A COGNITIVE NEUROSCIENCE EXAMINATION OF RHYTHM AND READING AND THEIR TRANSLATION TO NEUROLOGICAL CONDITIONS

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ABSTRACT

The goal of the current research was to provide a novel and comprehensive examination of the connection between rhythm and reading through the combination of multiple experimental stimuli, and to translate the reading aloud research to neurological patients.

Both speech and music perception/production involve sequences of rhythmic events that unfold over time, and the presence of rhythm in both processes has motivated researchers to consider whether musical and speech rhythm engage shared neural regions (Patel, 2008), and whether musical rhythm can influence speech processing (Cason & Schön, 2012). The experimental paradigm involved examining whether reading aloud is affected by the presentation of a rhythmic prime that was either congruent or incongruent with the syllabic stress of the target letter string. The experiments in Chapter 2 used targets that were words that placed the stress on either the first or second syllable (*prac*tice vs. po*lice*), as well as their corresponding pseudohomophones (*prak*tis vs. po*leese*), which allowed us to compare lexical and sublexical reading, respectively. In Chapter 3, the experiments involved a paradigm in which target words have stress on the first syllable for nouns, and on the second syllable for verbs. Thus, the design used identical noun-verb word pairs (*con*flict vs. con*flict*), as well as their corresponding pseudohomophones (*kon*flikt vs. kon*flikt*). The results from the behavioural experiments demonstrated that naming reaction times were faster for words and pseudohomophones when the rhythmic prime was congruent with the syllabic stress, and slower when the rhythmic prime was incongruent, which suggests that a rhythmic prime matched to the syllabic stress of a letterstring aids reading processes. Functional magnetic resonance imaging (fMRI) was also used in Chapters 2 and 3 to test whether a network involving the putamen is involved in the effect of rhythm on reading aloud. The fMRI results revealed that a network involving the putamen is associated with the effect of congruency between rhythmic stress and syllabic stress on reading aloud, which is consistent with previous literature that has shown this region is involved in reading, rhythm processing, and predicting upcoming events. Chapter 4 was to provide a behavioural and neuroanatomical examination of reading processes in two patients. Case Study 1 examined the effect of rhythmic priming on reading aloud in a patient with Parkinson's disease (PD), given that these patients exhibit abnormalities in the putamen, which has been associated with rhythm and reading processes. The patient demonstrated the same behavioural effect as normal participants, whereby individuals benefited from the rhythm prime being congruent with the syllabic stress of the target letter string, and the fMRI results revealed that despite disruptions in basal ganglia functioning following PD, there was still activation in the putamen for reading real words. Case Study 2 examined a patient with intractable left temporal lobe epilepsy (TLE) who was undergoing a temporal lobectomy that involved removing regions of the left temporal lobe that are often thought to be important in language processing. The fMRI results showed that all four reading tasks activated the right posterior occipitotemporal region in the ventral visual stream, confirming the right hemisphere dominance in this patient. Together, these findings have implications for developing neurobiological models of reading, translation to localization of function in neurological conditions such as PD and TLE, and may also reveal potential remedial applications for treating speech deficits in patient populations, such as Parkinson's disease, stuttering, aphasia, and dyslexia.

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LIST OF ABBREVIATIONS

Confidence Interval – CI

Deep Brain Stimulation – DBS

Diffusion Tensor Imaging - DTI

Echo-Planar Images - EPI

Frontal Operculum – FO

General Linear Model – GLM

Inferior Frontal Gyrus – IFG

Inferotemporal gyrus – ITG

Lateral Occipital Complex – LOC

Magnetization Prepared Rapid Acquisition Gradient Echo – MPRAGE

Middle Temporal Gyrus – MTG

Parkinson’s Disease - PD

Pseudohomophone – PH

Reaction Time – RT

Specific Language Impairment – SLI

Superior Temporal Gyrus – STG

Supplementary Motor Area – SMA

Temporal Lobe Epilepsy - TLE

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CHAPTER 1

AN INTRODUCTION TO RHYTHM AND SPEECH PROCESSING

Portions of this chapter have been previously published:

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Rhythm is omnipresent in communication. Since ancient times, humans have universally engaged in activities that involve rhythm, such as drumming, dancing, and playing musical instruments as a form of communication, and rhythm has long been associated with language in the form of song (Conard, Malina, & Münzel, 2009; d'Errico et al., 2003; Mithen, 2005; Fitch, 2006). Thus, it has been speculated that the neural mechanisms involved in rhythm processing may be quite ancient, and furthermore, that rhythmic abilities may be a fundamental organizing principle of brain function (Buzsaki, 2006). Not only is rhythm vital to artistic forms of communication, it is also essential to the perception and production of speech and provides important cues about the meaning of speech. Both music and speech involve the perception of sequences of acoustic events that unfold over time with both rhythmic and tonal features. Furthermore, like musical rhythm, speech rhythm involves organized acoustic sequences and complex cognitive and motor processes. More specifically, many define speech rhythm as the patterns of stressed and unstressed tones and syllables that compose the meter of spoken utterances (Cason & Schön, 2012; Cutler, 1994; Hausen, Torppa, Salmela, Vainio, & Särkämö, 2013; Jusczyk, Houston, & Newsome, 1999). These rhythmic features are essential for speech comprehension as they allow listeners to segment an ongoing speech stream into discrete and meaningful units (Kotz & Schwartze, 2010; Patel, 2011; Peele & Davis, 2012), and allow listeners to identify syllables, segment words from fluent speech, and convey prosody (Cutler & Foss, 1977; Cutler & Norris, 1988; Houston, Santelmann, Jusczyk, 2004; Vroomen, Tuomainen, & de Gelder, 1998). Speech rhythm also plays an important role in speech processing because alternating regular rhythmic patterns help build up an expectation when the next stressed syllable might appear (Cutler & Foss, 1977; Cutler & Norris, 1988; Pitt & Samuel, 1990). Furthermore, there is a degree of perceptual regularity in musical and speech rhythm, albeit to a lesser degree in speech (Patel, 2008), which leads to the prediction of upcoming salient auditory events (i.e., sounds, tones, and speech units; Large & Jones, 1999). The presence of rhythm in both speech and music has motivated researchers to consider whether musical and speech rhythm engage shared neural regions (Patel, 2008), and whether musical rhythm can influence speech processing (Cason & Schön, 2012; Cason, Astésano, & Schön, 2015).

The degree to which music and language share cognitive and neural resources has long been debated by scientists. In particular, researchers have long sought to understand why humans have evolved a sense for musical rhythm at all and, in particular, whether musical ability is inextricably linked to our human capacity for speech (Zatorre, 2005). The similarities between speech rhythm and musical rhythm have led to debates in the literature as to what extent their processing draws on similar or different mechanisms (Patel, 2008), and whether there may be a cross-domain effect of one process onto the other (Cason & Schön, 2012). On one hand, theorists have argued for a shared evolutionary origin (Mithen, 2006), as well as extensive structural similarities between music and language (Lerdahl & Jackendoff, 1983; Botha, 2009), while on the other hand, theorists have argued for differences between music and language processing and specificity of the two domains (Peretz & Coltheart, 2003). Evidence for shared processing of music and language comes from reading studies in which musical and linguistic syntax are manipulated simultaneously, such as using garden path sentences (i.e., a grammatically correct sentence that starts in such a way that a reader's most likely interpretation will be incorrect) and harmonically expected/unexpected musical chord progressions (Slevc et al., 2009; Jung et al., 2015). The results of these studies demonstrate interactive effects when linguistic and musical syntax were violated simultaneously, suggesting the use of the same neural and cognitive resources for these processes.

When investigating how rhythm can influence speech processing, Morton, Marcus, and Frankish (1976) determined that speakers and listeners gauge temporal intervals in speech based on stressed syllables, rather than syllable onsets, and referred to this concept as ‘perceptual centres’ or ‘p-centres’. In other words, p-centres in speech are a measure of time that rhythmic emphasis is heard. Morton and colleagues found that adults hear alternating syllables like “ba” and “la” as non-rhythmic when syllable onset times were isochronous (i.e., occurring at equal time intervals), but heard them as rhythmic when the syllable stresses were isochronous. In other words, adults attend to the stressed syllables or ‘p-centres’ to determine speech rhythm, and not to syllable onsets. This concept has also been demonstrated to occur in speech production (Fowler, 1979), whereby participants that are asked to *produce* isochronous sequences will generate a rhythmic pattern in their speech that listeners require to *hear* a sequence as isochronous. Furthermore, the expectations that listeners hold regarding the timing of stressed syllables have also been shown to contribute to speech perception (Lehiste, 1980; Port, 2003; cf. Quené & Port, 2005). Lastly, it has been proposed that attention is more focused on stressed syllables during speech processing, which has been termed the "attentional bounce hypothesis" (Pitt & Samuel, 1990).

Brain Regions Associated with Rhythm and Speech Processes

A potential link between speech and rhythm processing has been shown in several neuroimaging studies, which have revealed that the brain recruits similar cortical and subcortical regions for the processing of both music and speech stimuli. These cortical regions are comprised of the left superior and middle temporal gyri, including the primary, secondary, and association areas of auditory cortex (Abrams, Bhatara, Ryali, Balaban, Levitin, & Menon, 2011), as well as the middle and superior temporal sulci (Brown, Martinez, Hodges, Fox, & Parsons, 2004; Koelsch, Gunter, Cramon, Zysset, Lohmann, & Friederici, 2002; Schon et al., 2010), planum polare (Brown, Martinez, Hodges, Fox, & Parsons, 2004; Koelsch et al., 2002), and the anterior transverse temporal area (Koelsch et al., 2002). Frontal regions implicated in the processing of temporal information in speech and music involve the left inferior frontal gyrus (IFG; Gelfald & Bookheimer, 2003; Schön et al., 2010; Tillmann, Janata, & Bharucha, 2003), including the pars orbitalis region, as well as its right hemisphere homologue (Abrams et al., 2011; Levitin & Menon, 2003), Broca's area (Abrams et al., 2011; Brown et al., 2004; Koelsch et al., 2002; Maess, Koelsch, Gunter, & Friederici, 2001), the frontal sulcus (Abrams et al., 2011), motor cortex and supplementary motor area (SMA; Brown et al., 2004), as well as the insula (Koelsch et al., 2002). The subcortical regions implicated in processing both speech and music include the brain stem, basal ganglia, thalamus, and cerebellum. The cerebellum is responsible for encoding of event-based temporal structure, and relays information to motor regions via the thalamus, which further transmits information to the frontal cortex (Kotz & Schwartze, 2010). The basal ganglia, particularly the putamen, are assumed to continuously evaluate temporal relations, extract temporal regularity, and engage in sequencing temporal events (Fujii & Wan, 2014; Grahn & Rowe, 2009). In addition, the basal ganglia and SMA respond more strongly during beat perception than during listening to irregular auditory sequences that lack a steady beat (Grahn & Brett, 2007). Taken together, these neuroimaging studies provide evidence that many of the same brain regions may subserve the processing of both language and musical information.

In addition to studies seeking to investigate the underlying neural mechanisms of musical rhythm and speech processing, there are also several neuropsychological and neuroimaging studies that have studied timing more broadly, and have identified that the timing network in the brain includes the cerebellum (Irvy & Keele, 1989; Irvy, 1993; Nichilli et al., 1996; Penhune et al., 1998; Xu et al., 2006; Lee et al., 2007; Gooch et al., 2010; Grube et al., 2010ab; Teki et al., 2011), basal ganglia (Artieda et al., 1992; Pastor et al., 1992; Harrington et al., 1998; Grahn and Brett, 2007; Teki et al., 2011), pre-SMA and SMA (Halsband et al., 1993; Shima and Tanji, 2000; Macar et al., 2004, 2006; Kotz and Schwartze, 2011), and pre-motor and prefrontal cortex (Oshio, 2011; for reviews see: Ivry et al., 2002; Lewis and Miall, 2003; Ivry and Spencer, 2004; Meck and Malapani, 2004; Buhusi and Meck, 2005; Meck, 2005; Grahn, 2009; Grondin, 2010; Wiener et al., 2010; Coull et al., 2011). Thus, it has been posited that these areas contain specialized timekeeping mechanisms necessary to coordinate temporally precise and structured movement, as well as perceptual timing (Teki et al., 2012). Among these regions, the cerebellum has been implicated in the encoding of time intervals (Irvy & Keele, 1993; Grube et al., 2010ab), whereas the basal ganglia have been implicated in the perception of rhythmic sequences with a regular beat (Grahn, 2009), and the perception of time intervals relative to beat duration (Grahn & Brett, 2007; Grahn & Rowe, 2009).

Music and Speech Processing in Atypical Populations

Further support for a link between speech and rhythm processing comes from studies of neuropsychological patients, which provide strong evidence that many of the same brain regions are involved in the processing of both music and speech. For example, patients with Broca's aphasia (who have impairments in structural processing of language) may also show problems in structural processing of music (e.g., Patel, 2005; Patel et al., 2008). It has also been shown that musical practices like choral singing are useful in the rehabilitation of language abilities of patients with non-fluent aphasia (Racette, Bard, & Peretz, 2006; Schlaug, Norton, Marchina, Zipse, & Wan, 2010). Contrary to the idea that singing may be the key aspect in rehabilitation in non-fluent aphasics, where rehabilitation is attributable to melodic intonation, Stahl, Kotz, Henseler, Turner, and Geyer (2011) instead proposed that rhythm may be the critical aspect in rehabilitation of speech, particularly for patients with lesions in areas such as the basal ganglia. Their findings indicate that benefits typically attributed to melodic intonation actually have their roots in rhythm and, importantly, point to a crucial contribution of the basal ganglia for rhythmic segmentation in speech production. Other studies have also implicated the basal ganglia as a critical region involved in production and perception of rhythm (Cameron & Grahn, 2014; Grahn, 2009; Grahn, Henry, & McAuley, 2011; Grahn & Rowe, 2009; Harrington, Haaland, & Hermanowitz, 1998), as well as organizing and enacting sequences of simple speech sounds (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Bohland & Guenther, 2006; Kuljic-Obradovic, 2003; Oberhuber et al., 2013; Riecker et al., 2005; Sakurai, Momose, Iwata, Watanabe, Ishikawa, & Kanazawa, 1993). As such, musical rhythm is also used as a speech rehabilitation method in various patient populations. Sacks (2007) describes how musical rhythm, such as playing the piano, can improve speech and movement in patients with Parkinson's disease, as well as patients with aphasia. He has proposed that rhythm helps to coordinate movement, organize sequences, or retain great volumes of information, which then helps patients perform procedures they might otherwise be incapable of completing.

There is also a noteworthy literature regarding the effect of musical rhythm on speech processing in children with specific language impairment (SLI) and dyslexia. For example, Przybylski et al. (2013) compared the influence of regular and irregular musical rhythmic patterns, in which the meter extraction was easy or difficult, respectively, on syntax processing in these children. The task involved auditorily presenting a musical excerpt followed by sentences that were either grammatically correct or incorrect, and asking the children to indicate whether a given sentence was correct or not. They found that these children were better able to make judgments of grammaticality after the presentation of a regular rhythmic prime than after an irregular prime. Schön and Tillmann (2015) also aimed to test whether the beneficial effect associated with a regular rhythmic prime could extend to syllable segmentation in a reading task. In this task, children with SLI and dyslexia, as well as matched controls, were asked to read words and pseudowords following a rhythmic prime. The items of both types of stimuli were constructed to differ in their syllabic complexity as instilled by sonority cues, which allowed the authors to manipulate the difficulty level of segmentation. The results showed some improvement for syllable segmentation in reading after regular primes. For the more difficult items (containing the ambiguous syllable boundaries), SLI children produced more correct syllable boundaries after regular than irregular primes. For SLI and dyslexic children, the quality of reading increased after the regular prime, such as producing reduced phoneme omissions. Schön and Tillmann concluded that these findings promote the use of musical primes to boost language processing, and that such a technique may have great potential for rehabilitative purposes and for stimulating language development in children who are not acquiring language typically. Furthermore, Cason, Hidalgo, Isoard, Roman, and Schön (2014) investigated whether rhythmic priming can affect phonological production in hearing impaired children with hearing devices. They asked children to repeat sentences that were or were not preceded by a rhythmical prime, which could be either matched or mismatched with the meter (i.e., stress contrasts) of the sentence. Cason and colleagues found that the matching conditions resulted in a greater phonological accuracy of spoken sentences compared to baseline and mismatching conditions. Thus, these results suggest that musical rhythmic priming can enhance phonological production in hearing impaired children via an enhanced perception of the target sentence.

The Effect of Rhythm on Speech Processes

A neuroimaging study by Gordon, Magne, and Large (2011) explored the idea that musical rhythm could affect speech processing. Their study involved manipulating the temporal alignment between strong syllables (i.e., emphasized syllables) and strong beats (i.e., emphasized beats) to see if temporal alignment would help listeners to better understand song lyrics by directing their attention to instances where strong syllables occur on strong beats. Electroencephalographic (EEG) recordings were taken while participants listened to the sung sentences in which some, none, or all of the strong syllables aligned with metronome clicks. The results indicated that temporal alignment between strong/weak syllables and strong/weak musical beats were associated with modulations of frequency of EEG responses in the beta range (15 – 30 Hz) over mostly frontal and central regions, and gamma range (30 – 100 Hz) over the left parietal, central, and right frontotemporal regions, which have been shown to fluctuate with rhythmic expectancies. Furthermore, targets that followed well-aligned primes elicited greater induced alpha (8 – 15 Hz) and beta activity in the right and left hemispheres and better lexical decision task performance compared with targets that followed misaligned and varied sentences. Gordon and colleagues interpreted these findings as evidence for the notion of shared neural resources underlying speech rhythm and musical rhythm.

In order to study the cross-domain effect of rhythm on speech production, Cason and Schön (2012) examined whether a rhythmic prime could enhance phonological processing. As previous research has shown that the expectancy of the timing of stressed syllables contributes to speech perception (Lehiste, 1980; Port, 2003; Quené & Port, 2005), they developed a paradigm in which a brief rhythmic pattern would induce expectancy about where a target phoneme would be in a pseudoword. Like music, speech perception and production are dependent on beat (stressed, 'strong' syllables) and meter (the alternation of stressed and unstressed –'strong' and 'weak' – syllables). Cason & Schön (2012) recorded EEG and behavioral reaction time (RT) data while participants listened to pronounceable French pseudowords preceded by a simple rhythm prime. The participant's task was to decide whether a target phoneme was present in a word following the beat prime that was either 'on-beat' or 'off-beat' with the target phoneme. They found that when the target phoneme was presented on-beat with the rhythmic stress, participants yielded significantly faster RTs compared to when the target phoneme was off-beat. Moreover, they found a larger N100 amplitude for the metrical mismatches than matches, which is thought to reflect a violation of rhythmical expectations (Cason & Schön, 2012), as a larger N100 response is also elicited by mismatch negativity from the primary auditory cortex (Sams, Kaukoranta, Hämälainen, & Näätänen, 1991). Thus, their results indicate that speech processing can be enhanced by the temporal expectations generated by the prime and, further, that there is a cross-domain effect of musical rhythm on the processing of speech rhythm. Of particular interest to the present research, their results indicate that using a rhythmic prime matched to the prosodic features of speech can enhance phonological processing of spoken words.

A potential explanation of this phenomenon is that rhythm has an effect on reading aloud via entrainment. There are many existing definitions of entrainment but, for our purposes, we refer to it as the process of synchronizing our internal rhythmic processes to an external rhythm (Patel, 2014; Repp, 2005). The internal rhythmic processes are described as oscillators. Stimuli that occur at expected times are said to be "in phase" with the internal oscillator, whereas stimuli that do not occur at the expected time are considered "out of phase." Previous research has indicated that there is entrainment of neural oscillations to the rate of a perceived stimulus and, further, that auditory rhythmic patterns may have an effect on motor entrainment (Thaut, Kenyon, Schauer, & McIntosh, 1999). As well, there is evidence that internal synchronization to the outside world may be regulated by subcortical structures, such as the lateral geniculate nucleus, the thalamic reticular nucleus, and the pulvinar, which regulate activity across various cortical regions (Saalmann & Kastner, 2011). Further support for this notion comes from observations that during attentional studies there are increases in higher frequency synchrony between cortical areas along with an increase in low frequency synchrony between regions of the pulvinar and the cortex (Saalmann, Pinsk, Wang, & Kastner, 2012). Saalmann et al. propose that these low frequencies may provide the basis for which higher frequency oscillations across cortex can become entrained to external stimuli. These oscillations between regions in the basal ganglia and other regions of the cortex provide a viable explanation for the synchronization between speech and musical rhythm as in the studies described above. Relatedly, Giraud and Poeppel (2012) proposed that neural oscillations are engaged by quasi-rhythmic properties of speech and are fundamental in speech and language processing by parsing and decoding speech, as well as ‘packaging’ information into the appropriate temporal structure. In other words, cortical oscillations provide ways to temporally organize incoming speech signals.

There are several theories that have attempted to explain how the rhythmic structures of music and language are connected, and how entrainment may play a role in the influence of one modality on the other. For example, the Dynamic Attending Theory (DAT) is an entrainment model that proposes a mechanism by which neural oscillators synchronize to external rhythms (Large & Jones, 1999). This theory posits that rhythm processing is a fluid process in which attention is involuntarily entrained to a dynamically oscillating array of external rhythms, with attention peaking with stimuli congruent with the regularity of a given oscillator (Large & Jones, 1999; Grahn, 2009). In this case, rhythmic entrainment is thought to occur via neural resonance (i.e., neurons form a circuit that periodically align with the stimuli; Grahn et al., 2009; Henry et al., 2015). More recently, Large and colleagues (e.g., Large, 2008, Large & Snyder, 2009) have proposed a theory, the “neural resonance” theory, which builds on the DAT theory. According to this theory, beat perception arises when oscillations in the nervous system entrain to external rhythmic stimuli.

Another theory is the Shared Syntactic Integration Resource Hypothesis (SSIRH), which proposes that syntactic integration occurs as a result of overlap between neural areas and operations between music and language (Patel, 2003). In other words, the same mechanisms act on both speech and musical representations, and thus one modality may affect the other based on their shared neural resources. The hypothesis reconciles contrasting findings between studies that show that neural resources are shared (Slevc & Okada, 2015) versus studies that show domain specificity (Perruchet & Poulin-Charronnat, 2013) by explaining that there is *some* shared processing of music and language processes. Other studies that have provided evidence for some shared processing comes from behavioural manipulations of syntactic expectancy in music and language (e.g., Fedorenko et al., 2009; Slevc et al., 2009; Hoch et al., 2011; Jung et al., 2015), and brain imaging techniques such as event-related potentials that coincide for neural processing of music and language (e.g., Koelsch et al., 2005; Steinbeis & Koelsch, 2008; Fitzroy & Sander, 2012). Taken together, these studies suggest that rhythmic expectancy plays an important role in the shared processing of musical and linguistic structure.

Lastly, Patel and Iversen (2014) recently proposed the Action Simulation for Auditory Prediction (ASAP) hypothesis. The ASAP hypothesis suggests that the motor planning system uses a simulation of body movement to entrain its neural patterns to the beat period, and that these patterns are communicated from motor planning regions to auditory regions where they serve as a predictive signal for the timing of upcoming beats and shape the perceptual interpretations of rhythms. The hypothesis proposes that musical beat perception depends on strong functional connections between motor and auditory regions by which motor planning signals can influence auditory processing and perception. These motor planning regions include a collection of regions including the PMC, SMA, and the putamen, which is consistent with previous neuroscience findings (e.g., Grahn & Brett, 2007; Chen et al., 2008a; Grahn & Rowe, 2009; Geiser et al., 2012; Teki et al., 2012; Kung et al., 2013). Thus, it may be speculated that musical rhythm could have an effect on speech processes due to the motor system becoming entrained to the musical rhythm stimulus.

