checking of the phonological lexicon (as evidenced by a significant base-word frequency effect; Borowsky et al., 2002).

Analysis

For optimal sensitivity, the experiment used a blocked design, as described above, and was analyzed using a previously developed and validated regularized BOLDfold approach (Borowsky et al., 2005; 2006; 2002; Borowsky, Loehr et al., 2005; Owen et al., 2004; Sarty, 2006; Sarty, & Borowsky, 2005; Vakorin, Borowsky, Sarty, 2007). The BOLDfold method of analysis requires that sufficient time elapse between task conditions for the hemodynamic response (HRF or BOLD function) to fully return to baseline levels. After correcting for baseline drift, the mean BOLD function for each voxel, collapsing across the repetitions of task and baseline, was empirically determined with the BOLDfold method (which is a general linear model [GLM] parameterization of the HRF) and then repeated and correlated to the actual data as a measure of consistency across repetitions. A consistency threshold correlation of 0.65 (which has been shown to be optimal; Borowsky et al., 2002; Owen et al., 2004; Sarty & Borowsky, 2005) was used for the analyses that follow. The corresponding *p*-value for the correlation is *p*<0.05 (two-tailed) when using a conservative Bonferroni-correction for 100,000 comparisons (approximately 100,000 voxels). Given that the BOLDfold maps are robust to false activation due to motion, we used the gap paradigm to effectively deal with head motion and, we carefully inspected the original voxel timecourses in active regions to confirm smooth (i.e., no high-frequency component) HRF response, no correction for motion was necessary nor implemented

Region of Interest

To extract the relevant BOLD data, regions of interests (ROIs) were delineated for each participant (Figure 7; Strupp, 1996). The inferior frontal gyrus has been implicated as a region involved in motor output and Broca's area is the last cortical region to be activated in overt naming prior to the motor cortex (Lui et al., 2004; Price, Noppeney, & Friston, 2006). Thus, Broca's area is an obvious region of interest for examining how SV and PD processing interact in terms of the BOLD response measures. The ROIs were drawn in one or two slices (depending on the participant) in the lateral inferior frontal gyrus of both the right and left hemisphere.

Extracting BOLD measures

Given the discrete and noisy nature of the fMRI response, extracting temporal measures of the hemodynamic response requires some kind of smoothing (see Vakorin et al., 2007 and Cummine et al., 2008 for complete details). The method adopted was within the framework of signal averaging techniques that increase the signal-to-noise ratio of fMRI signals (DeYoe, Bandettini, Neitz, Miller, & Winans, 1994). For active voxels in the ROI, the smoothed hemodynamic responses were used to create the full width at half maximum (FWHM) maps as well as maps for the first derivative at the initial point (i.e., initial slope of the BOLD response), intensity (maximum response value), and time to peak. These four hemodynamic response measure values were averaged over all the active voxels included in the ROI. It is these ROI averaged hemodynamic response measures that were used for further analysis of the relationships between reaction time and the properties of the hemodynamic response.

Normalized Measures

Behavioural response times were calculated by averaging each participant's correct offset response times for each stimulus type. The expression of mathematical independence requires
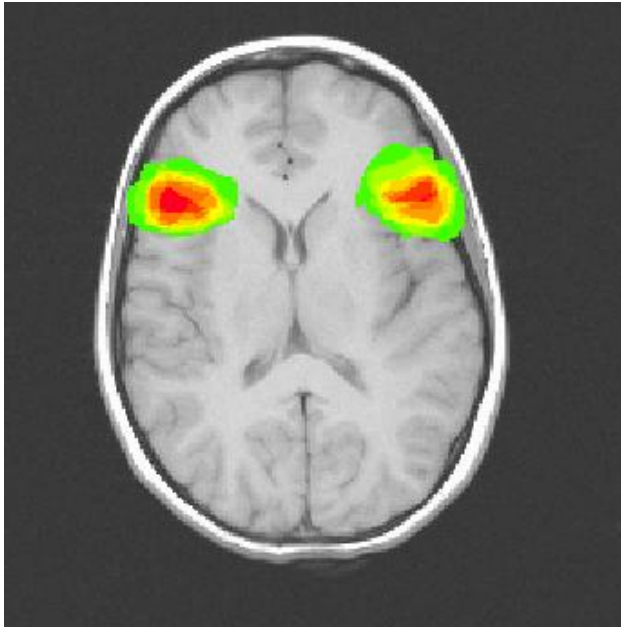
Figure 7. Inferior frontal gyri masked in axial view, representing the selected region of interest (ROI) for each participant, overlaid on the axial anatomical image of one of the participants. Colour gradations represent amount of individual variability in the specific region (i.e., red is the region that was masked for all participants).

that values be normalized, dimensionless, values in the range 0 to 1. To normalize, the response time of each stimulus type was divided by the maximum time available to name the stimulus (i.e., 1850ms) to convert the values to the range [0, 1]. Individual predicted REG response times were derived for each model (based on NWs or PHs) via:

$$RT_{PredREG} = RT_{EXC} + RT_{NW} - RT_{EXC}RT_{NW} \qquad (1.7)$$

and

$$RT_{PredREG} = RT_{EXC} + RT_{PH} - RT_{EXC}RT_{PH} \qquad (1.8)$$

Where RT_{REG} is the normalized response time for REGs, RT_{EXC} is the normalized response time for EXCs, RT_{NW} is the normalized response time for NWs and RT_{PH} is the normalized response time for PHs (see Eq. 1.2), for each participant. Regression analyses were conducted to compare the actual REG normalized response time, RT_{REG}, to the two model $RT_{PredREG}$ values. The dependent variable for the regression analyses was actual REG normalized response time, RT_{REG}. The independent variables were the two predicted REG normalized response times, $RT_{PredREG}$ of equations (1.7) and (1.8).

Similar to response time values, the BOLD response measure values also had to be normalized to a range of 0 to 1 to test the mathematical independence model. This was accomplished by dividing each of FWHM and Time to Peak value, in seconds, by the time per block (i.e., 19 volumes x 3.7 seconds (T_R) = 70.3 seconds) to produce normalized values W and P, respectively. Intensity (in grayscale (gs) units), Volume (in cc) and Initial Slope (gs/s) were normalized to I, V and S respectively by dividing the measured values by a value that was more than the maximum obtained value identified for the corresponding measure (to prevent values > 1; i.e., I = Intensity/1000, V = Volume/150, S = Initial Slope/10). Individual predicted REG FWHM, $W_{PredREG}$, REG P, $P_{PredREG}$, REG I, $I_{PredREG}$, REG V, $V_{PredREG}$, and REG S, $S_{PredREG}$, were

derived for each model similar to the schemes of equations (1.7) and (1.8) (i.e., independence with NWs or PHs) for each participant. Regression analyses were conducted to compare the prediction of $W_{PredREG}$, $P_{PredREG}$, $I_{PredREG}$, $V_{PredREG}$, and $S_{PredREG}$ from the models to actual REG FWHM, W_{REG}, actual REG P, $P_{REG,}$ actual REG I, I_{REG}, actual REG V, V_{REG}, and actual REG S, S_{REG}.

Results

The mean response times, accuracy rates and BOLD response measures for each stimulus type are presented in Table 4. We assessed the extent to which behavioural response times and BOLD response measures displayed a pattern of mathematical independence similar to that found with accuracy scores when reading SV and PD stimuli (Castles et al., 2006; McDougall et al., 2005). The initial correlation analyses revealed significant (and marginally significant) relationships between stimulus types for Response Times, BOLD FWHM, BOLD Intensity, and BOLD Volume (with a Bonferroni adjusted p-value corrected for the six correlations within each set, i.e., *p*<.008). These relationships reflect typical findings that are reported for accuracy scores (e.g., significant relationships between REGs and EXCs and between REGs and NWs; see Table 5; McDougall et al., 2005). Thus, it was expected that some of these variables (e.g., Response Times, BOLD FWHM, and BOLD Intensity) would display a relationship of mathematical independence between SV and PD processes. The results of the regression analyses are presented in Table 6.

Response Time. The linear regression used to assess the extent to which actual RT_{REG} could be accounted for given the independence model with PHs was significant, as was the independence model with NWs.

Table 4. Mean BOLD function parameters and Behaviour Parameters (Standard Deviation) for each Stimulus Type

	Regular Words		Exception Words		Nonwords		Pseudohomophones	
FWHM (s)	32.90	(8.0)	31.02	(7.4)	35.07	(4.5)	37.67	(6.9)
Intensity (gs)	666.70	(120.8)	702.36	(173.6)	716.94	(67.0)	710.92	(120.4)
Time to Peak (s)	42.00	(9.3)	41.62	(8.9)	42.82	(5.8)	43.96	(6.0)
Initial Slope (gs/s)	3.07	(1.9)	2.63	(1.6)	4.31	(1.6)	3.84	(1.8)
Volume (cc)	36.00	(23.1)	35.30	(28.0)	70.50	(52.2)	66.80	(60.6)
Mean Reaction Time (ms)	794.75	(76.4)	838.55	(102.6)	1084.30	(165.6)	1008.40	(118.3)
Mean Accuracy (%)	98	(.03)	98	(.04)	83	(.09)	87	(.07)

Abbreviations:

s – seconds

gs – grayscale (not normalized)

cc – cubic centimeter

ms – milliseconds

Table 5. Pearson Correlation Matrix Values of Measured Parameters for the Different Stimulus Types

Reaction Time	T_{EXC}	T_{NW}	T_{PH}
T_{REG}	.789**	.926**	.582
T_{EXC}		.905**	.506
T_{NW}			.655+
BOLD Width	W_{EXC}	W_{NW}	W_{PH}
W_{REG}	.902**	.593	.427
W_{EXC}		.544	.440
W_{NW}			.324
Intensity	I_{EXC}	I_{NW}	I_{PH}
I_{REG}	.671+	.528	.610
I_{EXC}		.378	.721*
I_{NW}			.541
Time to Peak	P_{EXC}	P_{NW}	P_{PH}
P_{REG}	.676+	.507	.306
P_{EXC}		.631+	.016
P_{NW}			-.211
Volume	V_{EXC}	V_{NW}	V_{PH}
V_{REG}	.369	.276	-.122
V_{EXC}		.765*	.007

| V$_{NW}$ | | | -.012 |

Initial Slope	S$_{EXC}$	S$_{NW}$	S$_{PH}$
S$_{REG}$	.767*	.078	.182
S$_{EXC}$		.160	.545
S$_{NW}$			.321

**. $p<.008$ (Bonferroni correction two-tailed)

 *. $p<.016$ (Bonferroni correction one-tailed)

 +. $p<.05$ (uncorrected two-tailed)

Table 6. Regression Analyses of *Actual* Regular Word Parameters as a function of *Predicted* Regular Word Parameters

	Adj. r^2	Slope	Standardized Slope	$t(9)$	p
Reaction Time					
$T_{PredREG (EXC \& PH)}$	.55	.581	.775	3.47	.008
$T_{PredREG (EXC \& NW)}$	.82	.512	.981	6.55	<.001
BOLD Width					
$W_{PredREG (EXC \& PH)}$	.30	1.381	.615	2.21	.058
$W_{PredREG (EXC \& NW)}$	.63	2.154	.818	4.02	.004
Intensity					
$I_{PredREG (EXC \& PH)}$	.44	.901	.708	2.83	.022
$I_{PredREG (EXC \& NW)}$	.44	1.416	.710	2.85	.021
BOLD Time to Peak					
$P_{PredREG (EXC \& PH)}$	.47	1.652	.726	2.99	.017
$P_{PredREG (EXC \& NW)}$	.38	1.143	.667	2.53	.035
Volume					
$V_{PredREG (EXC \& PH)}$	-	-	-	1.57	.161
$V_{PredREG (EXC \& NW)}$	-	-	-	.75	.479
Initial Slope					
$S_{PredREG (EXC \& PH)}$	-	-	-	1.66	.137
$S_{PredREG (EXC \& NW)}$	-	-	-	1.18	.272

FWHM. The linear regression used to assess the extent to which actual W_{REG} could be accounted for given the independence model with PHs was, $t(9) = 2.21$, $p=.058$. Given our prediction based on the initial correlation analyses and accuracy analyses of Experiment 1 this regression can be considered significant at the one-tailed level ($p=.029$). The linear regression used to assess the extent to which actual W_{REG} could be accounted for, given the independence model with NWs was also significant.

Intensity. The linear regression used to assess the extent to which actual I_{REG} could be accounted for, given the independence model with PHs was significant, as was the independence model with NWs.

Time to Peak. The linear regression used to assess the extent to which actual P_{REG} could be accounted for given the independence model with PHs was significant, as was the independence model with NWs.

Volume and Initial Slope. The linear regression used to assess the extent to which actual V_{REG} could be accounted for given the independence model with PHs was not significant, nor was the independence model with NWs. The linear regression used to assess the extent to which actual S_{REG} could be accounted for given the independence model with PHs was not significant, nor was the independence model with NWs.

<p style="text-align:center">*Discussion*</p>

A relationship exists between behavioural and functional BOLD response measures of naming, whereby both types of measures demonstrate mathematical independence between SV and PD processes. Previous endeavors to test this hypothesis have only been supported with accuracy measures in behavioural paradigms (Castles et al., 2006; McDougall et al., 2005); our current work demonstrates that this relationship is evident in response time and several

functional measures as well. Our analyses revealed that the assumption of mathematical independence, previously applied to accuracy scores, can also be applied to behavioural response times and functional BOLD measures such as FWHM, Time to Peak and Intensity. Thus, under the assumption that the SV and PD systems are mathematically independent one can account for REG response time, REG BOLD FWHM, REG BOLD Time to Peak and REG BOLD Intensity given the corresponding EXC and NW or PH measures (i.e., Response Time, FWHM, Time to Peak or Intensity). Therefore, we have provided converging behavioural and neurobiological evidence that a dual-route model of reading which makes detailed predictions about the mathematically independent nature of SV and PD systems and subsequent behavioural accuracy scores can be extended to these other behavioural and functional imaging measures.

The fact that we were able to model the mathematical relationship between SV and PD with some BOLD measures but not others is understandable given current findings regarding the relationship between BOLD measures and behavioural data. Our results suggest FWHM, Time to Peak and Intensity all model mathematical independence relatively well, whereas Volume and Initial Slope do not. Past research that has attempted to link behavioural measures with functional measures has consistently demonstrated relationships between Time to Peak, Intensity and FWHM of the hemodynamic function and behavioural events (Lui et al., 2004; Menon & Kim, 1999; Menon, Luknousk & Gati 1998; Miezin, Maccotta, Ollinger, Petersen & Buckner, 2000; Neumann, Lohmann, Zysset, & von Cramon, 2003; Richter et al., 1997). In contrast, Initial Slope (i.e., onset) and Volume have either not been included in studies involving behavioural and functional relationships or they have not demonstrated consistent findings (Miezin et al., 2000; Neumann et al., 2003; Richter et al., 1997). Thus, Initial Slope and Volume have not been shown to be reliably related to behavioural measures of various cognitive tasks,

and therefore it is not surprising that they do not display the same mathematical relationship as is found with behavioural measures.

Conclusions

Experiment 1 and 2 provide important information about the relationship between SV and PD processes. Specifically, we replicated previous findings of mathematical independence between SV and PD processes on behavioural naming accuracy and extended these findings to include a skilled adult population. Furthermore, we advanced the development of equation-based models of cognitive behaviour and neurophysiology whereby we showed that the relationship of mathematical independence that exists for predicting REG accuracy given EXC and NW or PH naming accuracy was present for naming Response Time, as well as three BOLD parameters in Broca's Area: BOLD Width, BOLD Time to Peak, and BOLD Intensity. Therefore, we provide converging behavioural and neurobiological evidence for a mathematically independent relationship between SV and PD systems, consistent with a dual-route model of reading. In addition, we provide evidence against single mechanism models by directly comparing models of independence and redundancy and demonstrating that only models of independence account for significant unique variance in actual REG reading performance.

Chapter 2: An Evaluation of Mathematical Independence via Functional Pathways

Summary

The following experiments examined the neural underpinnings associated with SV and PD processes when participants read several different types of letter strings (e.g., REGs, EXCs, NWs and PHs) as well as the relationships between these systems. Results reveal that SV processing (as measured by EXC naming) consistently activates an occipito-temporal network along the ventral stream and PD processing (as measured by PH naming) consistently activates an occipito-parietal-frontal network along the dorsal stream. Neurobiological evidence for mathematical independence between SV and PD systems was evaluated by examining unique versus shared fMRI activation maps.

Experiment 3, (published in Borowsky, R., **Cummine, J.**, Owen, W.J., Friesen, C. K., Shih, F., & Sarty, G. (2006). *Brain Topography; Journal of Neurophysiology, 18,* 233-239) replicated and extended previous findings regarding SV and PD processing streams in basic reading. Specifically, EXC naming activated a ventral visual processing stream in the brain and PH naming activated a dorsal visual processing stream in the brain. Furthermore, this study emphasized the role of the insular cortex in phonological processing during basic reading tasks and suggests future neurobiological models must include this region.

Experiment 4 extends the previous findings by including an examination of all possible stimuli (REGs, EXCs, NWs, and PHs) and the extent to which ventral and dorsal processing streams were active during the naming of these critical letter strings. Again, support for a spatial dual-route model is provided whereby the ventral route is involved in naming SV stimuli and the dorsal route is involved in naming PD stimuli. NWs, which are correctly read via the PD system, produced an abundance of activation across both streams while REGs, which are correctly read

by either or both the SV and PD system, activated a predominantly dorsal stream similar to PHs.

All stimuli produced activation in regions associated with visual input (e.g., occipital cortex) and

motor output (e.g., premotor cortex).

Introduction

Experiment 3

Although researchers may disagree about the particular mechanisms at work during basic reading (e.g., dual-route models vs. single mechanism models), it is widely acknowledged that certain stimuli are named in markedly different ways. For example, researchers who subscribe to models with separable processing routes assume that some stimuli are correctly read by a SV route whereas others are correctly read by a PD route (Coltheart et al., 2001). Similarly, researchers who subscribe to single mechanism models assume a division of labour where some stimuli are influenced by semantic processing whereas others are not (Plaut et al., 1996; Plaut & Booth, 2006). The use of functional imaging in word recognition research has shown that different stimulus types activate different brain regions. The neural underpinnings associated with reading such stimuli as they relate to one theory or another has been the subject of much research (Borowsky, Cummine, et al., 2006; Borowsky, Esopenko, Cummine & Sarty, 2007; Binder, Medler, Desai, Conant, & Liebenthal, 2005; Cohen, Dehaene, Vinckier, Jobert & Montavont, 2008).

It has been argued that reading SV and PD stimuli activates anatomical pathways that are part of the ventral "what" stream (Ungerleider & Mishkin, 1982) and dorsal-frontal "how" stream (Borowsky et al., 2006, 2007; Goodale & Milner, 2005; see Figure 8). That is, the ventral stream has been implicated in cognitive tasks which require identifying "what" an object is (Goodale & Milner, 2005; Ungerleider & Mishkin, 1982) and accordingly, should be active when participants are naming familiar letter strings which have SV representations. The dorsal stream, on the other hand, has been implicated in more analytical cognitive tasks such as identifying "how" one might interact with an object. PD processing also involves analytical
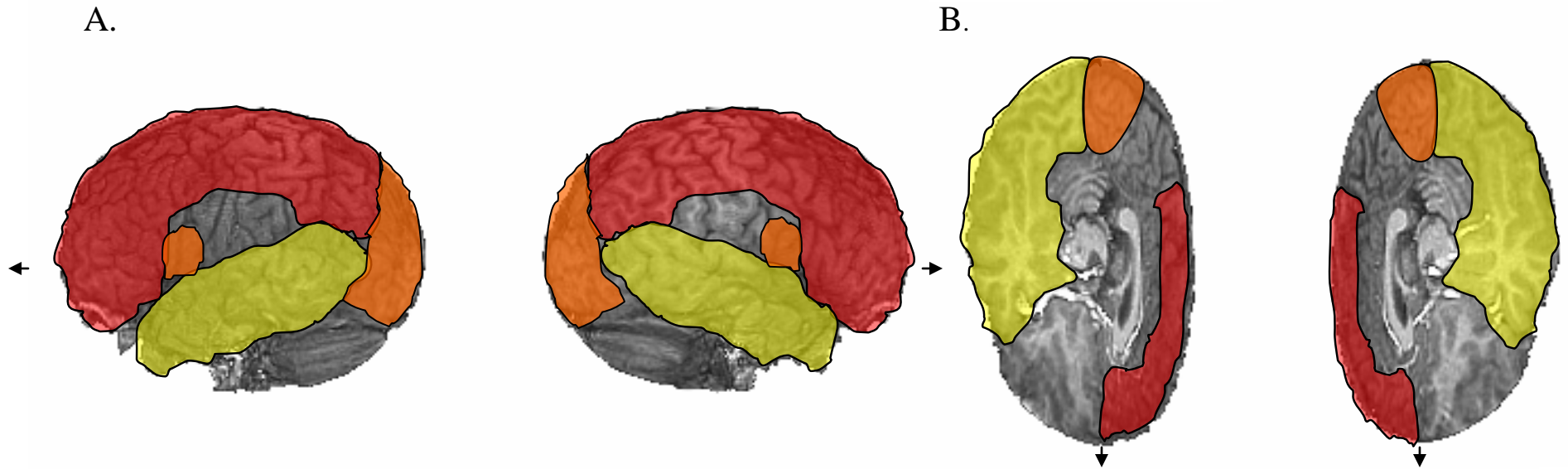
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Figure 8. Functional representation of the SV and PD routes in basic reading processes from A. lateral and B. ventral perspectives. PD stimuli (i.e., NWs, and PHs) are processed via a dorsal stream (red) and SV stimuli (i.e., EXCs) are processed via a ventral stream (yellow). Both share early activation in the occipital cortex and later activation in the motor cortex (orange).

processing as one maps graphemes onto phonemes to name novel letter strings and thus, should produce activation in the dorsal stream. A straightforward comparison of fMRI activation maps from naming basic letter strings would advance our understanding of the underlying SV and PD processes and the corresponding ventral and dorsal pathways involved in basic word recognition.

Several neurobiological models specific to basic visual word recognition have been proposed. For example, Pugh et al. (1996; 1997; 2000; 2001) have suggested that participants rely on two routes to name words and novel words: a dorsal route and a ventral route. The dorsal route (occipital-temporal-parietal) is involved in phonologically demanding tasks such as nonword rhyming. Areas in this route include the posterior portion of the superior temporal, supramarginal and angular gyri of the temporal-parietal region. The ventral route (occipital-temporal) is involved in orthographically demanding tasks such as letter case discrimination. Areas in this route include the medial extrastriate, left inferior occipito-temporal regions and the fusiform gyrus in the occipital lobe and the inferior and medial temporal gyri in the temporal lobe. The dual-pathway model proposed by Pugh et al. (1996; 1997; 2000; 2001) parallels that of the behavioural dual-route model given that there is a specific pathway that processes lexical orthographic stimuli (i.e., SV), there is a specific pathway that processes sub-lexical phonological stimuli (i.e., PD) and both routes share in early visual feature analysis and orthographic processing in the occipital cortex and motor activation in the frontal cortex during reading aloud tasks (see Figure 8).

Similarly, Posner and Raichle (1994) have proposed a dual-route neurobiological model of reading. They suggest that readers rely on both an automatic stream and non-automatic stream in the processing of word stimuli. The automatic stream represents SV access and includes such areas as the medial extrastriate in the occipital lobe and the insular cortices of the

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frontal lobe. The non-automatic stream represents processing of words that are not in our lexicon or are unfamiliar to us and includes such areas as the posterior portion of the superior temporal gyrus, supramarginal and angular gyri of the temporal-parietal region and the inferior frontal gyrus and Broca's area. Notably, Posner and Raichle emphasize the importance of the insular cortices in basic reading processes. In a semantic verb generation task, they found increased insular cortical activity as a function of familiarity with noun-verb associations and subsequently suggested the insular cortices represent an enhanced word form system. Posner and Raichle's (1994) model is similar to the Pugh et al., (2000) model in that both suggest there are independent routes for processing basic words with an overlap in the lateral occipital regions. In contrast to Pugh et al.'s (2000) model, Posner and Raichle (1994) also suggest the insular cortices play an important role during speech production.

The ventral-dorsal model and automaticity model are sufficiently well-developed to allow researchers to derive predictions regarding whether the same or different neurobiological regions respond to familiar orthographic and familiar phonological representations. Both Pugh et al.'s and Posner and Raichle's models would be consistent with predominantly ventral activation unique to the reading of EXCs and predominantly dorsal activation unique to the reading of PHs. However, the involvement of the insular cortices allows one to distinguish between these models in that Posner and Raichle claim that the insula is sensitive to word familiarity whereas Pugh et al.'s model does not refer to the insula. If we do not find the insula to be activated for EXC reading or PH reading then Pugh et al.'s model would be more parsimonious. However, if Posner and Raichle are correct then the insula should be active during the reading of these stimuli but it is not clear from their research as to exactly what type of familiarity the insula is most sensitive to. If the insula is primarily sensitive to orthographic lexical processing then the reading of EXCs

should result in greater activation of this structure. However, if the insula is primarily sensitive to sub-lexical spelling-to-sound translation then the reading of PHs should result in the most activation. Finally, if the insula is primarily sensitive to phonological lexical processing, which both EXCs and PHs share then there should be very little *unique* activation in the insula for either stimulus type and a substantial amount of *shared* activation.

The goals of Experiment 3 were to examine the neural underpinnings of SV and PD processes, directly evaluate the extent to which they involve unique (i.e., modular) versus shared (i.e., intersection) regions of the brain as described in Pugh et al.'s (1996, 2000; Sandak et al. 2004) and Posner and Raichle's (1994) models and to further determine the role of the insular cortices in basic reading processes. However, most functional neuroimaging studies have examined the modularity of cognitive and perceptual function in the physiological tradition using Donders' (1868:1969) subtractive logic. This approach, as it is typically applied to task subtraction in functional neuroimaging, allows only the more dominant process to earn a placement on the resulting brain activation map. Given that the question of modularity is one that requires knowledge about unique regions of activation (i.e., activation attributable to only one stimulus or task), information about dominance cannot, by itself, serve as a means of isolating task-or stimulus-specific functions. Here we examine both the modularity of cognitive processing by defining unique maps (showing activation that is unique to each condition, relative to the other), and the intersection of cognitive processing by defining intersection maps (showing activation that is common to both conditions), for EXC and PH naming (see also Borowsky et al. 2005; 2006).

Methods

Participants

Six participants (four female, mean age = 33, two male, mean age = 28, one participant in each sex subgroup was left-handed) performed the EXC and PH naming tasks, in an alternating order across participants. Inclusion criteria and ethical approval was identical to Experiment 1.

Stimuli

The stimuli were identical to those used in Experiment 1; however, forty stimuli were randomly selected from the EXCs or PHs and presented in five blocks of eight stimuli to be consistent with, and thus comparable to, another experiment that was run concurrently.

Materials, Procedure and Analyses

The materials, procedure and analysis were identical to Experiment 2 with the following exceptions. For each experiment 88 volumes of 12 slice axial single-shot echo-planar images (EPI) were obtained (T_R = 3300 ms, with a 1650 ms gap of no image acquisition in each gap, T_E = 55 ms, 64 × 64 acquisition matrix, 128 × 128 reconstruction matrix). The first 8 volumes were used to achieve a steady state of image contrast and were discarded prior to analysis. The remaining volumes were organized into 5 blocks of 16 volumes each. Each block consisted of 8 volumes of response followed by 8 volumes of relaxation. A consistency threshold correlation of 0.60 was used for the analyses that follow.

For each stimulus-type C, for each subject, two maps were computed, a threshold map η_C (p) of η goodness of-fit values and a visibility or intensity map V_C (p) (BOLD amplitude), where p is a voxel coordinate. The corresponding activation map for C was defined as M_C (p) = $K_{C,\theta}$(p) V_C (p) where $K_{C,\theta}$(p) = 1 if η_C (p) > θ and zero otherwise. Intersection (shared) maps (*M*int) maps, and unique (modular) maps (*M*uni) maps were computed for paired conditions A and B (i.e., EXC naming and PH naming) for each subject according to the following equations:

$$M\text{int}(p) = K_{A,\theta}(p) K_{B,\theta}(p)(V_A(p) + V_B (p))/2 \qquad (2.1)$$

$$M\text{uni}(\,p) = [K_{A,\theta}(p)V_A(\,p) - K_{B,\theta}(p)V_B\,(p)] \times [1 - K_{A,\theta}(\,p)K_{B,\theta}(p)] \quad\quad (2.2)$$

The intersection map shows activation common to both conditions A and B, and this type of map has been referred to as a *conjunction map* by previous researchers (Friston, Holmes, Price, Buchel, & Worsley, 1999; Price & Friston 1997). The unique map represents a difference and shows task subtraction for activations that are not common to conditions A and B. The maps were averaged across participants to produce the final maps (see also Borowsky et al. 2005).

Using AFNI (Cox 1996), voxels separated by 1.1 mm distance were clustered and clusters of volume less than 100 μL were clipped out. The data were then spatially blurred using an isotropic Gaussian blur with a FWHM of 3.91 mm. Averaging of images across subjects was done after standard piecewise affine transformation of individual data to a standardized brain atlas (Talairach & Tournoux, 1988). Visual inspection of the individual participant anatomical images did not reveal any structural abnormalities that would compromise the averaging of data in Talairach space. Mean activation maps in Talairach coordinates were determined for each map along with the corresponding one sample *t* statistic for each voxel. The maps that follow simply show regions of activation that surpass both the consistency threshold at the individual level and a one-tailed *t* test against zero at the group level. Given that consistent low intensity BOLD functions are as important to understanding perception and cognition as are consistent high intensity BOLD functions, the maps are presented without scaling the color to vary with intensity (i.e. the maps are binary). Regions of activation on the resulting maps are significant at $t(5) = 2.228$, $p < 0.05$, one-tailed.

Results

The fMRI maps that follow are portrayed with the left hemisphere on the left side of each pair of brain images. Given the well-documented specialization of cortical neurons into columnar

arrangement by stimulus characteristics across the senses of vision, hearing and touch (Goldstein, 2002; Hubel, Wiesel, & Stryker, 1978; Young, 1995), 90% brain anatomical underlay maps (which strip away 10% of the lateral cortex and cerebellum, from the anatomical underlay only) are used here to better visualize the extent and location of function.

Shared Regions of Activation for EXC and PH Reading

As seen in Figure 9A, the shared regions of activation from reading EXCs and PHs included the lateral occipital region, Broca's area, the motor cortex and posterior insular cortex.

Unique Regions of Activation for EXC or PH Reading

As seen in Figure 9B, unique activation patterns from reading PHs primarily included regions along the dorsal stream from the lateral occipital region through the parietal lobule, motor cortex and insular cortex (including both anterior and posterior regions). Unique activation patterns from reading EXCs primarily included regions along the ventral stream from the lateral occipital gyrus through the temporal gyri.

Discussion

Consistent with both the Pugh et al. (1996, 2000; Sandak et al. 2004) ventral-dorsal model and Posner and Raichle's (1994) automaticity model, the present results support the notion that SV-based reading (as stimulated by the reading of EXCs) relies primarily on the ventral stream whereas PD phonological assembly route (as stimulated by the reading of PHs) relies primarily on the dorsal stream. The comparison of unique and shared fMRI activation from EXC reading and PH reading provided a useful assessment of SV and PD processing during reading.