Speech Rhythm and Language Processing

Prosodic reading, or reading with rhythmic expression, is considered one of the hallmarks of fluent reading. Several researchers argue that sensitivity to speech rhythm is an important predictor of reading ability, and a number of recent findings suggest that children and adults with dyslexia show reduced awareness of syllabic stress patterns (Goswami, 2011; Goswami, 2002; Goswami, Gerson & Astruc, 2009; Leong, Hämäläinen, Soltész, & Goswami, 2011). Longitudinal studies also demonstrate that sensitivity to syllabic stress accounts for literacy performance of typically developing children (Holliman, Wood, & Sheehy, 2010).

The role of speech rhythm in reading development (e.g., Holliman, Wood, & Sheehy, 2010; Schwanenflugel, Hamilton, Kuhn, Wisenbaker, & Stahl, 2004; Wood & Terrell, 1998) and, more specifically, in phonological development (Abrams, Nicol, Zecker, & Kraus, 2009; Goswami, 2002) has also been widely investigated. Speech rhythm is one of the earliest cues used by infants to discriminate syllables. Cutler and Mehler (1993) suggest that children are born with an innate predisposition to attend to the rhythm of their native language (the *periodicity bias*), and that infants' sensitivity to the rhythmic features of speech (such as syllabic stress in particular) may facilitate spoken word recognition (Cutler, 1994), vocabulary development (Newman, Bernstein Ratner, Jusczyk, Jusczyk, & Dow, 2006; Walley, 1993), and reading development (Metsala & Walley, 1998). Goswami (2002) proposed that a failure to detect speech rhythm may underlie the language deficits observed in individuals with dyslexia, and more specifically, that phonological difficulties in dyslexia may be due to a deficit in the perceptual experience of rhythmic timing.

Speech rhythm in reading is often studied using multisyllabic words through the examination of responses to words with varying syllabic stress. Seminal work by Cutler and colleagues has studied the role of syllabic stress in lexical retrieval by using word fragment primes and examining the responses to words in which the syllabic stress either matched or mismatched the stress of the prime. For example, Cutler and Van Donselaar (2001) examined Dutch listeners' use of syllabic stress information in spoken-word recognition in a word-spotting task. They found that mismatching syllabic stress between a prime and a target word resulted in reduced lexical representation of the target word. That is, they suggest that a stress-matched fragment like *mu-ZEE* facilitated the recognition of *museum* more effectively than a stress-mismatched fragment like *MU-zee*. Similar studies have also demonstrated that speech fragments like ***octo-***, which matched the stress of one of either *OC-to-pus* or *oc-TO-ber*, resulted in faster lexical decisions when the prime and the target matched compared to when they were mismatched (Soto-Faraco, Sebastián-Gallés, & Cutler, 2001; Van Donselaar, Koster, & Cutler, 2005). Lastly, a study by Cooper, Cutler, and Wales (2002) presented English and Dutch speaking participants sentences that ended with a truncated portion of a word (e.g., *mu-*) and then measured their lexical decision responses to visually presented words (e.g., *MU-sic* vs. *mu-SE-um*) as a function of whether the stress pattern of the prime fragment matched the target word. They found that both listener groups recognized visually presented target words faster in the stress-matched priming condition compared to the stress-mismatched condition. Taken together, these results suggest that listeners exploit syllabic stress information in spoken-word recognition.

Related studies by McQueen, Norris, and Cutler (1994), as well as Cutler and Van Donselaar (2001), demonstrated that syllabic stress information could remove competition from a word in which it mismatches. These studies used word-spotting tasks whereby listeners monitored lists of short nonsense strings for the presence of an embedded real word. Cutler and Van Donselaar found that words were detected faster in nonsense contexts in which the target word was embedded within a string of nonwords that have no strong competitor compared to words that were embedded within a string of nonwords that had strong competitors for the target word. McQueen, Norris, and Cutler reported analogous findings in Dutch. These results suggest that listeners were able to use the syllabic stress information to facilitate the selection of one of two competitors for lexical recognition.

Several studies confirm that regularity of spelling-stress can also influence naming and lexical decision performance. For example, Arciuli and Cupples (2006) found that skilled adult readers produce significantly more errors in response to atypically stressed words than in response to typically stressed words. Further, Mundy and Carroll (2013) investigated the effects of spelling-stress regularity on the lexical decision performance of skilled adult readers and adults with developmental dyslexia. They used words in which the orthographic structure of the final syllable was a reliable indicator of lexical stress assignment (e.g., *sham-POO*), as well as words in which the orthographic structure of the final syllable was an unreliable indicator of lexical stress assignment (e.g., *COM-pass*). They found that participants in both reading groups were faster and more accurate in making lexical decision responses to words in which the orthographic structure of the final syllable was a reliable indicator of lexical stress assignment compared to words in which orthographic structure was an unreliable indicator of lexical stress assignment. Analogous findings have also been reported in Spanish (Gutiérrez-Palma & Palma-Reyes, 2008) and Greek (Protopapas, Gerakaki, & Alexandri, 2006). These findings are also supported by neuroimaging evidence that shows that violations of the stress pattern of spoken words elicits a neural response known as the mismatched negativity in the fronto-central electrode sites (Honbolygó, Csépe, & Ragó, 2004). These data suggest that the mismatched negativity component can be used to investigate syllabic stress patterns and, more specifically, spelling-stress regularity.

The aforementioned studies illustrate that a variety of experimental tasks can be influenced by a word fragment prime in which the stress either matches or mismatches the syllabic stress of the target word. Nevertheless, it is still unclear if simply reading aloud can be affected by a congruent or incongruent rhythmic beat, and whether the effect would be significant for familiar words that are likely read lexically, and for pseudohomophones (PHs; (letter strings that sound like actual words when read phonetically but are spelled differently; e.g., “praktis” is a PH for “practice”) that must be read phonetically. In the upcoming chapters, the experiments will provide an examination of the reading aloud task, as well as the interaction of processing between musical and speech rhythm by using newly developed stimulus sets and rhythm priming reading paradigms. The behavioural experiments aim to determine *when* in the cognitive chronometry this interaction is occurring, and the neuroimaging experiments aim to determine *where* in the brain is associated with the effect. In order to examine the brain-behavioural relationship, correlation analyses between brain activation and behavioural RT are also conducted for congruent rhythm priming conditions, which are thought to reflect the entrainment of the congruent rhythm prime with the target. Moreover, Chapter 4 will demonstrate the utility of the reading aloud task to patient applications (i.e., 'bench to bedside'), and elucidate how these tasks may be used to localize function in neurological conditions such as Parkinson's disease and temporal lobe epilepsy (TLE). The results provide a novel set of findings about this connection, and are consistent with the idea that musical rhythm can affect speech production and that these processes share at least partly overlapping brain regions.

CHAPTER 2

AN EXAMINATION OF THE EFFECTS OF RHYTHM ON READING ALOUD

Portions of this chapter have been previously published:

Gould, L., McKibben, T., Ekstrand, C., Lorentz, E., & Borowsky, B. (2016). The Beat Goes on: The Effect of Rhythm on Reading Aloud. *Language, Cognition, and Neuroscience, 31*(2), 236-250, doi: 10.1080/23273798.2015.1089360

As described in Chapter 1, previous research has shown that rhythm processing can influence various parts of speech, including speech segmentation (Endress & Hauser, 2010; Lee & Todd, 2004), phonological development (Abrams, Nicol, Zecker, & Kraus, 2009; Goswami, 2002), language acquisition (Jusczyk et al., 1999), spoken word recognition (Cutler, 1994; Cutler & Norris, 1988), vocabulary development (Newman, Bernstein Ratner, Jusczyk, Jusczyk, & Dow, 2006; Walley, 1993), reading development (Metsala & Walley, 1998), speech comprehension (Gordon, Magne, & Large, 2009), and phonological processing (Cason & Schön, 2012). Importantly, it has also been shown that speech processing can be enhanced by the temporal expectations generated by rhythmic primes, and more specifically, that a rhythmic prime matched to the prosodic features of speech can enhance auditory phonological processing of spoken French words (Cason & Schön, 2012). Moreover, it has been shown that manipulations in temporal alignment between musical and speech rhythm modulates brain activity (Gordon, Magne, & Large, 2009). Thus, the aim of Experiment 1 was to extend this research by investigating whether reading aloud of individual words is affected by the presentation of a rhythmic prime that was either congruent or incongruent with the syllabic stress of the target letter string. These results would provide further evidence for a connection between rhythm and reading processes, and would have important implications for connecting models of visual word recognition and basic reading processes with models of rhythm processing. Such research may also reveal potential remedial applications in certain patient populations, as rhythm-based therapy techniques have been shown to be effective for treating speech deficits in patients with Parkinson's disease (Liotti et al., 2003; Ramig, Fox, & Sapir, 2004, 2007; Ramig, Sapir, Fox, & Countryman, 2001; Sackley et al., 2014; Sapir, Ramig, & Fox, 2011; see Fujii & Wan, 2014 for review), stuttering (Toyomura, Fujii, & Kuriki, 2011), aphasia (Stahl et al., 2011;

Stahl, Henseler, Turner, Geyer, & Kotz, 2013), as well as the potential remediation of dyslexia (e.g., Goswami, 2011).

Experiment 1

Experiment 1 included real words that were selected to have stress on the first or second syllable, as well as the corresponding PHs, which allowed us to examine the effect of lexical versus sublexical reading in a tightly controlled manner (i.e., within items as well as within participants). We predicted that a rhythmic prime sequence would induce expectations about the position of the syllabic stress in the upcoming word and, thus, affect reading aloud. Previous research has shown that individuals expect events to occur more often 'on-beat' than 'off' and that we make predictions about how rhythmic patterns will continue on the basis of what has come before (Grahn, 2012). Specifically, a target word or PH whose syllable stress conforms to the temporal structure of the rhythm prime ('congruent'; e.g., a prime with stress on the first tone would be congruent with a word like 'practice') and, thus, to the listeners' temporal expectations, would facilitate naming RT compared to when a target word does not conform to the temporal structure of the prime ('incongruent'; e.g., a prime with the stress on the first tone would be incongruent with a word like 'police'). Accordingly, naming RT should be faster for words compared to PHs and, specifically, RT should be faster for the words and PHs whose syllable stress is congruent with the stressed element of the rhythmic prime compared to words and PHs whose syllable stress is incongruent. Further, there should be a stronger effect on sublexical processing than lexical processing (i.e., enhanced priming effects for PHs compared to words), as Oberhuber et al. (2013) demonstrated that a well-known structure involved in processing rhythm (the anterior putamen; see Grahn, 2009 for review) is significantly more active during sublexical processing.

2.1 Materials and Methods

2.1.1 Participants

Twenty-four undergraduate students (7 male, 1 left-handed; 17 female, all right-handed; M_{age} = 20.2 years of age) from the University of Saskatchewan recruited through the Department of Psychology participant pool participated for extra credit in their introductory psychology course. All reported normal or corrected-to-normal vision, and spoke English as their first language. The participants gave written informed consent to participate in the study and all testing procedures were approved by the University of Saskatchewan Research Ethics Board and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and its later amendments.

2.1.2 Stimuli

Experimental trials consisted of an auditory binary prime sequence followed by a written disyllabic word or PH. Auditory prime sequences were created in Audacity 2.0.6 for Mac OS X (http://audacity.sourceforge.net). Volume intensity was manipulated as it has been shown that sound intensity is one of the most dominant prosodic cues for word stress (Lieberman, 1960; Morton & Jassem, 1965; Kochanski & Orphanidou, 2008), and volume has been shown to strongly establish a beat (Grahn & Rowe, 2009). The sine tone primes consisted of weak tones (i.e., quieter in volume) and strong tones (i.e., louder in volume), and each tone sequence had a duration of 150 ms with a 50 ms gap between the strong-weak/weak-strong tone sequence (see Figure 1). Thus, the sine tone primes consisted of either a weak-strong structure (i.e., soft-loud volume) or a strong-weak structure (i.e., loud-soft volume). In both cases, the two-tone prime lasted 350 ms and repeated with a 100 ms silent gap in between, yielding a prime-target stimulus onset asynchrony (SOA) of 800 ms. Treating each tone as a beat, there was one beat every 175 ms in each 350 ms prime (i.e., a temporal frequency of 5.7 Hz, which falls within the theta band (4 – 8 Hz) of temporal frequencies, which has been argued as an important temporal frequency for tracking syllabic coding in reading (Goswami, 2011; see also Giraud & Poeppel, 2012 for description of phonemic sampling within the low gamma bandwidth [25-35 Hz]). The strong tones had a frequency of 225 Hz at an intensity of 70 dB, and weak tones had a frequency of 225 Hz at an intensity of 60 dB, as measured by a Scosche SPL1000 sound level meter. Sixty disyllabic words, 30 with first syllable stressed, 30 with second syllable stressed, were selected and matched on length ($t(29) = .14$, $p = .89$), word frequency ($t(29) = .71$, $p = .48$), orthographic neighborhood ($t(29) = 1.23$, $p = .23$), phonological neighborhood ($t(29) = 1.47$, $p = .15$), bigram sum ($t(29) = .65$, $p = .52$), bigram mean ($t(29) = .55$, $p = .59$), and number of phonemes ($t(29) = .47$, $p = .64$). All stimuli were presented in all conditions of interest and, thus, any differences in responding were due to the manipulation of interest and no any pre-existing differences between the stimuli. The PHs corresponding to these words were constructed by spelling the words phonetically (see Appendix A).

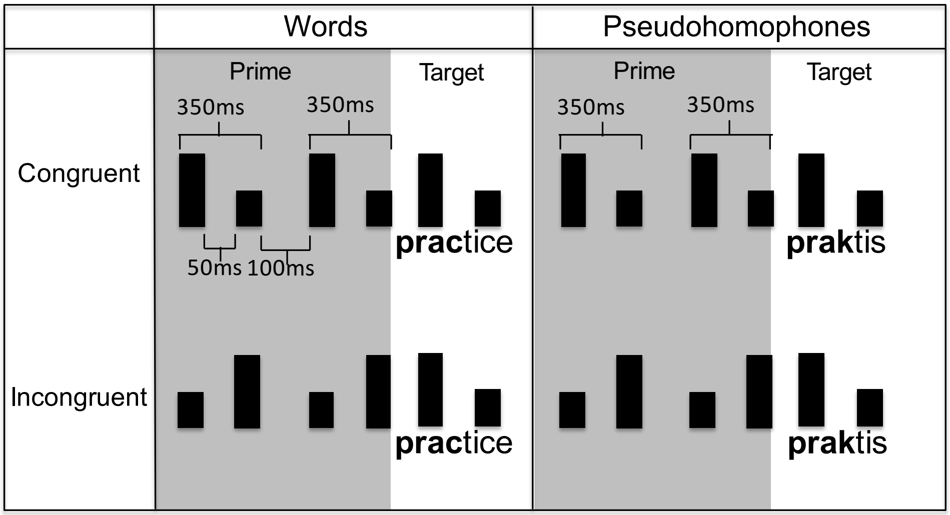

Figure 1. Illustration of the congruency manipulation between syllable stress and rhythmic stress in which the volume intensity of the tones (rhythmic stress) either matched (congruent condition) or mismatched (incongruent condition) the syllabic stress of the target word.

2.1.3 Apparatus and Procedure

Stimuli were presented on a 14.5-inch (35.56-cm) Compaq 7500 color monitor. E-prime software (Version 2.0; Psychology Software Tools) was used to control the presentation of the stimuli, as well as for data collection. Vocal responses made by the participants were collected via an Audio-Technica ATR 1200 microphone interfaced with the voice key in the E-prime serial response box and RTs were measured to the nearest millisecond. Participants sat in front of a computer screen and wore Audio-Technica ATH-M30x headphones to listen to the auditory prime stimuli presented through the E-prime software. Participants were told that they would hear a rhythm and then a see word or PH on the screen, which they were to name aloud as quickly and accurately as possible. They were told that “PHs are letter strings that are spelled in a way that it does not look like a word, but when sounded out should sound like a real word”. If the participants placed the stress on the incorrect syllable (e.g., *AB*-uv rather than *a-BUV*), or the resulting pronunciation did not sound like the intended word, the trial was considered an error. The words and PHs were presented in separate blocks, and each block contained 120 trials, consisting of 30 first syllable stressed words/PHs and 30 second syllable stressed words/PHs in the congruent condition, as well as 30 first syllable stressed words/PHs and 30 second syllable stressed words/PHs in the incongruent condition. The order of the blocks was counterbalanced across participants. For each trial, the target letter string was presented on the computer screen in lower case font until the voice-key logged the participant’s RT. The presentation of letter strings was randomly selected across the trials. In each trial a letter string followed the prime and the strong-weak or weak-strong prime sequence was randomly selected. The letter strings could either match or mismatch the metrical structure of the prime (a strong-weak word is considered to match a strong-weak prime, while a weak-strong word is considered to mismatch it). Specifically, participants received both a matched and a mismatched prime for each target (i.e., each target was presented twice).

2.2 Results

The naming onset RT that it took participants to correctly name the word or PH was measured in milliseconds (ms) for each trial, and the mean error rate of each condition was also computed for each participant. Incorrect and spoiled trials (e.g., trials in which participants failed to trigger the microphone with their first vocalization) were removed before analyses were conducted on mean RTs and error rates (9.1% of word trials, 12.6% for PH trials).

Mean RT ANOVA

Correct mean RT data were analyzed using a 2 (Congruency [congruent, incongruent]) x 2 (Stimulus Type [word, PH]) x 2 (Syllable Stress [first, second]) repeated measures general linear model (GLM) ANOVA. The mean RT was 505.10 ms for first syllable stressed words and 506.87 ms for second syllable stressed words in the congruent condition, 522.79 ms for first syllable stressed words and 517.93 ms for second syllable stressed words in the incongruent condition, 715.33 ms for first syllable stressed PHs and 757.31 ms for second syllable stressed PHs in the congruent condition, and 769.23 ms for first syllable stressed PHs and 835.32 ms for second syllable stressed PHs in the incongruent condition (Figure 2). There was a significant main effect of Congruency, $F(1, 23) = 10.94$, $MSE = 7079.37$, $p = .003$, $\eta_p^2 = .32$, whereby items in the congruent conditions ($M = 621.15$ ms) were named faster than items in the incongruent conditions ($M = 661.32$). There was also a significant main effect of Syllable Stress, $F(1, 23) = 8.95$, $MSE = 3693.26$, $p = .007$, $\eta_p^2 = .28$, whereby items with first syllable stress ($M = 628.11$ ms) were named faster than items with second syllable stress ($M = 654.36$), which likely reflects the more common trochaic (first syllable stress) rather than iambic (second syllable stress) prosodic template in English (Cutler & Carter, 1987; Schreuder & Baayen, 1994). As well, we found a significant main effect of Stimulus Type, $F(1, 23) = 65.78$, $MSE = 47878.69$, $p < .001$, $\eta_p^2 = .74$, indicating that words ($M = 513.17$ ms) were named faster than PHs ($M = 769.30$ ms). The Congruency x Stimulus Type interaction was also significant, $F(1, 23) = 5.15$, $MSE = 6199.98$, $p = .03$, $\eta_p^2 = .18$, indicating that the PHs show a larger effect of Congruency priming than words. There was also a significant Syllable Stress x Stimulus Type interaction, $F(1, 23) = 9.40$, $MSE = 3942.59$, $p = .005$, $\eta_p^2 = .29$, indicating that PHs showed a larger effect of Syllable Stress than words, which may reflect PHs' slower RTs and greater likelihood to show significant differences. There was no significant Congruency x Syllable Stress interaction, $F(1, 23) = .58$, $MSE = 1585.38$, $p = .46$, $\eta_p^2 = .03$, nor was there a significant Congruency x Syllable Stress x Stimulus Type interaction, $F(1, 23) = 1.79$, $MSE = 1580.29$, $p = .19$, $\eta_p^2 = .07$. The 95% confidence interval (CI; Loftus & Masson, 1994) was ± 32.58 ms, which demonstrates that participants named PHs faster when the target's syllable stress was congruent with the temporal structure of the rhythmic prime (i.e., a prime with stress on the first tone preceding the word 'praktis') compared to when the target's syllable stress was incongruent (Figure 2).[1]

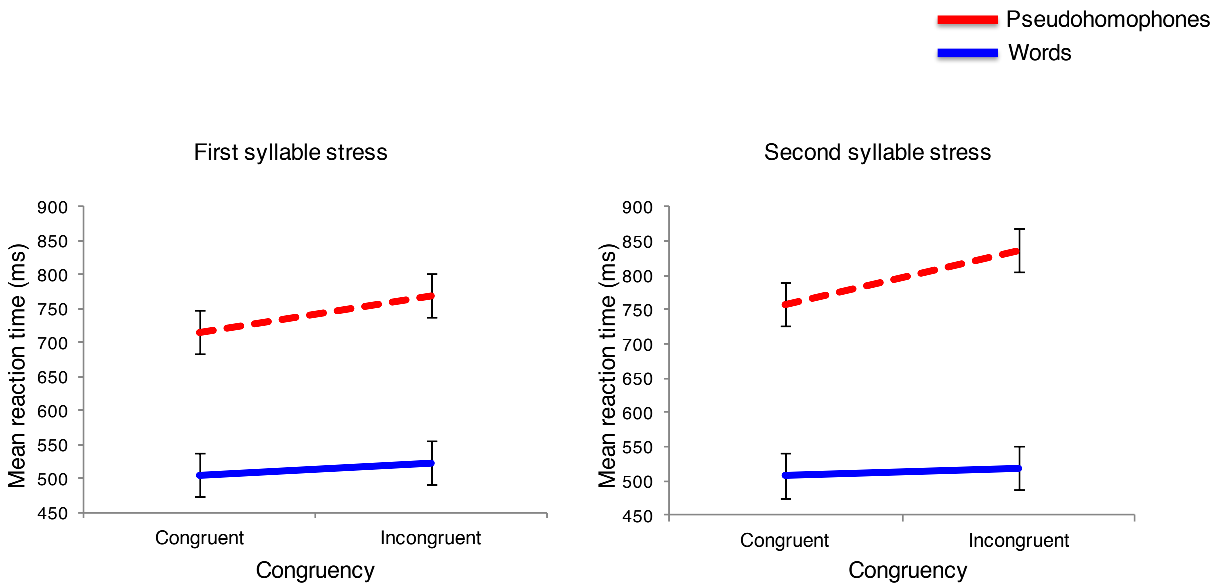

Figure 2: Mean reaction time (RT) representing the onset time taken to correctly name first syllable stressed words and pseudohomophones (PHs), as well as second syllable stressed words and PHs, as a function of Congruency and Stimulus Type. The 95% confidence interval (CI; Loftus & Masson, 1994) for word and PH naming RT was ± 32.58 ms. The means of two

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[1] We also conducted all the same analyses by-items. The by-item analyses were consistent with the by-subject analyses (i.e., each main effect and interaction in the by-items analyses led to the same conclusion as the by-subjects analyses), and thus strongly support the notion that a rhythmic prime affects reading aloud, particularly while reading sublexically.

conditions are considered statistically different if the mean of one condition is not captured by the 95% CI of the other condition. The 95% CI demonstrates that participants named PHs faster when the target's syllable stress was congruent with the temporal structure of the rhythmic prime (i.e., a prime with stress on the first tone preceding the word 'praktis') compared to when the target's syllable stress was incongruent.

Error Rates

The accuracy of participants' responses was computed by determining the percentage of errors in each of the word and PH conditions. However, the analyses revealed that in the PH conditions three out of four conditions were significantly skewed, and in the word conditions two cells have means of zero with zero variance. As such, the mean error rate values are reported, but we do not conduct an ANOVA on these data. The mean error rate was .89% for first syllable stressed words and 0% for second syllable stressed words in the congruent condition, .28% for first syllable stressed words and 0% for 'second syllable stressed words in the incongruent condition, 6.39% for first syllable stressed PHs and 3.64% for second syllable stressed PHs in the congruent condition, and 6.89% for first syllable stressed PHs and 2.80% for second syllable stressed PHs in the incongruent condition.

2.3 Discussion

Experiment 1 aimed to determine whether speech production of individual words in a reading aloud task would be affected by a prior presentation of a rhythmic prime, which has important implications for further developing models of basic reading processes. The results demonstrated that a target word or PH whose syllable stress conforms to the temporal structure of the rhythm prime, and thus to the listener's temporal expectations, resulted in a faster naming RT compared to when a target word or PH does not conform to the temporal structure of the prime. That is, RTs were faster for letter strings whose syllable stress was congruent with the stressed element of the rhythmic prime compared to letter strings whose syllable stress was incongruent. Lastly, there was also a larger priming effect for PHs compared to words, indicating that rhythm has a stronger effect on sublexical processing than it does on lexical processing. Overall, the results of both the by-subjects and by-items analyses supported the hypotheses and suggest that a rhythmic prime matched to the syllabic stress of a letter string can enhance reading aloud. Furthermore, the interaction between congruency and stimulus type confirmed the expected stronger effect of rhythm on sublexical processing (see Figure 2).

Underlying Cognitive Systems Involving Rhythm and Speech during Reading

Interpreting these results in terms of underlying cognitive systems can be aided through applying the Additive Factors Method (Sternberg, 1969, 1998; Gould et al., 2012). The additive factors method posits that if two variables are affecting a temporally common cognitive system, this would result in an overadditive interaction pattern on RT. The results of Experiment 1 revealed an ideal example of an overadditive interaction between Stimulus Type and Congruency, which can be interpreted as these two factors influencing at least one common system in time (Figure 3). Through the use of real words and PHs, we were able to control for reading strategy, as PHs must be phonetically decoded, whereas real words would typically be read via lexical access. In this cognitive model of reading, stimulus type is assumed to have its effect early in the cognitive architecture, specifically at the inputs to the grapheme-to-phoneme conversion system and the orthographic lexical system, as correct identification of PHs will rely more on phonetic decoding, whereas word identification would rely more on orthographic lexical access. The results illustrate that sublexical reading was more affected by a rhythmic prime than lexical reading, which was shown in the form of an interaction. Specifically, there was a larger difference between the congruent and incongruent conditions for the PHs (65.96 ms difference), than for the words (14.38 ms difference), which represent significant differences when assessed by the 95% CIs. This interpretation of these data provides support for the conclusion that rhythm and speech production in a reading task are interacting at a common cognitive system, specifically the grapheme-to-phoneme conversion system (i.e., phonetic decoding).

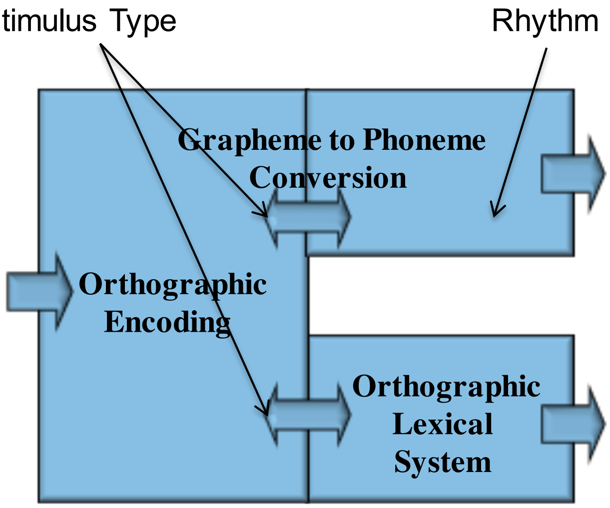

Figure 3: A subset of relevant cognitive systems based on our ongoing development of a ventral-lexical, dorsal-sublexical model of basic reading processes (e.g., Borowsky et al., 2013;

Cummine et al., 2013; Gould et al., 2012). The results of the present experiment support the idea of a connection between the rhythm processing system and the reading system via grapheme-to-phoneme conversion.

Overall, the results of Experiment 1 support the idea of a connection between the rhythm processing system and models of reading via grapheme-to-phoneme conversion, as shown in Figure 3. This figure is based on our ongoing development of a ventral-lexical, dorsal-sublexical model of basic reading processes (e.g., Borowsky, Esopenko, Gould, Kuhlmann, Sarty, & Cummine, 2013; Cummine et al., 2013; Gould, Cummine, & Borowsky, 2012; see also Hickok & Poeppel, 2007). Experiment 1 pointed clearly to 'when' in the stages of reading processes that rhythm processing may be interacting. An examination of the underlying neural substrates associated with the processing of rhythm and speech production, and specifically, with the differential effects for congruent and incongruent stimuli, will be addressed in Experiment 2a.

2.4 Conclusions

The results from Experiment 1 revealed that naming RTs were faster when preceded by a rhythmic prime that was congruent with the syllable stress of the target word or PH compared to when the rhythmic prime was incongruent. Furthermore, the rhythmic primes had a larger effect on PHs, which suggests that rhythm has a larger influence on stimuli that must be phonetically decoded than stimuli that can be read lexically. Taken together, the results suggest that priming with a structured and anticipatory repetitive rhythm matched to speech rhythm provides cues that may facilitate reading aloud. This paradigm may also be useful for optimizing the role of rhythm in speech and language rehabilitation, whereby rhythmic priming could enhance reading and speech production in various populations.

Experiment 2a

Portions of this experiment have been submitted for publication, and redundant information has been removed: Gould, L., Mickleborough, M., Ekstrand, C., Lorentz, E., & Borowsky, R. (2016). Examining the Neuroanatomical and the Behavioural Basis of the Effect of Rhythm on Reading Aloud. *Language, Cognition, and Neuroscience.*

Experiment 2a used fMRI to examine the brain regions associated with the effect of congruency between rhythmic stress and syllabic stress on reading aloud (i.e., Experiment 1). Specifically, the aim of this study involved elucidating the neural mechanisms underlying the effect of rhythmic priming on reading aloud, which has important implications for revealing the underlying neurobiological mechanisms of reading processes. The results would be especially useful in delineating the commonalities and cross-boundaries between rhythm and reading in the brain. As Gould et al. (2016; Experiment 1) pointed clearly to 'when' in the stages of processing rhythm and reading processes may be taking place, the obvious next step is to explore 'where' in the brain the rhythm priming effect may be occurring using functional neuroimaging.

Given that previous neuroimaging studies have implicated the IFG and superior temporal gyrus (STG), SMA, basal ganglia, cerebellum, anterior insula, and thalamus for processing both musical and speech rhythm (for speech: Aleman et al., 2005; Geiser et al., 2008; Klein et al., 2011; Kotz & Schwatze, 2010; for music: Chen et al., 2008; Grahn & Brett, 2007; Grahn & Rowe, 2009), we predicted that these regions should be activated during the reading tasks, as it involved both speech and rhythmic stimuli. Furthermore, given that the behavioural findings in Experiment 1 (Gould at al., 2016) showed that PHs displayed a greater effect of congruency compared to words, it was predicted that PHs preceded by a rhythmic prime that was either congruent or incongruent with its syllabic stress would activate separate brain regions, and particularly in the putamen, which has been shown to be involved in sublexical processing (Oberhuber et al., 2012), beat processing (Grahn & Rowe, 2009), and predicting upcoming events leading to optimized speech comprehension (Rothermich & Kotz, 2013).

2.5 Materials and Methods

2.5.1 Participants

Sixteen healthy participants (11 females, all right-handed; 5 males, all right-handed; M_{age} = 26.7 years of age) with normal or corrected-to-normal vision who spoke fluent English participated in the experiment. The participants' consent was obtained according to the Declaration of Helsinki (2008) and the experiment was performed in compliance with the relevant laws and institutional guidelines, and was approved by the University of Saskatchewan Research Ethics Board.

2.5.2 Stimuli

The same stimuli were used as described in Experiment 1, with the exceptions that target stimuli were presented at the fixed MRI-synchronized rate of one per TR, and the stimuli were presented using EPrime software (Psychology Software Tools, Inc., http://www.pstnet.com) through goggles by Cinemavision, which the participants wore in the MRI.

2.5.3 Behavioural Analysis

Vocal responses were recorded at 96KHz, 24bit, through the CinemaVision system using an Olympus LS11 digital recorder. These recordings were analyzed using PRAAT software (Boersma & Weenink, 2009), and the waveforms and broadband spectrograms were used to localize vocalization onset RT. Given that we used a sparse-sampling (gap paradigm) fMRI method that allows the participant to respond during a gap in image acquisition (e.g., Borowsky et al., 2006; Cummine, Stockdale-Winder, Crossley, & Borowsky, 2009; Cummine et al., 2010; Esopenko, Borowsky, Cummine, & Sarty, 2008), the stimulus onset was synchronized with the last gradient sound before the gap. This provided an acoustic marker for the onset on the recording while the gap allowed for a clear recording of the participant's vocal response.

2.5.4 Protocol

All imaging was conducted using a 3 Tesla Siemens Skyra scanner. Whole-brain anatomical scans were acquired using high resolution axial magnetization prepared rapid acquisition gradient echo (MP RAGE) sequence, consisting of 192 T1-weighted echo-planar images (EPI) of 1-mm thickness (no gap) with an in-plane resolution of 1 x 1 mm (field of view 256; TR = 1900 ms; TE = 2.08 ms).

For the functional tasks, T2*-weighted functional single shot gradient-echo echo-planar imaging (EPI) scans were acquired using an interleaved ascending EPI sequence, consisting of 65 volumes of 25 axial slices of 4-mm thickness (1-mm gap) with an in-plane resolution of 1-mm X 1-mm (field of view = 250) using a flip angle of 90°. In order to obtain verbal behavioural data from the MRI, we used a sparse-sampling (gap paradigm) fMRI method that allows the participant to respond during a gap in image acquisition (TR = 3300 ms, with a 1650 ms gap of no image acquisition, TE = 30 ms; e.g., Borowsky et al., 2006; Cummine, Stockdale-Winder, Crossley, & Borowsky, 2009; Cummine et al., 2010; Esopenko, Borowsky, Cummine, & Sarty, 2008). A within-subjects design was used, and participants responded vocally during the regular, periodic gap in the image acquisition that followed the offset of each volume of image acquisition, which allowed the participants to respond with no noise interference from the MRI. That is, a stimulus was presented at the offset of an image acquisition for 1650ms, providing a silent gap for participants to name aloud the stimulus. The first two volumes of each functional scan were discarded to allow for scanner equilibration.

2.5.5 fMRI Analysis

All preprocessing and statistical analyses for functional images were performed using Brain Voyager QX Version 2.6.1 (www.brainvoyager.com). Functional images were preprocessed and corrected for slice scan time acquisition (cubic spline interpolation), 3D motion correction (trilinear/sync interpolation), and temporal filtering with a high-pass (GLM Fourier) filter to remove frequencies less than two cycles/time course. The functional data were assessed for head motion and/or magnet artifacts by viewing cine-loop animation and examining motion detection parameter plots following the 3D motion correction. Functional volumes were then individually co-registered to their respective anatomical brain images before being transformed into Talairach space (Talaraich & Tournoux, 1988). The first five image volumes were used to achieve steady state of image contrast and were discarded prior to analysis. Blocked analyses were conducted in order to compared words versus PHs, and event-related analyses were conducted to examine the differences between congruent and incongruent rhythm and syllabic stress conditions for both the words and PHs separately.

2.6 fMRI Results

Rhythm Prime Manipulation Check

The regions that were activated for the rhythm prime manipulation check significant at a statistical threshold of $t(15) = 3.50$, $p < 0.005$ are listed in Table 1. The results demonstrated significant bilateral anterior and middle putamen activation (see Figure 4; Talairach coordinates, x, y, z: -20, 5, 11/20, 5, 11), as well as significant activation in the brainstem (2, -24, -37), bilateral cerebellum (-28, -44, -37/ 28, -43, -37), bilateral STG (-57, -26, 3/57, -26, 3), bilateral insula (-48, 7, 3/48, 7, 3), bilateral precentral gyri (-37, -16, 31/37, -16, 31), left middle frontal gyrus (-33, 38, 31), bilateral cingulate gyri (-6, 10, 39/6, 10, 39), and bilateral SMA (-6, -8, 60/6, -8, 60).

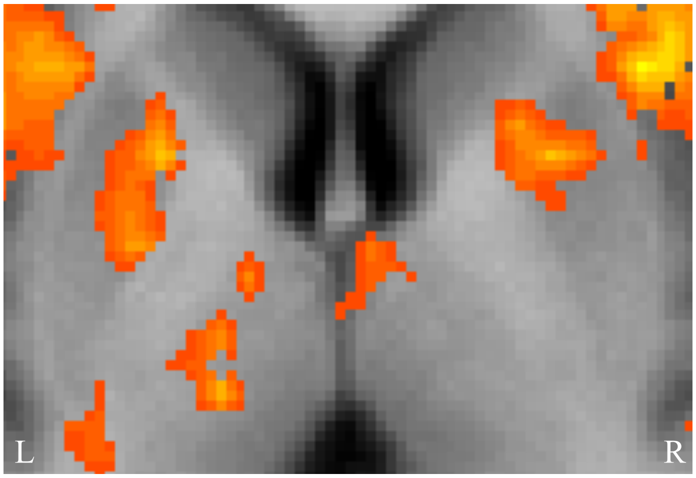

Figure 4: Activation in Bilateral Putamen for Rhythm Prime Alone

Table 1: Regions of Activation for Rhythm Prime Alone

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Rhythm Prime Manipulation Check				
Brainstem		2	-24	-37
Cerebellum	L	-28	-44	-37
	R	28	-43	-37
Superior Temporal Gyrus	L	-57	-23	3
	R	57	-23	3
Insula	L	-48	7	3
Putamen	L	-20	5	11
	R	20	5	11
	R	48	7	3
Precentral Gyrus	L	-37	-16	31
	R	37	-16	31
Middle Frontal Gyrus	L	-33	38	31
Cingulate Gyrus	L	-6	10	39
	R	6	10	39
Supplementary Motor Area	L	-6	-8	60
	R	6	-8	60

Unique Regions of Activation for Word or PH Reading

The regions that were uniquely activated for PHs greater than words are displayed in Figure 5 and listed in Table 2, $t(15) = 2.50$, $p < 0.01$. As predicted, there was significant activation in the left putamen (-16, 4, 11/ -20, 6, 13/-21, -8, 15; Figure 6). There was also activation in the right superior occipital gyrus (30, -71, 28), bilateral precuneus (-24, -71, 22/ 24, -71, 22), left precentral gyrus (-41, 3, 32), midbrain (-2, -22, -2), and right cingulate gyrus (3, 28, 32), predominantly in the dorsal visual processing stream for PHs greater than words is consistent with Borowsky et al. (2006). There were no regions of activation greater for words compared to PHs.

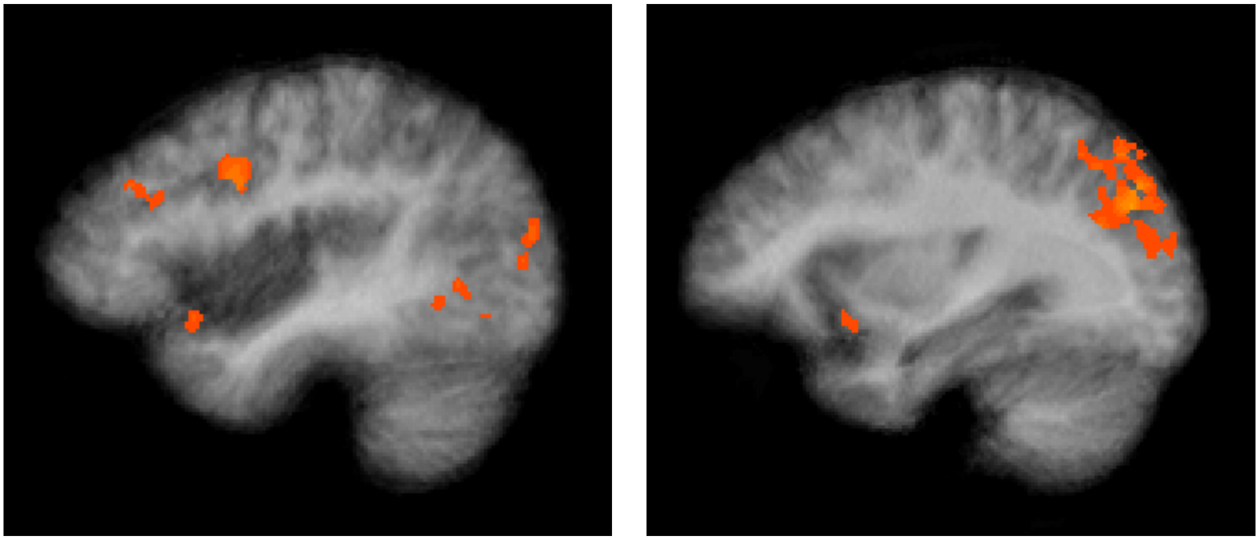

Figure 5: Regions uniquely activated for pseudohomophones (PHs) greater than words, including the left putamen, right superior occipital gyrus, bilateral precuneus, left precentral gyrus, and and right cingulate gyrus.

Table 2: Regions of Activation Greater for Pseudohomophones than Words

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
PHs > Words				
Midbrain		-2	-22	-2
Putamen	L	-16	4	11
	L	-20	-6	13

	L	-21	-8	15
Superior Occipital Gyrus	R	30	-71	28
Precuneus	L	-24	-71	22
	R	24	-71	22
Precentral Gyrus	L	-41	3	32
Cingulate Gyrus	R	3	28	32

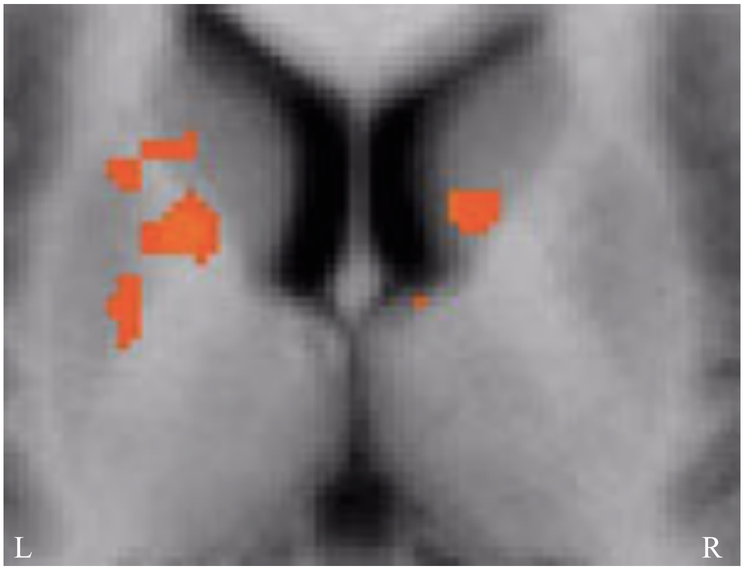

Figure 6: Activation in the Left Putamen for Pseudohomophones (PHs) Greater than Words.

Shared Regions of Activation for Word and PH Reading

The regions of shared activation for reading words and PHs are listed in Table 3, and included the right cerebellum (20, -58, -20), bilateral occipital lobe (-23, -82, -11/ 26, -82, -11), bilateral middle occipital gyrus (-30, -92, 6/ 30, -92, 6), left thalamus (-11, -16, 8), left IFG (pars orbitalis; -41, 6, 8/ -40, 3, 28), left anterior insula (-32, 19, 8), bilateral putamen (-20, 4, 8/ 20, 4, 8), bilateral precentral gyri (-51, -10, 28/ 44, -14, 34), right cingulate gyrus (6, 10, 39), and bilateral SMA (-3, -4, 59/ 5, -4, 59) at a statistical threshold of $t(15) = 3.50$, $p < 0.01$. The significant putamen activation is shown in Figure 7.

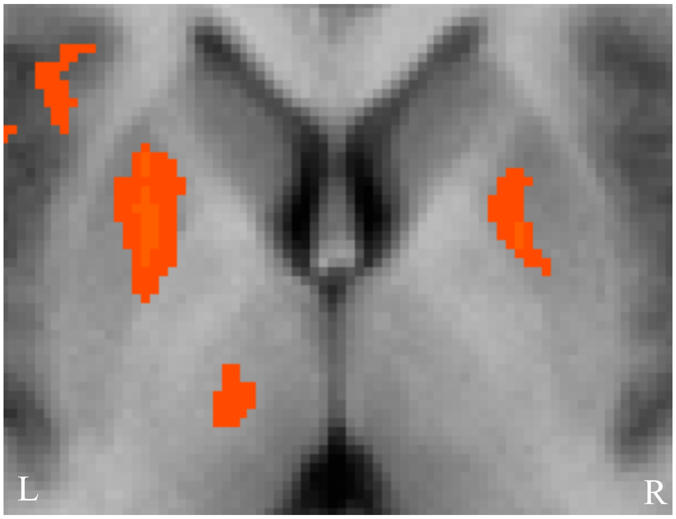

Figure 7: Activation in bilateral putamen for shared pseudohomophones (PHs) and words.

Table 3: Regions of Activation Shared Between Words and Pseudohomophones

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Shared Words and PHs				
Cerebellum	R	20	-58	-20
Occipital lobe	L	-23	-82	-11
	R	26	-82	-11
Middle Occipital Gyrus	L	-30	-92	6
	R	30	-92	6
Thalamus	L	-11	-16	8
Inferior Frontal Gyrus	L	-41	6	8
	L	-40	3	28
Insula	L	-32	19	8
Putamen	L	-20	4	8
	R	20	4	8
Precentral Gyrus	L	-51	-10	28
	R	44	-14	34
Cingulate Gyrus	R	6	10	39
Supplementary Motor Area	L	-3	-4	59

	R	5	-4	59

Unique Regions of Activation for Congruent or Incongruent Words and Rhythm

The regions of activation greater for incongruent versus congruent word rhythmic conditions are listed in Table 4, and included the brainstem (0, -22, -33), bilateral cerebellum (-35, -62, -33/ 18, -62, -23), right middle temporal gyrus (MTG; 38, -17, -12), left cuneus (-4, -69, 7), right lateral occipital complex (LOC; 50, -67, 10), left premotor cortex (-33, 15, 53), right STG (28, 49, 28), right supramarginal gyrus (34, -46, 34), left precentral gyrus (-36, -19, 42), right postcentral gyrus (37, -22, 42), and the right cingulate gyrus (9, -19, 40) with a statistical threshold set at $t(15) = 2.50$, $p < 0.01$. There were no regions of activation greater for congruent words compared to incongruent words.