Our work is in line with current neuroimaging research that supports the broad distinction of ventral and dorsal processing streams in reading (Borowsky et al., 2006; 2007; Cohen et al.,
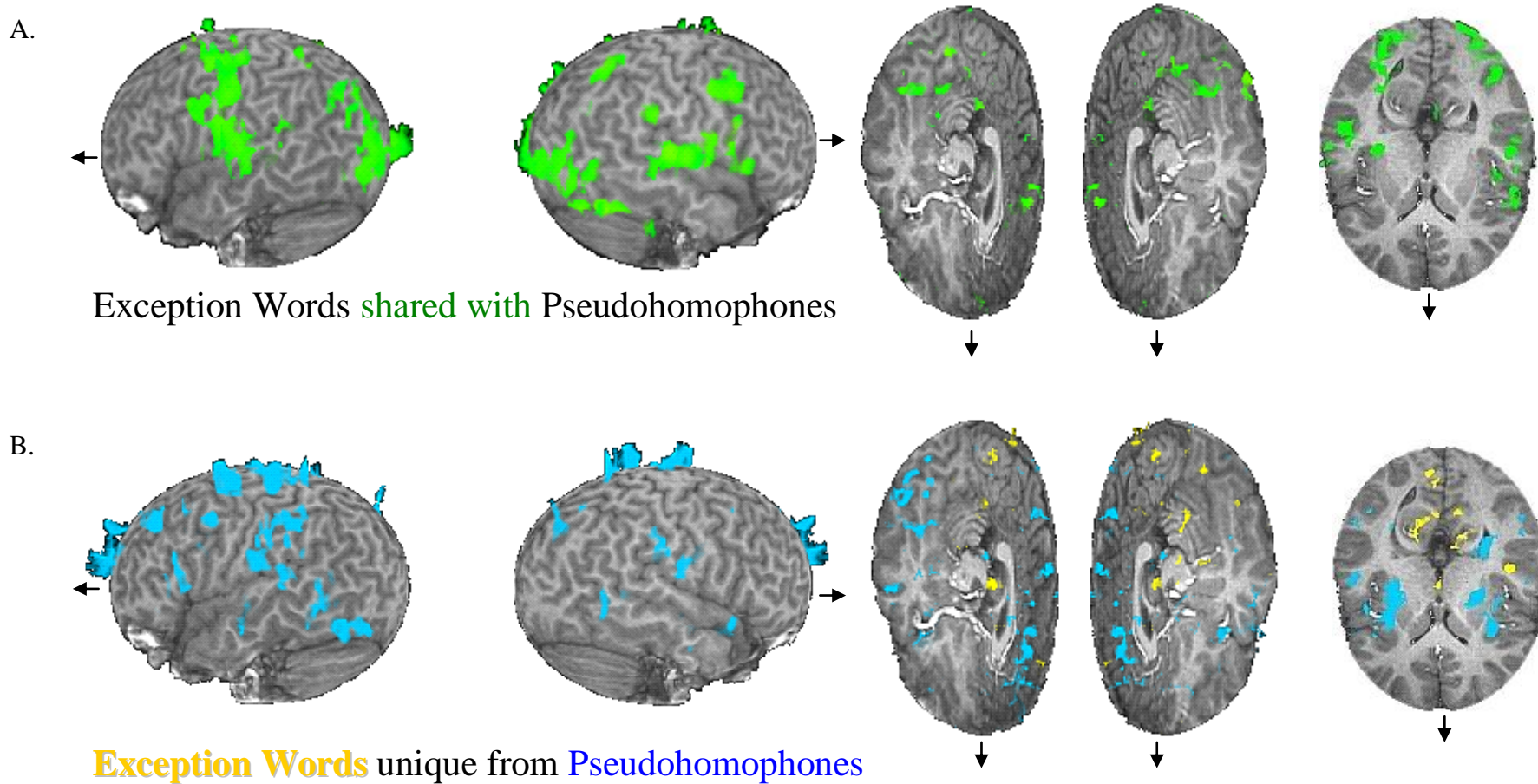
A.

Exception Words shared with Pseudohomophones

B.

Exception Words unique from Pseudohomophones

Figure 9. A. Shared activation between EXCs and PHs. Shared regions of activation between EXCs and PHs included the lateral occipital gyrus (LOG), inferior temporal gyrus (ITG), posterior portion of the superior temporal gyrus (STG), inferior parietal lobule (angular gyrus; IPLAG), inferior parietal lobule (supra-marginal gyrus; IPLSG), superior parietal lobule (SPL), post-central gyrus (PoG), precentral gyrus (PrG), inferior frontal gyrus (IFGPT and IFGPO), middle frontal gyrus (MFG), superior frontal gyrus (SFG), lingual gyrus (LG), cuneus, occipitotmeporal gyrus (OG), cingulate gyrus (CG), paracentral lobule (PL), cerebellum and posterior portion of the insula. *B. Unique activation to **EXCs** and PHs.* Activated regions include LOG, ITG, middle temporal gyrus (MTG), STG, IPLAG, IPLSG, SPL, PoG, PrG, IFGPT, IFGPO, MFG, SFG, LG, cuneus, preCuneus (PreC), OG, orbital gyri, thalamus, CG, paracentral lobule (PL), cerebellum, midbrain, parahippocampal gyrus (PG), gyrus rectus (GR), putamen, and insula. Arrows point to face direction.

2008; Posner & Raichle, 1994; Pugh et al., 2001). In addition to the previously outlined models, recent work by Cohen et al. (2008) provides support for a similar ventral – dorsal model using normal and degraded stimuli in a reading task. In their study, participants were presented with words that were progressively degraded via word rotation, letter spacing and displacement in the visual periphery. Their fMRI results indicated that regions in the ventral stream such as the bilateral occipital-temporal cortex were highly activated when words were presented in a familiar format consisting of no degradation due to rotation, spacing or displacement. Comparatively, regions in the dorsal stream such as the bilateral occipital-parietal cortex were highly activated when participants read progressively degraded stimuli. Similar to our findings of SV and PD processing streams, Cohen et al. (2008) concluded that the ventral stream acts as a visual word system that is employed during familiar reading and the dorsal stream is activated during tasks that require serial reading strategies.

Also consistent with our findings is research on dyslexia, which provides support for independent pathways during basic reading processes. Such research has demonstrated that there is a ventral-dorsal pathway distinction that is active during basic reading (Cao, Bitan, Chou, Burman, & Booth, 2006; Hoeft, Hernandez, McMillon, Taylor-Hill, Martindale, Meyler, et al., 2006; Menghini, Hagberg, Caltagirone, Petrosini, & Vicari, 2006; Shaywitz & Shaywitz, 2005). Functional studies reveal that both children and adults who have been diagnosed with dyslexia demonstrate deficits in either or both of these routes. Specifically, people with phonological processing deficits demonstrate reduced activation in the temporo-parietal pathway during reading when compared to controls (Coa et al., 2006; Hoeft et al., 2006; Menghini et al., 2006) and people with dyslexia who have deficits in orthographic representations show reduced activation patterns in the ventral temporal cortex when compared to controls (Cao et al., 2006).

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Given recent interest in the diagnostic (and prognostic) utility of fMRI for assessing two of the major forms of dyslexia: (1) surface dyslexia, which represents a functional impairment of the SV reading system (i.e., ventral stream), and (2) phonological dyslexia, which represents a functional impairment of the PD phonological assembly system (i.e., dorsal stream), such an assessment tool is timely.

Given the goal of elucidating the role of the insular cortex in basic reading processes the present study has clearly added to Posner and Raichle's (1994) work. Posner and Raichle suggested that the insula represents an extended word form system that is sensitive to one's familiarity with words. The nature of this relationship between insular activation and "familiarity" is now considerably clearer. Although there is a small portion of shared activation in the posterior insular cortices for both EXCs and PHs (i.e., suggestive of sensitivity in the insula to phonological lexical processing) EXCs did not show any unique activation in the insula (i.e., suggestive of a lack of sensitivity in the insula to orthographic lexical processing) whereas PHs showed a large portion of unique insular cortex activation anterior to the region of shared activation (i.e., indicative of insular sensitivity to PD spelling-to-sound processing).

Overall, Experiment 3 supports the notion of ventral and dorsal processing streams and the relationship to independent SV and PD reading, respectively. The present study did not reveal any evidence of insular sensitivity to orthographic lexical processing (i.e., SV ortho-graphic representations, which is unique to EXCs in this study). Our results suggest that in reading aloud the insular cortex may be sensitive to lexical phonological processing (i.e., whole-word pronunciation, which is a characteristic shared by both EXCs and PHs) only in a small region of the posterior insula, but is clearly sensitive to PD spelling-to-sound processing (i.e.,

mapping letters to sounds, which is unique to PHs in this study) in more anterior regions of the insula.

The implications for models of the neurophysiology of reading are twofold: the ventral-SV and dorsal-PD distinction is supported (e.g., Posner and Raichle 1994; Pugh et al. 2000; Sandak et al. 2004) and the insular cortices are clearly involved (e.g., Posner and Raichle 1994). The present study elucidates the involvement of the insula to be mainly that of sensitivity to PD spelling-to-sound processing with some suggestion of a small region of sensitivity to lexical phonology in the posterior insula. We argue that ventral-dorsal models of basic reading processes should be further explored with attention paid to the insular cortices and extended to accommodate the effects noted here.

Experiment 4

Importantly, to provide a more comprehensive investigation of the ventral – dorsal dual-route model, several other stimuli must be included and compared. As previously mentioned, letter strings that are commonly used in word recognition research include not only EXCs and PHs, but also REGs and NWs. There are many critical differences and similarities among these four important letter strings with respect to their orthographic and phonological whole- and sub-word processing characteristics. Recall that REGs (e.g., *hint*) are letter strings which have both SV and PD phonological and orthographic representations. In contrast, EXCs (e.g., *pint*) have SV and PD orthographic representations but must activate SV phonological representations in order to be named correctly. NWs (e.g., *bint*) are letter strings that only have PD orthographic and phonological representations and PHs (e.g., *bote*) have PD phonological and orthographic representations but also have SV phonological representations. See Table 7 for a summary.

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Table 7. Summary of Critical Stimulus Types as a Function of Level of Representation (Sub-word versus Whole-word) and Type of Representation (Orthographic versus Phonological) for Correct Naming

	PD (Sub-word)		*SV (Whole-word)*	
Orthographic	REG	EXC	REG	EXC
	NW	PH		
Phonological	REG		REG	EXC
	NW	PH		PH

Abbreviations:
REG – Regular Word
EXC – Exception Word
NW – Nonword
PH – Pseudohomophone

As previously mentioned, traditional subtraction maps are customary in functional imaging of language whereby activation foci are attributed to the more dominant process instead of being identified as shared (Donders, 1969; see also Binder et al., 2005). Evaluating what is unique and shared between stimuli is critical in the present investigation given that REGs, EXCs, PHs and NWs differ on SV and PD phonological and orthographic characteristics. For example, Binder et al. (2005) used traditional subtraction maps in their investigation of word stimuli and attempted to identify regions involved in SV processing by visually comparing activation across maps. Specifically, they searched for commonly activated regions between EXCs and REGs in two separate comparisons, working under the assumption that SV regions would include areas more strongly activated by EXCs relative to REGs and areas more strongly activated by REGs relative to NWs. In our analyses, we will compute each individual's shared map and average them providing a more direct evaluation of regions that are commonly activated for two stimulus types. Given that the use of each of the four stimulus types discussed here are ubiquitous in word recognition research knowing what activation is shared versus unique is essential for developing accurate models of basic reading processes.

In summary, functional imaging of basic word recognition has provided support for a global ventral-dorsal pathway distinction (Borowsky et al., 2006; 2007; Cohen et al., 2008; Fiebach, Friederici, Muller & von Cramon, 2002; Posner & Raichle, 1994; Pugh et al., 2000; see Figure 8). However, further examination of the activation of several stimulus types including REGs, EXCs, PHs and NWs, would serve to clarify the nature of these processing streams and provide useful information about how these streams are engaged during reading. For example, REGs are often assumed to primarily activate SV representations given their high familiarity (Binder et al., 2005; Fiez, Balota, Raichle & Petersen, 1999; Joubert, Beauregard, Walter,

Bourgouin, Beaudoin, Leroux, et al. 2004). Similarly, EXCs must activate SV representations if they are to be named correctly (Binder et al., 2005; Borowsky et al., 2006; Fiez et al., 1999). Would reading these stimuli then activate primarily the same regions, subsequently producing large regions of shared activation and relatively smaller regions of unique activation? However, REGs can also be named correctly via the activation of PD representations whereas EXCs cannot.   Past research has found that PD stimuli such as PHs and NWs primarily activate dorsal regions (Binder et al., 2005; Borowsky et al., 2006; Joubert et al., 2004) and thus it may be the case that REGs activate primarily a dorsal stream similar to PHs and/or NWs. In this case, we should see large amounts of shared activation when REGs are compared with PHs or NWs and relatively smaller amounts of shared activation when REGs are compared with EXCs. Or perhaps REGs activate both processes equally in which case we should see similar patterns of unique and shared activation with SV and PD stimuli. As such, it remains to be seen to what extent REGs activate ventral, dorsal or both processing streams. However, it is clear that EXCs should primarily activate ventral processing regions and that NWs and PHs should primarily activate dorsal processing regions. To date, an experiment including all four of these stimulus types has yet to be conducted.

Methods

Participants, *Stimuli, Materials, and Analyses*

The participants, stimuli, and materials were identical to those used in Experiment 2. The functional map computation was identical to that presented in Experiment 3 with the following exceptions: a consistency threshold of 0.65 was used and regions of activation on the resulting maps are significant at $t(9) = 1.833$, $p < 0.05$, one-tailed.

Results

A total of six comparisons were made, which included unique and shared activation maps for each pair of stimuli. When EXC reading was compared with NW reading, EXC reading elicited predominantly ventral activation and NW reading elicited both dorsal and ventral activation (see Figure 10). Similarly, when EXC reading was compared with PH reading, EXC reading elicited predominantly ventral activation and PH reading elicited predominantly dorsal activation (see Figure 11). When REG reading was compared with EXC reading, by and large REG reading elicited predominantly dorsal activation and EXC reading elicited predominantly ventral activation (see Figure 12). When REG reading was compared with NW reading, both REG reading and NW reading elicited predominantly dorsal activation (see Figure 13). Similarly, when REG reading was compared with PH reading both REG reading and PH reading elicited predominantly dorsal activation (see Figure 14). Finally, when NW reading was compared with PH reading, NW reading and PH reading elicited predominantly dorsal activation; however, NWs produced activation that was not as constrained to the dorsal stream as PHs (see Figure 15). All stimuli produced activation in the regions associated with visual input (e.g., occipital cortex) and motor output (e.g., precentral gyrus).

Discussion

Our results are in line with other research that suggests SV based reading activates ventral regions in the brain, whereas analytical-based PD reading activates dorsal-frontal regions in the brain (Borowsky et al., 2006; 2007; Cohen et al., 2008; Fiebach et al., 2002; Posner & Raichle, 1994; Pugh et al., 2001). The maps revealed both distinguishable foci of activation that are unique to stimulus type (REGs, EXCs, PHs, and NWs) and a considerable volume of intersecting regions of activation. From a global perspective, EXC naming, which activates whole-word phonological and orthographic representations, was processed predominantly in a
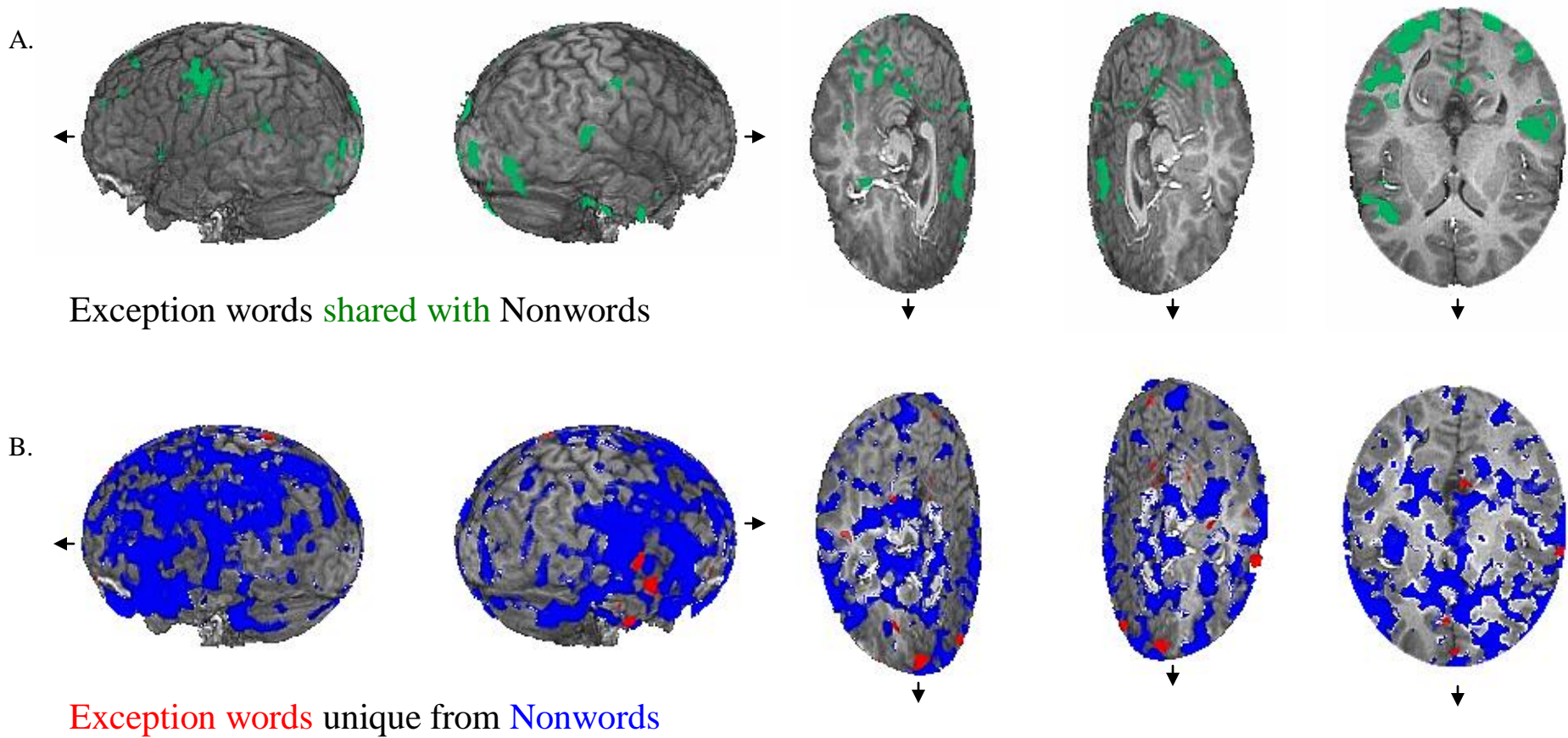
61

A.

Exception words shared with Nonwords

B.

Exception words unique from Nonwords

Figure 10. A. *Shared activation between EXCs and NWs*. Activation shared between EXCs and NWs was found in the LOG, cerebellum, SPL, IPLSG, PrG, IFGPT, MFG, and the SFG in the left hemisphere, and the LOG, cerebellum, ITG, STG, and PoG in the right hemisphere. Shared activation was also found in the LG, OG, cuneus, PreC, CG, SFG and insular cortex. B. *Unique activation to EXCs and NWs*. Activation unique to EXCs was found in the SPL in the left hemisphere, and the ITG, MTG, and STG in the right hemisphere. Activation unique to NWs was found in the cerebellum, LOG, ITG, MTG, STG, SPL, AG, SG, PoG, PrG, SFG, MFG, and IFG bilaterally. Unique activation for EXCs was also found in the cuneus, CG, PG, orbital gyri, and SFG. Activation unique to NWs was also found in the LG, OG, PG, PreC, cuneus, midbrain, PL, CG, orbital gyri, SFG and insular cortex. Arrows point to face direction.

Figure 11. A. *Shared activation between EXCs and PHs.* Activation shared between EXCs and PHs was found in the LOG, posterior STG, and PrG in the left hemisphere, as well as, posterior ITG and IFGPO in the right hemisphere. Shared activation was also found in the cuneus, OG, MTG (right hemisphere), SFG and anterior left insula. B. *Unique activation to EXCs and PHs.* Activation unique to EXCs was found bilaterally in the cerebellum, LOG, ITG, anterior STG, SPL, and orbital gyrus, as well as, right hemisphere MTG AG, SG, and MFG. Activation unique to PHs was found bilaterally in the cerebellum, LOG, ITG, MTG, AG, SG, SPL, PoG, PrG, SFG, MFG, IFG, and the orbital gyri. Unique activation for EXCs was also found in the cuneus, PreC, SFG, STG, MTG, midbrain, gyrus rectus, and orbital gyrus. Activation unique to PHs was also found in the cuneus, PreC, PL, cingulate, midbrain, SFG and right anterior insula.   Arrows point to face direction.

A.

Regular words shared with Exception words

B.

Regular words unique from Exception words

Figure 12. A. *Shared activation between REGs and EXCs.* Activation shared between REGs and EXCs was found in bilateral LOG, STG, PoG, right MTG and ITG, and left PrG and MFG. Shared activation was also found in the OG, cuneus, PL, SFG and CG. B. *Unique activation to REGs and EXCs.* Activation unique to REGs was found in the right LOG and bilateral cerebellum, ITG, MTG, STG, AG, SG, SPL, PoG, PrG, SFG, MFG, IFG. Unique activation for EXCs was found in the LOG, ITG, MTG, STG bilaterally, the PoG, SFG, and MFG in the left hemisphere, and the SPL, and IFGPO in the right hemisphere. Activation unique to REGs was also found in the right LOG and cerebellum, bilateral PreC, STG, MTG, PL, CG, SFG, orbital gyri and gyrus rectus and mid-to-posterior insula, while activation unique to EXCs was found in the cerebellum, cuneus, PreC, SFG, CG, midbrain, gyrus rectus, left orbital gyri, and mid-to-anterior insula. Arrows point to face direction.
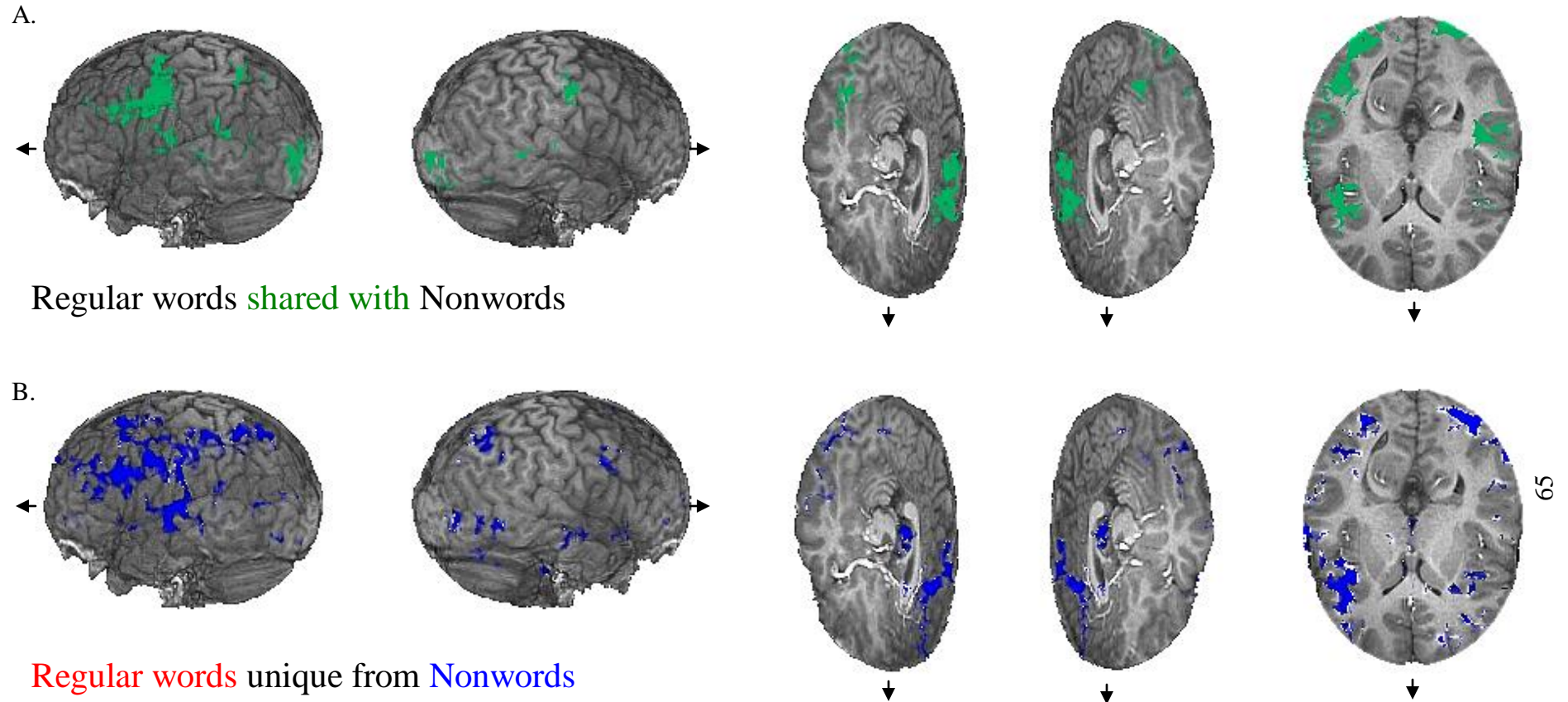
A.

Regular words shared with Nonwords

B.

Regular words unique from Nonwords

Figure 13. A. *Shared activation between REGs and NWs*. Activation between REGs and NWs was found in bilateral LOG, STG, left SG, SPL, PrG, IFG-PO, MFG, and right MTG, and PoG. Shared activation was also found in the right cerebellum, and bilateral LOG, OG, CG, SFG, and mid-to-anterior left insular cortex. B. *Unique activation to REGs and NWs*. There was no unique activation found for REGs when compared to NWs. Activation unique to NWs was found in the LOG, MTG, STG, SPL, and MFG bilaterally, and the SG, PoG, PrG, IFG, and SFG in the left hemisphere. Activation unique to NWs was also found in the LOG, LG, midbrain, cingulate gyrus, SFG, and bilateral anterior insular cortex. Arrows point to face direction.
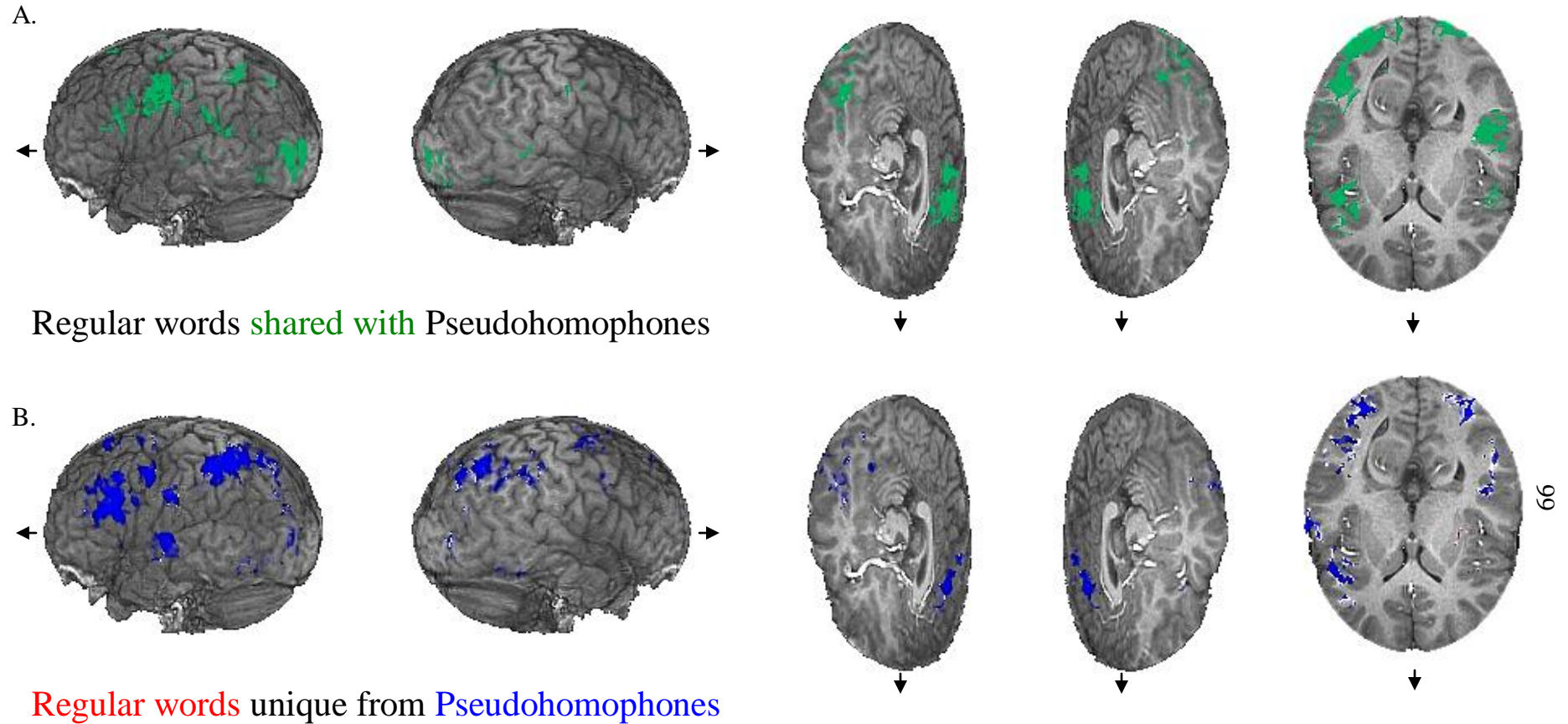
A.

Regular words shared with Pseudohomophones

B.

Regular words unique from Pseudohomophones

Figure 14. A. *Shared activation between REGs and PHs.* Activation shared between REGs and PHs was found in bilateral LOG, ITG, PoG, SPL, right MTG, and left STG, SG, PrG, and MFG. Shared activation was also found in bilateral LOG, OG, CG, SFG, right LG, and left mid-to-anterior insular cortex. B. *Unique activation to REGs and PHs.* There was no unique activation found for REGs when compared to PHs. Activation unique to PHs was found in the LOG, ITG, SPL, PrG, MFG and SFG bilaterally, and activation was seen in the left STG, AG, and PoG. Activation unique to PHs was also found in the OG, CG, SFG, and left anterior insular cortex. Arrows point to face direction.
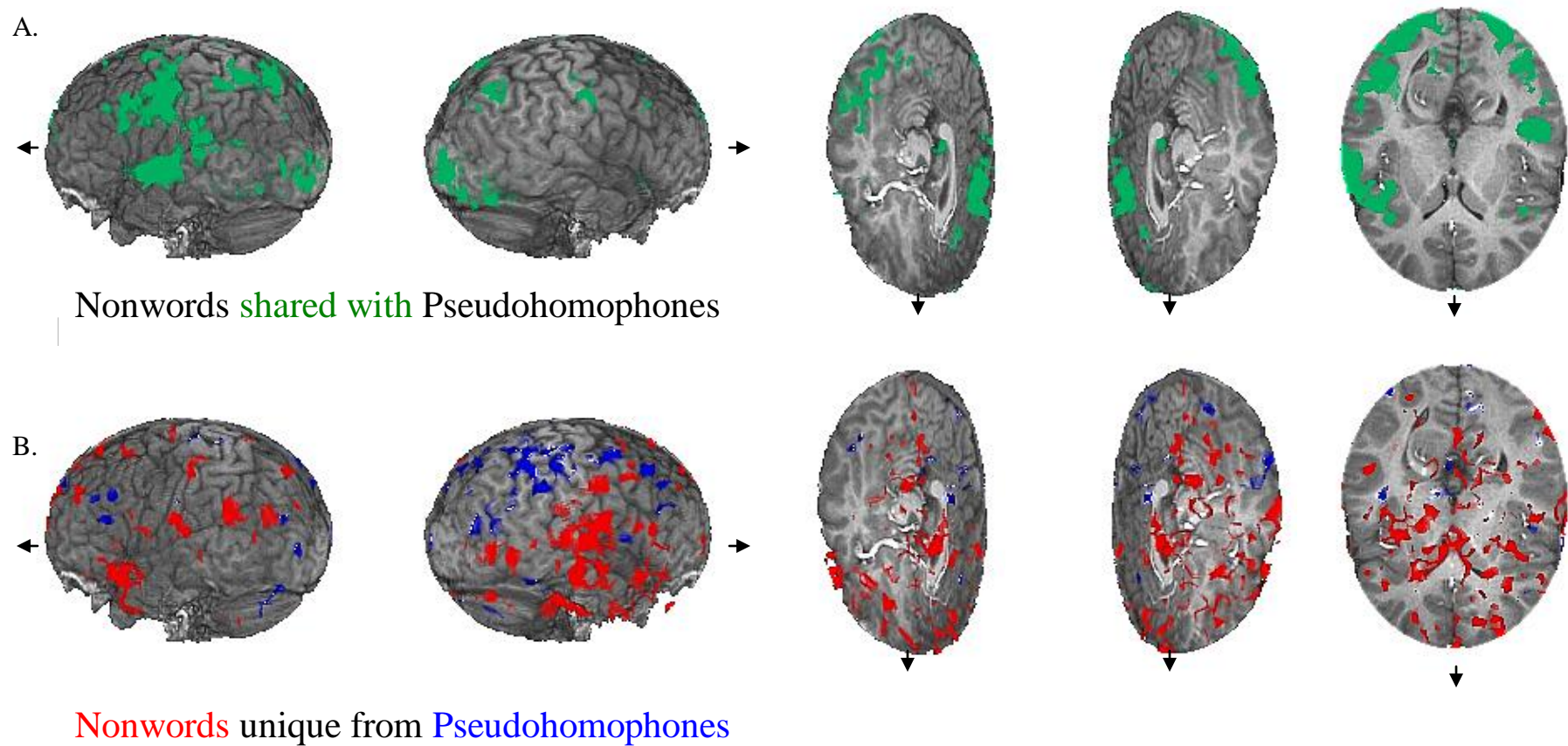
A.

Nonwords shared with Pseudohomophones

B.