Table 4: Regions of Activation Greater for Incongruent than Congruent Word Conditions

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Incongruent > Congruent Words				
Brainstem		0	-22	-33
Cerebellum	L	-35	-62	-33
	R	18	-62	-23
Middle Temporal Gyrus	R	38	-17	-12
Cuneus	L	-4	-69	7
Lateral Occipital Complex	R	50	-67	10
Premotor Cortex	L	-33	15	53
Superior Frontal Gyrus	R	28	49	28
Supramarginal Gyrus	R	34	-46	34
Precentral Gyrus	L	-36	-19	42
Postcentral Gyrus	R	37	-22	42
Cingulate Gyrus	R	9	-19	40

Unique Regions of Activation for Congruent versus Incongruent PHs and Rhythm

The regions of activation greater for incongruent versus congruent PH rhythmic conditions are listed in Table 5, and included the left cerebellum (-38, -36, -36/ -19, -74, -27), right LOC (41, -74, -27), right fusiform gyrus (18, -55, -5), right parahippocampal gyrus (25, -39, -5), right lentiform nucleus (10, 2, -2), right IFG (pars orbitalis; 45, 32, -3), left caudate (-9, 8, 8), left medial frontal gyrus (-7, 45, 29), left frontal eye fields (-23, 27, 35) and right precental gyrus (48, -27, 45) with a statistical threshold set at $t(15) = 2.50$, $p < 0.01$. Regions of activation that were greater for congruent versus incongruent PH conditions included the right cerebellum [13, -62, -16], and the right anterior putamen [19, 10, 5; see Figure 8].

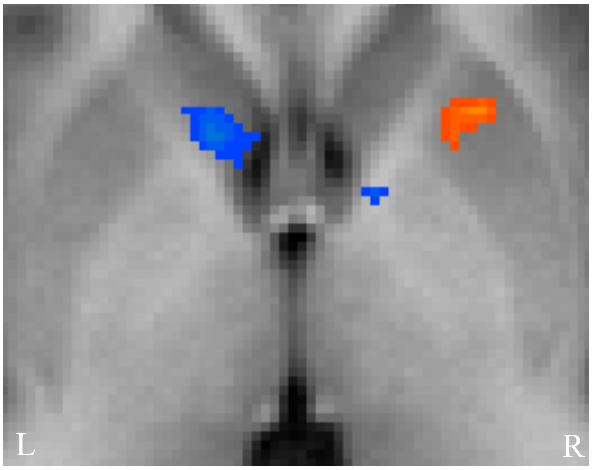

Figure 8: Activation in the right anterior putamen greater for congruent versus incongruent pseudohomophones (PHs) and rhythm conditions.

Table 5: Regions of Activation Greater for Incongruent Versus Congruent PH Condition

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Incongruent > Congruent PHs				
Cerebellum	L	-38	-36	-36
	L	-19	-74	-27
Lateral Occipital Cortex	R	41	-74	-14
Fusiform Gyrus	R	18	-55	-5
Parahippocampal Gyrus	R	25	-39	-5
Lentiform Nucleus	R	10	2	-2
Inferior Frontal Gyrus	R	45	32	-3
Caudate	L	-9	8	8
Medial Frontal Gyrus	L	-7	45	29
Frontal Eye Fields	L	-23	27	35
Postcentral Gyrus	R	48	-27	45

Shared Regions of Activation for Congruent and Incongruent Words

The regions of shared activation for congruent and incongruent words are listed in Table 6, and included the right cerebellum (18, -56, -19), bilateral inferior occipital gyrus (-15, -90, -6/ 16, -86, -6), right middle occipital gyrus (30, -86, 4), bilateral transverse temporal area (-57, -31, 8/ 59, -31, 8), left superior temporal gyrus (STG; -48, -13, 8/ 48, -13, 8), right thalamus (-11, -18, 8), left insula (-36, 11, 11), left putamen (-19, 3, 13), left precentral gyrus (-50, -9, 26), bilateral postcentral gyrus (-45, -16, 33/ 45, -14, 33), bilateral cingulate cortex (-4, 5, 41/8, 5, 41), and bilateral SMA (-2, -9, 60/ 2, -9, 60) at a statistical threshold of $t(15) = 3.50$, $p < 0.01$.

Table 6: Regions of Shared Activation for Congruent and Incongruent Words

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Shared Congruent & Incongruent Words				
Cerebellum	R	18	-56	-19
Inferior Occipital Gyrus	L	-15	-90	-6
	R	16	-86	-6
Middle Occipital Gyrus	R	30	-86	4
Transverse Temporal Area	L	-57	-31	8
	R	59	-31	8
Superior Temporal Gyrus	L	-48	-13	8
	R	48	-13	8
Thalamus	R	-11	-18	8
Insula	L	-36	11	11
Putamen	L	-19	3	13
Precentral Gyrus	L	-50	-9	26
Postcentral Gyrus	L	-45	-16	33
	R	45	-14	33
Cingulate Cortex	L	-4	5	41
	R	8	5	41
Supplementary Motor Area	L	-2	-9	60
	R	2	-9	60

Shared Regions of Activation for Congruent and Incongruent PHs

The regions of shared activation for congruent and incongruent PHs are listed in Table 7, and included the right cerebellum (17, -54, -20), bilateral occipital cortex (-15, -86, -10/ 16, -82, -10), bilateral LOC (-29, -89, 5/ 27, -85, 5), left occipitotemporal gyrus (-44, -66, -10), right STG (59, -22, 5), left transverse temporal gyrus (-53, -16, 9), left putamen (-20, 3, 9), bilateral insula (-32, 15, 9/ 30, 21, 10), left IFG (-39, 3, 28), bilateral precentral gyrus (-50, -11, 28/ 46, -13, 35), bilateral superior parietal lobe (-23, -65, 44/ 26, -62, 44), bilateral cingulate cortex (-5, 3, 44/ 8, 3, 44), and bilateral SMA (-2, -9, 61/ 2, 8, 58) at a statistical threshold of $t(15) = 3.50$, $p < 0.01$.

Table 7: Regions of Shared Activation for Congruent and Incongruent PHs

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Shared Congruent & Incongruent PHs				
Cerebellum	R	17	-54	-20
Occipital Cortex	L	-15	-86	-10
	R	16	-82	-10
Lateral Occipital Cortex	L	-29	-89	5
	R	27	-85	5
Occipitotemporal Gyrus	L	-44	-66	-10
Superior Temporal Gyrus	R	59	-22	5
Transverse Temporal Gyrus	L	-53	-16	9
Putamen	L	-20	3	9
Insula	L	-32	15	9
	R	30	21	10
Inferior Frontal Gyrus	L	-39	3	28
Precentral Gyrus	L	-50	-11	28
	R	46	-13	35
Superior Parietal Lobule	L	-23	-65	44
	R	26	-62	44
Cingulate Cortex	L	-5	3	44
	R	8	3	44
Supplementary Motor Area	L	-2	-9	61
	R	2	8	58

2.7 Discussion

Experiment 2a used fMRI to help uncover the underlying brain regions associated with the behavioural effect of rhythm on reading aloud. Analogous to the finding reported by Oberhuber et al. (2013) for pseudowords, the results revealed that the left anterior putamen was activated for PHs, which also require sublexical grapheme-to-phoneme conversion. The finding of greater activation in the anterior putamen is also consistent with prior studies that have associated the anterior putamen with the initiation of unskilled, difficult movements (Okuma & Yanagisawa, 2008; Aramaki et al., 2011), which occurs during sublexical reading of both pseudowords (Oberhuber et al., 2012) and for PHs given that the participant is producing a novel, unskilled movement at the beginning of their pronunciation until the phonological output is recognized. Conversely, as mentioned by Oberhuber et al. an alternative explanation could be that multiple other variables are influencing activity in the putamen such as eye movements, which have been associated with the anterior putamen (Petit et al., 2009; Neggers et al., 2012), and may explain the present findings, given that eye movements should increase when reading novel relative to familiar letter strings. However, the current study found differences in the putamen when comparing congruency, thus controlling for such factors, which is an additional advantage of the present design. Further investigation is required to clarify the different possibilities described above.

In contrast to Oberhuber et al. (2012), the results of the present experiment did not reveal significant activation in the posterior putamen for words compared to PHs. One potential explanation is that since this study used words and PHs (which result in the same phonological output), our subtraction map may have removed any activation for ‘phonological lexical activation’ as both words and PHs would contribute to that representation, and thus our contrast is able to isolate activation for differences in sublexical versus lexical orthography. In the Oberhuber et al. study, it may be the case that the word activation in the posterior putamen is a result of a familiar phonological lexical representation. Our stimuli were matched in all aspects of speech except orthographic lexical representation, thus controlling for many of the differences between lexical and sublexical reading. Furthermore, the PHs allowed for phonetic decoding with phonological access, which has far greater ecological validity than reading pseudowords, as learning to read generally involves mapping novel orthographic letter strings onto familiar phonological lexical representations. The other regions of activation showing greater activation for PHs compared to words (i.e., midbrain, superior occipital gyrus, precuneus, precentral gyrus, and cingulate gyrus) may represent levels of processing beyond orthography, such as grapheme-to-phoneme conversion or phonological retrieval (e.g., Borowsky et al., 2006, 2012).

There was also consistent activation in the cerebellum for the rhythm and reading tasks for both words and PHs. With respect to the rhythm prime manipulation check, the results revealed bilateral cerebellum activation, which is consistent with previous research that implicates the cerebellum with the encoding of time intervals (Irvy & Keele, 1993; Grube et al., 2010ab). There was also activation in the right cerebellum in the shared map for words and PHs, as well as the shared maps for congruent and incongruent words and PHs, which supports the suggestion that the cerebellum is involved in early sequence learning and language processes (Doyon, Penhune, & Ungerleider, 2009). Lastly, greater activation in the cerebellum for incongruent compared to congruent rhythm prime and words/PHs corroborates the finding that the cerebellum is associated with the timing of irregular sound sequences (Teki, Grube, Kumar, & Griffiths, 2011).

Word and Pseudohomophone Processing

The regions of shared activation between words and PHs, including the cerebellum, occipital lobe, middle occipital gyrus, thalamus, IFG, putamen, precentral gyrus, and SMA, are consistent with previous literature that has implicated these regions in language related tasks (see also Price, 2012 for review). As predicted, there was also activation in the bilateral STG given that the tasks involved auditory processing. Lastly, insular cortex activation was found for the shared word and PH processing map, which is consistent with findings that the insula is also associated with auditory processing (Bamiou et al., 2003), and language processing (Borowsky et al., 2006). The finding of greater activation in the left putamen for PHs compared to words supports the idea that the left putamen is involved in increased articulatory demands and complex motor processes involving articulation and fine motor skills (Crosson, 1992; Wing & Miller, 1984). A complementary role for the right putamen in motor control of prosody has also been suggested (Volkmann, Hefter, Lange & Freund, 1992).

The finding that PHs, but not words, elicited unique activation could reflect a typical frequency effect, whereby lower frequency letter strings tend to produce greater activation than higher frequency letter strings in linguistically-relevant regions (e.g., Cummine, Sarty, Borowsky, 2010). Nevertheless, the unique activation for reading PHs in the occipital region, precuneus, and cingulate gyrus is consistent with previous literature that has shown these regions to be uniquely activated for PHs (Borowsky et al., 2006). Furthermore, similar to Borowsky et al. we found a portion of shared activation in the insular cortex for both words and PHs, which may suggest that this region is sensitive to phonological processing. However, our results did not demonstrate any unique activation in the insular cortex for PHs (cf. Borowsky et al., 2006).

2.8 Conclusions

Experiment 2a investigated the neurobiological basis associated with the effect of rhythm priming on reading aloud. Specifically, the experiment used fMRI to identify the brain networks that underlie the priming effect of rhythm on speech, and particularly the putamen's involvement given recent research suggesting its role in phonetic decoding. The neuroimaging results revealed that separate brain regions, with particular focus on the putamen, are associated with congruent compared to incongruent conditions, and that words and PHs uniquely activate the brain. Unlike previous studies that examined rhythm and reading in the putamen in which stimuli were not matched in aspects of speech such as orthographic lexical representation, or other studies that did not directly explore reading processes, the advantage of the present design current paradigm is that it controls for such factors and thus, might be better for pursuing the real underlying shared regions for rhythm and reading.

Experiment 2b

The aim of Experiment 2b was to replicate and extend the behavioural findings of Experiment 1 (Gould et al., 2016) in the MRI environment. Thus, the current experiment included real words that were selected to have stress on the first or second syllable, as well as the corresponding PHs, which allowed us to examine the effect of lexical versus sublexical reading in a tightly controlled manner (i.e., within items as well as within participants). It was predicted that a target PH whose syllable stress conforms to the temporal structure of the rhythm prime would result in a faster naming RT compared to when the PH does not conform to the temporal structure of the prime. In the Gould et al. study there was a stronger effect on sublexical processing than lexical processing (i.e., enhanced priming effects for PHs compared to words), and Oberhuber et al. (2013) demonstrated that a structure well-known to be involved in processing rhythm (the anterior putamen; see Grahn, 2009 for review) is significantly more active during sublexical processing. However, given the possibility that a lack of rhythm priming effects on word stimuli in that study may partly reflect a floor effect (i.e., mean RTs for words were ~500-525 ms), we were also interested in whether slower RTs may allow for a significant rhythm priming effect to emerge for words also, given that trials are presented at a slower rate in the MRI in order to allow for the synchronization with the TR used (i.e., 3300ms, see Protocol below). Lastly, naming RT should be faster for words compared to PHs.

2.9 Materials and Methods

2.9.1 Participants and Stimuli

The participants and stimuli were the same as Experiment 2a.

2.9.2 Behavioural Analysis

Vocal responses were recorded at 96KHz, 24bit, through the CinemaVision system using an Olympus LS11 digital recorder. These recordings were analyzed using PRAAT software (Boersma & Weenink, 2009), and the waveforms and broadband spectrograms were used to localize vocalization onset RT. Given that we used a sparse-sampling (gap paradigm) fMRI method that allows the participant to respond during a gap in image acquisition (e.g., Borowsky et al., 2006; Cummine, Stockdale-Winder, Crossley, & Borowsky, 2009; Cummine et al., 2010; Esopenko, Borowsky, Cummine, & Sarty, 2008), the stimulus onset was synchronized with the last gradient sound before the gap. This provided an acoustic marker for the onset on the recording while the gap allowed for a clear recording of the participant's vocal response.

2.10 Behavioural Results

The naming onset RT that it took participants to correctly name the word or PH was measured in ms for each trial, and the mean error rate of each condition was also computed for each participant. Spoiled trials were removed before analyses were conducted on mean RTs and error rates (12.2% for word trials, 19.1% for PH trials).

Mean RT ANOVA

Correct mean RT data were analyzed using a 2 (Congruency [congruent, incongruent]) x 2 (Stimulus Type [word, PH]) repeated measures GLM ANOVA. The mean RT was 1087.27 ms for words in the congruent condition, 1145.80 ms for words in the incongruent condition, 1211.08 ms for PHs in the congruent condition, and 1246.19 ms for PHs in the incongruent condition. The behavioural results are displayed in Figure 9. There was a significant main effect of Congruency, $F(1, 15) = 29.27$, $MSE = 1198.09$, $p < .001$, $\eta_p^2 = .66$, whereby items in the congruent conditions ($M = 1149.18$ ms) were named faster than items in the incongruent conditions ($M = 1196.0$ ms). There was also a significant main effect of Stimulus Type, $F(1, 15) = 66.49$, $MSE = 3024.10$, $p < .001$, $\eta_p^2 = .82$, indicating that words ($M = 1116.54$ ms) were named faster than PHs ($M = 1228.64$ ms). There was no Congruency x Stimulus Type interaction, $F(1, 15) = 2.71$, $MSE = 810.02$, $p = .12$, $\eta_p^2 = .15$. The 95% CI (Loftus & Masson, 1994) was ± 20.58 ms, which clearly show that the rhythm priming effect on mean RT is significant for both words and PHs.[2]

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[2] The same analyses were conducted by-items, and the results were consistent with the by-subject analyses (i.e., each main effect and interaction in the by-items analyses led to the same conclusion as the by-subjects analyses).

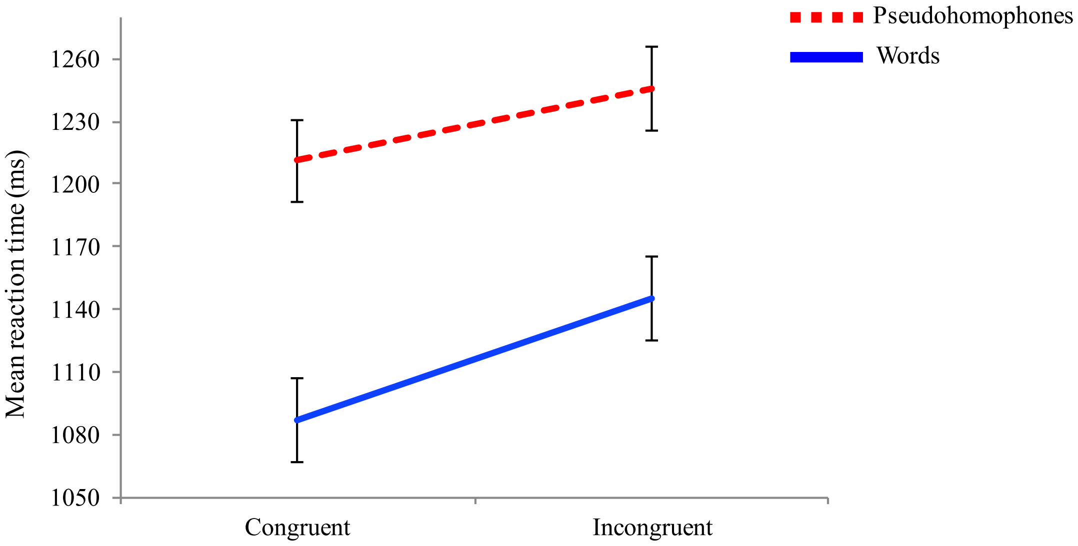

Figure 9: Mean reaction time (RT) representing the onset time taken to correctly name words and PHs as a function of Congruency and Stimulus Type. The 95% confidence interval (CI; Loftus & Masson, 1994) for word and pseudohomophones (PHs) naming RT was ± 20.58 ms. The 95% CI demonstrates that participants named items faster when the target's syllable stress was congruent with the temporal structure of the rhythmic prime (i.e., a prime with stress on the first tone preceding the word 'practice') compared to when the target's syllable stress was incongruent.

Error Rates

The accuracy of participants' responses was computed by determining the percentage of errors in each of the word and PH conditions. The mean error rate was 1.4% for words in the congruent condition, 1.9% for words in the incongruent condition, 1.8% PHs in the congruent condition, and 1.7% for PHs in the incongruent condition. There was no main effect of Congruency, $F(1, 15) = .60$, $MSE = .10$, $p = .45$, $\eta_p^2 = .04$, no main effect of Stimulus Type, $F(1, 15) = .004$, $MSE = .21$, $p = .95$, $\eta_p^2 < .001$, and no Congruency x Stimulus Type interaction, $F(1, 15) = 2.98$, $MSE = .04$, $p = .10$, $\eta_p^2 = .17$. The 95% CI (Loftus & Masson, 1994) was ± .17%, which clearly indicate that the rhythm priming effect on error rates is significant for words.

2.11 Brain-Behaviour Correlations

In order to examine the brain-behavioural relationship, correlational analyses were also conducted between number of active voxels and active regions of the putamen in congruent conditions (Experiment 2a), with mean RTs (Experiment 2b) for those conditions, which are thought to reflect the entrainment of the congruent rhythm prime with the target. In Experiment

2a, there were only significant activations in the right putamen, and only for congruent PHs. There was a significant correlation between number of active voxels and RTs, *r*(14) = .45, *p* = .04, as well as a trend towards significance for mean intensity and RTs, *r*(14) = .42, *p* = .051, indicating that as RTs for congruent PHs increased so did the number of active voxels and the activation intensity in the anterior putamen.

2.12 Discussion

Behavioural Effect of Rhythmic Priming on Reading Aloud

The behavioural results from the MRI replicated several of the findings reported in Experiment 1 (Gould et al., 2016). Firstly, analogous to Experiment 1, naming RTs were shown to be faster when preceded by a rhythmic prime that was congruent with the syllable stress of the target word or PH compared to when the rhythmic prime was incongruent. Moreover, it was found that words were named faster than PHs, which is consisted with previous literature (Herdman et al., 1996; Marmurek & Kwantes, 1996; McCann & Besner, 1987, 1988). In contrast to Gould et al. however, the behavioural data indicated that words elicited a rhythm priming effect that is not significantly different from the size of effect obtained for PHs. Given the possibility that a lack of rhythm priming effects on word stimuli in Gould et al. (2016) may partly reflect a floor effect (i.e., mean RTs for words were ~500-525 ms), words may be showing the effect in the present environment because of the slower pace of trials in the fMRI environment (i.e., the TR of 3300ms served to slow participants' RTs to ~1100-1150ms). Given that a significant rhythm priming effect emerged for words, it may be the case that rhythm priming may also have a locus along the lexical reading pathway in the dual route model (Figure 3; e.g., Borowsky et al., 2013; Cummine Gould, Zhou, Hrybouski, Siddiqi, Chouinard, & Borowsky, 2013; Gould, Cummine, & Borowsky, 2012). In this cognitive model of reading, stimulus type is assumed to have its effect early in the cognitive architecture, specifically at the inputs to the grapheme-to-phoneme conversion system and the orthographic lexical system, as correct identification of PHs will rely more on phonetic decoding, whereas word identification would rely more on orthographic lexical access. The results illustrate that both sublexical and lexical reading were affected by a rhythmic prime, which was shown in the form of additivity.

The finding that the congruency of a rhythmic prime has an effect on speech production while reading words and PHs aloud suggests that external auditory stimuli can serve to entrain reading aloud, thereby producing faster RTs in the congruent condition where the stimulus stress is "in phase" with the expected stress initiated by the rhythmic pattern. In other words, it may be the case that faster RTs for the congruent conditions were induced by a rhythmic prime (via entrainment) through an implicit temporal expectation about the stress of the word or PH. Moreover, given the fact that the prime validity is non-predictive and that the stimulus appears 450 ms after the first tone occurs (which is not long enough for the participant to consciously process whether the prime is congruent or incongruent with the syllabic stress), there must be some degree of automaticity for this effect. Further research is necessary to confirm this possibility.

The results of the analyses that examined the brain-behavioural relationship revealed correlations between brain activation and behavioural RT, whereby RTs for congruent PHs increased as the number of active voxels and activation intensity in the anterior putamen for congruent PHs increased. By focusing on congruent conditions, these correlation analyses reflect the entrainment of the congruent rhythm prime with the target. The fact that they were only significant with PH targets suggests there may be a floor effect occurring with the word targets (i.e., faster RTs and less opportunity to show an effect), and that the more difficult-to-process PHs were more sensitive to detecting a brain-behaviour relationship whereby greater activation volume and intensity corresponds to longer RTs.

2.12 Conclusions

The behavioural results from Experiment 2b revealed that naming RTs were faster for both words and PHs when they were preceded by a rhythmic prime that was congruent with the syllable stress of the letter string compared to when it was incongruent. These results demonstrate that the rhythm priming effect does extend to real words when trials are presented at the slower pace in the MRI environment, thereby suggesting that the lexical reading pathway is also affected by rhythm. Taken together, these results suggest that priming with a structured and anticipatory repetitive rhythm, matched to speech rhythm, provides cues that may facilitate reading aloud, and further support the idea of a connection between the rhythm and reading systems.

CHAPTER 3

A BEHAVIOURAL AND FMRI EXAMINATION OF THE EFFECT OF RHYTHM ON READING NOUN-VERB HOMOGRAPHS ALOUD

Portions of this chapter have been submitted for publication, and redundant information from previous chapters has been removed:

Gould, L., Mickleborough, M., Lorentz, E., Ekstrand, C., and Borowsky, R. (2016). A Behavioural and fMRI Examination of the Effect of Rhythm on Reading Noun-Verb Homographs Aloud. Submitted to *Brain Topography.*

In order to explore the connection between rhythmic and syllabic stress with stimuli that allow for a stronger within-stimulus comparison of syllabic stress, Experiment 3 used stimuli that undergo a process in English called initial-stress derivation, in which disyllabic noun-verb homographs display differing stress patterns depending on whether the homograph is used as a noun or a verb. In general, stress is placed on the first syllable for nouns (trochaic stress), whereas stress is placed on the second syllable when the word is used as a verb (iambic stress). These words are commonly referred to as "initial-stress derived nouns" (ISDNs). For example, the word 'record' can be used as a noun (e.g., "I'll keep a récord of that request), or as a verb (e.g., "Remember to recórd that show"). As the example illustrates, stress patterns become particularly relevant in the lexical and syntactic distinction of homographic forms, and it has been demonstrated that this noun-verb stress differentiation is learned early in childhood (Kelly, 1992).

A series of experiments by Kelly and his colleagues has demonstrated that language users capitalize on this asymmetry in both language production and perception. For example, Kelly and Bock (1988) showed that participants make use of stress patterns when producing novel words. They asked participants to pronounce disyllabic nonwords in sentences that framed them as either verbs or nouns, and found that they were significantly more likely to give the words initial stress if they were functioning as nouns. In another experiment, Kelly (1988) showed that participants classified disyllabic nonwords as nouns if they had word-initial stress, and as verbs if they had word-final stress. A final piece of evidence comes from an experiment by Kawamoto, Farrar, and Overbeek (1990), in which participants were asked to rapidly classify words by their grammatical category. They found that participants classified nouns significantly more quickly if they had word-initial stress than if they had word-final stress, while the reverse was found for verbs.

Experiment 3

The aim of Experiment 3 was to use ISDNs to examine the effect of congruency between rhythmic and syllabic stress, thereby extending the results of Experiments 1 and 2. The ISDNs allow for the same word in both the first and second syllable stressed conditions (i.e., fully within-item) for all participants (i.e., within-participants), thus providing maximal experimental control and the strongest test of the effect of rhythm priming on reading aloud. Based on the results from Experiments 1 and 3 it was predicted that RTs should be faster for both words and PHs whose syllable stress is congruent with the stressed tone of the rhythmic prime compared to words and PHs whose syllable stress is incongruent. Moreover, naming RT should be faster for words compared to PHs.

3.1 Materials and Methods

3.1.1 Participants

Twenty-four undergraduate students (10 male [all right-handed], 14 female [2 left-handed]; $M_{\text{age}} = 24$ years of age) from the University of Saskatchewan recruited through the Department of Psychology participant pool participated for extra credit in their introductory psychology course. All reported normal or corrected-to-normal vision, and spoke English as their first language. The participants gave written informed consent to participate in the study and all testing procedures were approved by the University of Saskatchewan Research Ethics Board and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and its later amendments.

3.1.2 Stimuli

The stimuli consisted of 30 ISDN words (presented once in the noun condition, and once in the verb condition, thus totaling to 60 presented word stimuli), as well as their corresponding PHs (see Appendix B). All stimuli were presented in all conditions of interest and, thus, any differences in responding were due to the manipulation of interest and no any pre-existing differences between the stimuli. In the case of written ISDNs, the grammatical category of the word is ambiguous without a cue to tell the participant to read the word as a noun or a verb. Thus, we separated the nouns/verbs into blocks, and instructed the participant to "read the word as if it is a noun" or "read the word as if it is a verb." The target stimulus was presented in the middle of the computer screen, and directly above the word was the word ‘to’ or ‘the’ to cue the participants’ to name the stimulus as a noun or a verb, but were told not to read the word ‘to’ or ‘the’ aloud. Experimental trials and auditory prime sequences were the same as Experiment 1 (see Figure 1).

3.2 Results

The naming onset RT that it took participants to correctly name the word or PH was measured (in ms) for each trial, and the mean error rate of each condition was also computed for each participant. Incorrect and spoiled trials (e.g., trials in which participants failed to trigger the microphone with their first vocalization; 10.3% of word trials, 14.1% for PH trials) were removed before analyses were conducted on mean RTs and error rates.

Mean RT ANOVA

Correct mean RT data were analyzed using a 2 (Congruency [congruent, incongruent]) x 2 (Stimulus Type [word, PH]) x 2 (Syllable Stress [first=noun, second=verb]) repeated measures GLM ANOVA. The mean RT was 730.42 ms for first syllable stressed words (i.e., nouns) and 719.31 ms for second syllable stressed words (i.e., verbs) in the congruent condition, 748.74 ms for nouns and 757.19 ms for verbs in the incongruent condition, 810.96 ms for PH nouns and 824.24 ms for PH verbs in the congruent condition, and 824.68 ms for PH nouns and 838.14 ms for PH verbs in the incongruent condition. There was a significant main effect of Congruency, $F(1, 23) = 11.83$, $MSE = 1780.71$, $p = .002$, $\eta_p^2 = .34$, whereby items in the congruent conditions ($M = 771.23$ ms) were named faster than items in the incongruent conditions ($M = 792.19$). There was also a significant main effect of Stimulus Type, $F(1, 23) = 6.5$, $MSE = 53983.58$, $p = .01$, $\eta_p^2 = .22$, indicating that words ($M = 738.91$ ms) were named faster than PHs ($M = 824.51$ ms). There was no significant main effect of Syllable Stress, $F(1, 23) = .10$, $MSE = 17262.76$, $p = .75$, $\eta_p^2 = .004$, nor was there a Congruency x Stimulus Type interaction, $F(1, 23) = 1.58$, $MSE = 1546.87$, $p = .22$, $\eta_p^2 = .06$. There was no significant Syllable Stress x Stimulus Type interaction, $F(1, 23) = .18$, $MSE = 14398.20$, $p = .67$, $\eta_p^2 = .008$, no Congruency x Syllable Stress interaction, $F(1, 23) = .45$, $MSE = 2615.76$, $p = .51$, $\eta_p^2 = .019$, nor was there a significant Congruency x Syllable Stress x Stimulus Type interaction, $F(1, 23) = .851$, $MSE = 1324.88$, $p = .37$, $\eta_p^2 = .036$. The 95% CI (Loftus & Masson, 1994) was ± 39.70 ms.

In order to better understand the 3-way interaction effects, correct mean RTs were also analyzed separately for each stimulus type (i.e., words and PHs) using 2 (Congruency) x 2 (Syllable Stress) repeated measures ANOVAs (Figure 10). For words, there was a significant main effect of Congruency, $F(1, 23) = 15.24$, $MSE = 1243.08$, $p = .001$, $\eta_p^2 = .40$, whereby words in the congruent condition ($M = 724.87$ ms) are named faster than words in the incongruent condition ($M = 752.97$ ms). There was no main effect of Syllable Stress, $F(1, 23) = .003$, $MSE = 12519.27$, $p = .95$, $\eta_p^2 < .001$, and no Congruency x Syllable Stress interaction, $F(1, 23) = 1.38$, $MSE = 1660.47$, $p = .25$, $\eta_p^2 = .06$. For PHs, the main effect of Congruency did not reach significance, $F(1, 23) = 2.20$, $MSE = 2084.49$, $p = .15$, $\eta_p^2 = .09$, and there was no main effect of Syllable Stress, $F(1, 23) = .22$, $MSE = 19141.69$, $p = .64$, $\eta_p^2 = .01$, and no significant interaction, $F(1, 23) < .001$, $MSE = 2280.17$, $p = .99$, $\eta_p^2 < .001$. The 95% CI (Loftus & Masson, 1994) for words was ± 29.13 ms and 35.95 ms for PH naming.

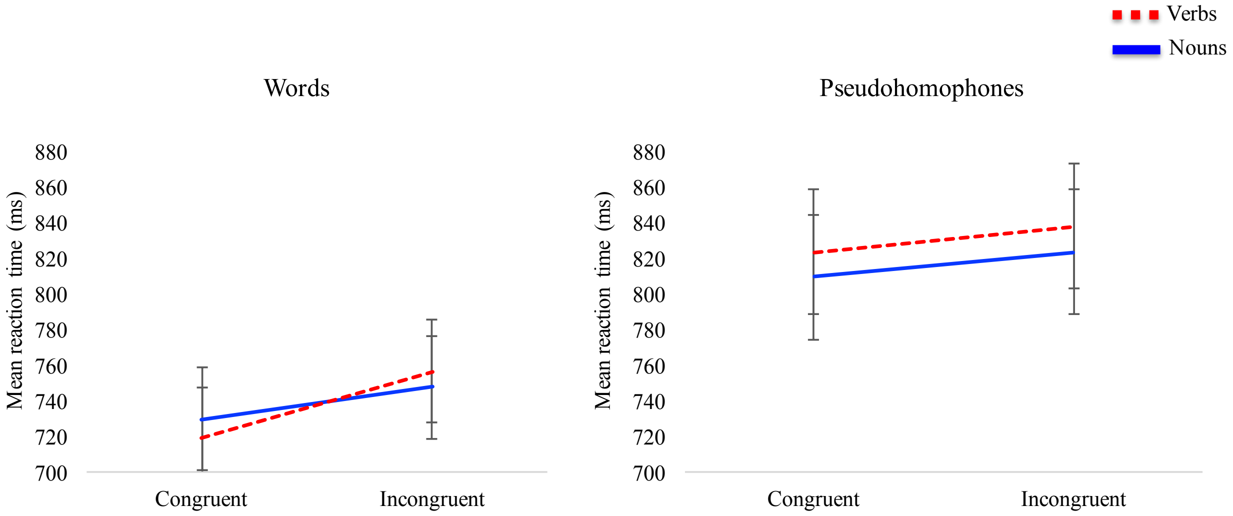

Figure 10: Mean reaction time (RT) representing the onset time taken to correctly name nouns and verbs as a function of Congruency and Part-of-Speech. The 95% confidence interval (CI; Loftus & Masson, 1994) for word naming RT was ± 29.13 ms and ± 35.95 ms for PH naming.

Error rates

The accuracy of participants' responses was computed by determining the percentage of errors in each of the word and PH conditions. The mean error rate was 1.3% for first syllable stressed words and 1.2% for second syllable stressed words in the congruent condition, 1.4% for first syllable stressed words and 1.9% for 'second syllable stressed words in the incongruent condition, 1.3% for first syllable stressed PHs and 1.4% for second syllable stressed PHs in the congruent condition, and 1.3% for first syllable stressed PHs and 2.4% for second syllable stressed PHs in the incongruent condition. There was a significant main effect of Congruency,

$F(1, 23) = 6.99$, $MSE = 13.0$, $p = .015$, $\eta_p^2 = .23$, whereby items in the congruent conditions ($M =$ 12.85%) has fewer errors than items in the incongruent conditions ($M = 17.25\%$). There was no main effect of Stimulus Type, $F(1, 23) = 1.96$, $MSE = .06$, $p = .18$, $\eta_p^2 = .08$, nor was there was a significant main effect of Syllable Stress, $F(1, 23) = 2.24$, $MSE = .32$, $p = .15$, $\eta_p^2 = .09$. There was a significant Congruency x Syllable Stress interaction, $F(1, 23) = 5.22$, $MSE = .14$, $p = .03$, $\eta_p^2 = .19$, indicating that the effect of congruency is larger for second syllable stress items compared to first syllable stressed items. There was no Congruency x Stimulus Type interaction, $F(1, 23) = .28$, $MSE = .07$, $p = .60$, $\eta_p^2 = .012$. There was no significant Syllable Stress x Stimulus Type interaction, $F(1, 23) = .09$, $MSE = .05$, $p = .09$, $\eta_p^2 = .12$. Lastly, there was no significant Congruency x Syllable Stress x Stimulus Type interaction, $F(1, 23) = .79$, $MSE = .05$, $p = .38$, $\eta_p^2 = .03$. The 95% CI (Loftus & Masson, 1994) was ± 0.08%.[3]

3.3 Discussion and Conclusions

As previously described, the aim of Experiment 3 was to determine whether speech production in a reading aloud task would be affected by prior presentation of a rhythmic prime using noun-verb homographs, which allows for a strong within-item comparison of noun and verb processing. The results provide converging evidence for Experiments 1 and 2b, whereby target words whose syllabic stress conformed to the temporal structure of the rhythm prime, and thus entrained to the prime, resulted in a faster naming RTs compared to when a target word did not conform to the temporal structure of the prime. Furthermore, as predicted, naming RT was faster for words compared to PHs. Overall, the results of both the by-subjects and by-items analyses supported the hypotheses and suggest that a rhythmic prime matched to the syllabic stress of a letter string enhances reading aloud. The congruency effect did not reach significance for the PHs, most likely due to high variance. The larger 95% CIs for PHs compared to words reflects greater variance in the PH conditions, which could reflect a limitation of using a voice-key for detecting vocalization onset (Gould, Cummine, & Borowsky, 2012). Specifically, participants may be naming the orthographically unfamiliar PHs with a lower vocalization volume, which would result in failed triggering of the voice-key, as the higher spoiled trial rate

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[3] The same analyses were conducted by-items, and the patterns were consistent with the by-subject analyses.

for PHs suggests. In the following experiment, an intensity envelope analysis of a digital audio recording of the trials (Gould, Cummine & Borowsky, 2012) will be used to provide greater precision under a wide-range of vocalization volume, and avoid the limitation of voice-keys with respect to vocalization volume and spoiled trials.

Although Experiment 3 provided converging evidence for the behavioural effect of rhythm on reading words aloud, further research is still needed to better understand the source of the effect in terms of the underlying neural networks. Functional MRI will be used in Experiment 4a to further examine the effect of rhythm on reading and reveal the underlying brain regions associated with the differential effects for congruent and incongruent stimuli with these optimally controlled stimuli.

Experiment 4a

As previously mentioned, using ISDNs as critical stimuli provides a stronger within-stimulus comparison of syllabic stress, and thus noun/verb status, thereby allowing for a more tightly-controlled examination of the influence of rhythmic priming on speech production. Furthermore, the use of ISDNs also provides an opportunity to explore how the brain processes nouns and verbs, and whether shared or unique brain regions are involved in noun-verb processing.

Neuropsychological experiments have shown modality-specific deficits in producing verbs compared to nouns, and dissociations in which patients may perform significantly worse in oral production of verbs compared to nouns, but perform equally well in written production of both types, whereas other patients may display the opposite pattern (Caramazza & Hillis, 1991). Neuroimaging studies have provided mixed findings regarding the extent to which nouns and verbs activate a common or unique brain network. For example, Tranel, Martin, Damasio, Grabowski and Hichwa (2005) found that nouns and verbs primarily activate separate regions of the brain, whereby verbs activate the left frontal operculum (FO) and left MT regions, whereas nouns activate the left inferotemporal cortex (IT) region. Conversely, several studies have shown that the activation representing noun and verb processing involves a common neural network (Siri et al., 2008; Crepaldi et al. 2011; Soros, Cornelissen, Laine, & Salmelin, 2003; Tyler, Randall, & Stamatakis, 2008). However, these studies have all relied on a between-stimulus comparison to evaluate noun and verb processing. Borowsky, Esopenko, Gould, Kuhlmann, Sarty, and Cummine (2013) examined the distinction between nouns and verbs using a within-stimulus manipulation, and how the distinction may relate to the ventral and dorsal visual processing streams. Given that the ventral stream specialises in the identification of *what* a particular stimulus is, whereas the dorsal stream specialises in *where/how* processing, another hypothesis is that nouns may rely more on the ventral stream, while verbs may rely more heavily on the dorsal stream. Their experiment involved the participant reading homonymous homographs (e.g., *the* bank versus *to* bank) separately cued as nouns or verbs in order to reveal whether the fMRI activation would support either the shared or separate network hypothesis. Such stimuli allowed for the strongest within-item comparison of noun and verb processing based on their matched properties (e.g., word frequency, word length, bigram frequency, number of phonemes, orthography neighborhood density), similar to the ISDN stimuli used in the present experiment. The results demonstrated that activation was primarily shared by both the noun and verb conditions across both the ventral and dorsal streams, including the regions that had previously been implicated as noun processing regions (i.e., IT), or verb processing regions (i.e., FO, MT).

Summary and Hypotheses

The aim of Experiment 4a was to use fMRI to identify the brain networks that underlie the priming effect of rhythm on speech, and particularly the putamen's involvement given recent research suggesting its role in phonetic decoding. That is, the experiment aimed to elucidate whether similar or distinct brain networks are recruited when rhythmic and speech stress are congruent or incongruent with one another, which will contribute to the understanding of the cross-domain effect of musical rhythm on the reading aloud. Given that previous neuroimaging studies have implicated the left IFG and STG, SMA, basal ganglia, cerebellum, insula, and thalamus for processing both musical and speech rhythm (for speech: Aleman et al., 2005; Geiser et al., 2008; Klein et al., 2011; Kotz & Schwatze, 2010; for music: Chen et al., 2008; Grahn & Brett, 2007; Grahn & Rowe, 2009), we predicted that these regions should be activated during the reading tasks, as it involved both speech and rhythmic stimuli. Given the recent focus on the putamen in both reading (Oberhuber et al.) and rhythm processing (Grahn & Rowe, 2009), our analyses will focus on that region of interest.

In terms of noun versus verb processing, given that nouns and verbs activate primarily a shared network (as demonstrated by Borowsky et al., 2012), we predict that there should be mainly shared activation through the ventral and dorsal streams, including the left IT, MT, and FO regions.

3.4 Materials and Methods

3.4.1 Participants

Sixteen participants (6 males; 10 females; all right-handed; M_{age} = 29.3 years) performed both the word and PH naming tasks, with the task order counterbalanced across participants. All reported normal or corrected-to-normal vision, and spoke English as their first language. The participants gave written informed consent to participate in the study and all testing procedures were approved by the University of Saskatchewan Research Ethics Board and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and its later amendments.

3.4.2 Stimuli

The stimuli were identical to Experiment 3.

3.4.3 Behavioural Analysis

The behavioural analysis was conducted in the same manner as Experiment 2a.

3.4.4 Protocol and fMRI Analyses

The protocol and fMRI analyses were identical to Experiment 2a.

3.5 fMRI Results

Unique Regions of Activation for Word or PH Reading

The brain regions that were uniquely activated for PHs greater than words were the left anterior cingulate (Talairach coordinates, x, y, z: -4, 25, 0) and left caudate nucleus (-6, 20, 3), and the only region that was uniquely activated for words greater than PHs was the left anterior insula (-37, 10, 5) at a statistical threshold of $t(15) = 2.25, p < 0.01$.

Shared Regions of Activation for Word and PH Reading

The regions of shared activation for reading words and PHs are listed in Table 8, and included bilateral LOC (-31, -84, -8/28, -83, -8), bilateral STG (-54, -30, 5/58, -27, 5), bilateral insula (-32, 17, 8/38, 13, 8), bilateral putamen (-21, 1, 8/21, 2, 8), right caudate nucleus (15, 6, 8), bilateral precentral gyri (-48, 4, 9/-48, -15, 29/37, -1, 31), left precuneus (-26, -71, 21), left middle frontal gyrus (-39, 20, 26), bilateral superior parietal lobule (-26, -58, 40/24, -62, 40), bilateral cingulate gyri (-9, 1, 46/6, 1, 46), and bilateral SMA (-4, -11, 64/5, 11, 62) at a statistical threshold of $t(15) = 3.50, p < 0.01$.

Table 8: Regions of Shared Activation for Reading Words and Pseudohomophones

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Shared Words & Pseudohomophones				
Lateral Occipital Complex	L	-31	-84	-8
	R	28	-83	-8
Superior Temporal Gyrus	L	-54	-30	5
	R	58	-27	5
Insula	L	-32	17	8
	R	38	13	8
Putamen	L	-21	1	8
	R	21	2	8

Caudate Nucleus	R	15	6	8
Precentral Gyrus	L	-48	4	9
	L	-48	-15	29
	R	37	-1	31
Precuneus	L	-26	-71	21
Middle Frontal Gyrus	L	-39	20	26
Superior Parietal Lobule	L	-26	-58	40
	R	24	-62	40
Cingulate Gyrus	L	-9	1	46
	R	6	1	46
Supplementary Motor Area	L	-4	-11	64
	R	5	11	62

Unique Regions of Activation for Congruent or Incongruent Words and Rhythm

The regions of activation greater for congruent compared to the incongruent word and rhythm condition are listed in Table 9, and included the right cerebellum (39, -61, -38), right parahippocampal gyrus (23, -9, -17), right inferior temporal gyrus (59, -47, -10), right internal capsule (17, -14, -4), bilateral putamen (27, -5, 1/-27, -7, 8/26, -1, 9/-27, 4, 9; see Figure 11), bilateral insula (42, -16, 2/-38, -23, 4), right occipital cortex (9, -82, 10), right lingual gyrus (9, -80, -1), right transverse temporal gyrus (35, -25, 9), right medial frontal gyrus (23, 44, 9/6, -26/64), left thalamus (-10, -14, 13), right parietal lobe (51, -17, 18), bilateral cingulate gyrus (-6, -37, 21/-7, -37, 35/-9, -4, 35/8, 17, 35), left superior frontal gyrus (-5, 10, 51), left primary motor cortex (-27, 0, 51), and right postcentral gyrus (29, -33, 54) at a statistical threshold of $t(15) = 2.25$, $p < 0.01$. The only region of activation that was greater for the incongruent compared to congruent condition was the right superior frontal gyrus (23, 56, 29).

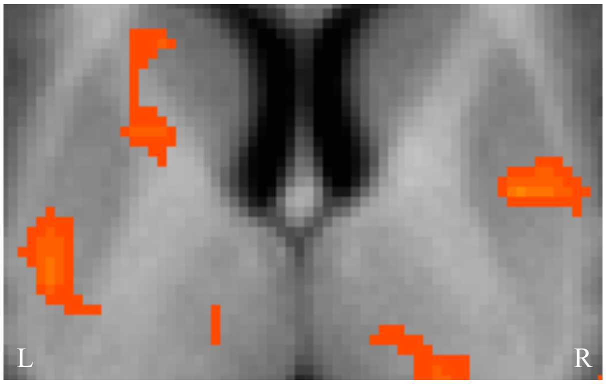

Figure 11: Activation in bilateral putamen (and right external capsule & left thalamus) for congruent compared to the incongruent word and rhythm priming condition.

Table 9: Regions of activation greater for congruent compared to the incongruent word and rhythm condition.