Nonwords unique from Pseudohomophones

Figure 15. A. *Shared activation between NWs and PHs*. Activation shared between NWs and PHs was found in the bilateral LOG, ITG, AG, SPL, PrG, MFG, and SFG, and left MTG, STG, PoG, IFG-PO. Shared activation was also found in the LG, OG, cuneus, PreC, PL, midbrain, CG, and SFG, and left mid-to-anterior insular cortex. B. *Unique activation to NWs and PHs*. Activation unique to NWs was found in bilateral STG, PoG, PrG, IFG-PT, MFG, SFG, cerebellum, and SG, left AG, SPL, and IFG-PO, and right MTG, ITG, and orbital gyri. Activation unique to PHs was found in bilateral LOG, MFG, cerebellum, AG, and PoG, and left SFG and right PrG and IFGPO. Activation unique to NWs was also found in the cerebellum, LG, OG, cuneus, PreC, midbrain, PL, CG, SFG, gyrus rectus, orbital gyrus, PG and insular cortex, while activation unique to PHs was found in the LG, OG, PreC, CG, and SFG. Arrows point to face direction.

ventral stream from the occipital cortex through to the temporal lobes. In contrast, PH naming, which must activate both orthographic and phonological sub-word representations as well as whole-word phonological representations, was processed predominately in a dorsal stream including the occipital, parietal and frontal gyri. Importantly, REG naming which is often assumed to rely on both whole-word and sub-word representations activated a predominately dorsal stream similar to PH naming. Finally, NW naming which only has sub-word orthographic and phonological representations activated numerous regions in the brain that were not restricted to either a dorsal or ventral stream. All stimuli comparisons shared activation in regions associated with visual input and motor output, in particular the occipital cortex and premotor and motor cortex, respectively.

What is particularly noteworthy is the finding that REG naming largely activated dorsal regions in the brain. While REG naming can activate both SV and PD processes, familiar REGs are commonly assumed to engage SV processes given their familiarity from both an orthographic and phonological perspective (Binder et al., 2005; Fiez et al., 1999; Joubert et al., 2004). Thus, one might have predicted that these stimuli would by and large activate a ventral SV processing stream. When we compared REG naming with EXC naming, which primarily has SV characteristics, there was considerable unique dorsal activation for REG naming. Furthermore, when we compared REG naming with PH and NW naming which primarily have PD characteristics there was no unique activation for REG naming. That is, all activation was shared between PD stimuli and REGs indicating that they are activating similar dorsal processing systems. Thus, in contrast to previous notions that familiar REG naming primarily activates regions responsible for SV processing our results suggest that familiar REG naming primarily activates regions that are considered to reflect PD processing. Noticeably REG stimuli,

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particularly when presented in a pure block format, are flexible in the extent to which naming them can rely on SV or PD processing. Future endeavors with REG stimuli must avoid assumptions about SV processing strategies and ventral brain regions, given that these stimuli engage more dorsal regions and likely more PD processing than typically assumed.

The fMRI maps clearly indicate that the stimuli used to engage SV and PD systems contribute both to unique activation foci and shared activation foci and thus spatially depict a relationship of mathematical independence. This was not a trivial finding. For example, if there was no unique activation for one class of stimuli (e.g., EXCs as a measure of SV processing) then a model of redundancy in which PD is the dominant system would have been supported. In contrast, if there was no shared activation between naming EXCs and PHs, then a neurobiological model of exclusivity (i.e., a model in which two systems that only process their representative stimuli are required) would have been supported. Indeed, we found that there are separate patterns of activation for SV and PD processing, as well as significant shared activation for each stimulus type. Such a pattern of results supports the dual-route models of basic reading processes put forth by Pugh et al. (2000), Posner and Raichle (1994), Borowsky et al. (2006) and Cohen et al. (2008).

The regions of activation that were robust across each of the maps included the lateral occipital gyri, anterior insula and the medial superior frontal gyri (including the supplementary motor cortex). Activation in the lateral occipital gyri was expected given its involvement in early visual information processing. We demonstrated in Experiment 3 that the insula is sensitive to PD phonology, a characteristic common to the naming of REG, PH and NW stimuli. Thus, the one issue that remains to be determined is the exact role of the medial superior frontal gyri (i.e., supplementary motor cortex) in basic reading processes. Past research dating back to

Penfield has consistently found activation in this region during speech production and has suggested it may be involved in programming complex motor activity (Posner & Raichle, 1994). Somewhat consistent with this notion, working memory research by Picard and Strick (1996) and Petit, Courtney, Ungerleider, and Haxby (1998) have examined the dorsomedial prefrontal cortex, which contains the supplementary motor area and anterior cingulate cortex. This research suggests that these regions are involved in preparing for and selecting a motor response. The present research outlined a more inferior supplementary motor cortex activation pattern that was shared between stimuli in all comparisons. Clearly, there is a need for future research that examines the exact role of the medial superior frontal gyri during the parsing of phonemes in an attempt to articulate letter strings, and we will return to this issue in Experiment 6.

The frontal lobes have also been shown to be involved in working memory, whereby there is a frontal-ventral stream that is involved in the maintenance of stimuli and a frontal-dorsal stream that is involved in the manipulation of stimuli (D'Esposito, 2001; Muller & Knight, 2006). Such working memory research may pertain to the extended activation in the ventral and dorsal frontal lobes that is found during the naming of PD stimuli. This activation might be a product of working memory-demanding phonological strategies. Given that PHs are completely novel to participants, strategies must be engaged when naming such stimuli. One such strategy during PD processing might include the following steps: 1. First the participant must parse the visual information and hold the parsed stimulus in memory. 2. The participant must engage in phonemic translation of sequential parsed components in order to form a phonological representation of the visual stimulus. 3. Next, the participant must check their phonological lexical system to determine if they have comprised an accurate phonological representation of the stimulus. 4. Finally, the participant must give a verbal response. However, this has not been

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established directly, and thus, the role of the supplementary motor cortex and frontal gyri during speech production is further investigated in Chapter 3.

Our findings are important for researchers interested in global ventral – dorsal models and specific regions of interest as they relate to basic reading processes. Specifically, we have provided clarification about the role of the insula in basic reading processes, demonstrating that this region plays a significant role in PD phonology. We also provide further evidence for the broad distinction between ventral and dorsal processing streams, such that SV based reading activates a ventral processing stream and PD based reading activates a dorsal processing stream. In addition, we demonstrate that NWs typically used to engage PD processing may be sub-optimal in fMRI in that they produce rather dispersed activation. Finally, familiar REGs typically assumed to be read via SV processes were found to be primarily activating regions associated with PD processing. This latter finding should be accommodated by any current model of basic reading processing. For example, both computational and neurobiological models of reading should be able to emphasize the PD dorsal processing stream more so for REGs than traditionally assumed. We look forward to seeing this implemented in future models.

Conclusion

Experiment 3 and 4 demonstrated that SV processing activates regions in the ventral stream as evidenced by EXC naming, which is primarily whole-word in nature, and PD processing activates regions in the dorsal stream as evidenced by PH naming, which is primarily sub-word in nature. While REG naming is in theory, equally whole-word and sub-word in nature, such stimuli primarily engaged regions within the dorsal frontal cortex similar to that seen with PH naming. This finding indicates that REGs are not unyielding to the particular reading process they employ (i.e., familiar REGs are not relying on the ventral stream to the

same extent as EXCs) and caution must be implemented when utilizing these stimuli to activate

ventral brain regions. Finally, NW naming appears to be an arduous task as evidenced by the

wealth of activation throughout the cortex, and produces less constrained and less interpretable

activation when compared to PHs; an issue that is revisited in Chapter 4. The latter two findings

emphasize the vigilance that must be exercised when assumptions are made about how a

cognitive description potentially maps onto a functional architecture.

Chapter 3: Converging Evidence from Behavioural and Functional Research

Summary

The purpose of the following experiments was to examine the ways in which behavioural and functional data can be compared to provide important information about basic reading processes. Such investigations are important to gain a more comprehensive understanding of basic reading processes and have the potential to provide another level of interpretation about the contribution of particular brain regions to SV and PD processing.

Experiment 5 (published in **Cummine** et al., 2008, *Magnetic Resonance Imaging*) examined the correlation between behavioural response time and fMRI BOLD width in Broca's Area during a naming task and whether the correlation varies as a function of four stimulus types: REGs, EXCs, NWs, and PHs. Participants named letter-strings aloud during an fMRI experiment. Naming response times were recorded during regular gaps in image acquisition and the BOLD width for active voxels was extracted. The results revealed that only PH naming response times were correlated with BOLD width, providing evidence that Broca's area supports PD processing accompanied with phonological lexical access.

Experiment 6 examined the typical Frequency X Regularity interaction reported for behavioural naming reaction times and the extent to which BOLD measures displayed the same pattern of results. Participants named aloud high and low frequency REGs and EXCs during an fMRI study. Initial activation maps revealed unique activation for EXCs in the supplementary motor association cortex (SMA; i.e., increased preparatory response), and unique activation for low frequency EXCs in the right middle temporal gyrus (i.e., increased SV processing). Functional BOLD time courses were extracted from four regions of interest including the middle temporal gyrus, SMA, insula and Broca's area. Importantly, BOLD intensities within the SMA

displayed an overadditive pattern parallel to that typically found with behavioural naming

reaction times, indicating that this region may play a critical role in the Frequency X Regularity

interaction.

Introduction

Experiment 5

Research that supports the utility of developing ways to analyze the temporal aspects of

fMRI comes from studies that have correlated onset measures (e.g., stimulus presentation) with

BOLD activity onset (e.g., inflection point from baseline; Menon et al., 1998; Richter et al.,

1997) and from studies that have correlated the behavioural processing time (e.g., reaction time)

with the BOLD width measure (i.e., FWHM of the BOLD response; Lui et al., 2004; Menon, &

Kim, 1999; Menon et al., 1998; Richter et al., 1997). For example, the study by Richter et al.

(1997) using time-resolved fMRI techniques, examined whether temporal resolution in fMRI

could provide information about the temporal sequence of neuronal events during the execution

of a mental rotation task. Time-resolved fMRI typically involves measuring the progress of the

BOLD signal from a single executed task, where it is important that individual trials are

distinguished from one trial to the next. Examination of the hemodynamic response in the

parietal lobe, presumed to be critical for mental rotation performance, revealed a correlation

between behavioural reaction time and FWHM of the BOLD response for the mental rotation

task. Assuming that the hemodynamic response is a linear function of neuronal activity, and

with evidence that the width of the peak in the fMRI time course is proportional to the reaction

time, Richter et al. (1997) concluded that the parietal lobe is active during the entire period of the

mental rotation task.

Following Richter et al. (1997), a recent study by Liu et al. (2004) sought to determine

whether the correlation between reaction time and FWHM of the BOLD response remained

during tasks of more rapid cognitive demands (around the order of 1 second for reading versus

the 5 seconds for mental rotation). Liu et al. (2004) examined whether the relationship between

behavioural measures (i.e., reaction times) and temporal measures in event-related fMRI BOLD responses (i.e., FWHM) could be replicated in a language task. While in the MRI, participants performed a lexical decision task (i.e., decide if the target is a word or a NW) for three types of stimuli: high-frequency REGs, low-frequency REGs and NWs. Looking at regions within the left inferior frontal cortex, Liu et al. (2004) found a positive correlation between behavioural reaction time and FWHM of the BOLD response. That is, faster reaction times were associated with narrower BOLD widths. This correlation between behavioural reaction time and BOLD width is an important finding with respect to our understanding of how word identification behaviour and neurophysiology are related in the inferior frontal gyrus.

More specifically, the inferior frontal gyrus and particularly Broca's area is important with respect to representing phonology (i.e., word sounds; Binder & Price, 2001; Borowsky et al., 2006; Gold, Balota, Kirchnoff, & Buckner, 2005; Price, et al., 1998) and word segmentation (Gold et al., 2005) in language. Manipulating the types of stimuli that participants are given in a word identification task can serve to focus on a specific type of linguistic representation, such as phonology (Borowsky et al., 2006; Cohen et al., 2008; Fiebach & Friederici, 2002; Fiez et al., 1999; Fiez, Tranel, Seager-Fririchs, & Damasio, 2006; McDougall et al., 2005; Owen et al., 2004; Perry, Ziegler, & Zorzi, 2007). For example, naming unfamiliar letter strings such as PHs serves as a way to isolate PD processes in reading (Fiez et al., 1999; see also Borowsky et al., 2006; McDougall et al., 2005). The study by Lui et al. (2004) did not evaluate the relationship of BOLD width and reaction time as a function of stimulus type nor did they evaluate the more ecologically valid task of naming. The correlation reported in their study was computed by combining all lexical decision reaction times (a task that is highly reliant on semantic access; Borowsky & Masson, 1996) and BOLD FWHMs for each participant and each stimulus type

revealing the significant overall relationship between the BOLD widths and reaction times. Therefore it cannot be determined whether the relationship reported by Lui et al. is particularly influenced by one of the stimulus types (i.e., REGs or NWs) nor whether it represents a particular linguistic representation such as PD phonological processing.

Refining the correlation between temporal FWHM of the BOLD response and reaction time

To determine whether the relationship between FWHM of the BOLD response and reaction time is dependent on a particular reading process, several different letter-strings must be compared in the context of an overt naming task (Borowsky et al., 2006), including REGs (e.g., *hint*), EXCs (e.g., *pint*), NWs (e.g., *bint*) and PHs (e.g., *pynt*). As outlined in Chapter 2, each of these letter-strings differs in some regard from the others in terms of which reading processes they rely on for accurate performance (see Table 7). The findings of Lui et al. (2004) can be elucidated to determine whether the correlation between reaction time and BOLD measures (such as FWHM) in Broca's Area is maximal for naming PHs (as a measure of the PD system and SV phonological processing) and less so for EXCs (as a measure of only SV phonological processing), NWs (as a measure of only PD phonological processing) and REGs (which can be read by either process). We hypothesize that the relationship between naming response time and BOLD measures (such as FWHM) should be strongest for the stimulus type that requires maximal activation of phonological representations (i.e., PHs, in that they involve PD *and* phonological lexical access) in Broca's area.

<div align="center">

Methods

</div>

Participants, Stimuli, Materials, Analyses

The participants, stimuli, materials and analyses are identical to those reported in Experiment 2. The time courses represent the average hemodynamic response extracted from Broca's area for each stimulus type (REGs, EXCs, NWs, PHs).

Statistics

Behavioural naming response times were calculated by averaging each participant's correct offset response times for each stimulus type. Initial correlation analyses were conducted to evaluate the relationship between the BOLD response measures and naming response time overall (collapsing across stimulus types) and then for each stimulus type (REG, EXC, NW, & PH).

<div align="center">

Results

</div>

Relationship between Response Time and FWHM

The mean response times, accuracy rates and BOLD response measures for each stimulus type are presented in Table 4 (see also Figure 16). Correlation analyses between response time and each of the BOLD measures, collapsed across stimulus type, revealed a significant relationship between Response Time and Volume, $r(39) = .323$, $p=.042$, Response Time and Initial Slope $r(39) = .464$, $p=.003$ and, consistent with Lui et al. (2004), a relationship between Response Time and FWHM, $r(39) = .269$, $p=.093$, that is significant at the one-tailed level ($p=.047$). We then examined the relationship between Response Time and BOLD measures for each stimulus type. There were significant correlations between PH Response Time and FWHM, $r(9) = .899$, $p<.001$, Intensity, $r(9) = .738$, $p=.015$, and Initial Slope $r(9) = .689$, $p=.027$. There was a significant correlation between NW Response Time and Time to Peak, $r(9) = -.655$, $p=.036$. There were no significant relationships between Response Time and any BOLD response measures for REGs or EXCs. Clearly the correlation between PH Response Time and
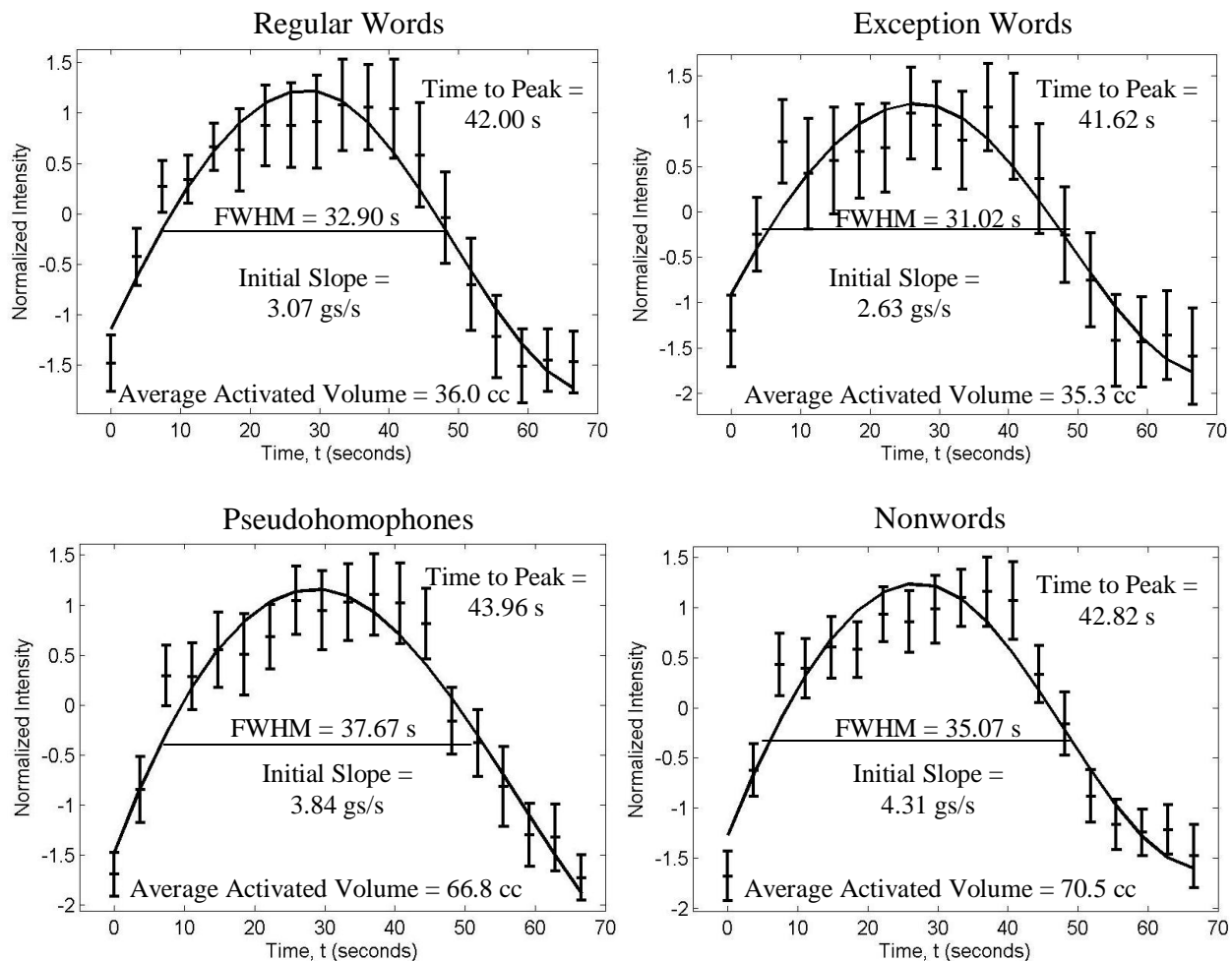
Figure 16. BOLD hemodynamic response (h; points with error bars) and smoothed BOLD hemodynamic response (H(t); solid line) as found in Broca's area and averaged across participants. (Note: Normalized Intensity = standardized (z-score) grayscale intensity values. Zeropoint is set to be the greyscale value of the first active volume).

FWHM is sufficiently strong to survive even the most conservative Bonferroni correction, and thus it is the focus of our attention in the discussion section.

Given that results revealed only PHs and NWs had significant relationships between Response Times and BOLD measures, multiple regression analyses were run with these variables to determine which BOLD measures were the best predictors of Response Times. The multiple regression that assessed the extent to which PH Response Time could be accounted for given FWHM, Intensity, Time to Peak, Volume and Initial Slope of the BOLD response was significant, $F(5, 9) = 6.95$, $p=.04$ ($R^2 = .897$, adjusted $R^2 = .768$). However, only FWHM remained significant within the overall model, $t(9) = 3.21$, $p=.033$ (partial $r^2 = .849$; see Figure 17). The multiple regression that assessed the extent to which NW Response Time could be accounted for given FWHM, Intensity, Time to Peak, Volume and Initial Slope of the BOLD response was not significant, $F(5, 9) = 1.84$, $p=.29$.[5]

Discussion

Our results revealed a relationship between the behavioural measure of response time and the neurophysiological measure of FWHM of the BOLD response that was dependent on stimulus type in a naming task. Specifically, only PH naming response time was significantly related to FWHM both in terms of simple correlation and in terms of accounting for unique variance in a multiple regression. Our work provides further support for the notion that fMRI and the BOLD response measures (i.e., FWHM) can provide valuable temporal information. Also, the relationship between FWHM of the BOLD response and response time in a language task was refined here to show that this relationship is dependent on the stimulus type. Upon investigation of specific letter-strings that can be read correctly via a SV system (i.e., EXCs), a PD system (i.e., PHs and NWs) or by both systems (i.e., REGs), it was found that only PH
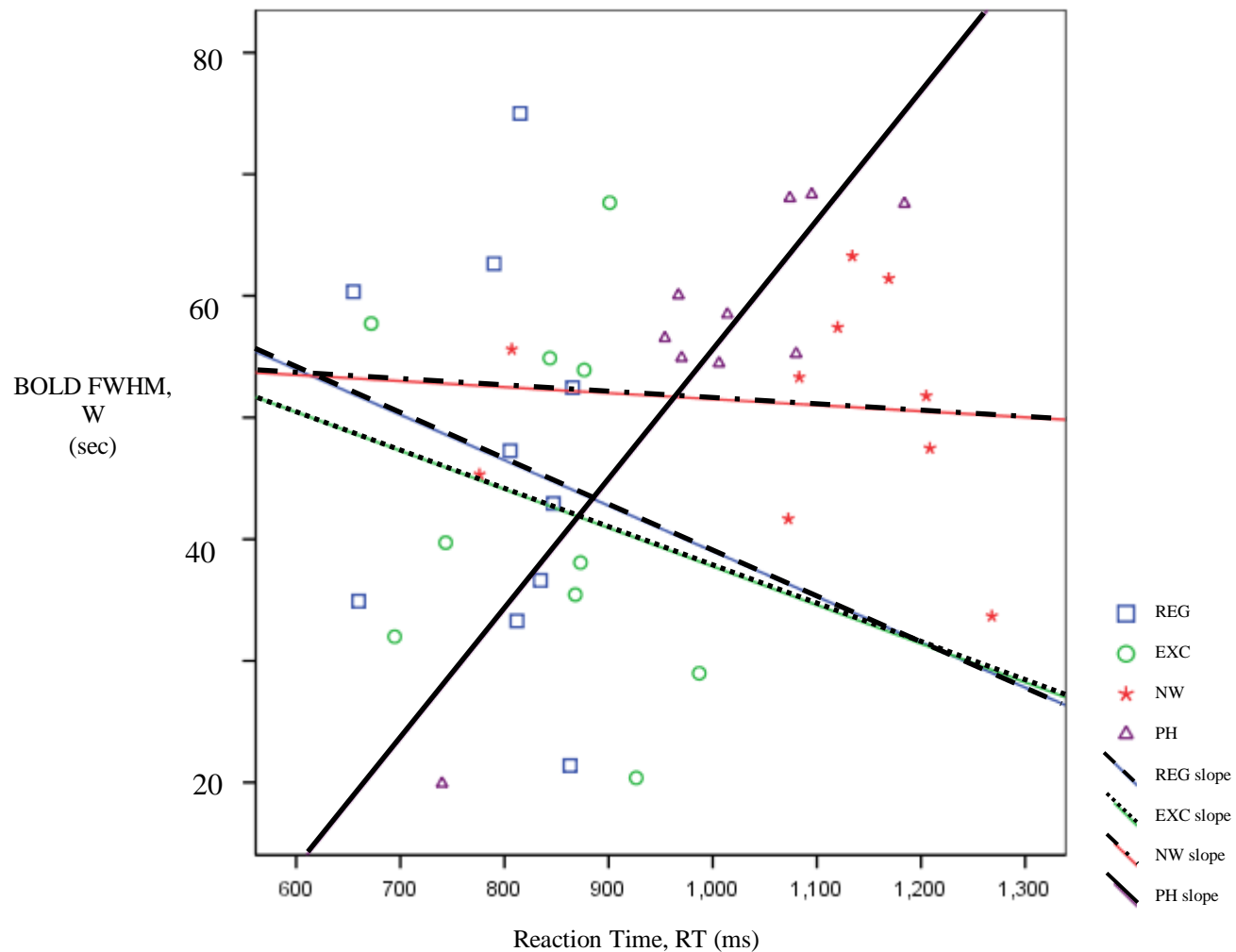
Figure 17. BOLD width at half maximum (as derived from the functional data) plotted as a function of response time (as derived from the behavioural data) for each stimulus type. There is a significant positive linear relationship between PH reaction time and FWHM of the BOLD response. (Note: There was one datum with z-score > ±2.5 (PH datum in the lower left). The correlation between FWHM and PH reaction time was reassessed after removing this participant, and remained significant.)

response times were correlated with FWHM of the BOLD response.   Before providing a

theoretical account of this finding, it should be noted the current results clearly show that

investigations of the relationship between behavioural measures and functional imaging

measures in language tasks must control for stimulus type.

Past research by Richter et al. (1997) suggested that the relationship between reaction

time on a mental rotation task and the FWHM of the BOLD response was related to the region of

interest investigated. Specifically, it was suggested the correlation between the two measures

was significant because the parietal lobe is involved in spatial orientation. Such an explanation

can be used to understand the unique relationship between response time and FWHM of the

BOLD response for PHs whereby our region of interest, namely Broca's Area, is involved in

naming such stimuli. Areas in the inferior frontal gyrus near Broca's area are particularly

sensitive to phonological lexical familiarity (Binder & Price, 2001; Borowsky et al., 2006;

Burton, 2001; Fiez et al., 2006 ; Price et al., 1998), a defining characteristic of PH processing.

While EXC and REG processing have this characteristic, the need to draw on such resources

might not be as demanding given that they are orthographically familiar (i.e., their spelling is

familiar) as well. NW processing, on the other hand, has no such characteristic of phonological

lexical familiarity, and thus would not be expected to draw on such resources (see Figure 2).

Lui et al. (2004) computed a correlation coefficient that combined all stimulus types in a

lexical decision task, which was the first demonstration that BOLD widths are related to

behavioural response time in word identification. We were interested in determining whether

reading a particular stimulus type (and thus engaging a particular reading process) is responsible

for the effect.   Although we found a significant relationship between FWHM and response time

overall, we established that only PH response time was uniquely related to FWHM of the BOLD

response. Lui et al. (2004) examined the left inferior frontal gyrus, broadly defined, whereas, our study focused on Broca's area within the inferior frontal gyrus, bilaterally. Our focus, accompanied with our use of a naming task as opposed to a lexical decision task has advanced Lui et al.'s finding and provides several new options for research involving BOLD measures and their relationship to behaviour.

As previously mentioned, the lexical decision task (as was used by Lui et al. (2004)) evokes considerably more semantic processing than a simple naming task and the extent and influence of such semantic processing is a question for future study. For example, research has implicated the anterior portion of the inferior frontal gyrus during semantic processing and the posterior portion of the inferior frontal gyrus during phonological processing (Binder & Price, 2001; Gold et al., 2005).   However, Lui et al. (2004) did not explicitly distinguish between anterior and posterior inferior frontal gyrus. In addition, the participants in Lui et al.'s (2004) study could have been relying on phonological lexical verification (i.e., does this stimulus 'sound' like a word, as opposed to simply assessing whether it 'spells' a word), which in light of our findings, is consistent with the possible role this region plays in basic reading processes. It remains to be seen whether a task that forces orthographic lexical verification (e.g., a lexical decision task containing words and PHs) produces the same effect and whether these effects are modulated by the anterior or posterior portion of the inferior frontal gyrus. Accordingly, our work provides valuable new information for research on basic reading processes, which should be studied using a variety of tasks including both naming and lexical decision.

Furthermore, our study provides important information regarding tasks that have relatively fast, and a limited range of, response times. While the relationship between PH response time and BOLD FWHM was significant, replication and extension is necessary for

several reasons. For example, naming tasks are relatively simple and thus produce a limited range of response times, whereas more difficult tasks (e.g., lexical decision, semantic decision, and mental rotation) provide the opportunity for a larger range of response times. Thus, future research should examine the nature of the relationship between BOLD measures and behavioural measures in the context of tasks that produce a variety of ranges of response times. Nonetheless, there appears to be a robust relationship between response time and certain BOLD measures (e.g., FWHM is reliably correlated with response time for mental rotation, lexical decision and naming; Lui et al., 2004; Richter et al., 1997).

Overall, Experiment 5 provides important information about the relationship between word identification behaviour and neurophysiology in Broca's area, bilaterally. Specifically, the BOLD response width (FWHM) from Broca's area is uniquely related to PH naming response time, a stimulus that forces PD processes during word reading. As such, our findings provide evidence in support of the hypothesis that Broca's area supports PD *accompanied with* phonological lexical access, and suggest that a PH naming task provides one way for elucidating this relationship.
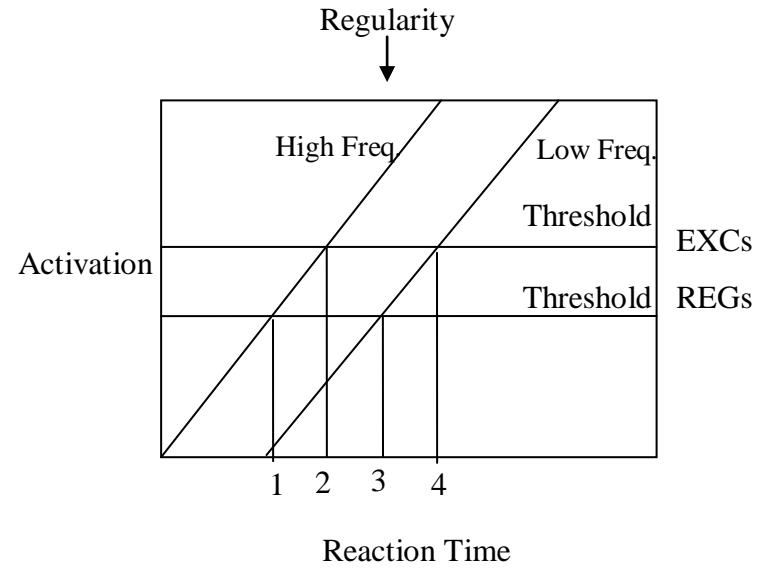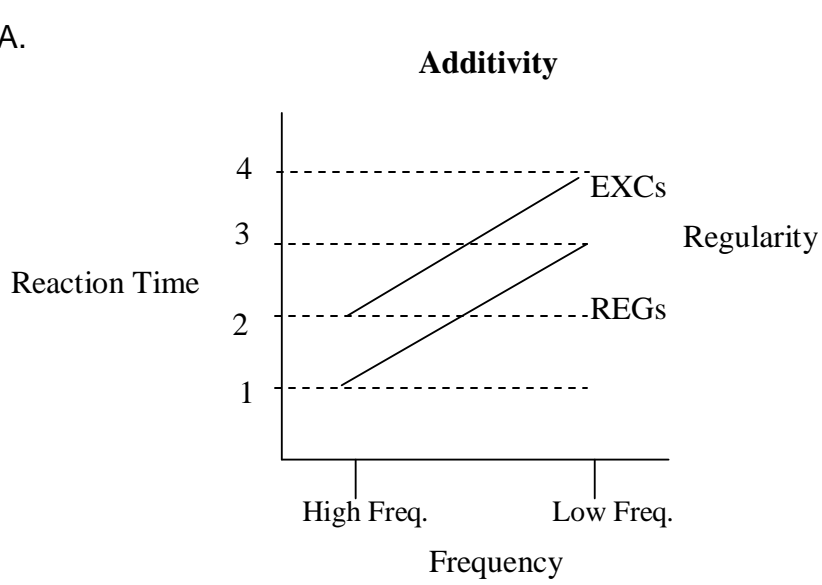
<div align="center">Experiment 6</div>

Importantly, we can investigate the relationship between behavioural and functional data in another way to further appreciate the involvement of particular brain regions during SV and PD processing. More specifically, the behavioural theories originally developed to understand cognitive architectures can be applied to the interpretation and understanding of functional architectures. For example, at one time subtractive logic dominated how cognitive experiments were conducted and reaction time results were interpreted (Donders, 1868; 1969). The introduction of Sternberg's (1969) additive factors logic (AFL) provided a new way of looking at
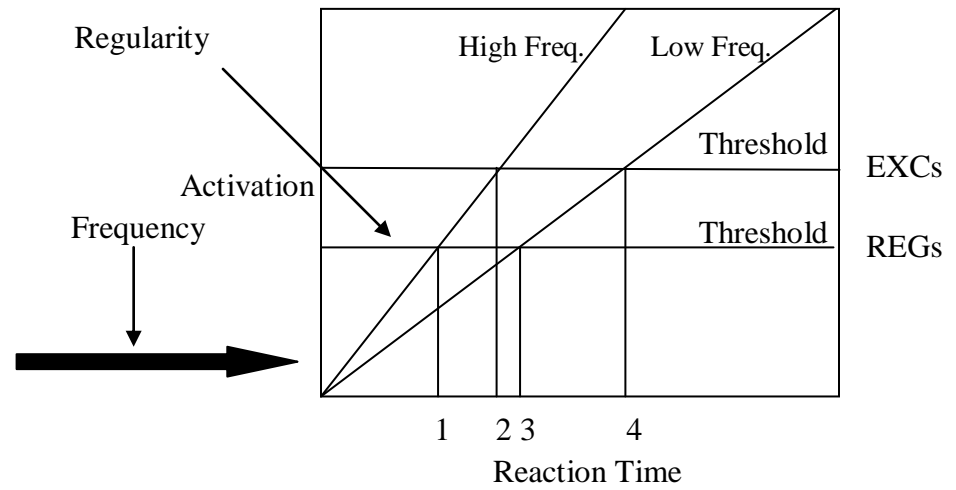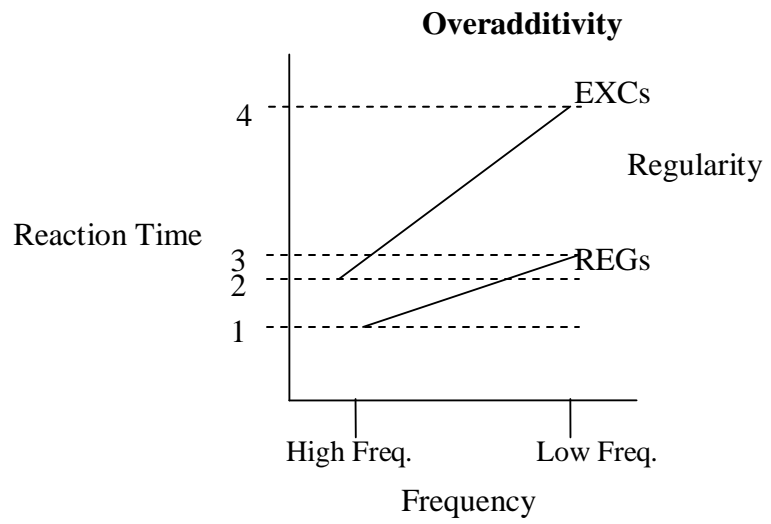
reaction times in cognitive experiments. Such logic has been useful in understanding stages of processing (underlying subsystems) and how factors affect a common stage versus separable stages of processing in basic reading tasks (see Figure 18; Borowsky & Besner, 1993; Borowsky & Besner, 2006). However, limited research has been conducted which applies AFL to measures other than reaction time (Miller & Hackley, 1992; Schweickert, 1989; 1985). More specifically, while AFL has advanced our understanding of how experimentally manipulated variables (factors) influence one another in time from a cognitive perspective, it remains to be seen whether such logic can be useful in our understanding of how factors influence one another in space (i.e., the brain), from a functional perspective. Little is known about the extent to which such logic can inform us about the underlying cortical regions involved in basic reading processes.