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Congruent > Incongruent Words				
Cerebellum	R	39	-61	-38
Parahippocampal gyrus	R	23	-9	-17
Inferior Temporal gyrus	R	59	-47	-10
Internal Capsule	R	17	-14	-4
Putamen	R	27	-5	1
	L	-27	-7	8
	R	26	-1	9
	L	-27	4	9
Insula	R	42	-16	2
	L	-38	-23	4
Occipital Cortex	R	9	-82	10
Lingual Gyrus	R	9	-80	-1
Transverse Temporal Gyrus	R	35	-25	9
Medial Frontal Gyrus	R	23	44	9
Thalamus	L	-10	-14	13

Parietal Lobe	R	51	-17	18
Cingulate Gyrus	L	-6	-37	21
	L	-7	-37	35
	L	-9	-4	35
	R	8	17	35
Superior Frontal Gyrus	L	-5	10	51
Primary Motor Cortex	L	-27	0	51
Postcentral Gyrus	R	29	-33	54
Medial Frontal Gyrus	R	6	-26	64

Unique Regions of Activation for Congruent versus Incongruent PHs and Rhythm

The regions of activation greater for incongruent compared to congruent PH and rhythm condition are listed in Table 10, and included the left cerebellum (-7, -67, -26), left fusiform gyrus (-41, -68, -7), left ITG (-55, -55, 0), left lingual gyrus (-19, -75, 0), bilateral STG (47, -25, 6/-37, -34, 15), right putamen (28, -7, 9; see Figure 12), left middle frontal gyrus (-40, 32, 20), left precentral gyrus (-26, -19, 40), and left cingulate gyrus (-11, -9, 42) at a statistical threshold of $t(15) = 2.25$, $p < 0.01$. The only region of activation greater for congruent compared to incongruent PHs and rhythm condition was the left cerebellum (-28, -37, -27).

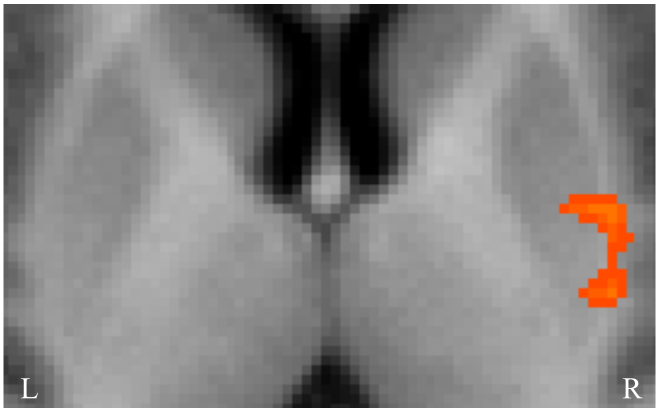

Figure 12: Activation in the right putamen for the incongruent greater than congruent PH and rhythm priming condition.

Table 10: Regions of activation greater for incongruent compared to congruent PH and rhythm condition

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Incongruent > Congruent PHs				
Cerebellum	L	-7	-67	-26
Fusiform Gyrus	L	-41	-68	-7
Inferior Temporal Gyrus	L	-55	-55	0
Lingual Gyrus	L	-19	-75	0
Superior Temporal Gyrus	R	47	-25	6
	L	-37	-34	15
Putamen	R	28	-7	9
Middle Frontal Gyrus	L	-40	32	20
Precentral Gyrus	L	-26	-19	40
Cingulate Gyrus	L	-11	-9	42

Shared Regions of Activation for Congruent and Incongruent Words

The regions of shared activation for congruent and incongruent words and rhythm are listed in Table 11, and included the left cerebellum (-27, -77, -21), bilateral inferior occipital gyri (-27, -88, -6/27, -85, -6), left precuneus (-25, -69, 23), bilateral STG (-55, -29, 6/58, -26, 6/-53, -17, 6/53, -17, 6), bilateral precentral gyri (-46, 4, 9/45, -13, 32/-45, -13, 32), bilateral insula (-31, 15, 9/31, 15, 9), bilateral putamen (-20, 5, 9/16, 4, 9; see Figure 13), left IFG (-40, 5, 28), and bilateral medial frontal gyri (-6, 2, 49/3, 2, 49) at a statistical threshold of $t(15) = 3.50$, $p < 0.01$.

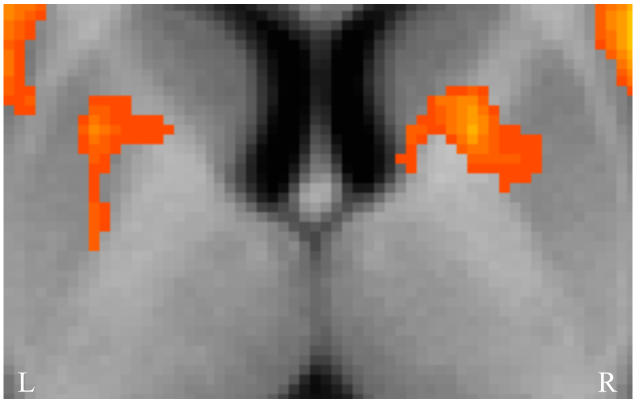

Figure 13: Activation in bilateral putamen for the shared congruent and incongruent word and rhythm priming condition.

Table 11: Regions of shared activation for congruent and incongruent words and rhythm

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Shared Congruent & Incongruent Words				
Cerebellum	L	-27	-77	-21
Inferior Occipital Gyrus	L	-27	-88	-6
	R	27	-85	-6
Precuneus	L	-25	-69	23
Superior Temporal Gyrus	L	-55	-29	6
	R	58	-26	6
	L	-53	-17	6
	R	53	-17	6
Precentral Gyrus	L	-46	4	9
	R	45	-13	32
	L	-45	-13	32
Insula	L	-31	15	9
	R	31	15	9
Putamen	L	-20	5	9
	R	16	4	9
Inferior Frontal Gyrus	L	-40	5	28

Medial Frontal Gyrus	L	-6	2	49
	R	3	2	49

Shared Regions of Activation for Congruent and Incongruent PHs

The regions of shared activation for the congruent and incongruent PHs and rhythm are listed in Table 12, and included the left fusiform gyrus (-30, -83, -11/-42, -61, -11), bilateral inferior occipital gyri (-22, -93, -3/25, -89, -3), left precuneus (-26, -71, 20), right middle occipital gyrus (29, -89, 7), left MTG (-52, -35, 7), bilateral STG (-51, -17, 4/57, -17, 4), left insula (-44, 4, 4), left IFG (-41, 3, 21), left precentral gyrus (-46, -11, 41), bilateral middle frontal gyri (-26, -11, 46/6, 2, 50/-5, 2, 50), and right superior parietal lobule (24, -60, 44) at a statistical threshold of $t(15) = 3.50$, $p < 0.01$.

Table 12: Regions of shared activation for the congruent and incongruent PHs and rhythm

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Shared Congruent & Incongruent PHs				
Fusiform Gyrus	L	-30	-83	-11
	L	-42	-61	-11
Inferior Occipital Gyrus	L	-22	-93	-3
	R	25	-89	-3
Precuneus	L	-26	-71	20
Middle Occipital Gyrus	R	29	-89	7
Middle Temporal Gyrus	L	-52	-35	7
Superior Temporal Gyrus	L	-51	-17	4
	R	57	-17	4
Insula	L	-44	4	4
Inferior Frontal Gyrus	L	-41	3	21
Precentral Gyrus	L	-46	-11	41
Middle Frontal Gyrus	L	-26	-11	46
	R	6	2	50
	L	-5	2	50

Superior Parietal Lobule	R	24	-60	44

Regions of Activation for Noun and Verb Word Processing

The shared regions for reading aloud of noun and verbs at a statistical threshold of $t(15) = 3.50$, $p < 0.01$ are listed in Table 13 and illustrated in Figure 14. Those regions included bilateral cerebellum (-25, -65, -21/25, -65, -21), left inferior temporal gyrus (-42, -65, -13), bilateral occipital cortex (-14, -88, -9/26, -84, -9), bilateral STG (-54, -28, 6/57, -27, 6), bilateral insula (-38, 12, 6/38, 12, 6), bilateral putamen (-21, 4, 6/21, 4, 6), bilateral thalamus (-10, -17, 6/7, -17, 9), left precuneus (-28, -73, 20), bilateral superior parietal lobule (-28, -63, 43/28, -63, 43), bilateral precentral gyri (-47, -11, 44/47, -11, 44), left IFG (-43, 2, 24), and bilateral medial frontal gyri (-5, 2, 48/5, 2, 48). There were only two regions of unique activation for noun processing, which were the IFG (-38, 26, -3), and the medial frontal gyrus (-5, 45, 32). There were no regions of unique activation for verb processing.

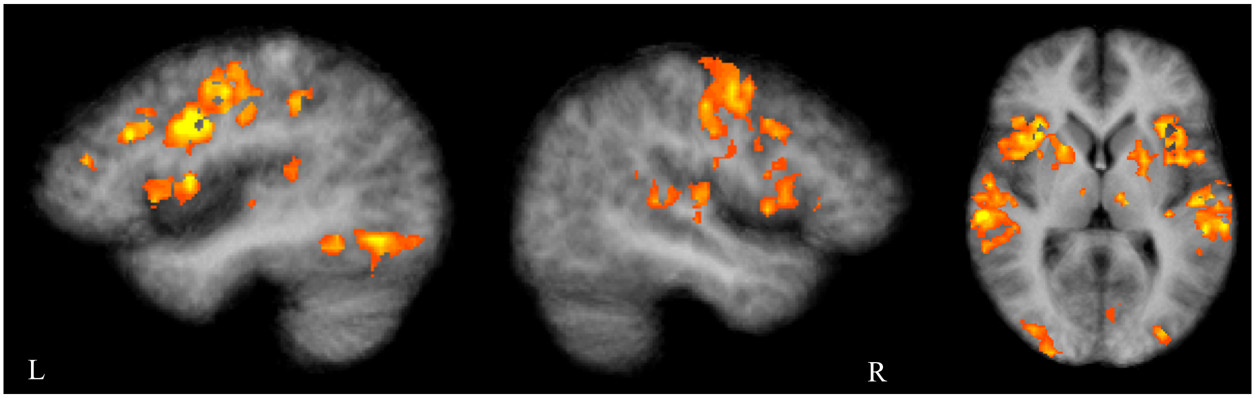

Figure 14: Shared regions of activation for noun and verb word processing.

Table 13: Shared regions of activation for noun and verb word processing

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Shared Nouns & Verbs Words				
Cerebellum	L	-25	-65	-21
	R	25	-65	-21
Inferior Temporal Gyrus	L	-42	-65	-13
Occipital Cortex	L	-14	-88	-9

	R	26	-84	-9
Superior Temporal Gyrus	L	-54	-28	6
	R	57	-27	6
Insula	L	-38	12	6
	R	38	12	6
Putamen	L	-21	4	6
	R	21	4	6
Thalamus	L	-10	-17	6
	R	7	-17	9
Precuneus	L	-28	-73	20
Superior Parietal Lobule	L	-28	-63	43
	R	28	-63	43
Precentral Gyrus	L	-47	-11	44
	R	47	-11	44
Inferior Frontal Gyrus	L	-43	2	24
Medial Frontal Gyrus	L	-5	2	48
	R	5	2	48

Regions for Noun and Verb PH Processing

The shared regions for reading aloud of noun and verb PHs at a statistical threshold of $t(15) = 3.50$, $p < 0.01$ are listed in Table 14 and displayed in Figure 15. The shared regions included the left cerebellum (-21, -60, -23), bilateral occipital cortex (-29, -87, -7/29, -87, -7), bilateral MTG (-46, -56, 7/39, -50, 9), bilateral insula (-31, 16, 9/31, 16, 9), bilateral transverse temporal gyri (-34, -29, 12/34, -29, 12), bilateral STG (-59, -29, 6/57, -30, 10), bilateral putamen (Talairach coor, dinates: -23, 0, 6/20, 1, 6), bilateral precentral gyri (-45, 1, 25/36, 0, 28), bilateral cingulate gyri (-6, -1, 46/6, -1, 46), and bilateral medial frontal gyri (-4, -8, 58/4, -8, 58). There were no regions of unique activation for either nouns or verbs.

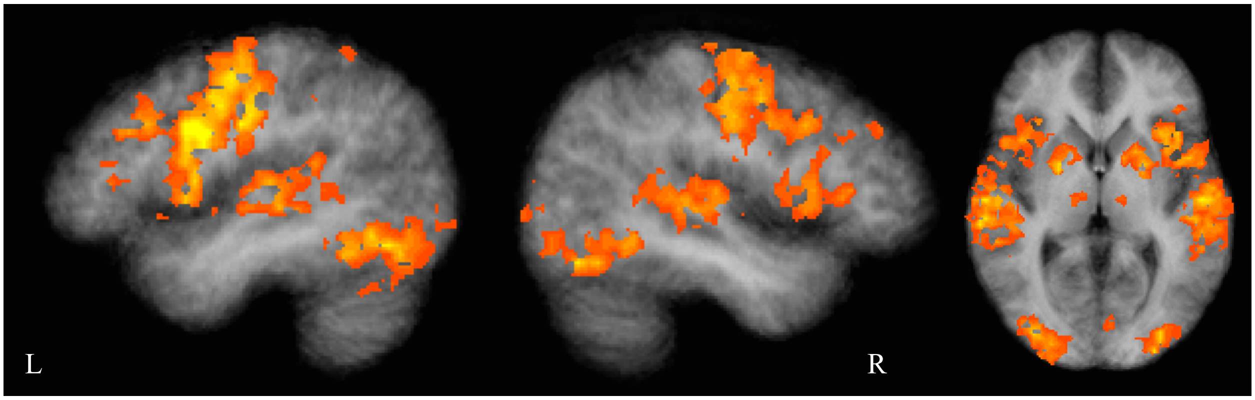

Figure 15: Shared regions of activation for noun and verb PH processing

Table 14: Shared regions of activation for noun and verb PH processing

		Talairach coordinates		
Anatomical region	**Laterality**	**x**	**y**	**z**
Shared Nouns & Verbs PHs				
Cerebellum	L	-21	-60	-23
Occipital Cortex	L	-29	-87	-7
	R	29	-87	-7
Middle Temporal Gyrus	L	-46	-56	7
	R	39	-50	9
Insula	L	-31	16	9
	R	31	16	9
Transverse Temporal Gyrus	L	-34	-29	12
	R	34	-29	12
Superior Temporal Gyrus	R	57	-30	10
	L	-59	-29	6
Putamen	L	-23	0	6
	R	20	1	6
Precentral Gyrus	L	-45	1	25
	R	36	0	28
Cingulate Gyrus	L	-6	-1	46
	R	6	-1	46

Medial Frontal Gyrus	L	-4	-8	58
	R	4	-8	58

3.6 Discussion

Experiment 4a identified brain regions associated with the effect of rhythm on reading aloud, which facilitates the development of models of basic reading processes in terms of the interaction of reading and rhythm processing. The functional neuroimaging results revealed that there was greater activation in the right putamen for incongruent compared to congruent PHs and rhythm, activation in bilateral putamen for shared congruent and incongruent word and rhythm conditions, and activation in bilateral putamen for congruent compared to the incongruent word and rhythm condition. This difference may reflect the fact that the putamen is involved in evaluating temporal relations between stimuli and extracting temporal regularity (Fujii & Wan, 2014; Grahn & Rowe, 2009), which may be heightened in conditions where the syllabic stress of the word or PH matches with the stress of the rhythmic prime. Furthermore, this finding supports the notion that the putamen is involved in predicting upcoming events, which leads to improved speech processing (Rothermich & Kotz, 2013).

As previously mentioned, the consistent activation in the cerebellum for the rhythm priming and reading tasks for both words and PHs is consistent with previous research that implicates the cerebellum with the encoding of time intervals (Irvy & Keele, 1993; Grube et al., 2010ab), and early sequence learning in language processes (Doyon, Penhune, & Ungerleider, 2009). In this experiment, greater activation in the left cerebellum for incongruent compared to congruent rhythm prime and PHs supports the notion that the cerebellum is associated with the timing of irregular sound sequences (Teki, Grube, Kumar, & Griffiths, 2011).

The regions of shared activation between words and PHs, including the occipital lobe, middle frontal gyrus, precuenus, putamen, insula, precentral gyrus, STG, superior parietal lobule, cingulate gyrus, and SMA are consistent with previous literature that has found these regions to be involved in processing both types of stimuli (Borowsky et al., 2006). Similar to Borowsky et al. we found a portion of shared activation in the insular cortex for both words and PHs, which may suggest that this region is sensitive to phonological processing, but our more tightly matched words and PHs showed that activation in the insula was greater for words compared to PHs.

Neural Representations of Noun and Verb Processing

Converging with Borowsky et al. (2013), the present fMRI results demonstrated that the vast majority of activation was shared by both noun and verbs across both the ventral and dorsal visual processing streams, in both the word and PH reading conditions (see Figures 13 & 14). There was very little unique activation for nouns in the word reading condition, and absolutely no unique activation in either the verb word reading or either of the PH reading conditions. Furthermore, we also found shared activation in regions that were previously considered by others to be verb-specific (i.e., left FO and MT), and noun-specific (i.e., left IT; e.g., Tranel, Martin, Damasio, Grabowski & Hichwa, 2005). These results provide converging evidence that after taking into account the inconsistencies between the stimuli and tasks used in the extant literature, the cerebral circuits underlying noun and verb processing are most likely shared.

3.7 Conclusions

The functional neuroimaging results revealed that several brain regions, including the putamen and the cerebellum, are involved in the rhythm priming effect on reading aloud, which has important implications for revealing the underlying neurobiological mechanisms of reading processes. Moreover, the results support the notion that the neurobiological mechanisms involved in reading nouns and verbs are primarily shared across both the ventral-lexical and dorsal-sublexical processing streams.

Experiment 4b

The aim of Experiment 4b was to replicate the behavioural results of Experiment 3 using the RTs collected in the MRI. Specifically, to test whether speech production in a reading aloud task would be affected by prior presentation of a rhythmic prime using noun-verb homographs. We predicted that target words whose syllabic stress conformed to the temporal structure of the rhythm prime, and thus to the listener's temporal expectations, resulted in a faster naming RTs compared to when a target word did not conform to the temporal structure of the prime. Furthermore, naming RT should be faster for words compared to PHs.

3.8 Materials and Methods

3.8.1 Participants and Stimuli

The participants and stimuli were the same as Experiment 4a.

3.8.2 Behavioural Analysis

The behavioural analysis was conducted in the same manner as Experiment 2b.

3.9 Behavioural Results

Mean RT ANOVA

Correct mean RT data were analyzed using a 2 (Congruency [congruent, incongruent]) x 2 (Stimulus Type [word, PH]) x 2 (Syllable Stress [first=nouns, second=verbs]) repeated measures GLM ANOVA. The mean RT was 1076.69 ms for nouns and 1119.01 ms for verbs in the congruent condition, 1182.60 ms for nouns and 1139.01 ms for verbs in the incongruent condition, 1203.93 ms for PH nouns and 1223.24 ms for PH verbs in the congruent condition, and 1220.05 ms for PH nouns and 1270.01 ms for PH verbs in the incongruent condition. There was a significant main effect of Congruency, $F(1, 15) = 75.49$, $MSE = 944.29$, $p < .001$, $\eta_p^2 = .84$, whereby items in the congruent conditions ($M = 1155.72$ ms) were named faster than items in the incongruent conditions ($M = 1202.92$ ms). There was also a significant main effect of Stimulus Type, $F(1, 15) = 87.41$, $MSE = 3659.49$, $p < .001$, $\eta_p^2 = .86$, indicating that words ($M = 1129.32$ ms) were named faster than PHs ($M = 1229.31$ ms). There was also a main effect of Syllable Stress, $F(1, 15) = 6.96$, $MSE = 1328.19$, $p = .20$, $\eta_p^2 = .32$, indicating that first syllable stressed items ($M = 1170.82$ ms) are named faster than second syllable stressed items ($M = 1187.82$ ms). There was a significant Congruency x Stimulus Type interaction, $F(1, 15) = 11.69$, $MSE = 679.06$, $p = .004$, $\eta_p^2 = .44$, whereby words demonstrated a larger effect of congruency ($M = 64$ ms) than PHs ($M = 32$ ms). There was also a significant Congruency x Syllable Stress interaction, $F(1, 15) = 6.04$, $MSE = 1010.05$, $p = .02$, $\eta_p^2 = .29$, and a significant Syllable Stress x Stimulus Type interaction, $F(1, 15) = 4.63$, $MSE = 2147.90$, $p = .04$, $\eta_p^2 = .24$, which indicates that PHs displayed a larger difference between first and second syllable items (M = 34.63 ms) compared to words (M = .64 ms). Lastly, the Congruency x Syllable Stress x Stimulus Type interaction was significant, $F(1, 15) = 19.04$, $MSE = 1427.19$, $p = .001$, $\eta_p^2 = .56$.[2]

In order to better understand the 3-way interaction effects, correct mean RTs were also analyzed separately for each stimulus type (i.e., words and PHs) using 2 (Congruency [congruent, incongruent]) x 2 (Syllable Stress [first, second]) repeated measures ANOVAs. The behavioural results are displayed in Figure 16. For words, there was a significant main effect of Congruency, $F(1, 15) = 187.72$, $MSE = 337.78$, $p < .001$, $\eta_p^2 = .93$, whereby words in the congruent condition (M = 1097.85 ms) are named faster than items in the incongruent condition (M = 1160.81 ms). There was no main effect of Syllable Stress, $F(1, 15) = .004$, $MSE = 1559.19$, $p = .95$, $\eta_p^2 < .001$, as it was qualified by a significant Congruency x Syllable Stress interaction, $F(1, 15) = 87.39$, $MSE = 337.78$, $p < .001$, $\eta_p^2 = .85$. The 95% CI (Loftus & Masson, 1994) for words was ± 13.71 ms. For PHs, there was a significant main effect of Syllable Stress, $F(1, 15) = 9.73$, $MSE = 1916.89$, $p = .007$, $\eta_p^2 = .39$, whereby first syllable stressed PHs (M = 1211.99 ms) were named faster than second syllable stressed PHs (M = 1246.63 ms). There was no main effect of Congruency, $F(1, 15) = 1.68$, $MSE = 2099.46$, $p = .22$, $\eta_p^2 = .10$, but there was a significant interaction, $F(1, 15) = 11.92$, $MSE = 1285.57$, $p = .004$, $\eta_p^2 < .44$. The 95% CI (Loftus & Masson, 1994) for PHs was ± 21.12 ms.

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[2] The same analyses were conducted by-items, and the patterns were consistent with the by-subject analyses.