Within research on basic reading processes, two factors that are commonly found to interact in basic naming paradigms are frequency and regularity (Hino & Lupker, 2000; Lupker, Brown, & Colombo, 1997; Visser & Besner, 2001). The Frequency X Regularity interaction is the finding that low frequency EXCs are named significantly slower than low frequency REGs, whereas higher frequency EXCs and REGs are named relatively faster and do not demonstrate the same magnitude of effect (Besner & Smith, 1992; Lupker et al., 1997; Paap & Noel, 1991). Two theoretical accounts have been put forth to explain the typical overadditive interaction of frequency and regularity. Dual route theorists explain the Frequency X Regularity effect in terms of the processing speeds between the SV and PD systems. Specifically, it is argued that high frequency EXCs can be processed fast enough via the SV route that naming can occur before the PD system can create a competing and incorrect phonological code. Low frequency EXCs, on the other hand, take longer to process and thus the PD system can produce a
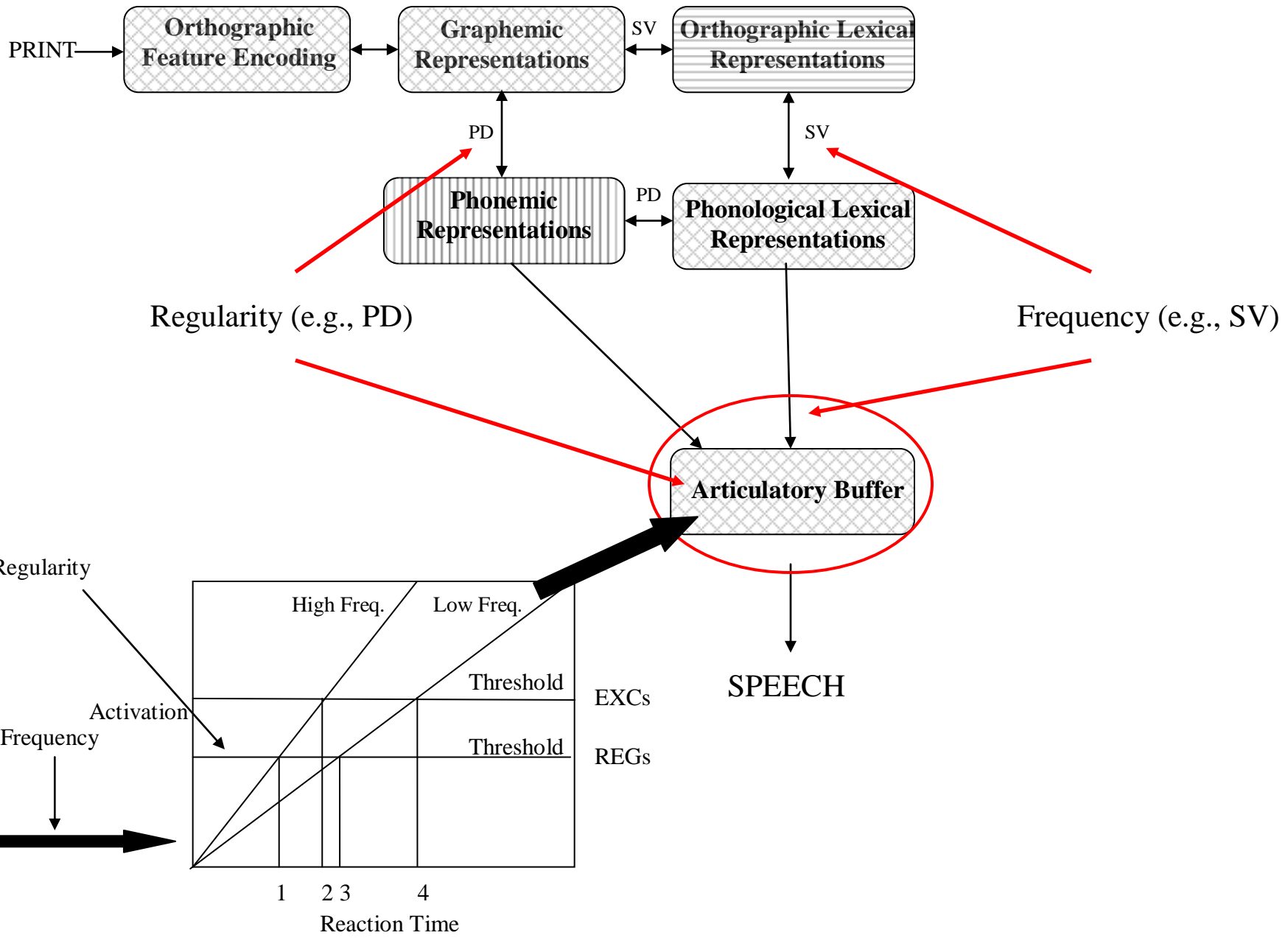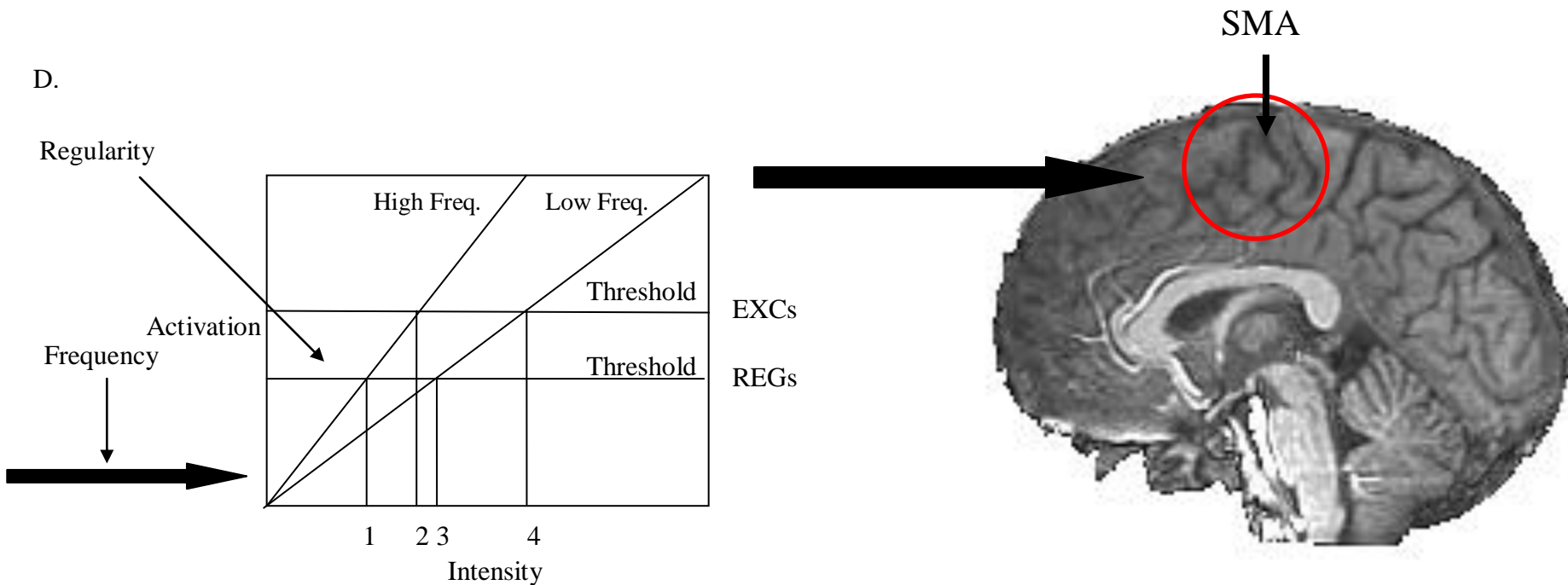
A.

Additivity

Reaction Time

4 ----------------- EXCs
3 ----------------- Regularity
2 ----------------- REGs
1 -----------------

High Freq.   Low Freq.

Frequency

Regularity

Activation

High Freq.   Low Freq.

Threshold EXCs

Threshold REGs

1 2 3 4

Reaction Time

B.

Overadditivity

Reaction Time

4 ----------------- EXCs

                    Regularity

3 -----------------
2 ----------------- REGs
1 -----------------

High Freq.   Low Freq.

Frequency

Regularity

Activation

Frequency

High Freq.   Low Freq.

Threshold EXCs

Threshold REGs

1   2 3   4

Reaction Time

C.

PRINT → Orthographic Feature Encoding ⟷ Graphemic Representations — SV — Orthographic Lexical Representations

PD

Phonemic Representations — PD — Phonological Lexical Representations

SV

Regularity (e.g., PD)

Frequency (e.g., SV)

Articulatory Buffer

Regularity

Activation

Frequency

High Freq.   Low Freq.

Threshold   EXCs

Threshold   REGs

SPEECH

1   2 3   4

Reaction Time

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D.

SMA

Regularity

High Freq.   Low Freq.

Activation

Frequency

Threshold   EXCs

Threshold   REGs

1   2 3   4

Intensity

Figure 18. A. Pattern of additivity on reaction time indicating that the two factors of interest are affecting separate stages of processing and a cognitive model which relates such additivity to factors of frequency and regularity (Time 1 = High frequency REGs; Time 2 = High frequency EXCs; Time 3 = Low frequency REGs; Time 4 = Low frequency EXCs) B. Pattern of overadditivity on reaction time indicating that the two factors of interest are affecting a common stage of processing and a cognitive model which relates such overadditivity to factors of frequency and regularity. C. An example of how AFL can be applied to the dual-route model of reading to understand where frequency and regularity influence one another in time (e.g., within the articulartory buffer). D. An example of how AFL can be applied to functional data to understand where frequency and regularity influence one another in the brain (e.g., within the SMA).
Abbreviations: Freq. = Frequency; AFL = Additive Factors Logic; SMA = Supplementary Motor Association cortex; REGs = Regular words; EXCs = Exception words; SV = Sight Vocabulary; PD = Phonetic Decoding.

competing phonological representation that must ultimately be resolved with the SV pronunciation prior to speech output. The resulting pattern of reaction times is an overadditive interaction, as described above.

Other theoretical accounts, which have been put forth by single mechanism theorists, do not make a distinction between different routes to account for the Frequency X Regularity interaction (Harm & Seidenberg, 2004; Plaut et al., 1996). Instead, these theorists treat spelling-sound correspondences as a continuum where REGs and EXCs represent different points on this continuum. For example, some connectionist models employ a sigmoid input-output function whereby the input levels of frequency and regularity serves to produce an output which parallels the typical Frequency X Regularity interaction found on basic naming reaction times (Plaut et al., 1996).[6] Other single mechanism theorists emphasize the distributed representations of orthographic, phonological and semantic units and it is the weights on the connections between these units that produces the typical Frequency X Regularity interaction (Harm & Seidenberg, 2004). Thus, the extent to which one subscribes to either a dual route or connectionist account of basic reading processes influences the way in which the Frequency X Regularity interaction is interpreted. However, there is no research on the Frequency X Regularity interaction in terms of an examination of the stages of processing, or AFL, of basic reading systems, which is useful for all theoretical frameworks. AFL provides another level of interpretation regarding the Frequency X Regularity interaction and the corresponding subsystems involved, which is not dependent on the model one endorses and consequently has the potential to inform and advance all models of word recognition.

In general, AFL interprets an additive pattern of reaction times as evidence for the factors affecting separate stages of processing (see Figure 18A; Sternberg, 1969; Roberts & Sternberg,

1993). Specifically, if frequency and regularity affect separate stages of processing then the effect of one factor will not depend on the levels of the other factor. For example, if frequency had effects at an earlier stage of processing than regularity then activation in a subsequent system would be delayed by a constant factor. The resulting pattern of reaction times is such that high frequency REGs pass a baseline activation threshold and are named first (Time 1), followed by high frequency EXCs (Time 2), low frequency REGs (Time 3) and low frequency EXCs (Time 4). However, in the presence of an overadditive pattern of reaction times the factors being investigated are interpreted as affecting a common stage of processing (see Figure 18B). The overadditive Frequency X Regularity interaction on basic reading performance would suggest that frequency and regularity are affecting a common stage of processing whereby the levels of one factor influences or depends on the levels of another factor (see Figure 18C for an example; see also Borowsky & Besner, 1993 and Borowsky & Besner, 2006 for a description of the effects of context, stimulus quality and word frequency). Incorporating AFL with the previously outlined interpretations of the Frequency X Regularity interaction provides a more comprehensive understanding of the underlying processes at work during basic reading. For example, do frequency and regularity influence one another in a system such as an articulatory buffer where the pronunciation codes are evaluated just prior to speech? Or do these factors influence one another at an earlier feature analysis system where orthographic representations are initially assessed? Thus, regardless of whether one subscribes to a dual-route or single mechanism account of basic reading, AFL is essential in our understanding of how factors influence one another in time from a cognitive perspective. Importantly, minimal work has been conducted that extends such logic to measures other than reaction time in particular those extracted from functional data. It is currently unknown to what extent AFL can be applied to

functional measures to further our understanding about where factors influence one another in the brain.

Functional Investigations of the Frequency x Regularity Interaction

From a functional perspective, research that examines the Frequency X Regularity interaction has been minimal. One study by Fiez et al. (1999) examined the functional location of several factors including frequency and regularity while participants named aloud letter strings. Their results indicated that the insula played a critical role in the Frequency X Regularity effect whereby the activation intensities for the stimuli in this region displayed a similar pattern of overadditivity as is typically found in behavioural studies on reaction time. That is, the intensities for the low frequency EXCs were noticeably larger than the intensities for all the other stimuli. Although Fiez et al. (1999) did not interpret their findings using AFL, an endeavour of this sort is important for our work. Accordingly, when AFL is used to interpret their findings we would suggest that frequency and regularity affect a common region in the brain, namely the insular cortex. Additionally, Fiez et al. (1999) demonstrated that the intensities of the four critical stimuli do not demonstrate overadditivity within the lateral inferior frontal gyri. Instead, the intensities display a pattern of additivity within this region. Again, if we interpret these findings using AFL it would be argued that frequency and regularity affect separate systems of processing within the lateral inferior frontal gyrus. Once more, given what we know about the functional purpose of the inferior frontal gyrus and its involvement in motor output, is not surprising that regularity and frequency produce effects in this region.

Importantly, Fiez et al. (1999) also reported increased activation in the SMA cortex for low frequency words and thus this region is another potential region involved in the Frequency X Regularity interaction. The SMA is a likely candidate for where frequency and regularity might

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converge within the brain given that much functional research has implicated the SMA as being involved in preparatory motor responses (see Figure 18D; Cavina-Pratesi, Valyear, Culham, Köhler, Obhi, Marzi & Goodale, 2006; Fiez et al., 1999; Möller, Jansma, Rodriguez-Fornells & Munte, 2007; Müller & Knight, 2006; Rauschecker, Pringle & Watkins, 2008; Richter et al., 1997). For example, if the Frequency X Regularity interaction is produced because of competing phonological codes for low frequency EXCs as is proposed by dual route theorists it is possible that the SMA is the region where such competition is resolved. Similar to the insular cortex the anatomical location of the SMA is near the motor cortex which is involved in the actual motor output. Thus, the SMA is another promising region of interest where the overadditive Frequency X Regularity effect may be located.

More recently, Frost et al. (2005) conducted a study that examined the effect of imageability, regularity and frequency on activation during reading aloud. Of particular interest is their finding of an overadditive interaction on frequency and regularity within the left hemisphere inferior frontal gyrus on low imageable words. That is, activation intensities for EXCs were significantly larger than activation intensities for REGs and this difference was limited to low frequency words in the low imageable condition. Applying AFL to this finding would lead us to conclude that the inferior frontal gyrus is the region in the brain where frequency and regularity influence one another. However, this finding is in contrast to the additivity of regularity and frequency that Fiez et al. (1999) reported in the inferior frontal gyrus and thus further investigation of this region and it's involvement in the Frequency X Regularity interaction is important.

Notably, the Frequency X Regularity interaction is primarily a product of the low frequency EXCs and thus regions involved in processing these stimuli are of primary interest to

us. Much research has implicated the temporal lobes as a region responsible for the processing of EXCs (Dhanjal, Handunnetthi, Patel & Wise, 2008; Frost et al., 2005; Glasser & Rilling, 2008; Hauk, Davis & Pulvermuller, 2008; Joubert et al., 2004; Simos, Pugh, Mencl, Frost, Fletcher, Sarkari & Papanicolaou, 2008; Simos, Breier, Fletcher, Foorman, Castillo & Papanicolaou, 2002; Spitsyna, Warren Scott, Turkheimer, & Wise, 2006). For example Frost et al. (2005) reported that activation in the middle temporal gyrus was modulated by frequency (and imageability) and Fiez et al. (1999) reported that the left hemisphere temporal region was more active when participants read low frequency words as compared to high frequency words. This region presumably plays a significant role in the processing of low frequency EXCs and thus we should see evidence of this in our activation maps.

Summary

Behavioural research on basic naming typically reports a Frequency X Regularity interaction on reaction time and AFL would suggest that these two factors are affecting a common stage of processing in time. However, such logic has yet to be applied to functional data in attempts to localize these factors in the brain. Functional research on basic word recognition utilizing naming tasks indicates that likely regions where such factors may be coming together include the inferior frontal gyrus, insular cortex and the SMA. Currently, an fMRI naming study has yet to be conducted that explicitly looks for the Frequency X Regularity interaction in these brain regions and that uses AFL with BOLD measures to localize factors in the brain. In addition, regions that are particularly active for low frequency EXCs are also of interest given that these stimuli are the motivating force behind the Frequency X Regularity interaction. Past research indicates that regions within the middle temporal gyrus are likely involved in the processing of these stimuli. Importantly, AFL provides a novel level of

interpretation to functional data and is an innovative technique in the extraction of information regarding sub-systems involved in basic reading processes, and thus, is relevant and applicable to all models of word recognition.

Methods

Give the nature of the stimuli and that the naming task is relatively undemanding, we wanted to maximize sensitivity by using a blocked design instead of an event related design. Thus, an initial behavioural study was run to ensure that presenting the stimuli in a purely blocked fashion (as opposed to the mixed stimulus design that is typically employed in behavioural studies) would still produce the expected results.

Participants

Psychology students (N=63) performed the naming tasks, for credit in their Introductory Psychology course. Inclusion criteria and ethical approval were identical to Experiment 1.

Stimuli

The stimuli were identical to those reported in Experiment 1 consisting of high and low frequency REGs and EXCs.[7] The 55 letter strings from each category were separated into either high (items = 27) or low (items = 28) frequency.

Materials and Procedure

The materials and procedure were identical to Experiment 1 except that participants now viewed stimuli blocked by regularity and frequency.

Results

Only correct responses and trials in which reaction times were >250ms were included in the subsequent analyses. A 2 (frequency) x 2 (regularity) repeated measures ANOVA was conducted. There was a significant main effect of frequency, $F(1, 62) = 218.81$, $p<.001$, where

high frequency words (Mean = 551.59 ms) were responded to faster than low frequency words (Mean = 602.53 ms). There was a significant main effect of regularity, $F(1, 62) = 47. 80$, $p<.001$, where REGs (Mean = 559.16 ms) were responded to faster than EXCs (Mean = 594.97 ms). There was a significant interaction between frequency and regularity, $F(1, 62) = 44.74$, $p<.001$ (see Figure 19). The effect of regularity was significantly greater for low frequency words with a difference of 57.59 ms between REGs and EXCs in comparison to high frequency words which only showed a processing difference of 14.03 ms. Response times to high frequency REGs (Mean = 544.58 ms) were significantly faster than high frequency EXCs (Mean = 558.61 ms), $t(62) = 2.30$, $p=.025$, and low frequency REGs (Mean = 573.74 ms) were significantly faster than low frequency EXCs (Mean = 631.33 ms), $t(62) = 9.40$, $p<.001$.[8]

The results from this behavioural study are in line with previous findings (e.g., Hino & Lupker, 1997; Smith & Besner, 2000). Specifically, when the stimuli are presented in a purely blocked format, we see a significant frequency effect, a significant regularity effect and most importantly, a significant overadditive interaction between frequency and regularity. Given these results we proceeded with the functional study.

Methods

Participants

Ten participants took part in the fMRI experiment. None had participated in the behavioural experiment. Inclusion criteria and ethical approval were identical to the behavioural experiment.

Stimuli

The stimuli were identical to those used in the behavioural experiment.
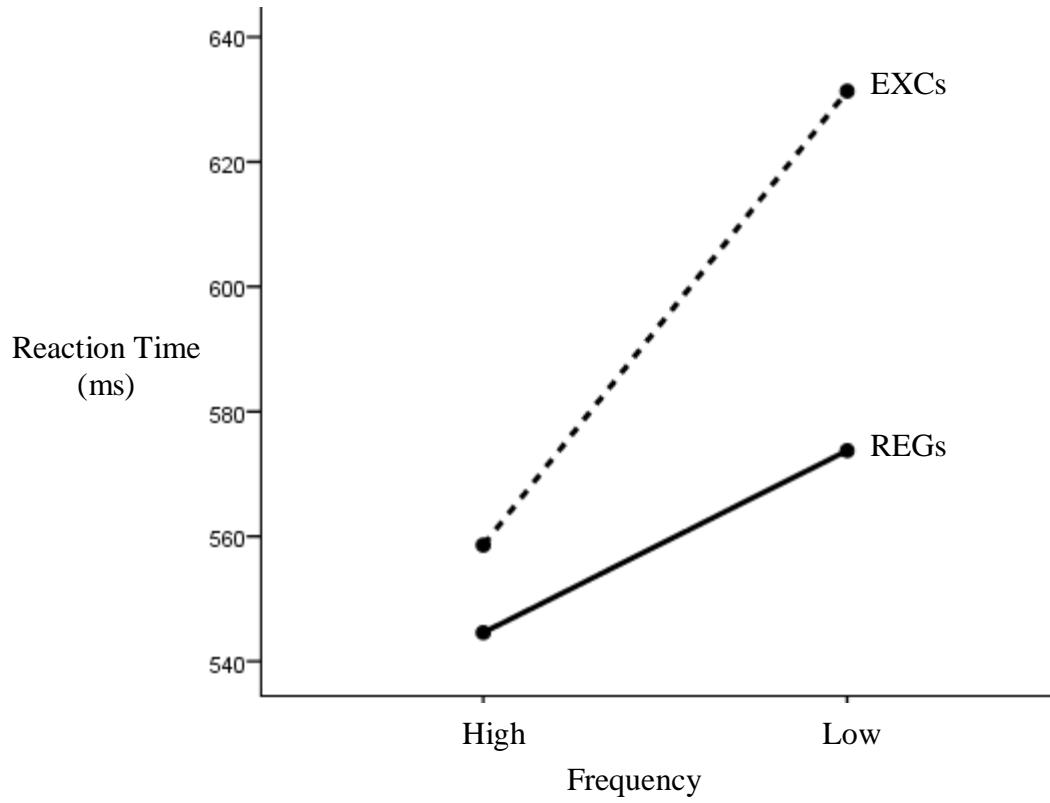
Figure 19. Significant Frequency (high vs. low) x Regularity (REG vs EXC) interaction on behavioural reaction time.

Materials and Procedure

Materials and procedure are identical to Experiment 2 except for the following changes. The volumes of images were organized into 5 blocks of 10 volumes each. Each block consisted of 5 volumes of response followed by 5 volumes of rest. That is, of the possible 28 stimuli in the low frequency conditions and 27 stimuli in the high frequency conditions, 25 items were randomly chosen for presentation (without replacement) for each of the four conditions. A BOLDfold correlation, η, of 0.60 or greater was used to define active voxels. The activation maps were rendered identically to Experiment 3, except resulting activation on the functional maps is significant at $t(9) = 1.833$, $p=0.05$, one-tailed.

Regions of Interest

To extract the relevant BOLD data, regions of interests (ROIs) were delineated for each participant. ROIs were drawn, using AFNI (Cox, 1996), in the insular cortex, lateral inferior frontal gyrus (Broca's area), SMA, and middle temporal gyrus of both the right and left hemisphere (see Figure 20). Stimulate (Strupp, 1996) was used to extract the hemodynamic response time courses for each participant, for each condition and in each ROI. Only time courses which were based on >5 active voxels were included in the analysis. The time courses were then averaged across participants to produce the average hemodynamic response.

<div align="center">*Results*</div>

The following results are focused on the regions of interest, namely the middle temporal gyrus, SMA, insula and inferior frontal gyrus (Broca's area).

High Frequency REGs and High Frequency EXCs. Shared activation between REGs and EXCs was found in the posterior LH temporal cortex, SMA and motor cortex (see Figure 21A). Unique activation to EXCs was also found in the middle temporal gyrus, SMA, inferior frontal
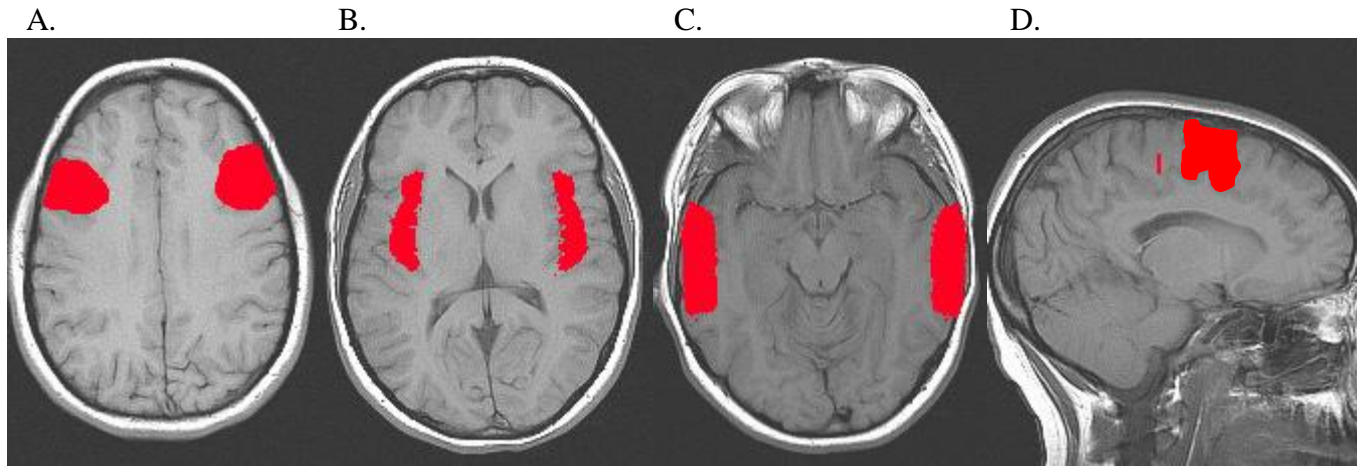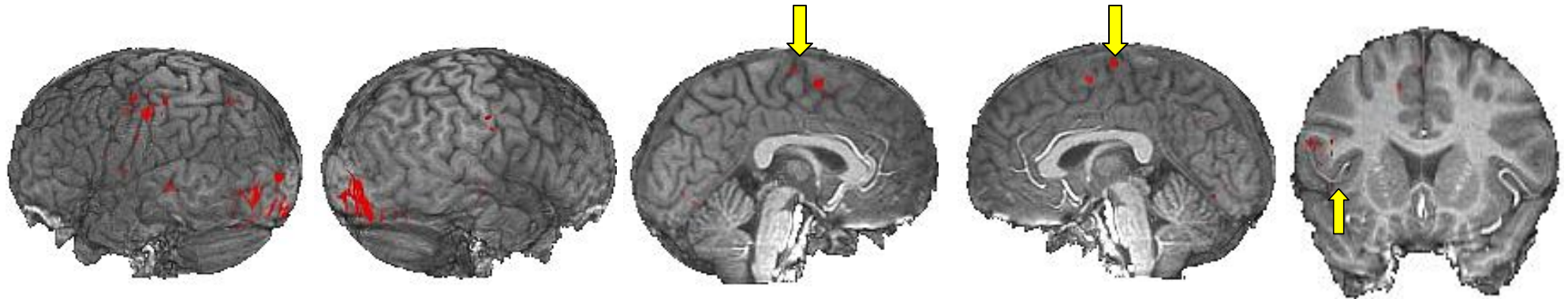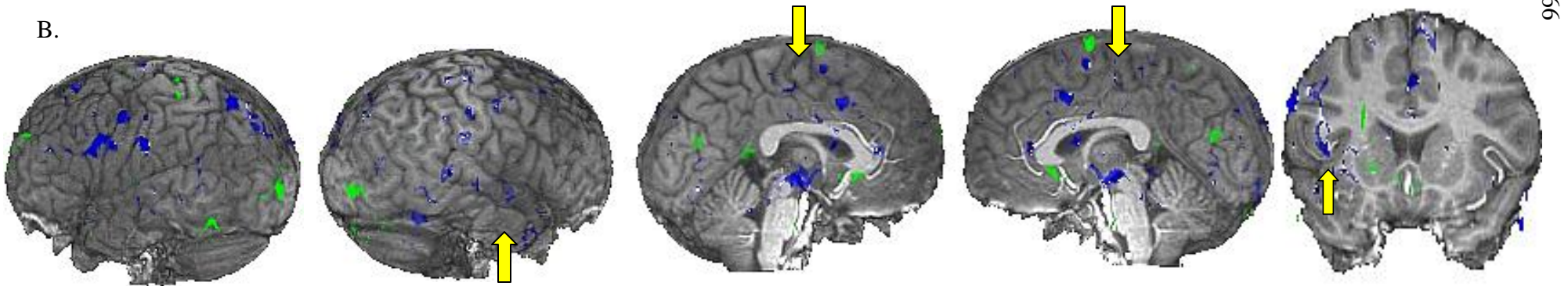
Figure 20. Examples of masked regions of interest (left = left) for one participant. A. The inferior frontal gyrus (center of right mask = -41, -65, 12). B. The insula (center of right mask = -42, -47, -8). C. The middle temporal gyrus (center of right mask = -61, -32, -28). D. The supplementary motor association cortex (-12, -40, 42).