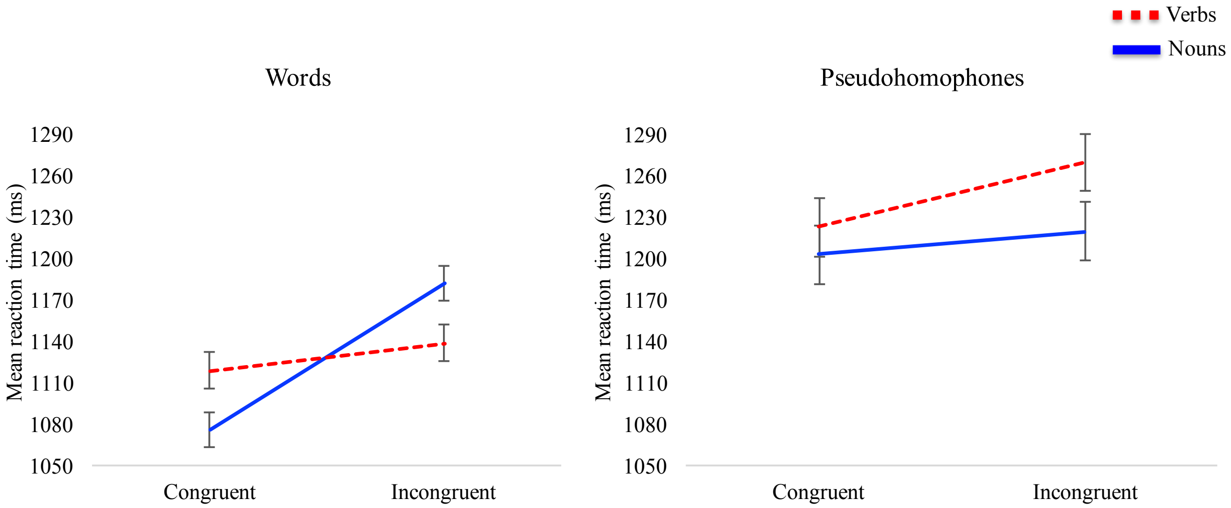


Figure 16: Mean reaction time (RT) representing the onset time taken to correctly name nouns and verbs as a function of Congruency and Part-of-Speech. The 95% confidence interval (CI; Loftus & Masson, 1994) for word naming RT was ± 13.71 ms and ± 21.12 ms for PH naming.

Error rates

The accuracy of participants' responses was computed by determining the percentage of errors in each of the word and PH conditions. The mean error rate was 2.8% for first syllable stressed words and 1.9% for second syllable stressed words in the congruent condition, 2.5% for first syllable stressed words and 2.2% for second syllable stressed words in the incongruent condition, 1.7% for first syllable stressed PHs and 2.5% for second syllable stressed PHs in the congruent condition, and 1.9% for first syllable stressed PHs and 2.3% for second syllable stressed PHs in the incongruent condition. There was no main effect of Congruency, $F(1, 15) = .39$, $MSE = .35$, $p = .54$, $\eta_p^2 = .03$, no main effect of Stimulus Type, $F(1, 15) = .94$, $MSE = .20$, $p = .35$, $\eta_p^2 = .05$, nor was there was a significant main effect of Syllable Stress, $F(1, 15) = .005$, $MSE = .46$, $p = .95$, $\eta_p^2 < .001$. There no significant Congruency x Syllable Stress interaction, $F(1, 15) = .55$, $MSE = .23$, $p = .47$, $\eta_p^2 = .04$, no Congruency x Stimulus Type interaction, $F(1, 15) = 1.22$, $MSE = .15$, $p = .29$, $\eta_p^2 = .08$, no significant Syllable Stress x Stimulus Type interaction, $F(1, 15) = 3.23$, $MSE = .40$, $p = .09$, $\eta_p^2 = .18$. Lastly, there was no significant Congruency x Syllable Stress x Stimulus Type interaction, $F(1, 15) = .02$, $MSE = .30$, $p = .88$, $\eta_p^2 = .001$.

3.10 Brain-Behaviour Correlations

In order to examine the brain-behaviour relationship, correlational analyses were also conducted between number of active voxels and active regions of the putamen (Experiment 4a), with mean RTs (Experiment 4b). In this case, there were no significant activations for congruent stimuli in the putamen, but given that there were for incongruent stimuli, brain-behaviour correlations were explored for those conditions. There were significant activations in the left putamen, only for PHs, and only for 13 of the participants. There were no significant correlations involving number of active voxels nor activation intensity with RT (all p's > .72)

3.11 Discussion and Conclusions

Experiment 4b aimed to examine whether speech production in a reading aloud task would be affected by a prior presentation of a rhythmic prime using optimally-controlled noun-verb homographs. The behavioural results replicated those of Experiment 3, and demonstrated that a target word or PH whose syllabic stress conformed to the temporal structure of the rhythm prime resulted in faster naming RTs compared to when a target word or PH did not conform to the temporal structure of the prime. The fact that there was no significant relation between brain activation and behavioural RT for PHs in the putamen, unlike Experiment 2b, may suggest that these matched first- and second-syllable stressed items are not optimal for detecting such relationships. Specifically, the representations for such stimuli likely correspond to both first and second syllable stress patterns, and thus are less sensitive for detecting entrainment relationships, although they do offer the optimal within-item matching for comparing noun and verb processing. Taken together, the behavioural results support the idea that rhythm may influence reading via grapheme to phoneme conversion or via the orthographic lexical system, as shown in Figure 10. The significant interaction of rhythm priming congruency with syllabic stress (i.e., nouns versus verbs) for both words and PHs, as well as the 3-way interaction with stimulus type, supports the notion that rhythm priming affects both the more dorsal sublexical reading process (via PHs), as well as the more ventral lexical reading process (via words).

CHAPTER 4

CASE STUDIES INVOLVING READING TASKS

Portions of this chapter have been previously published:

Gould, L., Mickleborough, M., Wu, A., Tellez, J., Ekstrand, C., Lorentz, E., Ellchuk, T., Babyn, P., & Borowsky, R. (2016). Pre-surgical language mapping in epilepsy: Using fMRI to identify functional reorganization in a patient with long-standing temporal lobe epilepsy. Epilepsy & Behavior, 5, 6-10. doi:10.1016/j.ebcr.2015.10.003

The goal of Chapter 4 is to provide a behavioural and neuroanatomical examination of reading processes in two patients. This chapter will: (1) examine the effect of rhythmic priming on reading aloud in a patient with Parkinson's disease (PD), given that these patients exhibit abnormalities in the putamen, which has been associated with rhythm (Cameron & Grahn, 2014; Grahn, 2009; Grahn, Henry, & McAuley, 2011; Grahn & Rowe, 2009; Harrington, Haaland, & Hermanowitz, 1998) and reading processes (Oberhuber et al., 2012; Experiments 2 & 5); and (2) we report a case in which a patient with intractable left temporal TLE who was undergoing a temporal lobectomy that involved removing regions of the left temporal lobe that are often thought to be important in language processing. The case involved using fMRI to localize language processing including reading of exception and regular words, pseudohomophones, and dual meaning words to determine whether these language functions were near the surgical resection plane in the left temporal lobe.

Case Study 1

The study of musical and speech rhythm and how those processes may interact with one another have been useful in determining the extent that entrainment (i.e., the process of synchronizing oscillators to external beats in auditory stimuli) can lead to an influence of one modality onto the other, and for elucidating the brain regions associated with these processes. Previous studies have examined the effect of rhythm on speech perception (Cason & Schön, 2012) and on reading aloud in normal populations (Gould et al., 2016), but studies have yet to examine the connection between musical and speech rhythm in patients, such as those with Parkinson's disease (PD), despite the fact that dysfunctions of the basal ganglia are frequently associated with impairments in the timing of motor functions. Moreover, aspects of speech, such as rhythm and timing organization have been shown to be impaired in patients with PD, and often lead to an accelerated rate of speech and a reduced number of pauses (Skodda & Schlegel, 2008; Skodda et al., 2010).

Pathologically, PD is characterized by a progressive degeneration of dopaminergic neurons projecting from the substantia nigra, which triggers a cascade of functional changes affecting the whole basal ganglia network (Delong & Wichmann, 2007; Jellinger, 2001). As a consequence, patients often show impairments of simple timing tasks such as motor timing and time perception (Harrington, Haaland, & Hermanowitz, 1998; Artieda et al., 1992; O'Boyle et al., 1996). Support for the notion that decreased dopamine levels in the striatum leads to these timing impairments comes from patients with PD who receive dopaminergic treatment showing improved motor timing (O'Boyle, 1997; Pastor et al., 1992; O'Boyle et al., 1996) and time perception (Malapani et al., 1998). Furthermore, impairments in timing tasks can be seen in healthy subjects following administration of dopamine receptor antagonist drugs (Rammsayer, 1999). In patients with PD, timing impairments in gait functions have been shown to improve in response to a metronome stimulus (e.g., Thaut et al., 1996; McIntosh et al., 1997; de Bruin et al., 2010; Nombela et al., 2013), but it remains to be seen whether PD patients will show a benefit in speech production following multiple-beat rhythm priming.

The putamen has received particular consideration in the study of rhythm processing, and has been found to be implicated in both the production and perception of rhythm (Cameron & Grahn, 2014; Grahn, 2009; Grahn, Henry, & McAuley, 2011; Grahn & Rowe, 2009; Harrington, Haaland, & Hermanowitz, 1998), organizing and enacting sequences of simple speech sounds (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Bohland & Guenther, 2006; Kuljic-Obradovic, 2003; Oberhuber et al., 2013; Riecker et al., 2005; Sakurai, Momose, Iwata, Watanabe, Ishikawa, & Kanazawa, 1993), and making predictions in upcoming events leading to optimized speech comprehension (Rothermich & Kotz, 2013). Grahn and Rowe (2009) suggest that a cortico-subcortical network, including the putamen, supplementary motor area (SMA), and premotor cortex, is engaged for the analysis of temporal sequences and prediction or generation of beats, especially under conditions that require internal generation of the beat. Moreover, the basal ganglia, and specifically the putamen, show a specific response to the beat during rhythm perception, regardless of musical training or how the beat is expressed (Grahn & Rowe, 2009).

A study by Grahn and Brett (2009) tested patients with PD and controls on a rhythm discrimination task in which patients listened to two identical rhythms, and then compared those to a third rhythm that could be the same or different. They found that controls showed a benefit in the task in which rhythms were beat-based (i.e., simple rhythmic sequences) compared to non-beat based (i.e., complex rhythmic sequences), but the patients with PD did not show that same benefit. That is, discrimination was significantly worse for patients with PD compared to controls, but only in the beat-based condition. The authors postulated that these data may suggest that PD patients are either impaired at extracting the beat structure when initially listening to the rhythms, or that they are less able to use the beat structure to improve their performance during the subsequent comparison of the rhythms. As the PD patients are not significantly impaired in the non-beat-based condition, the deficit appears to be specific to sequences that involve beat processing. Studies have also shown that patients with PD can show improved speech production, such as rate of speech and fluency, by speaking with a simple beat-based metronome cue compared with speech alone, which is a technique often referred to as rhythmic cueing (Thaut, McIntosh, McIntosh, & Hoemberg, 2001).

Neuroimaging studies have revealed many neurofunctional correlates underlying motor timing behavior of patients with PD, as well as the specific consequences of basal ganglia disruption on cerebral blood flow. Several fMRI studies have reported underactivation in neural structures, including the basal ganglia, as well as regions that receive output from the basal ganglia such as the SMA/pre-SMA (Lewis et al., 2007; Haslinger et al., 2001; Elsinger et al., 2003; cf. Cerasa et al., 2006). For example, Lewis et al. (2007) compared externally versus internally guided movements (i.e., participants were told to copy finger tapping sequences that were presented on a screen, or to continue a previously learned finger tapping sequence, respectively) in monozygotic twins in which one twin had PD and the other did not. They found that during the externally guided task there were no significant differences in activation between the twins in the basal ganglia-cortical pathways, but during the internally guided task the PD-twin had less activation than the non-PD-twin in the basal ganglia-cortical pathways. Another fMRI study by Elsinger et al. (2003) found underactivation in the basal ganglia, sensorimotor cortex, cerebellum, and SMA/pre-SMA in PD patients compared to controls in a simple paced finger-tapping task. These results are taken to indicate that impaired timing reproduction in PD patients is associated with reduced brain activation within motor and medial premotor circuits. Nevertheless, there is evidence that levodopa may partially improve impaired motor function and activation in the SMA during simple volitional movements (Haslinger et al., 2001). Taken together, these studies suggest that the network of brain regions associated with timing of motor and rhythm tasks in patients with PD may be distinct from the networks activated in control participants for the same tasks.

The Putamen and Reading

Another important experiment for the present case study is by Oberhuber et al. (2013), who compared fMRI brain activation for the reading of words and pseudowords relative to picture and colour naming. Their results demonstrated that the most significant effect was in the left putamen and revealed a functional dissociation between the anterior and posterior portions, whereby the anterior putamen was most activated by pseudowords and the posterior putamen was most activated by words. These findings motivated some of our previous work that explored the connection between rhythm and speech processes. Gould, McKibben, Ekstrand, Lorentz, and Borowsky (2016; Experiment 1) examined whether reading aloud was affected by the presentation of a rhythmic prime that was either congruent or incongruent with the syllabic stress of the target letter string. The targets were words that placed the stress on either the first or second syllable (*prac*tice vs. po*lice*, to investigate lexical processing), as well as their corresponding pseudohomophones (PHs; letter strings that sound like actual words when read phonetically but are spelled differently; *prak*tis vs. po*leese*, to investigate phonetic decoding). The results demonstrated that reaction times (RTs) were faster for PHs when the rhythmic prime was congruent with the syllabic stress, and slower when the rhythmic prime was incongruent. These results were taken to suggest that PHs showed a larger effect given that they must be phonetically decoded. In general, this suggests that a rhythmic prime matched to the syllabic stress of a letter string that requires phonetic decoding aids sublexical reading processes.

Subsequently, Experiment 2b further investigated the behavioural effect of rhythm priming on reading, and Experiment 2a studied the brain regions involved in the rhythm priming paradigm using fMRI. The behavioural results from the MRI demonstrated that naming RTs were faster for both words and PHs when preceded by a rhythmic prime that was congruent with the syllable stress of the target letter string compared to when the rhythmic prime was incongruent. It was posited that the lack of rhythm priming effects for word stimuli in Gould et al. (2016; Experiment 1) may have been due to a floor effect (i.e., mean RTs for words were ~500-525 ms), but in the fMRI environment the TR of 3300ms served to slow participants' RTs to ~1100-1150ms for words, thereby allowing the effect to be seen for words as well as PHs. The fMRI results converged with the findings reported by Oberhuber et al. (2013) for pseudowords, whereby activation was found in the left anterior putamen for PHs, which force reliance on phonetic decoding. There were also regions of shared activation between words and PHs, including the cerebellum, occipital lobe, middle occipital gyrus, thalamus, inferior frontal gyrus, putamen, precentral gyrus, and SMA, which is consistent with previous literature that has implicated these regions in language related tasks (see also Price, 2012 for review). Furthermore, the results revealed greater activation in the right anterior putamen for PHs in the congruent versus incongruent rhythm priming condition, suggesting that the putamen may be sensitive to subtle variations in rhythms in both musical and speech processes.

Given that the putamen has been associated with rhythm (Cameron & Grahn, 2014; Grahn, 2009; Grahn, Henry, & McAuley, 2011; Grahn & Rowe, 2009; Harrington, Haaland, & Hermanowitz, 1998) and reading processes (Oberhuber et al., 2012; Experiments 2 & 5), and that it is clear that PD is associated with dysfunction in this region, it was posited that patients with PD may display a different pattern of brain activity, and/or lower level of activity, compared to normal healthy participants in the rhythm priming reading task.

4.1 Case Report

The patient was a 68-year old female with early stages of PD (i.e., minimal tremors/shaking, no difficulties walking/moving, and no speech impairments). We restricted our sample to a PD patient in earlier stages of the disease progression so as to avoid a complete absence of putamen response. The patient had normal vision, was right-handed, and was on a standard levodopa medication regimen. The patient had no difficulties understanding task instructions, and their conversational speech was clear and comprehensible. Written informed consent to participate in the study was obtained, and all testing procedures were approved by the University of Saskatchewan Research Ethics Board and have therefore been performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and its later amendments.

4.2 Methods

4.2.1 Stimuli & Procedure

The stimuli were the same as Experiment 1. The patient was presented with two blocks of trials. The first was the word naming condition and the second was the PH naming condition, both of which had targets preceded by rhythm primes that were that were either congruent or incongruent with the syllabic stress of the target letter string. The letter strings were presented individually on a computer screen, and the participant was asked to read the letter strings aloud as quickly and accurately as possible. Participation took approximately 15 minutes.

All stimuli were presented using a PC running EPrime software (Psychology Software Tools, Inc., http://www.pstnet.com) through MRI compatible goggles (Cinemavision Inc., http://www.cinemavision.biz). The leading edge (10 μs) of the fiber-optic signal that is emitted by the MRI at the beginning of each acquisition volume was detected by a Siemens fMRI trigger converter and passed to the EPrime PC via the serial port. As such, perfect continuous synchronization between the MRI and the experimental paradigm computer was obtained at each volume. While speaking the patient was instructed to speak with his mouth kept slightly open to minimize mouth and jaw movements and was encouraged to not swallow or lick her lips during the experimental trials.

4.3 Behavioural Study

The rhythm priming reading task was also tested on 16 healthy participants with normal or corrected-to-normal vision who spoke fluent English (approved by the University of Saskatchewan Research and Ethics Board). This behavioural study design was the same as the patient's (Experiment 2), and also took place in an fMRI scanner.

4.3.1 Behavioural Analysis

Vocal responses were recorded at 96KHz, 24bit using an Olympus LS11 digital recorder. These recordings were analyzed using PRAAT software (Boersma & Weenink, 2009), and the waveforms and broadband spectrograms were used to localize vocalization onset RT. Given that we used a sparse-sampling (gap paradigm) fMRI method that allows the participant to respond during a gap in image acquisition, the stimulus onset was synchronized with the last gradient sound before the gap. This provided an acoustic marker for the onset on the recording while the gap allowed for a clear recording of the participant's vocal response. Moreover, recording participants' vocal responses allowed for the verification that each stimulus was being read as intended.

4.4 fMRI Protocol

All imaging was conducted using a 3 Tesla Siemens Skyra scanner. Whole-brain anatomical scans were acquired using a high resolution magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence consisting of 192 T1-weighted echo-planar images (EPI) slices of 1-mm thickness (no gap) with an in-plane resolution of 1 x 1 mm (field of view 256 x 256; TR = 1900 ms; TE = 2.08 ms).

For each of the functional tasks, T2*-weighted single shot gradient-echo echo-planar imaging (EPI) scans were acquired using an interleaved ascending EPI sequence, consisting of

55 volumes of 25 axial slices of 4-mm thickness (1-mm gap) with an in-plane resolution of 2.65-mm X 2.65-mm (field of view = 250) using a flip angle of 90°. The top 2 coil sets (16 channels) of a 20-channel Siemens head-coil were used. Additional foam padding was used to reduce head motion. In order to acquire verbal behavioural responses, we used a blocked (task vs relax) sparse-sampling (gap paradigm) fMRI method that allows the participant to respond during a gap in image acquisition (TR = 3300 ms, with a 1650 ms gap of no image acquisition; TE = 30 ms; Flip Angle = 90; e.g., Borowsky et al., 2005, 2006, 2007, 2013). The patient responded vocally during the regular, periodic 1650 ms gap in the image acquisition that followed the offset of each volume of image acquisition, which allowed the patient to respond with no noise interference from the MRI.

4.4.1 fMRI Analyses

All preprocessing and statistical analyses for functional images were performed using Brain Voyager QX Version 2.6.1 (*www.brainvoyager.com*). Functional images were preprocessed and corrected for slice scan time acquisition (cubic spline interpolation), 3D motion correction (trilinear/sinc interpolation), and temporal filtering with a high-pass (GLM-Fourier) filter to remove frequencies less than two cycles/time course. The functional data were assessed for head motion and/or magnet artifacts by viewing cine-loop animation and examining motion detection parameter plots following the 3D motion correction. The first five image volumes were used to achieve steady state of image contrast and were discarded prior to analysis. Blocked analyses were conducted in order to compare words versus PHs, and event-related analyses were conducted to examine the differences between congruent and incongruent rhythm and syllabic stress conditions for both the words and PHs separately. Instructing participants to name the word or PH in pure blocks (instead of mixed) maximized sensitivity of the neuroimaging experiment to detect regions of activation.

4.7 Behavioural Results

The naming onset RT that it took the patient to correctly name the word or PH was measured in ms for each trial, and the mean error rate of each condition was also computed. Spoiled trials were removed before analyses were conducted on mean RTs and error rates (3.3% for word trials, 10% for PH trials).

Naming Reaction Time

The patient's speech during the test trials was clear, and there was no sign of difficulty with the task. The mean RTs showed that the patient responded slower to both words and PHs compared to the normal healthy participants (Figure 17). Further, the patient responded faster for words (*M* = 1282.60 ms) compared to PHs (*M* = 1515.18 ms), which corroborates the results from the normal healthy participants, whose correct mean RTs were significantly faster for words (*M* = 1116.54 ms) compared to PHs (*M* = 1228.64 ms), $F(1, 15) = 66.49$, $MSE = 3024.10$, $p < .001$. In terms of the congruency effect, the patient's results were also similar to the results from the healthy participants in that the patient demonstrated a larger effect of congruency for words (*M* = 27 ms difference) compared to PHs (*M* = 12 ms difference), and the healthy participants demonstrated 58 ms difference for words and 35 ms difference for PHs, which trended towards a Congruency x Stimulus Type interaction, $F(1, 15) = 2.71$, $MSE = 810.02$, $p = .12$. The mean difference score between congruent and incongruent words was also compared to the mean difference score for congruent and incongruent PHs between healthy participants and the PD patient. This analysis is illustrated in Figure 18, and the blue bar displays the healthy participants' interaction effect size (i.e., difference of the congruency effect between words and PHs; 23 ms) and the asterisks displays the PD patient's difference score (15 ms). The 95% confidence interval (CI; Loftus & Masson, 1994) was ± 20.58 ms, which demonstrates that the PD patient's interaction effect falls within the 95% CI of the normal healthy participants' interaction effect (i.e., a significant interaction effect by this analysis given that the 95% CI does not include 0).

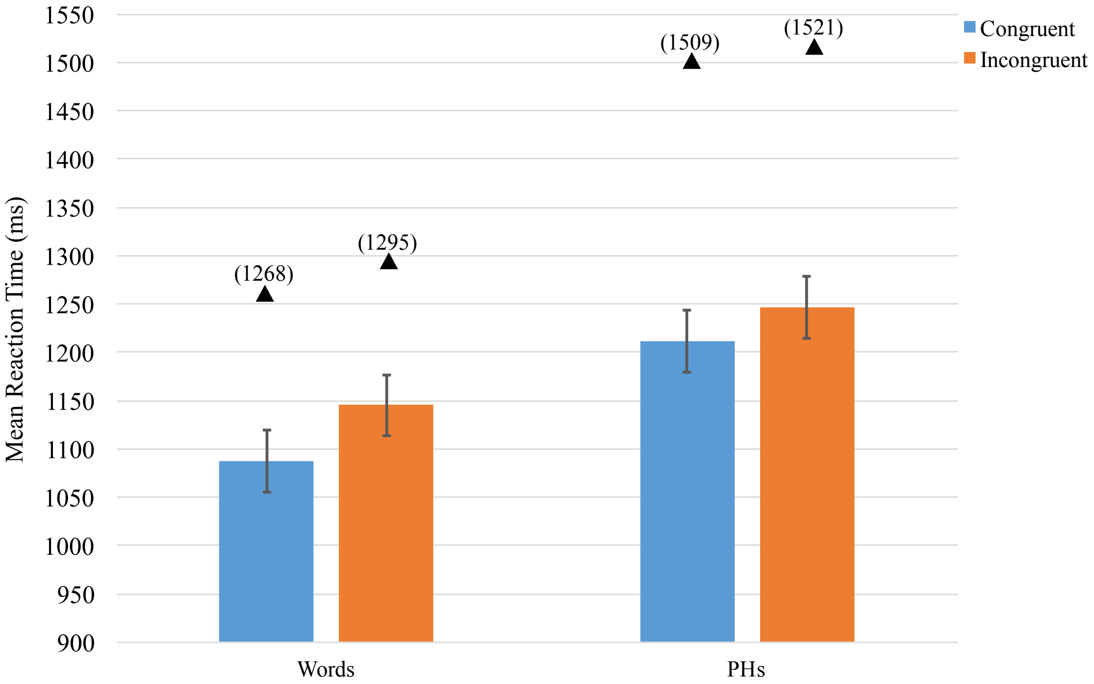


Figure 17: Mean reaction time (RT) representing the onset time taken to correctly name words and PHs as a function of Congruency and Stimulus Type for normal healthy participants (orange and blue bars) compared to the patient with PD (triangles). The 95% confidence interval (CI; Loftus & Masson, 1994) for word and pseudohomophones (PHs) naming RT was ± 20.58 ms.