High Frequency Regular Words shared with High Frequency Exception Words

High Frequency Regular Words unique from High Frequency Exception Words

Figure 21. A. Shared activation between high frequency REGs and EXCs. Shared activation between REGs and EXCs is found in the LOG, PrG, PoG, IFG, SMA and STG. *B. Unique activation to high frequency REGs and high frequency EXCs.* Unique activation to REGs was found in the LOG, ITG, PrG, SFG, PreC, and SMA. Activation unique to EXCs was found in the right hemisphere ITG, MTG, STG, bilateral SPL, PoG, PrG, IFG, MFG, SFG, SMA, CG, and midbrain. Arrows point to insula cortex.

gyrus and insular cortex (see Figure 21B). Unique activation to REGs was found in the inferior temporal cortex and SMA.
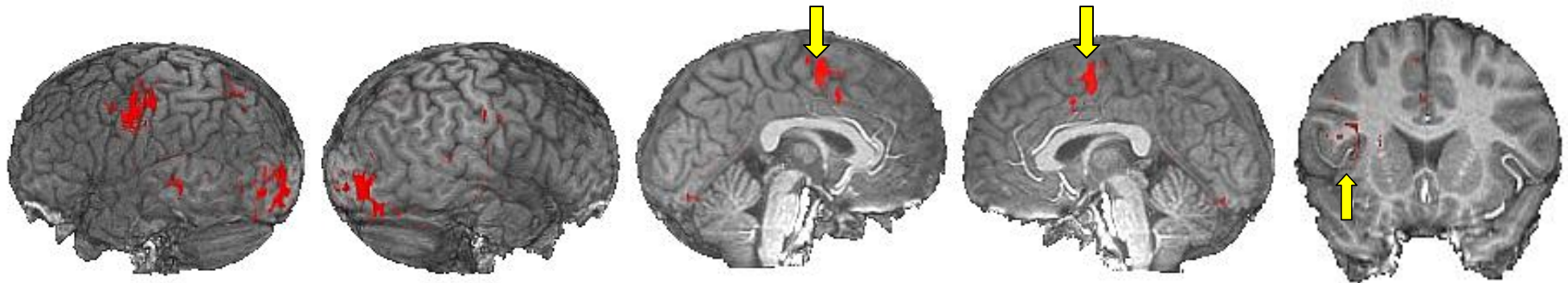
Low Frequency REGs and Low Frequency EXCs. Shared activation between REGs and EXCs was found in the left hemisphere temporal cortex, motor cortex, insular cortex and SMA (Figure 22A). Unique activation for EXCs was found in the right hemisphere middle temporal gyrus and SMA (see Figure 22B). Unique activation for REGs was found in the inferior temporal cortex.

Regions of Interest

Activation time courses were extracted for each stimulus type, from each region of interest and averaged across participants (see Figure 23). The mean peak intensities were plotted for each region of interest (see Table 8 and Figure 23). An ANOVA revealed a significant difference between peak time points among the regions of interest, $F(3, 132) = 4.051$, $p=.009$. A Student Newman-Keul posthoc test revealed that the time to peak in the inferior frontal gyrus (Broca's area; Mean = 4.65), was later than all other groups. We used the time to peak mean values to evaluate the extent to which the pattern of mean intensities resembles that typically found in behavioural reaction times.

Supplementary Motor Association cortex (SMA). Low frequency EXCs displayed an overall higher intensity function, followed by low frequency REGs. High frequency EXCs and REGs produced similar intensity functions in this region. The average intensity peak for each stimulus (time points two and three; see gray window in Figure 23A) were plotted.   Overall, EXCs produced higher intensity functions compared to REGs and low frequency stimuli produced higher intensity functions compared to high frequency stimuli. Notably, the pattern of

A.

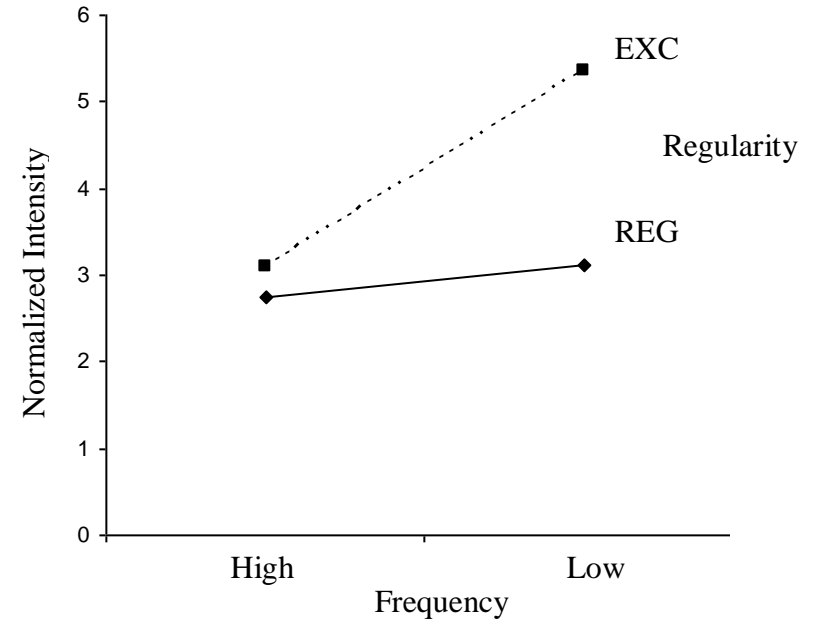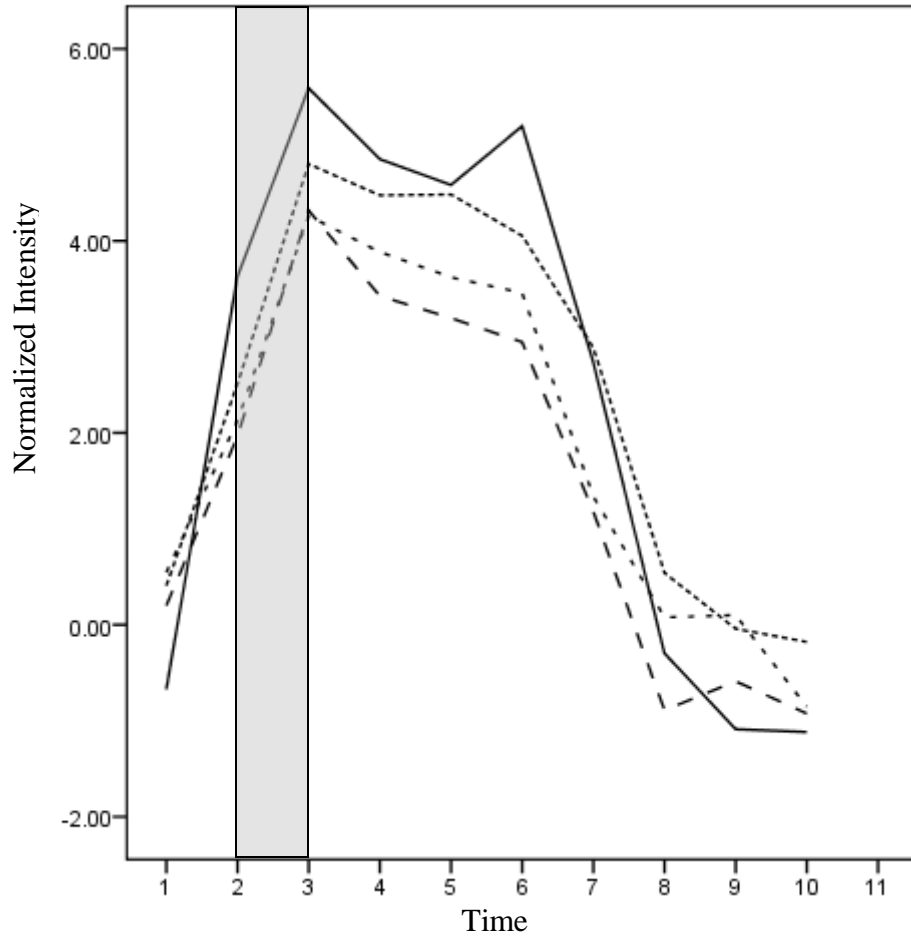Low Frequency Regular Words shared with Low Frequency Exception Words

B.
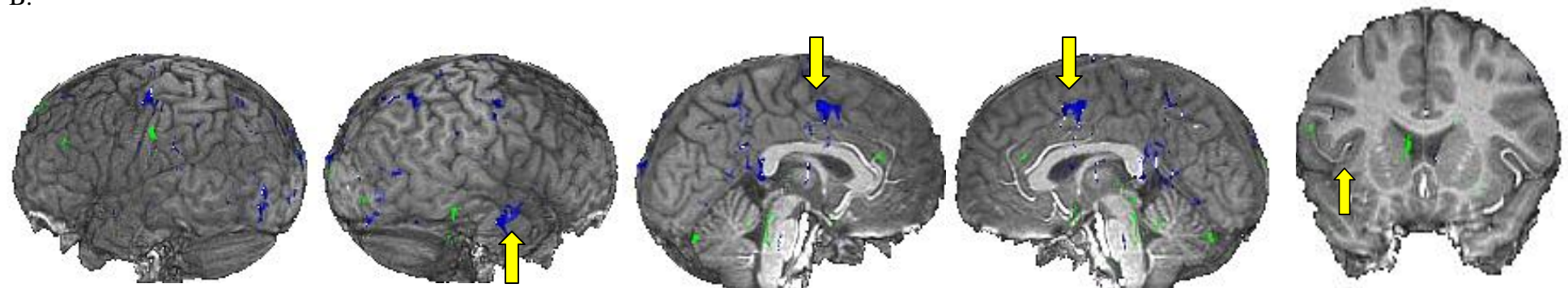
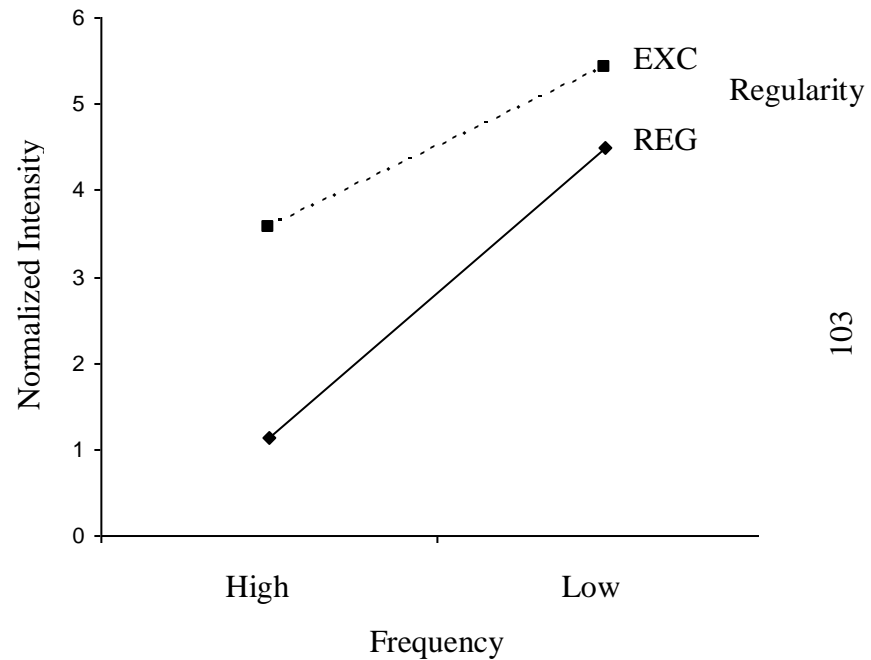Low Frequency Regular Words unique from Low Frequency Exception Words

Figure 22. A. Shared activation between low frequency REGs and EXCs. B. Shared activation between REGs and EXCs was found in the LOG, left hemisphere STG and SPL, right hemisphere IPL, PrG, PoG, SMA and cuneus. *Unique activation to low frequency REGs and low frequency EXCs.* Unique activation for REGs was found in the right hemisphere ITG, left hemisphere PrG, MFG, anterior CG and cerebellum. Unique activation for EXCs was found in the LOG, right hemisphere MTG, bilateral SPL, PrG, SMA, PL, and posterior CG. Arrows point to right MTG, bilateral SMA and insular cortex.

A.

Supplementary Motor Association Area

Normalized Intensity

Time

····· Low Frequency Regular Words
— — High Frequency Regular Words
—— Low Frequency Exception Words
- - - High Frequency Exception Words

Normalized Intensity

EXC

Regularity

REG

High   Low

Frequency

B.

Middle Temporal Gyrus

Normalized Intensity

8.00

6.00

4.00

2.00

0.00

-2.00

-4.00

Time

1 2 3 4 5 6 7 8 9 10 11

Normalized Intensity

6

5

4

3

2

1

0

EXC

Regularity

REG

High   Low

Frequency

103
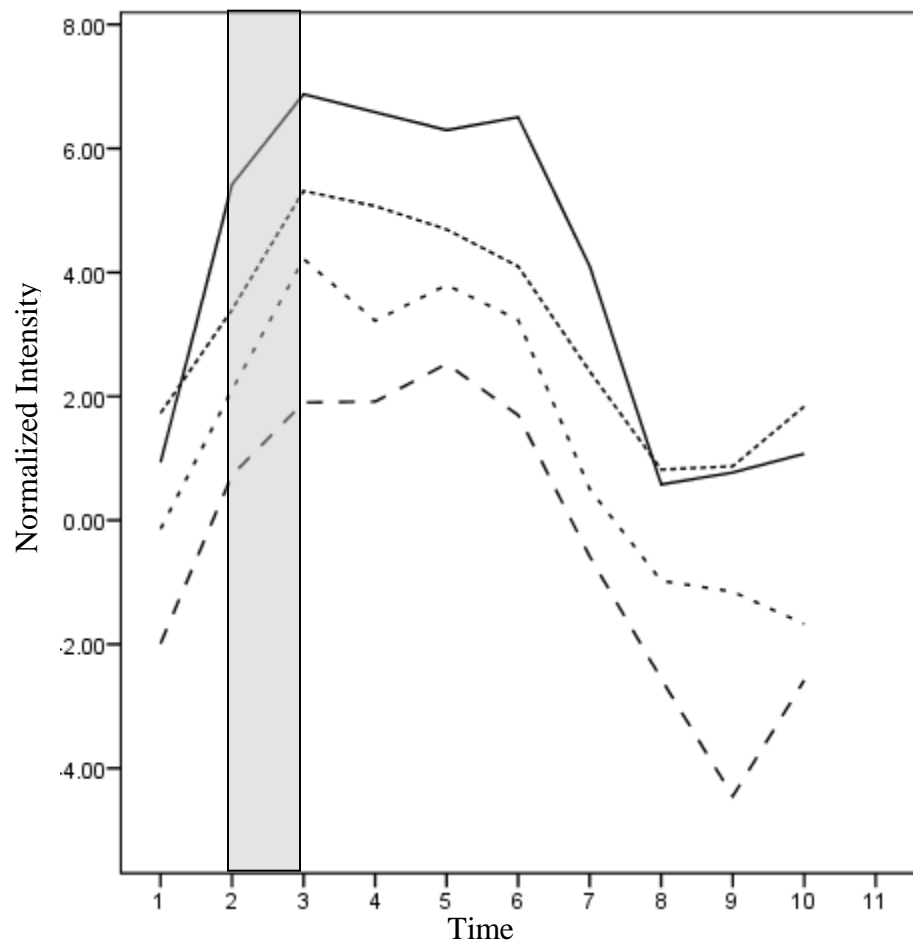
.... Low Frequency Regular Words

— — High Frequency Regular Words

———— Low Frequency Exception Words

- - - - High Frequency Exception Words

C.

Insular Cortex

Normalized Intensity

Time

.... Low Frequency Regular Words
— — High Frequency Regular Words
—— Low Frequency Exception Words
- - - High Frequency Exception Words

REG

Regularity

EXC

Normalized Intensity

High   Low

Frequency

104

D.

Broca's Area

Legend:
- .... Low Frequency Regular Words
- — — High Frequency Regular Words
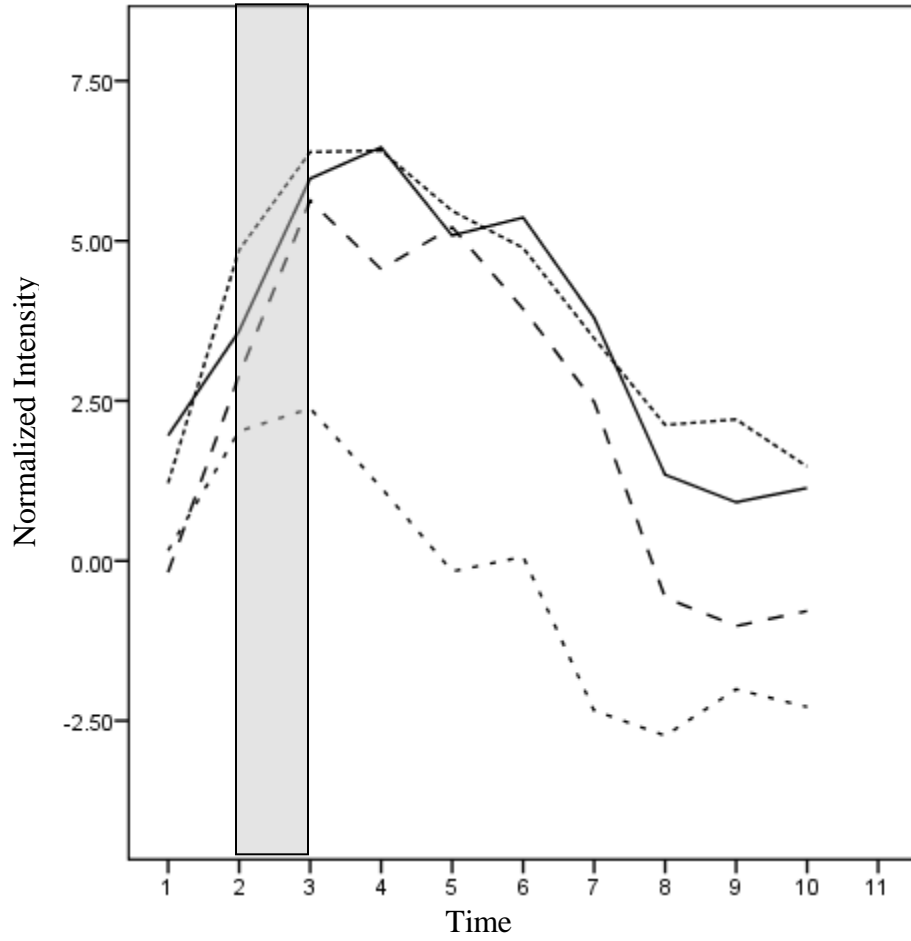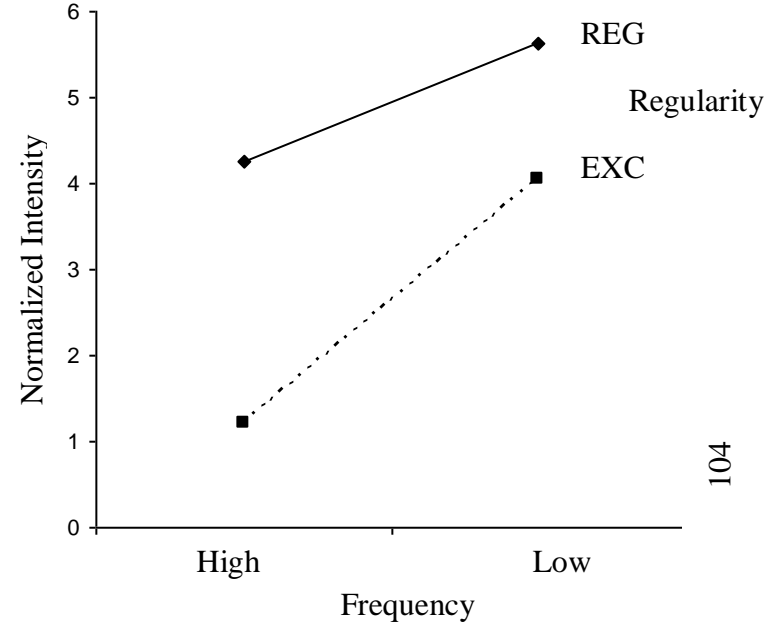- ———— Low Frequency Exception Words
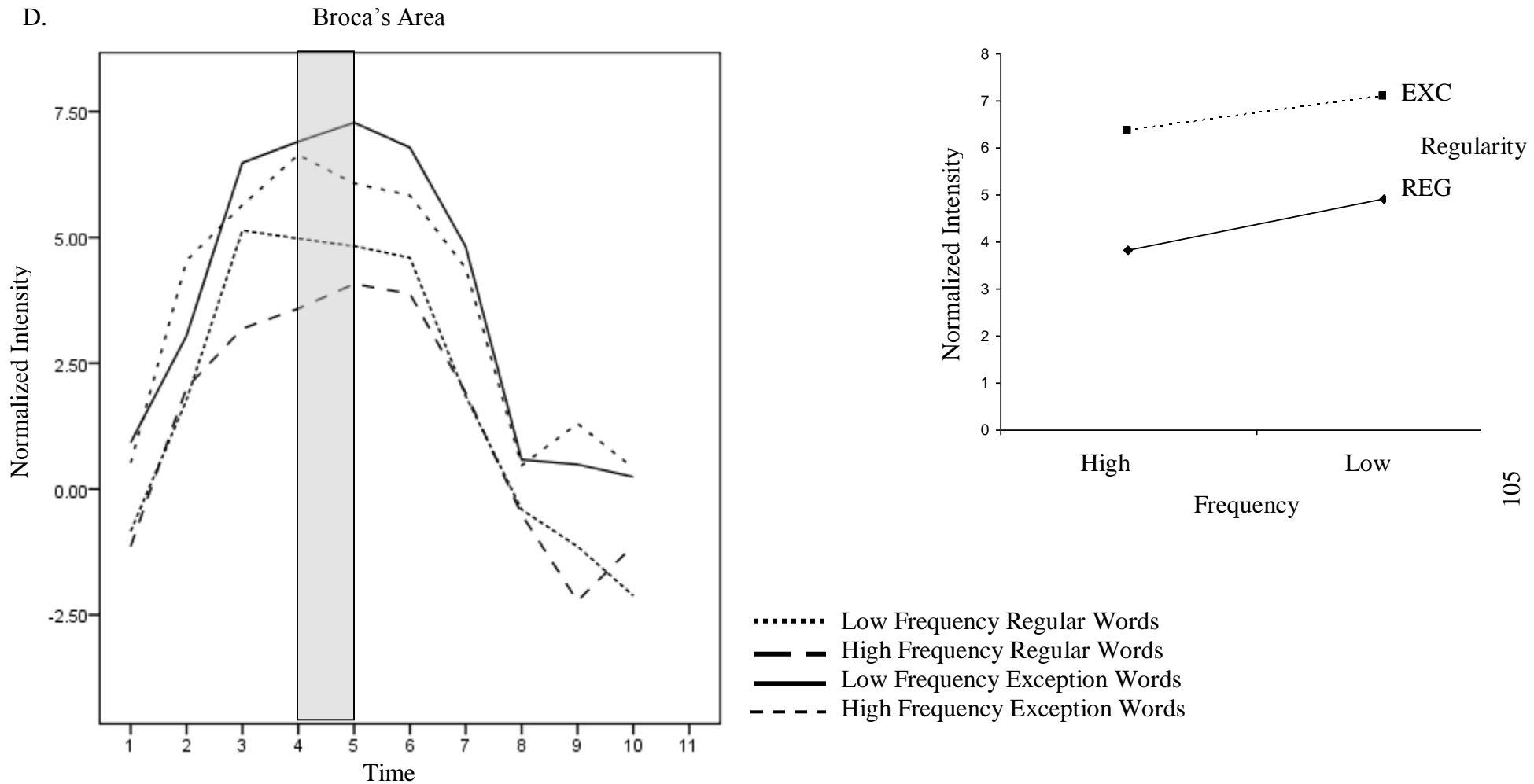- - - - - High Frequency Exception Words

Figure 23. Average hemodynamic response function and graph of the plotted mean peak intensities for: A. Supplementary Motor Association cortex, B. Middle Temporal Gyrus, C. Insula, and D. Inferior Frontal Gyrus (Broca's Area).

Table 8. Mean peak intensities (greyscale units) as a function of regularity, frequency and region of interest.

Region of Interest	Regular Words		Exception Words	
	High Frequency	Low Frequency	High Frequency	Low Frequency
MTG	1.132	4.490	3.565	5.415
Insula	4.265	5.625	1.200	4.040
SMA	2.755	3.115	3.085	5.365
Broca's	3.825	4.905	6.355	7.090

MTG = Middle Temporal Gyrus

SMA = Supplementary Motor Association Cortex

mean intensities parallels the overadditive interaction typically reported on behavioural naming reaction times.

Middle Temporal Gyrus (MTG). Low frequency EXCs displayed an overall higher intensity function than any of the other stimuli, followed by low frequency REGs, high frequency EXCs and high frequency REGs. The average intensity peak for each stimulus (time points two and three; see gray window in Figure 23B) were plotted. Overall, EXCs produced higher intensity functions compared to REGs and low frequency stimuli produced higher intensity functions as compared to high frequency stimuli.

Insular Cortex. Low frequency REG and EXCs produced similar intensities time courses, followed by high frequency REGs. High frequency EXCs produced a very small intensity function in this region. The average intensity peak for each stimulus (time points two and three; see gray window in Figure 23C) were plotted. Overall, REGs produced higher intensity functions compared to EXCs and low frequency stimuli produced higher intensity functions compared to high frequency stimuli.

Inferior Frontal Gyrus (Broca's Area). Low frequency EXCs displayed an overall higher intensity function, followed by high frequency EXCs, low frequency REGs and then high frequency REGs. The average intensity peak for each stimulus (time points four and five; see gray window in Figure 23D) were plotted. Overall, EXCs produced higher intensity functions compared to REGs and low frequency stimuli produced somewhat higher intensity functions compared to high frequency stimuli. Notably, the pattern of mean intensities displays additivity between frequency and regularity.

Discussion

We provide the first demonstration of the application of AFL to BOLD intensity in an attempt to understand where certain factors, namely frequency and regularity, interact in the brain. From our results, we conclude that the SMA is a region where frequency and regularity may interact in the brain. Our unique and shared maps illustrate that the SMA is more active for low frequency words than high frequency words, and more active for EXCs than REGs. Consistent with past research, this region appears to be involved in the preparation of a motor response, and such preparation produces higher intensity BOLD responses for low frequency EXCs than for any other stimuli. In addition, our maps illustrate that the middle temporal gyrus is maximally activated for low frequency EXCs and accordingly, a possible region where low frequency EXCs are initially slowed within the SV processing stream. Our region of interest analyses demonstrates that low frequency EXCs produce the highest intensity BOLD response in the middle temporal gyrus in comparison to the other three stimuli. In addition, EXCs produce more intense BOLD functions in the inferior frontal gyrus in comparison to REGs. Overall, the application of AFL has proven to be useful in the location of factors in the brain. More specifically, our results indicate that frequency and regularity influence a common structure, namely, the SMA.

Consistent with past research, we demonstrate that the middle temporal gyrus is sensitive to frequency (Fiez et al., 1999) whereby low frequency words produced more intense activation than high frequency words and, to a lesser degree, regularity (Frost et al., 2005) whereby EXCs produced more intense activation than REGs. Furthermore, we found that low frequency EXCs activate primarily the right middle temporal gyrus. Other research has shown that this region is particularly active during prosody tasks (e.g., detecting the rise in pitch at the end of a sentence,

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which indicates a question is being asked; see Glasser & Rilling, 2008). It is possible that similar processing demands are required for tasks involving the detection and production of proper prosody and naming low frequency EXCs. More specifically, prosody involves the manipulation and modification of phonemic pronunciations in order to transmit meaning. Low frequency EXCs are highly reliant on the particular pronunciation of the orthographic letter pattern if the correct pronunciation and subsequent word meaning is to be understood.

We found that the insula was particularly sensitive to regularity whereby REGs produced more intense activation than EXCs, and frequency, whereby low frequency words produced more intense activation than high frequency words. Notably, this is the only region in which we found REGs to produce more intense activation than EXCs. However, this is in line with previous notions about the insula's involvement in processing familiar stimuli (Posner & Raichle, 1994). While there is no difference in frequency between the REGs and EXCs in this study, REG naming involves the activation of familiar SV *and* PD representations, whereas EXC naming only involves activation of familiar SV representations. Contrary to other brain regions, the insula has been reported as producing more activation in response to familiar stimuli. However, we also demonstrate that the insula does display 'typical' neurophysiology relating to frequency whereby it responds more strongly to less familiar low frequency stimuli.

Importantly, we demonstrate that the peak intensities of our significant activation for each stimulus type produces a pattern of overadditivity within the SMA, which resembles that typically reported for behavioural reaction times. Interpreting these findings within the framework of AFL suggests that these factors influence one another within a common region in the brain. To our knowledge, this is the first study to apply AFL to BOLD measures in an attempt to localize factors in the brain. Such logic provides another level of interpretation for

factors affecting basic reading processes. This interpretation furthers our understanding of the underlying architecture of basic reading processes as it relates to neurobiological regions and more specifically how particular brain regions are influenced by frequency and regularity.

We demonstrated that the inferior frontal gyrus, namely Broca's area, is particularly sensitive to regularity whereby EXCs produced more intense response functions in this region than REGs. Interestingly, the peak of the time courses in Broca's area is later than all other regions emphasizing that Broca's area plays a role in later articulatory processes. In addition, the mean peak intensities display a pattern of additivity in this region similar to what we can see on the graphs presented by Fiez et al. (1999) which suggests that frequency and regularity do not influence one another within this region.

Notably, our results also reveal a small dissociation between frequency and regularity and their effects on intensity in different regions. More specifically, we found that frequency displays a large effect on intensity at early processing systems within the middle temporal gyrus (Mean difference between high and low stimuli = 2.604 greyscale/second (gs/s)), whereas the effect of regularity in this region is smaller (Mean difference between EXCs and REGs = 1.679 gs/s). In contrast, the effect of regularity on intensity is large within later processing regions such as Broca's (Mean difference between EXCs and REGs = 2.36 gs/s), whereas the effect of frequency in this region is much smaller (Mean difference between high and low frequency stimuli = 0.908 gs/s). This dissociation can be understood if we combine what is assumed within the behavioural dual route model with what is evidenced from the functional dual route model. That is, the cognitive dual route model suggests that the SV route is sensitive to frequency whereas the PD route is sensitive to regularity (Besner & Smith, 1992). The functional dual route model suggests that SV processing involves a ventral route in the brain whereas PD

processing involves a dorsal route in the brain (Borowsky et al., 2006; Cohen et al., 2008). Taken together, it is not surprising that the middle temporal gyrus in the ventral stream is sensitive to frequency whereas Broca's area in the dorsal stream is sensitive to regularity.

Our results underscore the importance of evaluating particular points on the hemodynamic response function. More specifically, we demonstrate that the time course peaks differentially as a function of stimulus type and region. We utilized a blocked design and, recall from Experiment 2, that blocked paradigms maximize sensitivity by creating a linear compounded BOLD response function (i.e., multiple single event BOLD functions are used to create a large response function). It was evident from our results that the hemodynamic response function in the middle temporal gyrus, insula and SMA was saturated by the third stimulus presentation. In contrast, the average peak in Broca's area was later than the other three regions and typically peaked around the fourth or fifth stimulus presentation. Furthermore, an evaluation of the entire hemodynamic response function provided interesting information about the specific stimuli. For example, low frequency EXCs produced a time course with two prominent peaks in the SMA. Such information is useful for understanding the role of the SMA in naming these stimuli. Future work should disentangle whether this double peak is a reflection of a feedback connection or an articulatory check of the derived pronunciation.

Overall, Experiment 6 demonstrates that the application of cognitive theories to interpreting functional architecture is quite useful. Specifically, we found that the SMA is critically involved in the Frequency X Regularity interaction and a region in the brain where frequency and regularity influence one another. In addition, within Broca's Area frequency and regularity produce additive intensity patterns suggesting that these factors do not influence one another within this region. While AFL has previously been used to localize factors within time

our research is the first demonstration of the use of AFL on functional intensities to localize the influence of psycholinguistic factors in the brain.

Conclusion

We demonstrate that comparing behavioural data with functional data is important for providing a more comprehensive understanding of basic reading processes and the contribution of particular brain regions to processing certain stimuli. More specifically, we demonstrate that Broca's area is critical for naming stimuli for which maximal phonological processing is involved (e.g., PHs). In addition, we provide the first demonstration of AFL to functional BOLD measures in an attempt to explore subsystems within SV and PD processes. While AFL has traditionally been used to localize factors in time we provide evidence that AFL is useful in understanding how variables influence one another in the brain. We provide evidence that the SMA may be important for resolving phonological conflict produced from the SV and PD routes when naming low frequency EXCs. The findings from both studies have broad implications for all models of word recognition that use these basic stimuli in the assessment of SV and PD processing.

Chapter 4: Methodological Considerations for the Use of PD stimuli

Summary

The purpose of Chapter 4 was to investigate the extent to which using NW naming performance as a reflection of PD processing can be challenging, and potentially raises concerns regarding the interpretation of functional data. Experiment 7 compared fMRI activation for naming aloud NWs and REGs (published in Farthing, **Cummine** et al. (2007), *MAGMA*). NW naming was associated with activation artefact in the ventricles and slower reaction time (RT), reflecting a strategy whereby breathing falls in synchrony with image acquisition. REG naming showed the expected behavioural RT distribution and frequency effect (reflecting lexical access) and no functional ventricle artefact. In addition, we revisit data from Experiment 4 that compared fMRI activation for naming aloud NWs and PHs. With the combination of this data, we discuss how PH stimuli are a preferable measure of PD processing over NWs. Relative to PHs, NWs produce an overabundance of activation that is noisy and not limited to the dorsal (i.e., PD) processing stream demonstrating that these stimuli are problematic.

Introduction

Experiment 7

Using fMRI to assess brain activation during overt naming tasks is challenging because head movement can be associated with false activations, especially if it is highly correlated with the task (Birn, Cox, & Bandettini, 2004). The degree of correlation between the task and motion may be more important than the magnitude of motion responsible for the false activations (Field, Yen, Burdette, Elster, 2000). Motion artefact confounds the validity of the activation maps and creates uncertainty about the regions of the brain that are truly activated due to the task (Johnstone et al., 2006).

One method of controlling for motion artefact associated with speech tasks in fMRI is by a gapped (or sparse sampling) acquisition, where a period of acquisition is alternated with a period of no acquisition (Borowsky, Loehr, et al., 2005; Borowsky et al., 2006; Gracco, Temblay, & Pike, 2005). The gapped paradigm is particularly advantageous for studying speech production in fMRI (Borowsky et al., 2005; Borowsky et al., 2006; Gracco et al., 2005) because overt speech can be monitored during the gap in the sequence (i.e., when there is no noise due to the MRI gradients). The gapped paradigm eliminates data acquisition during the execution of the speaking task where motion artefact is most likely to occur (Field et al., 2000; Johnstone et al., 2006). The reduction of motion artefacts is primarily due to the timing of the task. When the speech task is performed for brief periods, task-related motion artefacts are rapid and can be correlated with the timing of the task. Since the evoked BOLD response is slow, evolving over several seconds, looking at the periods where no task is performed can result in a cleaner BOLD signal without motion artefact.

Unfortunately, head motion is not the only means by which the validity of fMRI maps can be compromised. Several studies have demonstrated MRI signal fluctuation with respiration (Birn, Diamond, Smith, & Bandettini, 2006; Frank, Buxton, & Wong, 2001; Hu, Le, Parrish, & Erhard, 1995; Raj, Anderson, & Gore, 2001). Changes in fMRI signal intensity are known to correlate with changes in respiration (Birn et al., 2006), which could mask true activations or generate artefact (e.g., activation in the ventricles) if unaccounted for. Variations in breathing patterns that are correlated with the stimulus presentation can lead to activation artefact and ultimately compromise accurate detection of regions truly activated by the task of interest. If any phase of the respiratory cycle (inspiration or expiration) is task-correlated it could result in activation artefact since the fMRI signal fluctuates with respiration (Birn et al., 2006; Frank et al., 2001). Given that speech tasks can be associated with head motion and alterations to regular breathing, they present a challenge in fMRI.

Traditional fMRI experiments where image acquisition is continuous are not conducive to all behavioral studies of speech production. For example, behavioral research involving speech production typically examines such variables as reaction time (RT) and accuracy to identify a target stimulus (Andrews & Heathcote, 2001; Cusack, Cumming, Bor, Norris, & Lyzenga, 2005). Overt naming during fMRI studies of speech production is thus critical to fully examine word naming behaviour (Borowsky et al., 2005). Cusack et al. (2005) report a post-hoc method of extracting speech sounds from the noise of the scanner but admit that motion artefact from speech production remains problematic. The gapped paradigm aids in the investigation of speech production tasks in several ways. Being able to hear participants' responses during the fMRI experiment provides investigators with some confidence that the participant is properly engaged in the task (Borowsky, Owen, et al., 2005). More importantly, it allows investigators to

code important variables such as accuracy and RT during a period when no image acquisition is taking place.

The objective of Experiment 7 was to test whether ventricle activation artefact was present during an overt word-naming task where the use of a gapped paradigm is highly beneficial for the experiment and where breathing alterations would accompany naming the letter strings. First we compare NWs and REGs. Given that NWs are unfamiliar letter strings, they are highly susceptible to a mechanistic naming style. In contrast, REGs are familiar stimuli which activate lexical representations and thus should not result in a mechanistic naming strategy. In addition, we revisit data presented in Experiment 4 that compares NWs and PHs. PH stimuli are more similar to NWs in that they are unfamiliar, however, PHs are similar to REGs in that they also have phonological lexical representations that may discourage a mechanistic naming style.

Methods

Participants, Stimuli, Materials, Analyses

The participants, stimuli, materials and analyses are identical to those presented in Experiment 2 and 4.

Behavioural Analyses

Assessment of Mechanistic Naming Patterns: Frequency Effects and RT distributions. To examine the extent to which NWs and REGs displayed mechanistic naming patterns from a behavioural perspective, frequency and response time distributions were evaluated. In assessing the REG frequency effect, the word frequency for each item was determined from the Kucera and Francis (Kucera & Francis, 1967) corpus. These frequency counts were log transformed using the following formula: $\log(10)$ word frequency = $\log(10)$ (Kucera & Francis word

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frequency + 1; Borowsky, et al., 2002). A subject-by-item regression analyses was then used where each subject's regression coefficient is treated as a unit of analysis (i.e., performing a separate regression of correct item latency on the independent variable of word frequency for each subject, then determining whether the average regression coefficient differs from zero using a one-sample *t*-test; Lorch & Myers, 1990; see also Borowksy & Masson, 1999; Borowsky et al., 2002).

A pairwise *t*-test on the median offset response times was used to determine whether there was a significant difference in the speed with which REGs and NWs are named. The distribution of RTs for REGs and NWs was also tested for significant skewness, which is a hallmark characteristic in real word (e.g., REG) naming studies (Figure 24; Balota & Spieler, 1999). It has been suggested that the positively skewed (i.e., exponential distribution) nature of reaction time distributions in word naming tasks is related to attentional (or analytical) processes, whereas a normal (i.e., Gaussian) distribution in naming studies often reflects mechanistic (or non-analytical, e.g., NW) processing (Balota & Spieler, 1999).

Results

NWs versus REGs. Consistent with past research REGs display a frequency effect, whereby higher frequency words are named faster (response time is composed of time from stimulus onset until voice offset and thus is an offset response time) than are low frequency words (a regression analysis of each participant's offset response times (RT) yielded a slope coefficient of $b = -23.35$, $t(9) = -3.85$, $p = 0.004$). A pairwise *t*-test on the median offset response times revealed that REGs (median offset RT = 796.60 ms) are named significantly faster than NWs (median offset RT = 1103.90 ms; $t(9) = 9.68$, p<.001). REGs also displayed a positively skewed distribution of RTs (i.e., significant skewness [S] measures, S/[std error of S], in 7/10

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1: NW   # 1: REG   # 6: NW   # 6: REG

2: NW   # 2: REG   # 7: NW   # 7: REG

3: NW   # 3: REG   # 8: NW   # 8: REG

4: NW   # 4: REG   # 9: NW   # 9: REG
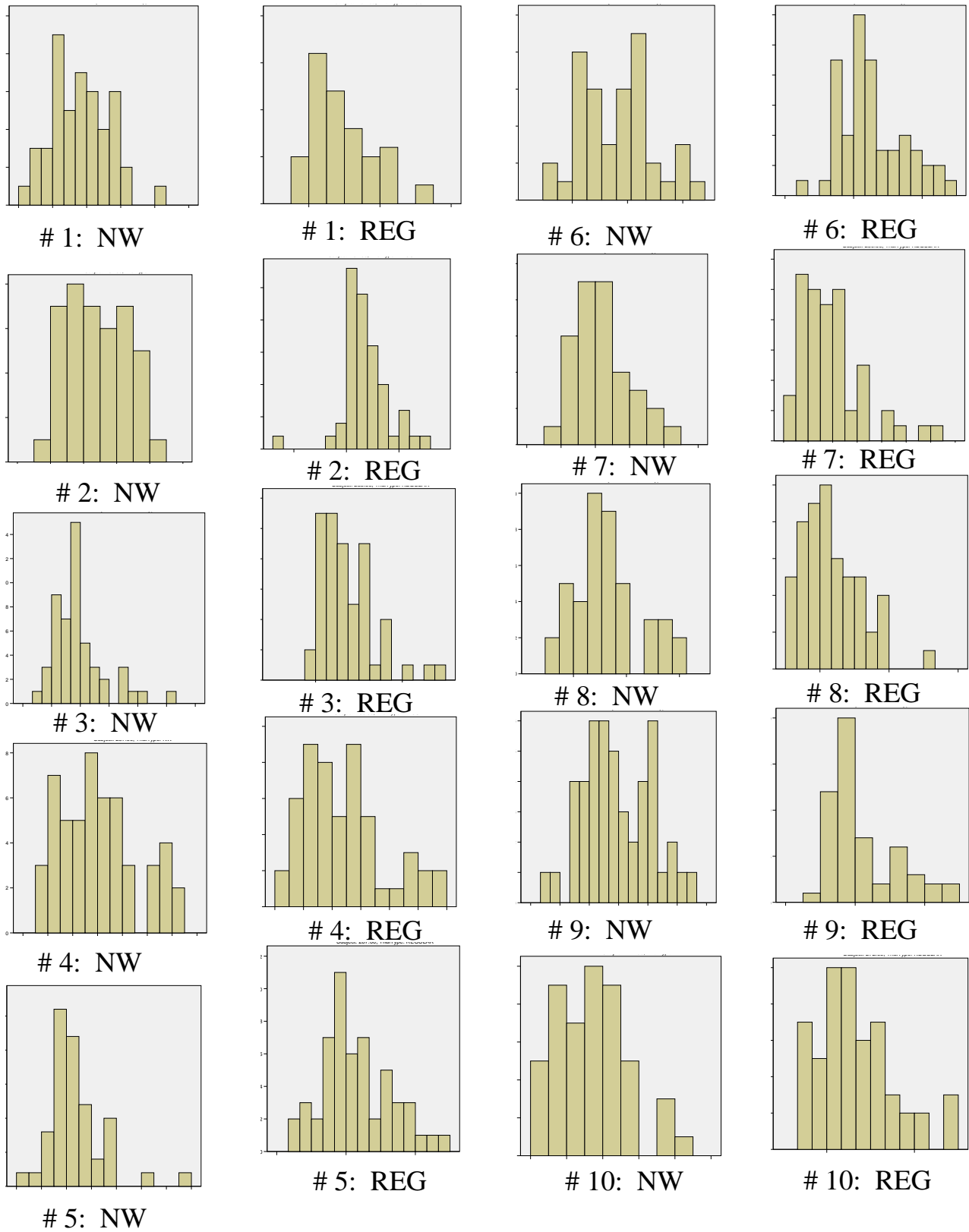
5: NW   # 5: REG   # 10: NW   # 10: REG

Figure 24. Histograms displaying skewness for NW and REG reaction times for each participant. The numbers on the graph correspond to subject number as shown in Table 9.

participants; Table 9). NWs did not typically elicit this positively skewed RT distribution (i.e., significant skewness measures were seen only in 2/10 participants), suggesting that NWs are being named in a more mechanistic fashion compared to the REGs. This mechanistic naming strategy allows for consistent breathing patterns that can be in synchrony with image acquisition in an fMRI experiment. We then evaluated the extent to which activation artefact was found in the ventricles for REGs and NWs (Figures 25 and 26). Both figures clearly demonstrate consistent activation in the ventricles for NW naming but not for REG naming.

Figure 27 displays the time course of voxel intensity across time for an activated region in the occipital cortex and in the brain ventricles for the NW reading condition. Figure 28 displays the time course of voxel intensity across time for an activated region in the occipital cortex and in the brain ventricles for the REG reading conditions. The time courses demonstrate task-correlated signal change in the brain ventricles for NW reading but not for REG reading.

NWs versus PHs. We revisit a previous comparison made in Experiment 4 that contrasted two orthographically unfamiliar stimuli types. PH naming (a task that also activates lexical phonological representations) elicited predominantly dorsal activation consistent with past research that suggests the dorsal route is active during PD processing. However, NW naming (a task that does not activate lexical phonological representations) produced activation that was noisy, overabundant and not as constrained to the dorsal stream as PHs (see Figure 15). That is, NW naming activated regions throughout both the dorsal (PD processing) and ventral (SV processing) streams.

Discussion

NW naming as compared to REG naming produced activation artefact in the ventricles and, as compared to PH naming, produced an abundance of activation across the brain. This is

Table 9. Skewness measures for Regular Words and Nonwords.

REG Naming Condition

Subject	Skewness	Std. Error of Skewness
1	1.064*	.352
2	-.461	.340
3	1.323*	.322
4	.779*	.327
5	.486	.325
6	.554	.325
7	1.355*	.322
8	.864*	.322
9	1.014*	.322
10	.932*	.322

NW Naming Condition

Subject	Skewness	Std. Error of Skewness
1	.300	.347
2	.209	.365
3	1.431*	.333
4	1.568*	.354
5	.509	.330
6	.296	.365
7	.603	.398

8	.506	.361
9	.219	.347
10	.618	.340

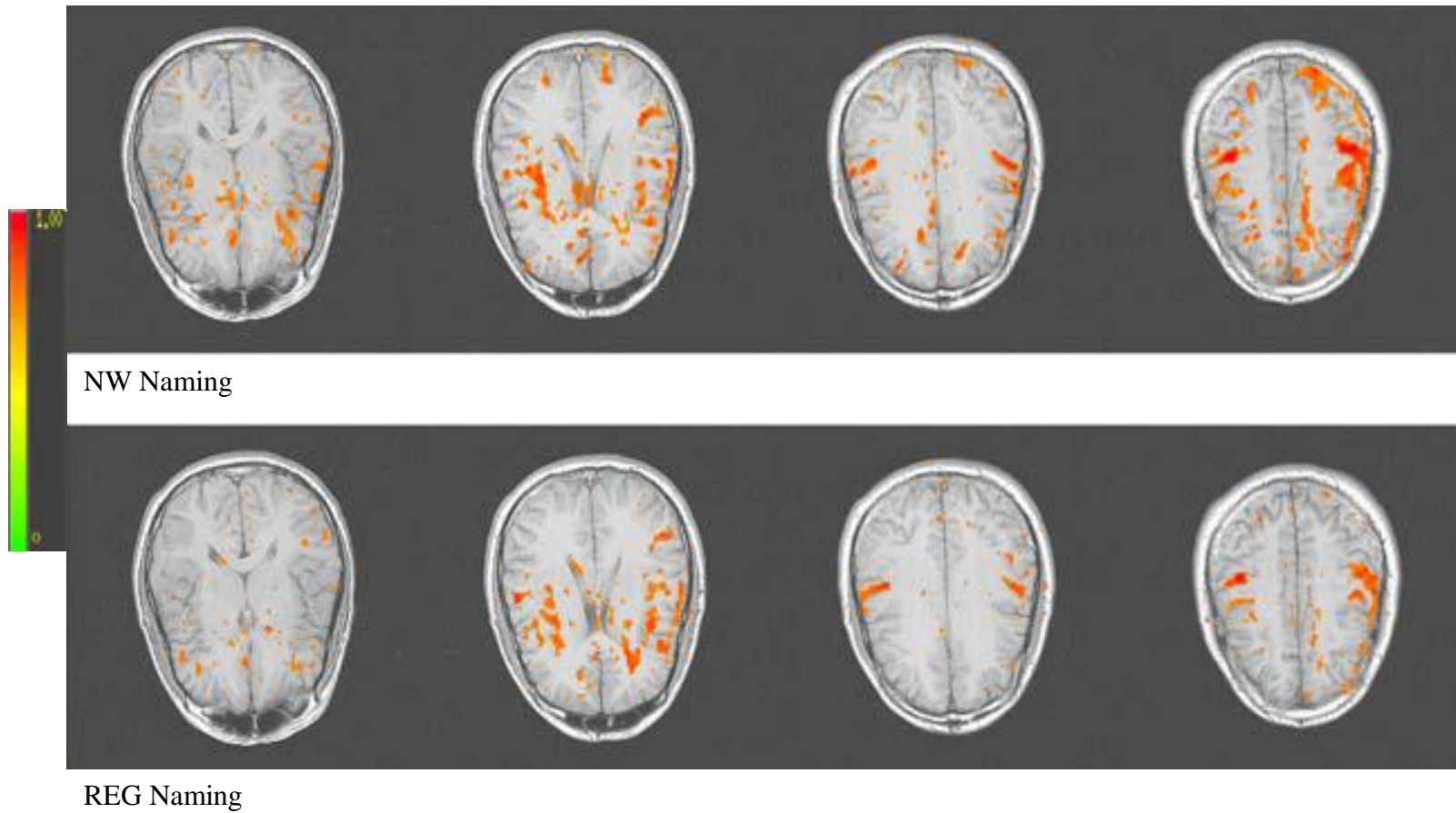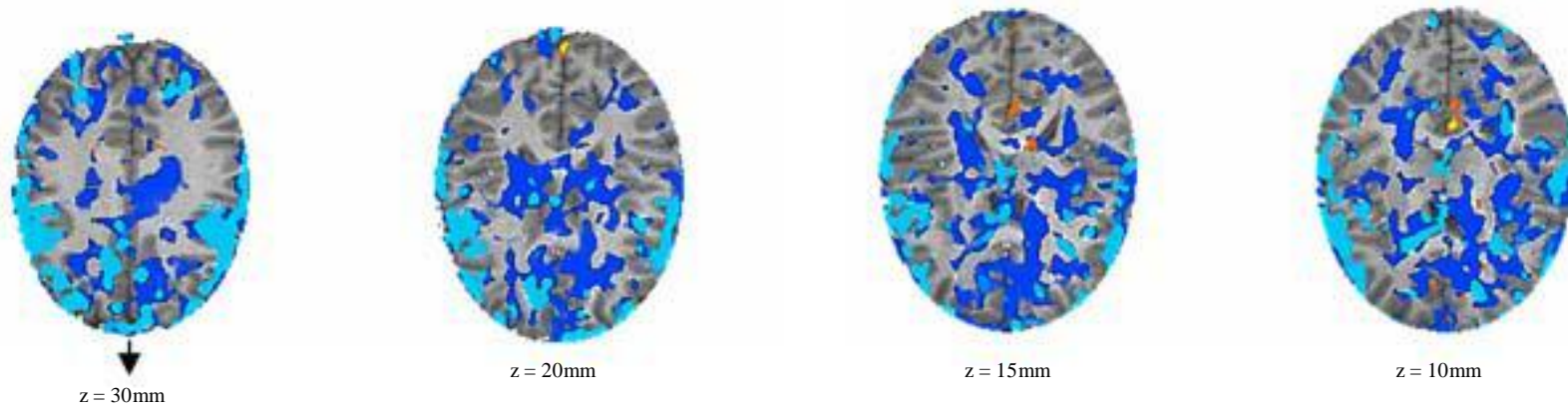* Indicates significant positive skewness.

Figure 25. Activation maps for a single participant that display ventricle activation during the NW naming task (*top*) and very little ventricle activation in the REG naming task (*bottom*). The third or fourth inferior-most slice was centered on the posterior commissure and represents z = 0. Each four-slice array displays right-to-left: z = ~ -10, 0, 10, and 20 mm, respectively. All activated regions exceed a threshold for activation of $\eta = 0.65$, and are color coded for intensity (arbitrary units). Maps are presented according to radiological convention (right = left).

z = 30mm   z = 20mm   z = 15mm   z = 10mm

Regular words unique from Nonwords

z = 30mm   z = 20mm   z = 15mm   z = 10mm
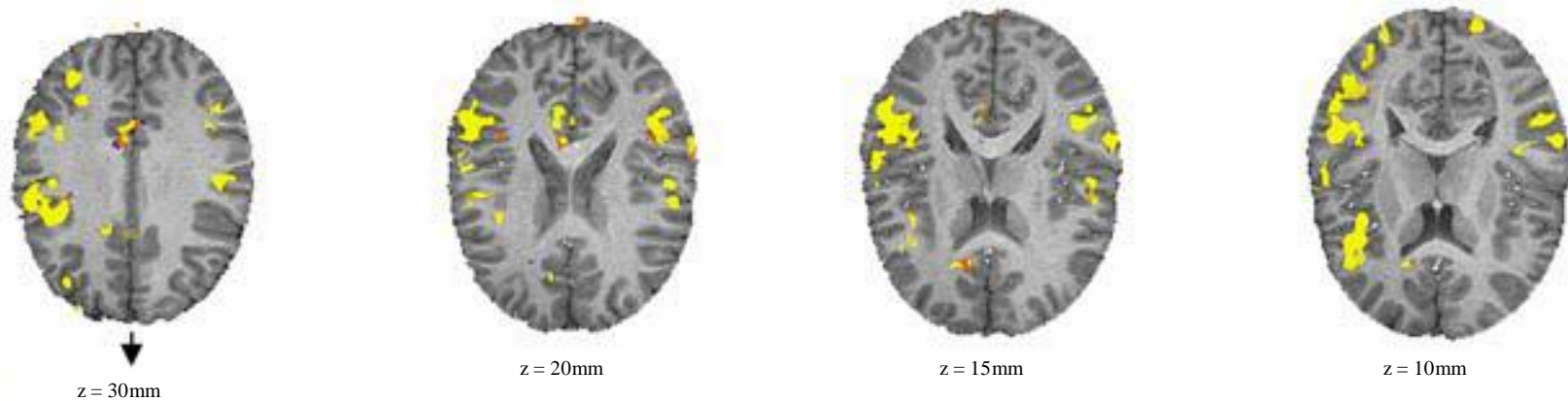
Regular words shared with Nonwords

Figure 26. Unique (top) map displaying activation for REG or NW naming. **Shared** (bottom) map displaying activation for REG and NW naming. The z-coordinate is centered on zero at the AC-PC line after Talairach transformation. The anatomical maps display right = right. The arrow direction indicates the anterior (orbital) direction.

Figure 27. Time course of voxel intensity as a function of time in an activated region (bottom; coordinates z = 92, y = 79, z = 5) and in the ventricles (top; coordinates x = 62, y = 68, z = 6) during NW reading. The shaded gray regions indicate the task blocks when participants were engaged in the word-naming task.
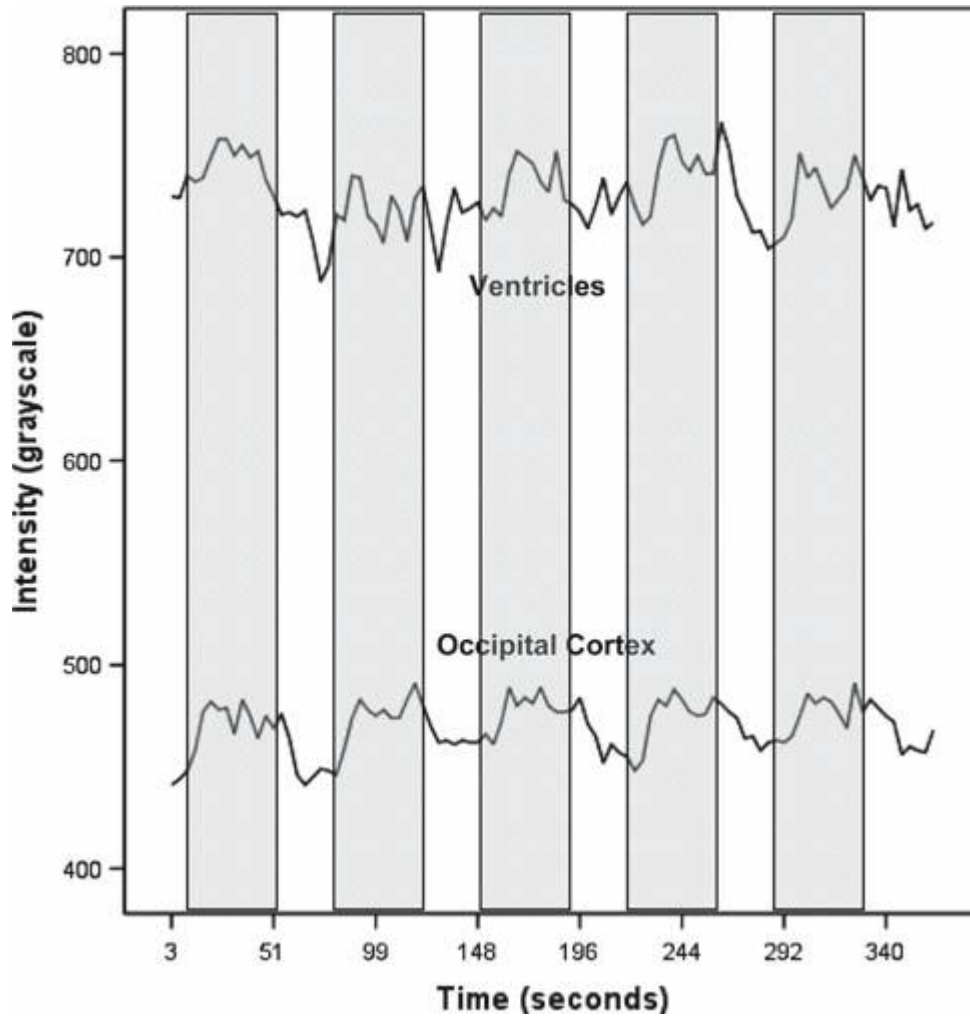
Figure 28. Time course of voxel intensity as a function of time in an activated region (bottom; coordinates z = 92, y = 79, z = 5) and in the ventricles (top; coordinates x = 62, y = 68, z = 6) during REG reading. The shaded gray regions indicate the task blocks when participants were engaged in the word-naming task.
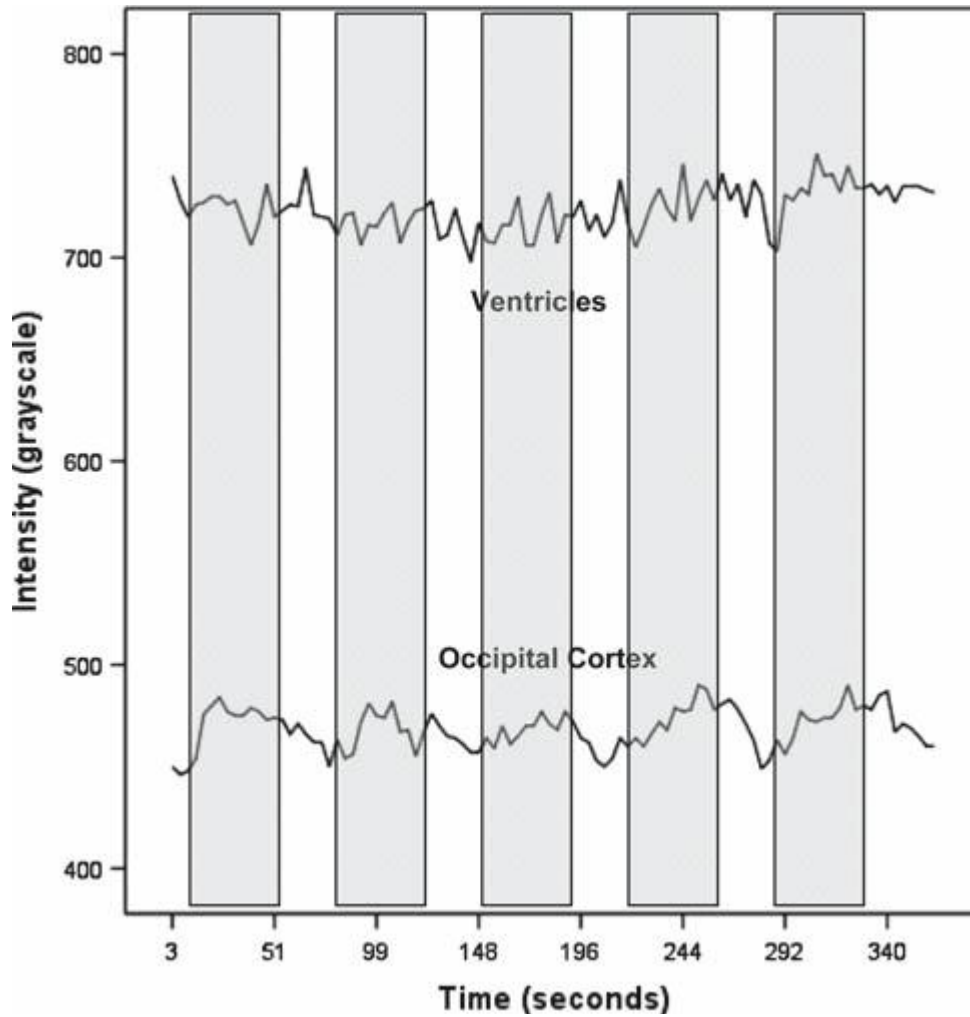
likely due to the NWs susceptibility to mechanistic naming and task-correlated breathing as expected given that NWs lack lexical representations. This mechanistic naming was also reflected in the RT distributions where NWs did not display the typical positively skewed RT of words. Participants were more likely to fall into a rhythmical response strategy. REG naming on the other hand exhibited a frequency effect (supporting the notion that they result in activation of frequency-sensitive lexical representations) and show a benefit in their RTs (i.e., positively skewed RT distributions) and thus the participants' responses did not reflect mechanistic naming and task-correlated breathing in the fMRI data (i.e., no ventricle activation). When engaged in reading REGs aloud participants have access to their lexical representations of these stimuli (word recognition) and can use this information to aid their response (as seen in the faster mean RT for REGs compared to NWs). The degree to which a given response is influenced by the word's lexical representation is itself influenced by the word's frequency in the language (as seen by the significant frequency effect). Therefore, breathing alterations are not a consistent influence on each trial, thus avoiding task-correlated artefact that is present with NW naming. Stimuli that lack lexical representations (and are consequently prone to mechanistic naming and task-correlated breathing artefact, e.g., NWs) should be avoided in gapped fMRI paradigms. While it may be possible to vary the timing of the presentation of such stimuli so as to avoid this problem, this remains an empirical question for future research.

When breathing became synchronized with the task, artefact activation in the brain ventricles was pronounced and may be an indicator of the presence of artefact activation in other brain regions, leading to misinterpretation of true activations associated with the task of interest. Normal respiration is known to cause fluctuations in fMRI signal intensity (Birn et al., 2006), but these are much less a concern if they are not correlated with the task. Fluctuations in fMRI signal

with breathing have been hypothesized to involve changes in arterial blood oxygen levels which lead to changes in BOLD signal intensity (Li, Kastrup, Takahashi, & Moseley, 1999; Stillman, Hu, & Jerosch-Herold, 1995). But if signal fluctuation with breathing results from blood oxygen level changes, then how is task-correlated breathing related to brain ventricle artefact where there is no blood supply? One speculation is that the artefact in the brain ventricles is caused by fluctuations in the static magnetic field due to bulk susceptibility or air volume variations in the lungs during respiration (Hu et al., 1995; Raj et al., 2001). Another explanation may involve movement of cerebral spinal fluid (CSF) in the brain ventricles. CSF pulsates in and out of the brain and spinal canal in direct relation to the cardiac cycle and respiration-induced pressure fluctuations, causing a signal change (Klose, Strik, Kiefer, & Grodd, 2000). If respiration becomes task-correlated, the signal fluctuation due to respiration could be mistaken for BOLD signal changes directly associated with the task, leading to misinterpretation of the functional data. The rhythmical nature of the gapped paradigm, both visually and acoustically, seemed to trigger breathing synchrony for NWs.

The gapped paradigm presents a distinct advantage in the case of studying overt naming. Importantly, our study demonstrates that the gapped paradigm can be used without showing ventricle artefact, depending on the nature of the stimulus (Figures 27, 28). That is, stimuli which contain some form of lexical representation (e.g., REGs) did not demonstrate activation artefact. The gapped paradigm is also advantageous for reducing motion artefact (Gracco et al., 2005) in any task where head motion is inherent. The problem with using acquisition gaps appears when breathing or an alteration to the normal breathing pattern (e.g., breath-hold) becomes task-correlated. Experimenters should be aware that when a particular paradigm is accompanied by a synchronized breathing pattern (e.g., always exhaling during the task), it will most likely result in

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task-correlated signal changes in the brain generating ventricle activation along with activation artefact that does not represent the task of interest.

The gapped paradigm presented here is a block design with a constant interstimulus interval (ISI). Event related designs where the ISI is variable minimize the correlation between motion-induced signal change and the BOLD signal change (Birn et al., 2004), and might reduce or eliminate the ventricle artefact we have shown here. However, event-related designs may not be realistic for all word-naming studies since the slow BOLD responses associated with speech production would require the collection of an appreciably large number of images.[9]

Importantly, our previous results that compare NWs to PHs also bring to light peculiarities about the nature of NW processing. Specifically, our results demonstrate that NWs activate numerous regions within the brain across both ventral and dorsal streams. This excessive activation may be evident for several reasons including difficulty in processing these stimuli, unfamiliarity of stimuli from both an orthographic and phonological perspective, uncertainty about correct pronunciation, and task-correlated motion/breathing artefact as demonstrated in the current experiment. Such factors could contribute to the abundance of activation that is evident when participants attempt to name such stimuli. This is not the case when participants are naming aloud PHs. These PD stimuli have familiar, whole-word phonological representations, which serve to provide some constraint to the response. The purpose of presenting novel sub-word letter strings is to encourage participants to use PD to translate orthography into phonology, and PHs serve this purpose while producing more constrained and interpretable activation when compared to NWs.

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Conclusion

NW naming appears to be an arduous task susceptible to a mechanistic naming style as evidenced by the wealth of activation in both ventral and dorsal streams and ventricle artefact. In general, NW naming produces less constrained and less interpretable activation when compared to REG naming and PH naming. Our results demonstrate a limitation for researchers using a gapped paradigm with speech tasks in fMRI. The gapped paradigm increases the likelihood that the signal increase in the brain ventricles will be detected in correlation with the signal changes from the task. However, the gapped paradigm does not always result in ventricle artefact and there are situations where it is advantageous such as for overt word naming experiments. As a precaution, fMRI researchers should carefully examine their functional data for activation artefact in the brain ventricles. The presence of this artefact may compromise the detection of true activations associated with the task of interest. Using stimuli that engage phonological lexical representations (e.g., REGs and PHs) appears to be advantageous and minimizes the presence of false activation.

Chapter 5: Application to Clinical Populations

Summary

The purpose of Experiment 8 (published in **Cummine**, Borowsky, Stockdale Winder & Crossley (2009), *Epilepsy and Behavior*) was to consider how models of basic reading processes can inform us about models of impaired reading processes (i.e., dyslexia). Dyslexia was explored within the framework of three explanations for language functioning following hemispherectomy (i.e., equipotentiality, hemispheric specialization, and crowding hypothesis/hierarchy of specialized functions) and the extent to which these models explain reading performance in SM (age 48; right hemispherectomy) and JH (age 49; left hemispherectomy). Basic reading performance was evaluated by assessing SV and PD processing. Both participants displayed severely impaired reading performance on PHs (e.g., *wun*), signifying poor PD processing. However, JH (remaining right hemisphere) also demonstrated impairments in reading EXCs (e.g., *one*), suggestive of poor SV processing. Thus, while SM clearly demonstrated phonological dyslexia and retention of the priority SV reading skills, JH presented with deficits more characteristic of mixed dyslexia. Taken as a whole, we suggest that some modification of the hierarchy of specialized functioning model and crowding hypothesis is needed, including stipulations about hemispheric specialization, to more accurately accommodate the present data.

Introduction

Experiment 8

The study of individuals following hemispherectomy presents a unique opportunity to evaluate the stability of hemispheric specialization of cognitive abilities and the potential of an isolated hemisphere to subsume typically lateralized higher brain functions. Previous research characteristically has examined basic language functioning following hemispherectomy (Curtiss, de Bode, & Mathern, 2001; Davidson, Howe, Worrall, Hicson, & Togher, 2008; Liegeois, Connelly, Bladeweg, & Vargha-Khadem, 2008; Menard, Le Normand, Rigoard, & Cohen, 2000; Ogden, 1996; Stark, Bleile, Brandt, Freeman & Vining, 1995; Stark & McGregor, 1997; Vanlancker-Sidtis, 2004), whereas recent work has focused on complex social behavior (Davidson et al., 2008; Fournier, Calverley, Wagner, Poock & Crossley, 2008; Kirsch, 2006; Schacher et al., 2006). Language and social functioning are intricately related (Davidson et al., 2008) and both factors are associated with post-hemispherectomy performance on particular cognitive tasks (e.g., simple reading, identification of emotions). For example, Fournier et al. (2008) explored complex social functioning in the same two participants who we studied, at the same time (30 years following their hemispherectomies). Important to the present paper, they reported differences between the participants in general language performance, whereby JH, the participant with a left-sided hemispherectomy and an intact right hemisphere, showed deficits in verbal fluency and language-related components of the assessments, whereas SM, the participant with a right-sided hemispherectomy and an intact left hemisphere, was fully fluent during conversational speech and demonstrated an excellent vocabulary. Nevertheless, SM did exhibit limitations in complex language-based tasks (e.g., speeded phonemic fluency, reading comprehension, etc.), suggesting that some of the functions typically associated with an intact

left hemisphere might also have been "crowded" following hemispherectomy during early development. Specifically, both SM and JH demonstrated impairments in basic reading skills suggestive of dyslexia. Consequently, the current study extends previous work with JH and SM by focusing on these basic reading processes -- skills presumed to contribute to overall cognitive and academic performance and to quality of life outcomes following hemispherectomy (Davidson et al., 2008).

In assessing individuals who have suffered from early acquired brain injury or developmental abnormality, and are consequently at a higher risk of developing reading impairments, understanding the underlying processes is crucial to the assessment, diagnosis and management of these deficits (Atchley, Halderman, Kwasny, & Buchanan, 2003; Atchley, Story & Buchanan, 2001). Dysfunction in basic reading processing is typically referred to as a form of dyslexia. The present paper focuses on three major types of dyslexia: (1) *phonological dyslexia;* (2) *surface dyslexia*; and, (3) *mixed dyslexia* (see Castles & Coltheart, 1993). Recall from Chapter 2 that *phonological dyslexia* is an impairment in reading aloud unfamiliar words (i.e., an impairment of the PD processing system). This is often assessed using a naming task that presents participants with novel letter-strings (i.e., PHs in the present cases). People with pure phonological dyslexia often display little or no difficulty in reading aloud REGs or EXCs, presumably because the SV processing system is intact. *Surface dyslexia* is an impairment in reading aloud EXCs (i.e., an impairment of the SV system) and the production of regularization errors (e.g., '*one*' pronounced as '*own*'). However, there is no difficulty in reading aloud REGs or novel letter-strings in cases of pure surface dyslexia, presumably because the PD processing system is intact. Finally, *mixed dyslexia* involves characteristics of surface dyslexia and phonological dyslexia subtypes. Individuals with mixed dyslexia typically present with severe

language difficulties and demonstrate problems with both SV and PD processing skills (Castles & Coltheart, 1993).

Within the hemispherectomy literature there are mixed findings regarding the extent of language ability and disability in right and left hemispherectomy patients (Ogden, 1996; Vanlancker-Sidtis, 2004). In keeping with cognitive neuropsychological models of normal language functioning, the theory of hemispheric specialization proposes that in most right-handed individuals the left hemisphere will have some specialization in language functions such as reading and spelling (Bode & Curtiss, 2000; Ogden, 1996; Stark & McGegor, 1997). This theory predicts that the right hemisphere (in the case of left hemispheric pathology) is limited in its potential to develop or subsume most language skills (e.g., reading). Thus, it would be predicted that an individual who had undergone a left hemispherectomy would have severe deficits on basic reading performance and typically would present with dyslexia. In contrast, an individual who had undergone a right hemispherectomy should have limited deficits on basic reading and perform within the normal range. Accordingly, the theory of hemispheric specialization would predict drastic differences in reading performance in SM and JH (see Table 10a).

In contrast to the hemispheric specialization model, cognitive neuropsychological testing involving individuals with acquired brain injury often support an equipotentiality model of language development. According to this model, at birth the two hemispheres are equipotential for most aspects of language and other higher brain functions (Mosch, Max, & Tranel, 2005; Stark et al., 1995). The equipotentiality model predicts that the non-injured right hemisphere is capable of subsuming most, if not all, language functions that might otherwise have been managed by the injured left hemisphere, provided that the injury has not occurred too late in

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Table 10. Predictions regarding language function following hemispherectomy according to the Hemispheric Specialization Model, Equipotentiality Model, and Hierarchy of Specialized Function/Crowding Hypothesis

	Side of Surgery	SV	PD
a. Hemispheric Specialization Model	Left	✘	✘
	Right	✓	✓
b. Equipotentiality Model	Left	✓	✓
	Right	✓	✓
c. Hierarchy of Specialized Function/Crowding Hypothesis	Left	✓	✘
	Right	✓	✘

✓ = Participant should retain function

✘ = Participant should not retain function

development. In particular, while the left hemisphere is presumed to be dominant for language processing in individuals with two functional hemispheres, the right hemisphere is able to perform these functions in the absence of a working left hemisphere (Liegeois et al., 2008; Liegeois, Cross, Polkey, Harkness & Vargha-Khadem, 2008). Importantly, the equipotentiality model would be supported by a completely different pattern of results than the hemispheric specialization model. More specifically, such a model would predict normal reading performance by individuals who had undergone an early hemispherectomy, *regardless* of surgical side (see Table 10b).

A crucial refinement to both the equipotentiality and the hemispheric specialization models is Ogden's theory of a hierarchy of preserved functions (Ogden, 1989; 1988). Ogden proposed that if left hemisphere injury occurs in infancy, and there is a recovery period spanning several years, the right hemisphere can subsume language functions (see also, Liegeois, 2008; Lucas, Drane, Dodrill & Ojemann, 2008), in addition to maintaining the basic visuospatial abilities typically associated with the right hemisphere. An important caveat is that functions presumed to be low on the hierarchy or non-essential will be less well preserved (Ogden, 1989). The hierarchy of preserved function model predicts that individuals who have undergone either a right or left hemispherectomy will display similar patterns of strengths and limitations across cognitive tasks. Specifically, if a function is high on the hierarchy it will be retained by the remaining hemisphere or subsumed (i.e., taken over) by the remaining hemisphere. If the function in question is low on the hierarchy, it will be lost (or less well preserved) to accommodate the transfer of higher ranked tasks, or the function will not be taken over by the remaining hemisphere (see Table 10c).

A very similar model is the crowding hypothesis that attempts to explain why a solitary right hemisphere loses some of its specialized functions in order to preserve language (Lansdell, 1969; Teuber, 1974). The crowding hypothesis proposes that each hemisphere has some specialized function; however, following left-sided hemispherectomy, the remaining right hemisphere will lose some traditional right hemisphere functions (e.g., visuospatial ability) in an attempt to take over the necessary language functions (e.g., speech). For example, Vanlancker-Sidtis (2004; see also Satz, Strauss, Hunter & Wada, 1994) examined a left-hemispherectomy participant and found that some circumscribed right hemisphere linguistic functions (e.g., comprehension of linguistic prosody) were "crowded out" by pragmatic language tasks. In addition, recent results with JH and SM suggest that not only are some traditional right hemisphere functions "crowded out" (e.g., evaluation of faces showing disgust or anger; Fourneir et al., 2008), but that some traditional left hemisphere functions are lost or compromised following right hemispherectomy. For example, when compared to JH, although our right hemispherectomy participant (SM) produced syntactically correct discourse, her narratives were succinct and limited in terms of complexity, color, and richness (Stockdale Winder, Cummine & Crossley, in preparation). Comparable to Ogden's hierarchical model of specialized functions (Ogden, 1989; 1988), the crowding hypothesis would predict that individuals who have undergone either right or left hemispherectomies should display similar patterns of results across most tasks.

The primary goal of the current study was to investigate with JH and SM the extent to which the right hemisphere can subsume basic reading processes (i.e., in JH), and conversely, the extent to which these functions are preserved (i.e., not 'crowded out' for critical right hemisphere functions such as the evaluation of emotions) in the left hemisphere (i.e., in SM). In particular,

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we explored aspects of language functioning presumed to be lower on the hierarchy of functions (i.e., PD processing), or more likely to be "crowded out", as well as language functions that are likely to be subsumed by the right hemisphere and unlikely to be "crowded out" in the left hemisphere (i.e., SV processing). Table 10 summarizes the predictions that follow from the three models: Hemispheric Specialization, Equipotentiality, and Hierarchy of Specialized Function/Crowding Hypothesis.

<div align="center">Methods</div>

Participants

  Clinical participants. The study included two female hemispherectomy participants, JH (age 49) and SM (age 48). Prior to taking part in the present study, both JH and SM participated in a clinical interview to determine their general health and specific seizure history, and completed a battery of neuropsychological tests. The present study was part of a larger investigation that assessed general cognitive functioning 30 years post-right or –left hemispherectomy and the effects of hemispherectomy on social cognition.

  Brief history of hemispherectomy participants. JH was born with a right-sided hemiplegia. Her seizures began at age 5 years and gradually increased in frequency. She underwent a complete left-sided hemispherectomy at age 16 for severe intractable seizure disorder. JH was 49 years when the current study was completed, has a Grade 11 education, her verbal intelligence was assessed to be within low normal range, and she had been seizure free for 33 years.

  SM was reportedly healthy until she began to have seizures at age 5. At age 6 she had a partial right-sided hemispherectomy. This was not successful in controlling her seizures and, consequently, she underwent a complete right-sided hemispherectomy at the age of 13. SM was

48 years when the current study was completed, has a Grade 12 education, her verbal intelligence was assessed to be within the low normal range, and although she continues to experience occasional complex partial seizures, these are generally well controlled by her medication. Both participants have normally fluent speech, display good language comprehension (for the purpose of everyday conversation), and have hemiplegia (i.e., one half of the body is paralyzed) and homonymous hemianopsia (i.e., loss of vision in the same visual field of both eyes) as predicted by their surgical side (left versus right hemispherectomy).

Normal comparison group. Normative reading data were collected from 12 females who ranged in age from 38 to 58 years (M = 47 yrs) and reported similar rural upbringing and educational backgrounds to JH and SM.

Measures and Procedures

The measures, procedures and stimuli are identical to those presented in Experiment 1.[10]

Assessment. Based on the assumption that SV and PD processing represent independent systems, and that both systems contribute to basic reading processes, a method of examining phonological and surface dyslexia involves assessing one process as a function of the other (Castles & Coltheart, 1993). This serves to isolate dyslexic participants who are markedly worse at one task than the other, given the linear relationship that exists between SV processing (i.e., EXC naming) and PD processing (i.e., PH naming). Thus, one can examine the scatterplot obtained from a simple linear regression of PH reading scores on EXC reading scores to provide an estimation of the expected number of PHs to be read correctly at varying levels of EXC reading (e.g., an assessment of phonological dyslexia). Similarly, regressing EXC reading scores on PH reading scores provides an estimation of the expected number of EXCs to be read correctly at varying levels of PHs (e.g., an assessment of surface dyslexia). Thus, the graphical

relationship between SV processing (as measured by EXC naming accuracy) and PD processing (as measured by PH naming accuracy) was used to determine whether dissociations existed between the two systems (Castles & Coltheart, 1993; McDougall, et al., 2005). Based on work by McDougall et al. (2005), 95% sample ellipses were placed around the normal participant's data to capture the normal reading performance. Participants whose performance fell below the 95% ellipsoids were classified as dyslexic.

<center>*Results*</center>

Naming accuracy. Naming accuracy was computed for SM (right hemispherectomy), JH (left hemispherectomy) and the twelve participants in the normal comparison group on each of the letter-string blocks. As shown in Table 11, SM's REG accuracy (100%) reflects performance, which is characteristic of the comparison group with similar age and educational backgrounds (99%). In addition, her EXC accuracy (96%) is also within the typical range of scores obtained by the comparison group participants (97%). In contrast to these findings, SM's PH accuracy (40%) is markedly lower (by over 6 standard deviations) than the accuracy found for the comparison group (83%), and reflects a clear impairment of the PD processing system.

In contrast to SM, JH's REG accuracy (96%) demonstrates an evident weakness when compared to the normal participants. In addition, her EXC accuracy (89%) falls significantly below the range typical of scores found in the comparison group (by over 3 standard deviations), indicating that JH has a mild deficit on SV processing. Finally, JH's PH accuracy (45%) is severely impaired (by about 5.5 standard deviations) when compared to the normal group and reflects a significant impairment of the PD processing system.

Regression-based analysis of dyslexia subtypes. Phonological dyslexia was assessed by plotting PH performance as a function of EXC performance. As demonstrated by Figure 29, JH

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Table 11. Naming percent accuracy for each participant and the comparison group (standard

deviation) as a function of stimulus type.

Participants	Regular Words	Exception Words	Pseudohomophones
SM	100	96	40
JH	96	89	45
Comparison Group	99 (.55)	97 (2.21)	83 (6.95)

SM – right-sided hemispherectomy

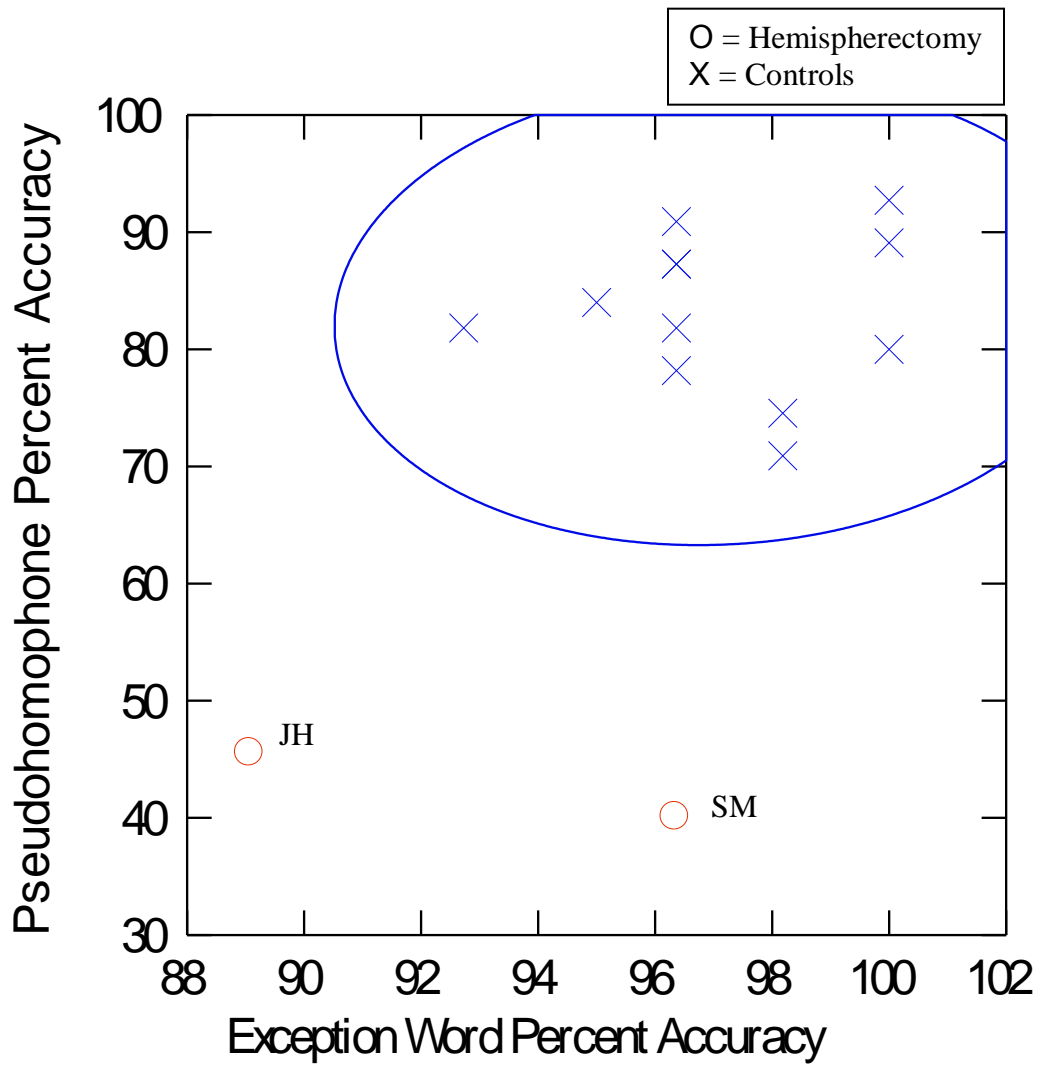JH – left-sided hemispherectomy

Figure 29. Assessment of phonological dyslexia via plotting PH naming accuracy as a function of exception word naming accuracy. A 95% sample ellipsoid is placed around the normal, age-matched, comparison group data.

and SM fell below the 95% ellipsoid of the normal comparison group and thus displayed phonological dyslexia. Notably, both participants' PH accuracy scores were extremely low when compared to the mean of the normal group, signifying severe impairments of the PD processing system. Surface dyslexia was assessed by plotting EXC performance as a function of PH performance. As demonstrated by Figure 30, JH fell below the 95% ellipsoid of the normal comparison group, indicative of surface dyslexia and a deficit of the SV processing system. In contrast, SM did not fall below the 95% ellipsoid, and from this perspective, demonstrates within-normal SV processing. Based on these findings, SM would receive a classification of phonological dyslexia and JH would receive a classification of mixed dyslexia.

Discussion

The present research provides some support for the hierarchical model of specialized function (Ogden, 1996) and crowding hypothesis (Lansdell, 1969) for language processing following hemispherectomy. Specifically, both SM and JH demonstrated deficits in naming PHs, suggesting that PD processing is lower on the hierarchy of specialized function and was 'crowded out' of the left hemisphere in the case of SM and not fully subsumed by the right hemisphere in the case of JH. When PH reading performance was assessed as a function of EXC reading performance, both JH and SM fell below the 95% normal ellipsoid and would be classified as having phonological dyslexia. However, the present results also provide some support for the hemispheric specialization model. That is, SM (right hemisperectomy) compared to JH (left hemispherectomy) displayed higher EXC accuracy (96% vs. 89%) providing evidence for a left hemisphere specialization of language processing. When EXC reading performance was assessed as a function of PH reading performance, only JH fell below
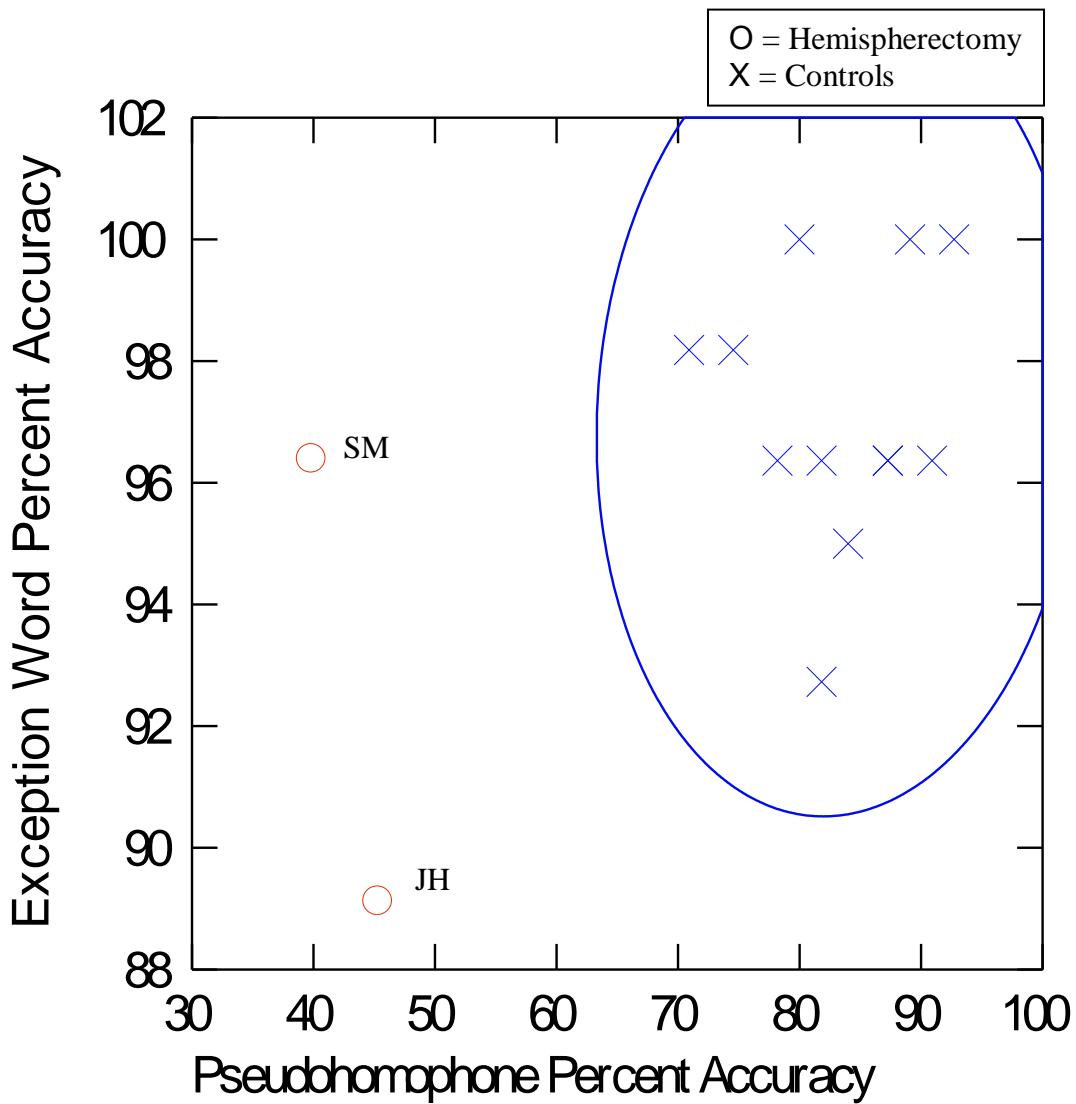
Figure 30. Assessment of surface dyslexia via plotting exception word naming accuracy as a function of PH naming accuracy. A 95% sample ellipsoid is placed around the normal, age-matched, comparison group data.

the 95% normal ellipsoid and, in conjunction with her performance on PH naming, would receive an overall classification of mixed dyslexia.

Importantly, SM's performance on PH naming was incongruent with her ability to name EXCs. Presumably, SM's left hemisphere had to crowd out specialized left hemisphere functions (i.e., PD processing; presumed to be lower on the hierarchy) to accommodate or take over functions otherwise monitored by the right hemisphere. In addition, JH displayed a similar impairment on PD processing, performing well below average when compared to age-equivalent peers. Together, SM's and JH's performance on PD processing provides support for the hierarchical model of specialized function and the 'crowding hypothesis' of language functioning following hemispherectomy (Lansdell, 1969; Ogden, 1996).

Nevertheless, overall reading performance was higher for SM (who had a remaining left hemisphere) than for JH (who had a remaining right hemisphere), indicating some support for an enduring left hemisphere advantage for basic language abilities (Bode & Curtiss, 2000; Ogden, 1996; Stark & McGregor, 1997). In particular, SM's performance on REG naming and EXC naming was not significantly different than the age-equivalent comparison group, whereas, JH's performance on both REG and EXC naming was below the range typical for her peers. Further, given that JH's reading scores on EXC naming were not markedly different than what would be predicted given her performance on PHs, it is suggested that the right hemisphere subsumed some components of both functions (i.e. SV and PD processing) following developmental failure and eventual loss of the left hemisphere. However, these functions were not fully subsumed as is indicated by her overall lower reading performance on both whole- and PD stimuli when compared to the age-equivalent comparison group. These findings provide evidence for the specialization of the left hemisphere in basic language processes.

Assessing the relationship between SV and PD processing to identify dyslexia proved to be useful with individuals who have undergone right or left hemispherectomy. In the present investigation, this technique revealed dissociation between SV and PD processing for SM. While SM had normal EXC naming accuracy (96%), her PH performance (40%) fell well below what would be predicted given her performance on EXC naming. Thus, SM's pattern of results (the dissociation between SV and PD systems) reflects a deviant or specific deficit pattern regarding the PD processing system. In contrast, JH's pattern of results (congruent SV and PD systems) reflects a broader spectrum of impaired reading skills. Although JH appeared to have relatively good EXC naming performance (89%), this score represented impairment when compared to age-equivalent controls (97%). Similarly her performance on EXC naming was consistent with what would have been predicted given her below normal performance on PH naming.

Notably, our results allow us to make inferences about the nature of the relationship between SV and PD processing following hemispherectomy. More specifically, our results support the notion that SV processing is high on the hierarchy of function and thus retained in the left hemisphere (i.e., SM) and subsumed by the right hemisphere (i.e., JH). The evidence also suggests that PD processing is low on the hierarchy of function and consequently is crowded out (i.e., SM) or minimally subsumed (i.e., JH). However, both SV and PD processing systems appear to contribute to the correct naming of REGs as evidenced by the higher REG naming accuracy, when compared to EXC accuracy and PH accuracy. Thus, while the PD system may be significantly impaired following hemispherectomy it is not the case that such functioning is completely abolished (following right hemispherectomy) nor is PD processing completely exempt from being integrated into the remaining hemisphere (following left hemispherectomy).

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The relationship between the SV and the PD processing systems following early brain injury is important to our understanding of the underlying processes at work during basic language functioning, so that we may better assess, diagnose and remediate individuals who suffer from language impairments as a result of their injuries.

Importantly, when we consider these findings amid what was reported by Fournier et al. (2008) our results continue to be consistent with the hierarchical model of specialized function and the 'crowding hypothesis'. Taken together, these studies indicate that identification of neutral, happy and fearful emotional expressions and SV processing are high on the hierarchy of specialized functions and thus retained in the left hemisphere and subsumed in the right hemisphere. In contrast, identification of emotional expressions depicting disgust and anger and PD processing were not retained in their traditional hemispheres, nor were these skills adequately subsumed by the remaining hemisphere. However, our results also indicate that traditional accounts of hemispheric specialization should be considered when assessing general functioning. That is, JH (remaining right hemisphere) displayed overall superior performance on emotional perception, a cognitive ability typically modulated by the right hemisphere. In contrast, SM (remaining left hemisphere) displayed overall superior performance on basic reading tasks, which are typically modulated by the left hemisphere.

Limitations

These results are qualified by the limitations of the research including our small sample of two hemispherectomy participants. In addition, although both participants began to experience seizures around age 5, JH suffered prenatal brain injury whereas SM reportedly had normal early development. Such differences may influence the retention or loss of cognitive functions. For example, JH, having an earlier brain injury than SM, theoretically has more potential for the

remaining hemisphere to take over functions typically modulated by the removed hemisphere, although this is not consistent with our reading results. Given that the extent of equipotentiality is significantly influenced by age of injury (Ogden, 1996), it is important to note that the presumed age of injury and the assumptions regarding the potential of the remaining hemisphere may be different for these two women. It also needs to be acknowledged that individual differences between the two participants might play a role, and cannot be fully disentangled from the effects of differences in hemispheric developmental injury and subsequent surgery.

Conclusions

Taken as a whole, it is clear that some modification is needed to the hierarchy of specialized functions model, which includes stipulations about hemispheric specialization. It is evident from our work with JH and SM that an isolated hemisphere is restricted in its ability to subsume functions typically mediated by the removed hemisphere, even when these functions are high on the hierarchy. Our results indicate that there are some functions that appear to be indispensable (e.g., SV processing and identification of happy emotions) and are retained or subsumed, consistently, following hemispherectomy. Other functions (e.g., PD processing and identification of angry emotions) appear to be dispensable and, consistently, are lost following hemispherectomy regardless of surgical side. Nevertheless, while subsuming some of the higher brain functions associated with the surgically removed side, the strengths and limitations of an isolated right or left hemisphere appear to demonstrate some lateralization of processing skills typically associated with the remaining hemisphere.

Chapter 6: General Conclusions

Overall, the purpose of the research in this dissertation was to evaluate basic reading processes, namely SV and PD systems, from both behavioural and functional perspectives. Our results from Experiment 1 support the notion of mathematical independence between SV and PD processes (Figure 1C). We provided a more thorough examination of models of basic reading processes by incorporating theoretical models of independence *and* redundancy and including all classes of stimuli (i.e., REGs, EXCs, NWs and PHs). When we compared predicted-REG reading accuracy from the equations of independence and redundancy, only predicted-REG reading accuracy from the independence equations accounted for a significant portion of the variance in actual-REG reading accuracy. Predicted-REG reading accuracy from the redundancy models failed to account for any unique variance. Thus, the data lends support for the dual-route architecture whereby basic reading processes (i.e., SV and PD) are mathematically independent systems (e.g., Castles et al., 2006; McDougall et al., 2005; Perry et al., 2007). Furthermore, our results showed that a measure of PD based on PH naming accuracy produced similar results as found with PD based on NW naming accuracy. These results suggest that PH naming not only has ecological validity but also appears to capture similar PD processing as NWs.

In addition, we provided the first demonstration of mathematical independence on behavioural naming reaction time and functional BOLD measures, which emphasizes the potential information that functional data has to offer in the investigation of basic language processes. Our results from Experiment 2 provided evidence that behavioural naming reaction time and BOLD width, time to peak and intensity measures all display a relationship of mathematical independence similar to that found with behavioural accuracy measures. Specifically, we demonstrated that actual-REG naming response time and BOLD measures can

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be predicted given the corresponding EXC and PH or NW measures and the application of mathematical independence equations. Such findings are important for all models of basic word recognition because they demonstrate how a cognitive architecture can be applied to functional data to provide further information about how SV and PD processes operate, and provide further support for dual-route models.

From a neurobiological perspective, we provide evidence for a spatial representation of mathematical independence between SV and PD systems (Figure 8). Our findings from Experiments 3 and 4 revealed that naming stimuli that engage SV processes (e.g., EXCs) activates regions in the brain along the ventral stream from the occipital cortex through to the temporal gyri. In contrast, naming stimuli that engage PD processes (e.g., PHs) activates regions in the brain along the dorsal stream from the occipital cortex through to the parietal gyri. Similar to the cognitive dual route architecture, both SV and PD systems overlap in several regions within the brain including the medial extrastriate (i.e., basic visual analysis) and motor cortex (i.e., output). Furthermore, our findings provide evidence against a neurobiological implementation of single mechanism models, whereby our functional maps representing activation for SV stimuli (e.g., EXCs) and PD stimuli (e.g., PHs) always revealed some unique activation for these stimuli. Consequently, neither a model that relies solely on lexical information (SV) nor a model that relies solely on phonological information (PD) was spatially represented in our analyses.

In Experiments 5 and 6, we then compared behavioural and functional data, which adds another level of interpretation and accordingly provides a more thorough investigation of basic reading processes. In Experiment 5 we demonstrated that the BOLD width in Broca's area is uniquely correlated with PH naming response time, providing evidence that Broca's area is

particularly sensitive to stimuli that have phonological lexical level representations (Figure 17; see also Figure 2). Experiment 6 provided the first demonstration of the application of AFL to BOLD intensity and our results suggest that the SMA is critically involved in the resolution of phonological information from SV and PD systems (Figure 18D and Figure 23A). When examining the average time courses from the middle temporal gyrus, SMA, insula and Broca's area, only the average intensity time course from the SMA displayed a pattern of overadditivity similar to results typically reported for behavioural naming reaction times. This work demonstrates that AFL, which is typically used to localize factors in time, can be used with functional data to localize the effects of factors in the brain. In fitting with the dual-route model, we suggest that the SMA is the region in the brain, analogous to an articulatory buffer, where the competing phonological codes produced from the SV and PD systems for low frequency EXCs is ultimately resolved prior to speech output. In general, comparing behavioural and functional measures provides more detailed information regarding basic reading processes and the contribution of particular brain regions to reading particular stimuli.

In Experiment 7, we provide critical information regarding methodological considerations that should be taken into account when conducting behavioural and functional research on basic reading processes. More specifically, we demonstrate that NWs can be problematic stimuli in the measurement of PD processing (Figure 25, Figure 26 and Figure 27). NWs produce false activation in the ventricles as well as an overabundance of activation throughout the brain, subsequently compromising the interpretation of functional MRI data. Furthermore, NW naming reaction times display a pattern of results that reflects a mechanistic naming style. We argue that naming PHs is more ecologically and functionally valid in the measurement of PD processing.

Finally, we provide information about how basic research regarding SV and PD processes can help inform and develop models of impaired reading, and allow us to make predictions about subsequent outcomes on basic reading processes following traumatic brain injury. In Experiment 8 we provided evidence for phonological dyslexia following right hemispherectomy and mixed dyslexia following left hemispherectomy. These findings indicate that SV processing skills are high on a hierarchy of preserved function and thus retained or subsumed by the remaining hemisphere, whereas PD processing skills are low on the hierarchy and subsequently lost or crowded out following hemispherectomy. Nonetheless, the left hemisphere did demonstrate some specialization in basic language processes as evidenced by a better reading performance in the participant with the remaining left hemisphere.

In conclusion, both behavioural and neurobiological support is provided for a mathematically independent, dual-route model of basic reading processes such that the correct naming of letter strings involves independent SV and PD processing systems. These results present a challenge to models that treat PD and SV as redundant processes (e.g., lexical analogy models such as Marchand & Friedman, 2005; single-process connectionist models such as Plaut et al., 1996) and support dual-route models (such as those proposed by Besner & Smith, 1992; Borowsky et al., 2006; Cohen et al., 2008; Coltheart et al., 2001; Forster & Chambers; 1978; McDougall et al., 2005; Paap & Noel, 1991; Posner & Raichle, 1994; Pugh et al., 2001).

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Footnotes

1. In order to help make research on basic reading processes more accessible to reading educators, the terms SV and PD are used here because they are more widely used and understood by a larger audience.

2. Another possible relationship that exists between SV and PD in basic reading processing is that of exclusivity. It is a dual-route model whereby two pathways exist and both contribute uniquely to naming words (i.e., there is no overlap). However, given that both SV and PD share orthographic encoding and phonological output processes, a theory of basic reading processing involving such a model as exclusivity could not be found, so we do not consider it here.

3. The lexical route can be further sub-divided with respect to whether the semantic system is involved or not, however, this subdivision is not relevant for the present work. Nonetheless, an important topic for future research would be to explore the relationship between the semantic-lexical route and the nonsemantic-lexical route.

4. Given our interest in extending these equations to normal skilled reading, and consequently, avoiding ceiling effects on naming accuracy, the present study implemented speeded naming instructions. Independence equations have been shown to be valid under conditions of sub-asymptotic accuracy. Lindsay and Jacoby (1994) have demonstrated that equations of independence can be used to test the contribution of independent processes under speeded naming conditions using the process dissociation procedure. Another important consideration from this research was that the proportion of item types could be experimentally manipulated from mixed blocks through to pure blocks. Pure block presentation ensures that PHs be named via the PD route with checking of the phonological lexicon (as evidenced by a

significant base-word frequency effect, Borowsky et al., 2002). Importantly, research that has

examined the extent to which people can emphasize or de-emphasize their PD processing system

has shown some differences in route emphasis in blocked versus mixed trials (Baluch & Besner,

1991; Monsell et al., 1992; Lupker, Brown & Colombo, 1997; Rastle & Coltheart, 1999;

Kinoshita et al., 2004). Such research, although mainly focused on reaction times, typically

reports no difference in accuracy scores between the two presentation types (Monsell et al.,

1992; Lupker et al., 1997; Kinoshita et al., 2004). Thus, we do not predict accuracy to be

affected by mixed versus blocked presentation. However, to ensure that the pure block version

of stimulus presentation did not compromise the validity of the independence equations, a

subsequent study was conducted that was identical in procedure, except that the stimuli were

presented in mixed block format. The results supported the same model as was supported in the

pure block version. That is, the independence model (with PHs) accounted for a significant

amount of variance of actual REG reading accuracy, $t(11) = 2.28$, $p = .046$. Predicted REG

accuracy as derived from the independence model accounted for 28% of the variance in actual

REG accuracy.

     5. It is worthwhile to note that while Lui et al. used an event related design, we chose to

use a block design. Thus, theoretically, we measured the FWHM of the hemodynamic response

H, whereas Liu et al. measured the FWHM of the impulse response function (IRF), h. However,

if B represents the paradigm function (the blocks) then H = B*h where * is convolution. Since B

is fixed the FWHM of H is essentially a constant multiple of the FWHM of h, and one could

argue that it should not matter which FWHM you measure. Nevertheless, there remains a

difference in magnitude between the correlation that we report, and the one that Liu et al report.

We believe that the main reason for the difference in magnitude of Liu et al's correlation reflects

the fact that they used a different task (i.e., lexical decision; see discussion section). Given that

block designs are well known to be more sensitive at detecting activation in fMRI studies, and

that naming tasks are known to be more sensitive to phonological processes, we chose to use a

block design naming task.

  6. In fitting with the connectionist framework that words are represented on a continuum,

the terms 'consistent' and 'inconsistent' are used to describe the relative consistency of spelling-

to-sound mappings, rather than 'regular' and 'exception', which reflects the dichotomous nature

of the dual route models. Such a distinction is not pertinent to the present investigation, and

thus, the terms 'regular' and 'exception' will be used throughout the remainder of the paper.

  7. The stimuli were presented as part of a larger behavioural experiment which also

included pure blocks of PHs (e.g., *pynt*) and NWs (e.g., *bint*). Importantly, the stimuli were

presented in concordance with a partial Latin square design to ensure no effects of presentation

order were present. In addition, using a database dictionary resource (MRC Psycholinguistic

Database: Machine Usable Dictionary. Version 2.00,

http://www.psy.uwa.edu.au/mrcdatabase/mrc2.html), which provides a count of the number of

occurrences of particular linguistic properties, we evaluated our stimuli on several

characteristics. The stimuli did not differ on imageabililty (ratings on a scale of 100-700;

p=.384, Mean REG = 477, Mean EXC = 454), Bi-gram sum (sum of frequencies for consecutive

bi-grams; p=.212; Mean REG = 4899, Mean EXC = 5544; as defined by Balota et al., 2007),

written frequency (counts per million; p=.496; Mean REG = 470, Mean EXC = 337; as defined

by Kucera & Francis, 1967), length (number of letters in a word; p=.817; Mean REG = 4.41,

Mean EXC = 4.45), phonological neighbourhood (number of correctly sounding words that can

be made by replacing one letter at a time; p=.491; Mean REG = 3.41 words, Mean EXC = 3.32

words) or orthographic neighbourhood (number of correctly spelled words that can be made by replacing one letter at a time; p=.172; Mean REG = 7.05, Mean EXC = 5.81) characteristics.

8. Given that the subsequent fMRI study was analyzed by-subjects, we focused our attention on the by-subject analyses in the behavioural experiment. However, the by-item analysis did not reveal a significant Frequency X Regularity interaction (p=.244).

9. Similar results to a gapped acquisition can be achieved by using a continuous (non-gapped) sequence and disregarding the time points during the task performance. However, this approach slightly reduces the sensitivity to detect activation in other regions of the brain not affected by the motion (Birn et al., 2004), and makes monitoring of the overt speech response very difficult.

10. Participants also read a block of NWs (e.g., *bint*). Given that the results of this block were similar to that of the PH block (i.e., both participants had poor performance and would be classified as phonological dyslexics) these analyses were not included.

Figure Captions

Figure 1. Models for the relationship between sight vocabulary (SV) and phonetic decoding

(PD) systems: A. Redundancy between SV and PD (i.e., single mechanism) whereby PD is the

encompassing system, B. Redundancy between SV and PD (i.e., single mechanism) whereby SV

is the encompassing system, C. The model of mathematical independence between SV and PD

(i.e., dual – route mechanisms) suggests that two systems (i.e., SV *and* PD) are necessary for

basic reading processes. The models of redundancy suggest a single system (i.e., SV *or* PD) is

necessary for basic reading processes.

Figure 2. Depiction of the relationship between sight vocabulary and phonetic decoding in a

dual-route model. A representation of the pathways involved in the translation of print to speech

using nonwords (NWs), pseudohomophones (PHs) and exception words (EXCs); regular words

(REGs; e.g., hint) can be read by either or both routes.

Figure 3. Partial regression plot of the residuals of actual REG reading accuracy as a function of

the residuals of predicted REG reading accuracy as derived from the independence model with

NWs after partialling out the unique contribution of the redundancy model with NWs from both

variables.

(Abbreviations: REG- regular word, NW- nonword)

Figure 4. Partial regression plot of the residuals of actual REG reading accuracy as a function of

the residuals of predicted REG reading accuracy as derived from the independence model with

NWs after partialling out the unique contribution of the redundancy model with EXCs from both

variables.

(Abbreviations: REG- regular word, NW- nonword, EXC – exception word)

Figure 5. Partial regression plot of the residuals of actual REG reading accuracy as a function of the residuals of predicted REG reading accuracy as derived from the independence model with PHs after partialling out the unique contribution of the redundancy model with PHs from both variables.

(Abbreviations: REG- regular word, PH- pseudohomophone)

Figure 6. Partial regression plot of the residuals of actual REG reading accuracy as a function of the residuals of predicted REG reading accuracy as derived from the independence model with PHs after partialling out the unique contribution of the redundancy model with EXCs from both variables.

(Abbreviations: REG- regular word, PH – pseudohomophone, EXC – exception word)

Figure 7. Inferior frontal gyri masked in axial view, representing the selected region of interest (ROI) for each participant, overlaid on the axial anatomical image of one of the participants. Colour gradations represent amount of individual variability in the specific region (i.e., red is the region that was masked for all participants).

Figure 8. Functional representation of the SV and PD routes in basic reading processes from A. lateral and B. ventral perspectives. PD stimuli (i.e., NWs, and PHs) are processed via a dorsal stream (red) and SV stimuli (i.e., EXCs) are processed via a ventral stream (yellow). Both share early activation in the occipital cortex and later activation in the motor cortex (orange).

Figure 9. A. Shared activation between EXCs and PHs. Shared regions of activation between EXCs and PHs included the lateral occipital gyrus (LOG), inferior temporal gyrus (ITG), posterior portion of the superior temporal gyrus (STG), inferior parietal lobule (angular gyrus; IPLAG), inferior parietal lobule (supra-marginal gyrus; IPLSG), superior parietal lobule (SPL), post-central gyrus (PoG), precentral gyrus (PrG), inferior frontal gyrus (IFGPT and IFGPO),

middle frontal gyrus (MFG), superior frontal gyrus (SFG), lingual gyrus (LG), cuneus, occipitotmeporal gyrus (OG), cingulate gyrus (CG), paracentral lobule (PL), cerebellum and posterior portion of the insula. *B. Unique activation to **EXCs** and PHs.* Activated regions include LOG, ITG, middle temporal gyrus (MTG), STG, IPLAG, IPLSG, SPL, PoG, PrG, IFGPT, IFGPO, MFG, SFG, LG, cuneus, preCuneus (PreC), OG, orbital gyri, thalamus, CG, paracentral lobule (PL), cerebellum, midbrain, parahippocampal gyrus (PG), gyrus rectus (GR), putamen, and insula. Arrows point to face direction.

Figure 10. A. *Shared activation between EXCs and NWs.* Activation shared between EXCs and NWs was found in the LOG, cerebellum, SPL, IPLSG, PrG, IFGPT, MFG, and the SFG in the left hemisphere, and the LOG, cerebellum, ITG, STG, and PoG in the right hemisphere. Shared activation was also found in the LG, OG, cuneus, PreC, CG, SFG and insular cortex. B. *Unique activation to EXCs and NWs.* Activation unique to EXCs was found in the SPL in the left hemisphere, and the ITG, MTG, and STG in the right hemisphere. Activation unique to NWs was found in the cerebellum, LOG, ITG, MTG, STG, SPL, AG, SG, PoG, PrG, SFG, MFG, and IFG bilaterally. Unique activation for EXCs was also found in the cuneus, CG, PG, orbital gyri, and SFG. Activation unique to NWs was also found in the LG, OG, PG, PreC, cuneus, midbrain, PL, CG, orbital gyri, SFG and insular cortex. Arrows point to face direction.

Figure 11. A. *Shared activation between EXCs and PHs.* Activation shared between EXCs and PHs was found in the LOG, posterior STG, and PrG in the left hemisphere, as well as, posterior ITG and IFGPO in the right hemisphere. Shared activation was also found in the cuneus, OG, MTG (right hemisphere), SFG and anterior left insula. B. *Unique activation to EXCs and PHs.* Activation unique to EXCs was found bilaterally in the cerebellum, LOG, ITG, anterior STG, SPL, and orbital gyrus, as well as, right hemisphere MTG AG, SG, and MFG. Activation unique

to PHs was found bilaterally in the cerebellum, LOG, ITG, MTG, AG, SG, SPL, PoG, PrG, SFG, MFG, IFG, and the orbital gyri. Unique activation for EXCs was also found in the cuneus, PreC, SFG, STG, MTG, midbrain, gyrus rectus, and orbital gyrus. Activation unique to PHs was also found in the cuneus, PreC, PL, cingulate, midbrain, SFG and right anterior insula. Arrows point to face direction.

Figure 12. A. *Shared activation between REGs and EXCs.* Activation shared between REGs and EXCs was found in bilateral LOG, STG, PoG, right MTG and ITG, and left PrG and MFG. Shared activation was also found in the OG, cuneus, PL, SFG and CG. B. *Unique activation to REGs and EXCs.* Activation unique to REGs was found in the right LOG and bilateral cerebellum, ITG, MTG, STG, AG, SG, SPL, PoG, PrG, SFG, MFG, IFG. Unique activation for EXCs was found in the LOG, ITG, MTG, STG bilaterally, the PoG, SFG, and MFG in the left hemisphere, and the SPL, and IFGPO in the right hemisphere. Activation unique to REGs was also found in the right LOG and cerebellum, bilateral PreC, STG, MTG, PL, CG, SFG, orbital gyri and gyrus rectus and mid-to-posterior insula, while activation unique to EXCs was found in the cerebellum, cuneus, PreC, SFG, CG, midbrain, gyrus rectus, left orbital gyri, and mid-to-anterior insula. Arrows point to face direction.

Figure 13. A. *Shared activation between REGs and NWs.* Activation between REGs and NWs was found in bilateral LOG, STG, left SG, SPL, PrG, IFG-PO, MFG, and right MTG, and PoG. Shared activation was also found in the right cerebellum, and bilateral LOG, OG, CG, SFG, and mid-to-anterior left insular cortex. B. *Unique activation to REGs and NWs.* There was no unique activation found for REGs when compared to NWs. Activation unique to NWs was found in the LOG, MTG, STG, SPL, and MFG bilaterally, and the SG, PoG, PrG, IFG, and SFG in the left

hemisphere. Activation unique to NWs was also found in the LOG, LG, midbrain, cingulate gyrus, SFG, and bilateral anterior insular cortex. Arrows point to face direction.

Figure 14. A. *Shared activation between REGs and PHs*. Activation shared between REGs and PHs was found in bilateral LOG, ITG, PoG, SPL, right MTG, and left STG, SG, PrG, and MFG. Shared activation was also found in bilateral LOG, OG, CG, SFG, right LG, and left mid-to-anterior insular cortex. B. *Unique activation to REGs and PHs*. There was no unique activation found for REGs when compared to PHs. Activation unique to PHs was found in the LOG, ITG, SPL, PrG, MFG and SFG bilaterally, and activation was seen in the left STG, AG, and PoG. Activation unique to PHs was also found in the OG, CG, SFG, and left anterior insular cortex. Arrows point to face direction.

Figure 15. A. *Shared activation between NWs and PHs*. Activation shared between NWs and PHs was found in the bilateral LOG, ITG, AG, SPL, PrG, MFG, and SFG, and left MTG, STG, PoG, IFG-PO. Shared activation was also found in the LG, OG, cuneus, PreC, PL, midbrain, CG, and SFG, and left mid-to-anterior insular cortex. B. *Unique activation to NWs and PHs*. Activation unique to NWs was found in bilateral STG, PoG, PrG, IFG-PT, MFG, SFG, cerebellum, and SG, left AG, SPL, and IFG-PO, and right MTG, ITG, and orbital gyri. Activation unique to PHs was found in bilateral LOG, MFG, cerebellum, AG, and PoG, and left SFG and right PrG and IFGPO. Activation unique to NWs was also found in the cerebellum, LG, OG, cuneus, PreC, midbrain, PL, CG, SFG, gyrus rectus, orbital gyrus, PG and insular cortex, while activation unique to PHs was found in the LG, OG, PreC, CG, and SFG. Arrows point to face direction.

Figure 16. BOLD hemodynamic response (h; points with error bars) and smoothed BOLD hemodynamic response (H(t); solid line) as found in Broca's area and averaged across

participants. (Note: Normalized Intensity = standardized (z-score) grayscale intensity values. Zeropoint is set to be the greyscale value of the first active volume).

Figure 17. BOLD width at half maximum (as derived from the functional data) plotted as a function of response time (as derived from the behavioural data) for each stimulus type. There is a significant positive linear relationship between PH reaction time and FWHM of the BOLD response. (Note: There was one datum with z-score > ±2.5 (PH datum in the lower left). The correlation between FWHM and PH reaction time was reassessed after removing this participant, and remained significant.)

Figure 18. A. Pattern of additivity on reaction time indicating that the two factors of interest are affecting separate stages of processing and a cognitive model which relates such additivity to factors of frequency and regularity B. Pattern of overadditivity on reaction time indicating that the two factors of interest are affecting a common stage of processing and a cognitive model which relates such overadditivity to factors of frequency and regularity. C. An example of how AFL can be applied to the dual-route model of reading to understand where frequency and regularity influence one another in time (e.g., within the articulartory buffer). D. An example of how AFL can be applied to functional data to understand where frequency and regularity influence one another in the brain (e.g., within the SMA).

Abbreviations: Freq. = Frequency; AFL = Additive Factors Logic; SMA = Supplementary Motor Association cortex; REGs = Regular words; EXCs = Exception words; SV = Sight Vocabulary; PD = Phonetic Decoding.

Figure 19. Significant Frequency (high vs. low) x Regularity (REG vs EXC) interaction on behavioural reaction time.

Figure 20. Examples of masked regions of interest (left = left) for one participant. A. The inferior frontal gyrus (center of right mask = -41, -65, 12). B. The insula (center of right mask = -42, -47, -8). C. The middle temporal gyrus (center of right mask = -61, -32, -28). D. The supplementary motor association cortex (-12, -40, 42).

Figure 21. A. *Shared activation between high frequency REGs and EXCs.* Shared activation between REGs and EXCs is found in the LOG, PrG, PoG, IFG, SMA and STG. *B. Unique activation to high frequency REGs and high frequency EXCs.* Unique activation to REGs was found in the LOG, ITG, PrG, SFG, PreC, and SMA. Activation unique to EXCs was found in the right hemisphere ITG, MTG, STG, bilateral SPL, PoG, PrG, IFG, MFG, SFG, SMA, CG, and midbrain. Arrows point to right MTG, bilateral SMA and insular cortex.

Figure 22. A. *Shared activation between low frequency REGs and EXCs. B.* Shared activation between REGs and EXCs was found in the LOG, left hemisphere STG and SPL, right hemisphere IPL, PrG, PoG, SMA and cuneus. *Unique activation to low frequency REGs and low frequency EXCs.* Unique activation for REGs was found in the right hemisphere ITG, left hemisphere PrG, MFG, anterior CG and cerebellum. Unique activation for EXCs was found in the LOG, right hemisphere MTG, bilateral SPL, PrG, SMA, PL, and posterior CG. Arrows point to right MTG, bilateral SMA and insular cortex.

Figure 23. Average hemodynamic response function and graph of the plotted mean peak intensities for: A. Supplementary Motor Association cortex, B. Middle Temporal Gyrus, C. Insula, and D. Inferior Frontal Gyrus (Broca's Area).

Figure 24. Histograms displaying skewness for NW and REG reaction times for each participant. The numbers on the graph correspond to subject number as shown in Table 9.

Figure 25. Activation maps for a single participant that display ventricle activation during the NW naming task (*top*) and very little ventricle activation in the REG naming task (*bottom*). The third or fourth inferior-most slice was centered on the posterior commissure and represents z = 0. Each four-slice array displays right-to-left: z = ~ -10, 0, 10, and 20 mm, respectively. All activated regions exceed a threshold for activation of $\eta = 0.65$, and are color coded for intensity (arbitrary units). Maps are presented according to radiological convention (right = left).

Figure 26. Unique (top) map displaying activation for REG or NW naming. **Shared** (bottom) map displaying activation for REG and NW naming. The z-coordinate is centered on zero at the AC-PC line after Talairach transformation. The anatomical maps display right = right. The arrow direction indicates the anterior (orbital) direction.

Figure 27. Time course of voxel intensity as a function of time in an activated region (bottom; coordinates z = 92, y = 79, z = 5) and in the ventricles (top; coordinates x = 62, y = 68, z = 6) during NW reading. The shaded gray regions indicate the task blocks when participants were engaged in the word-naming task.

Figure 28. Time course of voxel intensity as a function of time in an activated region (bottom; coordinates z = 92, y = 79, z = 5) and in the ventricles (top; coordinates x = 62, y = 68, z = 6) during REG reading. The shaded gray regions indicate the task blocks when participants were engaged in the word-naming task.

Figure 29. Assessment of phonological dyslexia via plotting PH naming accuracy as a function of exception word naming accuracy. A 95% sample ellipsoid is placed around the normal, age-matched, comparison group data.

Figure 30. Assessment of surface dyslexia via plotting exception word naming accuracy as a function of PH naming accuracy. A 95% sample ellipsoid is placed around the normal, age-matched, comparison group data.

Appendix A: Ethics Approval

UNIVERSITY OF SASKATCHEWAN

Behavioural Research Ethics Board (Beh-REB)

Certificate of Re-Approval

PRINCIPAL INVESTIGATOR	DEPARTMENT	Beh #
Ronald W. Borowsky	Psychology	Beh 00-09

INSTITUTION (S) WHERE RESEARCH WILL BE CARRIED OUT

SPONSORING AGENCIES
NATURAL SCIENCES & ENGINEERING RESEARCH COUNCIL OF CANADA (NSERC)

TITLE:
Basic Reading Processes: Reliance on Sight Vocabulary (SV) and Phonetic Decoding (PD) During Normal Reading Acquisition

RE-APPROVED ON	EXPIRY DATE
12-May-2009	11-May-2010

Full Board Meeting | |

Delegated Review |✔|

CERTIFICATION

The University of Saskatchewan Behavioural Research Ethics Board has reviewed the above-named research project. The proposal was found to be acceptable on ethical grounds. The principal investigator has the responsibility for any other administrative or regulatory approvals that may pertain to this research project, and for ensuring that the authorized research is carried out according to the conditions outlined in the original protocol submitted for ethics review. This Certificate of Approval is valid for the above time period provided there is no change in experimental protocol or consent process or documents.

Any significant changes to your proposed method, or your consent and recruitment procedures should be reported to the Chair for Research Ethics Board consideration in advance of its implementation.

ONGOING REVIEW REQUIREMENTS

In order to receive annual renewal, a status report must be submitted to the REB Chair for Board consideration within one month of the current expiry date each year the study remains open, and upon study completion. Please refer to the following website for further instructions: http://www.usask.ca/research/ethics_review/

John Rigby, Chair
University of Saskatchewan
Behavioural Research Ethics Board

Please send all correspondence to:

Research Ethics Office
University of Saskatchewan
Box 5000 RPO University
1607-110 Gymnasium Plac
Saskatoon SK Canada S7N 4J8

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Certificate of Re-Approval

PRINCIPAL INVESTIGATOR	DEPARTMENT	Bio #
Ronald W. Borowsky	Psychology	01-125

INSTITUTION (S) WHERE RESEARCH WILL BE CARRIED OUT

Royal University Hospital
103 Hospital Drive
Saskatoon SK S7N 0W8

SUB-INVESTIGATOR(S)

Gordon E. Sarty, Greg Kraushaar

STUDENT RESEARCHER(S)

Jacqueline Cummine, Carrie Esopenko

SPONSORING AGENCIES

CANADIAN INSTITUTES OF HEALTH RESEARCH (CIHR)
NATURAL SCIENCES & ENGINEERING RESEARCH COUNCIL OF CANADA (NSERC)

TITLE:

Correlation of Functional Magnetic Resonance Imaging (fMRI) with Direct Cortical Stimulation, Electroencephalography (EEG) and the WADA Test

RE-APPROVED ON	EXPIRY DATE
12-May-2009	11-May-2010

Full Board Meeting ☐

Delegated Review ✔

CERTIFICATION

The study is acceptable on scientific and ethical grounds. The principal investigator has the responsibility for any other administrative or regulatory approvals that may pertain to this research study, and for ensuring that the authorized research is carried out according to governing law. This re-approval is valid for the specified period provided there is no change to the approved protocol or consent process.

FIRST TIME REVIEW AND CONTINUING APPROVAL

The University of Saskatchewan Biomedical Research Ethics Board reviews above minimal studies at a full-board (face-to-face) meeting. Any research classified as minimal risk is reviewed through the delegated (subcommittee) review process. The initial Certificate of Approval includes the approval period the REB has assigned to a study. The Status Report form must be submitted within one month prior to the assigned expiry date. The researcher shall indicate to the REB any specific requirements of the sponsoring organizations (e.g. requirement for full-board review and approval) for the continuing review process deemed necessary for that project. For more information visit http://www.usask.ca/research/ethics_review/.

REB ATTESTATION

In respect to clinical trials, the University of Saskatchewan Research Ethics Board complies with the membership requirements for Research Ethics Boards defined in Division 5 of the Food and Drug Regulations and carries out its functions in a manner consistent with Good Clinical Practices. This re-approval and the views of this REB have been documented in writing.
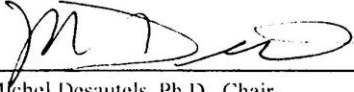
Please send all correspondence to:

Research Ethics Office
University of Saskatchewan
Box 5000 RPO University
1607-110 Gymnasium Place
Saskatoon SK Canada S7N 4J8

PRINCIPAL INVESTIGATOR
Ronald W. Borowsky

DEPARTMENT
Psychology

Michel Desautels, Ph.D., Chair
University of Saskatchewan
Biomedical Research Ethics Board

Appendix B: Stimuli from Experiments 1-8

Exception Words	Nonwords	Pseudohomophones	Regular Words
have	coaft	truhmp	off
both	leext	spawt	bridge
head	kruhmp	toon	saw
mow	nynd	bern	board
bush	flove	wyz	grew
flood	gawlt	phlash	speech
none	payt	theem	nine
heard	stroat	ehj	hand
foot	cleem	wyfe	wore
caste	ehp	boarn	well
move	plass	mohr	mug
love	gair	soke	land
swear	pryf	tule	bound
bread	brean	leest	ease
grow	brair	gyde	with
sew	helked	hoest	days
wood	swoam	dryv	cliff
month	nohr	pryd	fool
hearth	phlast	coalt	swell
where	loun	bote	carve
dread	swhin	helled	must
climb	fyce	dawt	hoarse
world	toov	seaks	which
won	theen	doun	mouth
four	drose	stroal	brown
heart	gerhn	mawths	dodge
prove	ghyt	swoar	while
comb	boam	layt	feel
bought	ost	flore	truce
give	hoert	foart	too
says	vyfe	feeld	home
touch	boarm	mylz	torn
broad	seafs	drore	heat
thread	hoaj	terhn	snatch
breath	sofe	swhis	goes
sweat	boke	mynd	twice
once	mamths	gawlf	dark
full	nyre	klass	bunch
front	berv	gaim	flame
whom	tufe	cleen	win
tour	woaf	woak	stack
spread	wawf	hedj	girl
tread	hoalt	fyne	food
two	dryn	breaz	brain
steak	gyfe	owt	hear
sieve	teeld	hoap	much
door	vyz	wawk	proud
most	sehn	boan	thrust
dough	spawl	stait	sweep
own	davt	braiv	free
earn	mydz	nyse	leave
gone	bedj	whyt	sag
learn	shait	wehn	had
does	hant	hawt	coil
one	loart	hoald	ditch

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List of Abbreviations

A_{EXC} – Accuracy in exception word naming
AFL – Additive factors logic
A_{NW} – Accuracy in nonword naming
A_{PH} – Accuracy in pseudohomophone naming
A_{REG} – Accuracy in regular word naming
BOLD – Blood oxygenated level dependent
cc – cubic centimetres
CG – Cingulate gyrus
CSF – Cerebral spinal fluid
EPI – Echo planar images
EXC – Exception word
fMRI –Functional magnetic resonance imaging
FWHM – Full width at half maximum
GLM – General linear model
GR – Gyrus rectus
gs – grayscale
I – Normalized intensity
I_{EXC} – Normalized intensity for exception word naming
IFGPO Inferior frontal gyrus (pars opercularis)
IFGPT – Inferior frontal gyrus (pars triangularis)
I_{NW} – Normalized intensity for nonword naming
I_{PH} – Normalized intensity for pseudohomophone naming
IPLAG – Inferior parietal lobule (angular gyrus)
IPLSG – Inferior parietal lobule (supra-marginal gyrus)
I_{REG} – Normalized intensity for regular word naming
IRF – Impulse response function
ISI – Interstimulus interval
ITG – inferior temporal gyrus
LG – Lingual gyrus
LOG – Lateral occipital gyri
MFG – Middle frontal gyrus
M*int* – Intersection map
mm – millimetres
ms – milliseconds
MTG – Middle temporal gyrus
M*uni* – Unique map
NW – Nonword
OG – Occipitotmeporal gyrus
P – Normalized time to peak
PD – Phonetic Decoding
P_{EXC} – Normalized time to peak for exception word naming
PG – Parahippocampal gyrus
PH – Pseudohomophone
PL – Paracentral lobule

PL – Paracentral lobule

P_{NW} – Normalized time to peak for nonword naming

PoG – Post-central gyrus

P_{PH} – Normalized time to peak for pseudohomophone naming

PreC – PreCuneus

P_{REG} – Normalized time to peak for regular word naming

PrG – Precentral gyrus

REG – Regular word

ROI – Region of Interest

RT – Reaction time

RT_{EXC} – Normalized response time for exception word naming

RT_{NW} – Normalized response time for nonword naming

RT_{PH} – Normalized response time for pseudohomophone naming

$RT_{PredREG}$ – Individual predicted regular word response time

RT_{REG} – Normalized response time for regular word naming

s – seconds

S – Normalized initial slope

S_{EXC} – Normalized initial slope for exception word naming

SFG – Superior frontal gyrus

SMA – Supplementary motor association cortex

S_{NW} – Normalized initial slope for nonword naming

S_{PH} – Normalized initial slope for pseudohomophone naming

SPL – Superior parietal lobule

S_{REG} – Normalized initial slope for regular word naming

STG – Superior temporal gyrus

SV – Sight vocabulary

T_E – Echo time

T_R – Repetition time

V – Normalized volume

V_{EXC} – Normalized volume for exception word naming

V_{NW} – Normalized volume for nonword naming

V_{PH} – Normalized volume for pseudohomophone naming

V_{REG} – Normalized volume for regular word naming

W – Normalized full width at half maximum

W_{EXC} – Normalized full width at half maximum for exception word naming

W_{NW} – Normalized full width at half maximum for nonword naming

W_{PH} – Normalized full width at half maximum for pseudohomophone naming

W_{REG} – Normalized full width at half maximum for regular word naming

µL – microlitres