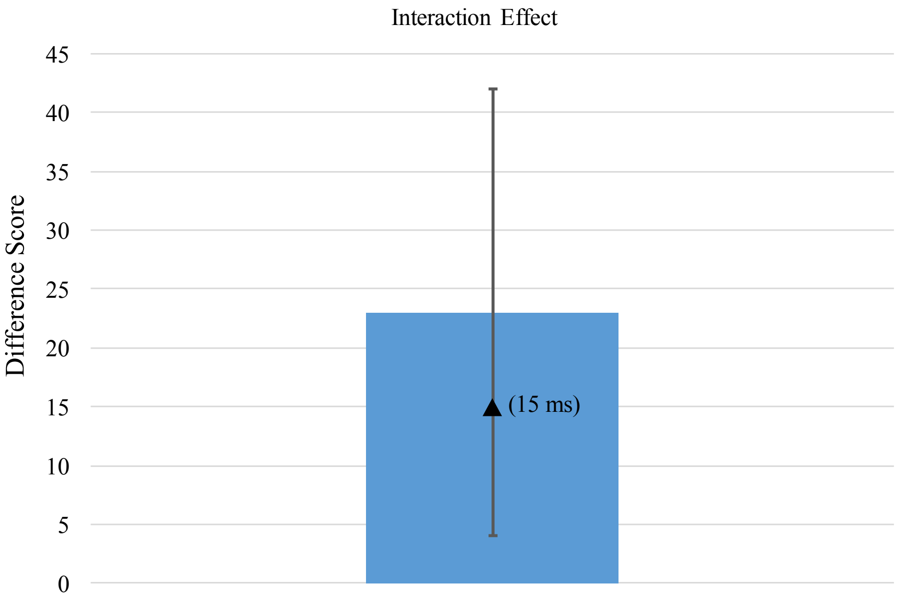


Figure 18: The mean difference score between congruent and incongruent words compared to the mean difference score for congruent and incongruent PHs between healthy participants and

the patient with PD. The blue bar shows the healthy participants' difference score (23 ms) and the triangle displays the PD patient's difference score (15 ms).

Naming Error Rates

The accuracy of the patient's responses was computed by determining the percentage of errors in each of the word and PH conditions (Figure 19). The error rates show that the patient made fewer errors in the word conditions ($M = 0\%$) than the PH conditions ($M = 6.6\%$) compared to 1.7% and 1.8% in the healthy participants, respectively, $F(1, 15) = .004$, $MSE = .21$, $p = .95$. The patient showed no difference in accuracy between the congruent words and incongruent words ($M = 0\%$), but displayed a larger difference for PHs such that there were lower errors for congruent PHs ($M = 0\%$) compared to incongruent PHs ($M = 6.6\%$). The mean difference score between congruent and incongruent words was also compared to the mean difference score for congruent and incongruent PHs between healthy participants and the PD patient. The healthy participants' interaction effect was .10% and the PD patient's difference score was 6.6%. The 95% CI (Loftus & Masson, 1994) was ± .17%, thus demonstrating that the PD patient's interaction effect on error rate was larger than the normal healthy participants' interaction effect. The normal healthy participants demonstrated no main effect of Congruency, $F(1, 15) = .60$, $MSE = .10$, $p = .45$, but a trend for a Congruency x Stimulus Type interaction, $F(1, 15) = 2.98$, $MSE = .04$, $p = .10$.

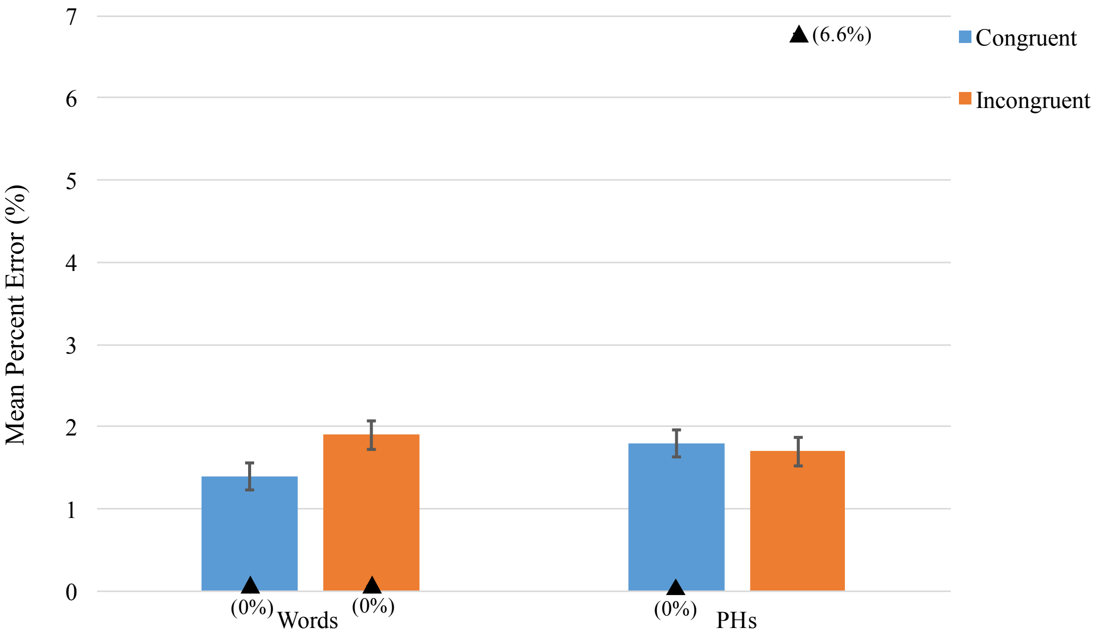
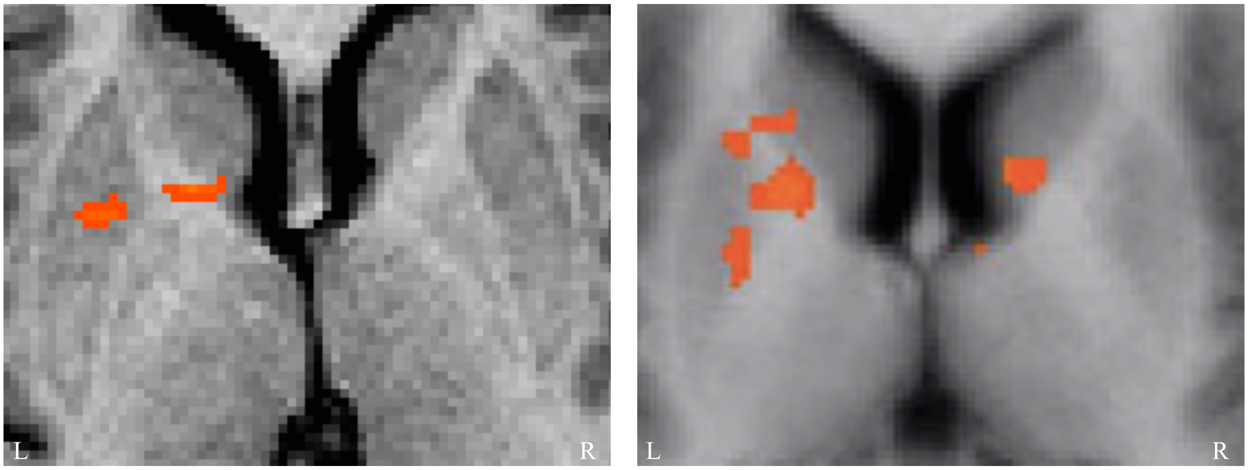


Figure 19: Mean percent error (%) for correctly named words and PHs as a function of Congruency and Stimulus Type for normal healthy participants (orange and blue bars) compared to the patient with PD (triangles). The 95% confidence interval (CI; Loftus & Masson, 1994) for word and pseudohomophones (PHs) error rate was ± .17%.

4.8 Neuroimaging Results

Regions of Activation for Greater for Words Compared to PHs

The regions of activation that were greater for words compared to PHs at a threshold of $t(112) = 2.50$, $p < .01$ include the left cerebellum (-16, -70, -24/-16, -54, 24), left anterior cingulate (-3, 41, -5), left putamen (-23, 0, 4; Figure 21), left internal capsule (-12, 2, 6), left superior frontal gyrus (-3, 50, 7), left middle temporal gyrus (-58, -5, -11), left middle frontal gyrus (-49, 43, 7), and left postcentral gyrus (-54, -23, 21). Figure 20 also illustrates the activation in the left putamen for PHs greater than words in the normal healthy participants as a comparison.



Words > PHs

PHs > Words

Figure 20: Activation in the left putamen for words greater than pseudohomophones (PHs) in the patient with PD (left image) and activation in the left putamen for PHs greater than words in the normal healthy participants (right image).

Regions of Activation Greater for PHs Compared to Words

The regions of activation that were greater for PHs compared to words at a threshold of $t(112) = 2.50$, $p < .01$ include the left cerebellum (-13, -62, -24), left middle frontal gyrus (-47, 16, 33), left postcentral gyrus (-38, -18, 45), and left IFG (-32, 30, -2).

Regions of Shared Activation for Words and PHs

The regions of shared activation for words and PHs at a threshold of $t(112) = 3.50$, $p < .01$ included the left cerebellum (Talairach coordinates, x, y, z: -27, -57, -24), bilateral occipital lobe (-29, -74, -17/29, -74, -17), bilateral inferior temporal gyrus (-47, -52, -11/33, -52, -11), bilateral superior temporal gyrus (-51, 6, 2/57, 7, 5), left inferior frontal gyrus (-47, 28, 8/-40, 5, 29), left posterior insula (-40, -40, 18), left postcentral gyrus (-55, -19, 18), right cuneus (25, -76, 20), bilateral precuneus (-21, -66, 35/23, -62, 35), left cingulate cortex (-10, 2, 35), bilateral precentral gyrus (-44, -18, 35/46, -14, 35), left superior parietal lobule (-28, -48, 41), right medial frontal gyrus (3, 3, 52), and bilateral superior frontal gyrus (-7, -1, 61/4, -1, 61).[4]

4.9 Discussion

The behavioural results demonstrated that the patient with PD showed the same benefit from congruent rhythm primes as normal healthy participants, which has implications for the development of a speech rehabilitation technique that uses entrainment (e.g., rhythmic cueing). In terms of gross motor rehabilitation in individuals with PD, studies have demonstrated the effectiveness of external auditory rhythmic cueing for motor entrainment to a beat (see Fujii & Wan, 2014). Given that the basal ganglia, which is impaired in patients with PD, is also susceptible to entrainment (Fujii & Wan, 2014; Guenther, Ghosh, Tourville, 2006; Kotz, Schwartze, & Schmidt-Kassow, 2009), it opens up important avenues of study with regard to the effect of auditory rhythm on impaired speech production. Indeed, rhythmic cueing has been shown to produce significant improvements in the rate of speech production in patients with PD, whereby individuals with speech impairments spoke more fluently to a simple metronome beat compared with speech alone (Thaut, McIntosh, McIntosh, Hoemberg, 2001). Furthermore, speech entrainment to simple, single beat rhythmic cues has been shown to improve speech production in individuals with traumatic brain injury (Pilon, McIntosh, Thaut, 1998), stuttering (Ingham, Bothe, Jang, Yates, Cotton, & Seybold, 2009; Ingham, Bothe, Wang, Purkhiser, & New, 2012), aphasia (Brendel, & Ziegler, 2008), as well as in children with underdeveloped motor coordination (LaGasse, 2013). The present study demonstrates that two-beat rhythms can

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[4] The event-related analyses that were conducted in order to examine the effect rhythm priming on reading words and PHs (i.e., the congruency effect) did not have enough power to pick up any effects given that it was based on a single patient's data.

effectively prime disyllabic words according to their syllabic stress, which further extends rhythmic cueing techniques beyond simple single-beat rhythms and captures the greater complexity of syllabic stress in speech production.

In terms of the fMRI results, normal healthy participants showed greater activation for PHs than words in the left anterior putamen, whereas the PD patient demonstrated greater activation for words than PHs in the left anterior putamen. Furthermore, the results revealed that the patient activated fewer brain regions for PHs compared to words, whereas the normal healthy participants showed activation in several regions for PHs, but no regions of activation higher for words compared to PHs. This finding may be explained by the hierarchical model of specialized function (Ogden, 1996) or the ‘crowding hypothesis’ for language processing (Lansdell, 1969). That is, it may be the case that sublexical reading is lower in the hierarchy of specialized function and was “crowded out” of some regions important for language processing (e.g., anterior cingulate, putamen, internal capsule, superior frontal gyrus, middle temporal gyrus).

However, both lexical and sublexical reading systems appear to be intact for the PD patient, as evidenced by their naming accuracy. Thus, although sublexical reading may show less brain activation compared to words, it is not the case that such functioning is completely abolished, nor is sublexical processing completely absent from brain regions involved in language processing. Considering previous findings that have reported underactivation in neural structures including the basal ganglia, and regions that receive output from the basal ganglia such as the SMA/pre-SMA in patients with PD (Lewis et al., 2007; Haslinger et al., 2001; Elsinger et al., 2003), it is noteworthy that the patient in the present study still demonstrated an effect within the region-of-interest (i.e., the putamen).

4.10 Conclusions

Taken as a whole, the fact that a patient with PD demonstrated the same behavioural effect as normal participants, whereby individuals benefited from the rhythm prime being congruent with the syllabic stress of the target letter string, provides promising support for the use of rhythm as an effective rehabilitation tool for the timing impairments seen in patients with PD. The fMRI results revealed that despite disruptions in basal ganglia functioning following PD, there was still activation in the putamen for reading real words, which is argued to be higher in the hierarchy of specialized functions model and thus, may be retained for longer following PD diagnosis. Additional studies are required to elucidate the exact nature of the process that the basal ganglia, and specifically the putamen, engage in during rhythm and reading processes in

PD, but these data suggest that a patient may benefit from rhythmic priming techniques to rehabilitate timing functioning. The following case study describes how the reading aloud task may be useful not only for studying speech impairments in patients with PD, but also for localizing brain regions near the surgical resection plane in patients undergoing brain surgery, such as for the treatment of TLE.

Case Study 2

Portions of this experiment have been previously published in:

Gould, L., Mickleborough, M., Wu, A., Tellez, J., Ekstrand, C., Lorentz, E., Ellchuk, T., Babyn, P., & Borowsky, R. (2016). Pre-surgical language mapping in epilepsy: Using fMRI to identify functional reorganization in a patient with long-standing temporal lobe epilepsy. *Epilepsy & Behavior, 5,* 6-10. doi:10.1016/j.ebcr.2015.10.003

The study of behavioural and neurofunctional correlates associated with reading tasks is not only useful for studying potential remedial techniques for patients with speech impairments, such as those with PD, but also for localizing brain regions near the surgical resection plane in patients undergoing brain surgery, such as for the treatment of TLE, brain tumours, cortical and vascular malformations, and other lesions in order to avoid disrupting these processes as much as possible. Given that each patient type presents unique challenges with respect to developing cognitive tasks that will serve to activate regions near their surgical margins, various paradigms can be developed to localize each patient's specific peri-lesional functional regions by using fMRI, which can also provide a relative index for language lateralization (Ekstrand, Mickleborough, Fourney, Gould, Lorentz, Ellchuk, & Borowsky, 2016; Mickleborough, Kelly, Gould, Ekstrand, Lorentz, Ellchuk, Babyn, & Borowsky, 2015).

We report a 55-year-old, right-handed patient with intractable left TLE, who previously had a partial left temporal lobectomy. The patient could talk during seizures, suggesting that he might have language dominance in the right hemisphere. Pre-surgical fMRI localization of language processing including reading of exception and regular words, pseudohomophones, and dual meaning words confirmed the clinical hypothesis of right language dominance, with only small amounts of activation near the planned surgical resection and thus minimal eloquent cortex to avoid during surgery. Post-operatively, the patient was rendered seizure free without speech deficits.

In patients with epilepsy, it is especially important to delineate language areas prior to surgery, as functional anatomy may be reorganized with transfer of functions to other areas in the ipsilateral or contralateral hemisphere (Duffau et al., 2003; Rasmussen & Milner, 1977; see also Cummine, Borowsky, Stockdale Winder, & Crossley, 2009 for evidence following hemispherectomy). For example, functional imaging studies of language processing in chronic epilepsy patients with a left hemisphere focus have provided evidence for a preoperative right hemispheric activation shift (Billingsley, McAndrews, Crawley, & Mikulis, 2001; Carpentier et al., 2001; Gaillard, 2002; Rutten, Ramsey, van Rijen, Alpherts, & van Veelen, 2002; Adcock, Wise, Oxbury, Oxbury, & Matthews, 2003; Sabsevitz et al., 2003). Surgical resection of epileptogenic regions requires knowledge of any shift of language function, as it may serve as a prognostic indicator and/or impact the surgical approach with the potential to minimize neurologic deficits post surgery.

Case Study 2 describes a case in which the surgical resection for a patient with epilepsy involved cortical regions that are known in the cognitive neuroscience literature to be a part of the language network (i.e., the left anterior-to-posterior temporal lobe; Grabowski, Damasio, Tranel, Boles Ponto, Hichwa, Damasio, 2001; Visser, Jefferies, & Lambon Ralph, 2010; Price, 2012; Borowsky, Loehr, Friesen, Kraushaar, Kingstone, & Sarty, 2005; Borowsky, Cummine, Owen, Friesen, Shih, Sarty, 2006; Borowsky, Esopenko, Cummine, Sarty, 2007; Cummine et al., 2010). The aim was to determine whether language functioning had shifted to the right hemisphere in this patient due to long-standing left TLE and a previous partial left temporal lobectomy. By including assessment of reading different types of letter strings in pre-surgical fMRI (see also Mickleborough et al., 2015), the case provided evidence that this type of language processing was localized primarily in the right hemisphere in this patient.

The study examined activation for reading aloud familiar exception words (words that do not follow regular spelling-to-sound mappings; e.g., one) and regular words (e.g., won), which have been shown to primarily activate brain regions in the temporal lobe, particularly the exception words which rely on ventral stream processing (Borowsky, Loehr, Friesen, Kraushaar, Kingstone, & Sarty, 2005; Borowsky, Cummine, Owen, Friesen, Shih, & Sarty, 2006; Borowsky, Esopenko, Cummine, Sarty, 2007; Cummine et al., 2010). The study also examined activation for pseudohomophones (letter strings that when phonetically decoded sound like real words, e.g., wun), which have been shown to activate regions of the dorsal visual processing stream (Borowsky, Cummine, Owen, Friesen, Shih, & Sarty, 2006). Lastly, dual-meaning words (e.g., bank) were used to maximally activate the language network (Borowsky, Esopenko, Gould, Kuhlmann, Sarty, & Cummine, 2013) by asking the patient to read the word aloud and to think about another word that was associated with it.

4.11 Case Report

The patient is a 55-year old right-handed male, presenting with intractable left TLE. The surgical resection involved planned access via the left anterior temporal pole. The patient had a previous partial left temporal lobe resection in conjunction with evacuation of a traumatic intracranial hematoma in 1979. Two years after the trauma he began to experience complex partial seizures with and without secondary generalization. Speech was not arrested during the seizures. Scalp EEG revealed an epileptogenic focus in the left temporal lobe. On the MRI, the left amygdala and hippocampus were noted to still be present, with evidence of post-traumatic hippocampal encephalomalcia/gliosis. The neurosurgeon and neurologist requested clinical fMRI to localize speech, and better delineate the area of planned resection (typically a coronal plane 60 mm posterior to the anterior temporal pole on the lateral surface, and 40 mm posterior on the medial surface). As the patient could speak during seizures, the neurologist suspected that the patient might be right hemisphere language dominant. The patient's consent was obtained and the experiment was performed in compliance with the Declaration of Helsinki (2008) and the relevant laws and institutional guidelines, and was approved by the University of Saskatchewan Research Ethics Board.

4.12 Materials and Methods

4.12.1 fMRI Protocol

All imaging was conducted using a 3 Tesla Siemens Skyra scanner. Whole-brain anatomical scans were acquired using a high resolution magnetization prepared rapid acquisition gradient echo sequence consisting of 192 T1-weighted EPI slices of 1-mm thickness (no gap) with an in-plane resolution of 1 x 1 mm (field of view 256 x 256; TR = 1900; TE = 2.08). For each of the functional tasks, T2*-weighted single shot gradient-echo EPI scans were acquired using an interleaved ascending sequence, consisting of 55 volumes of 25 axial slices of 4-mm thickness (1-mm gap) with an in-plane resolution of 2.65-mm X 2.65-mm (field of view = 250) using a flip angle of 90°. The top 2 coil sets (16 channels) of a 20-channel Siemens head-coil were used. In order to acquire verbal behavioural responses, a blocked (task vs relax) sparse-sampling method was used that allows the participant to respond during a gap in image acquisition (TR = 3300 ms, with a 1650 ms gap of no image acquisition; TE = 30 ms; Flip Angle = 90; e.g. 18-21; 25). The patient responded vocally during the regular, periodic 1650 ms gap in the image acquisition that followed the offset of each volume of image acquisition, which allowed the patient to respond with no noise interference from the MRI and task-compliance could be monitored.

4.12.2 Stimuli & Language Tasks

The stimuli were presented using a PC running EPrime software (Psychology Software Tools, Inc., http://www.pstnet.com) through MRI compatible goggles (Cinemavision Inc., http://www.cinemavision.biz). The leading edge (10 µs) of the fiber-optic signal that is emitted by the MRI at the beginning of each acquisition volume was detected by a Siemens fMRI trigger converter and passed to the EPrime PC via the serial port. As such, perfect continuous synchronization between the MRI and the experimental paradigm computer was obtained at each volume.

The patient was presented 100 monosyllabic letter strings, which consisted of 25 regular words, 25 exception words, 25 PHs, and 25 dual meaning words in separate runs, in blocks of 5, interspaced with blocks of relaxation. These stimuli were matched on several of the characteristics available from the E-Lexicon Database (http://elexicon.wustl.edu/; Balota et al., 2007). The patient was asked to read the stimulus aloud during the gap in image acquisition. For the dual meaning word task, the patient was also asked to think about another word that is associated with it.

4.12.3 fMRI Analyses

All preprocessing and statistical analyses for functional images were performed using Brain Voyager QX Version 2.6.1 (www.brainvoyager.com). Functional images were preprocessed and corrected for slice scan time acquisition (cubic spline interpolation), 3D motion correction (trilinear/sinc interpolation), and temporal filtering with a high-pass filter to remove frequencies less than two cycles/time course. The first five image volumes were used to achieve steady state of image contrast and were discarded prior to analysis.

4.13 Neuroimaging Results

All four reading tasks revealed clear activation of the right posterior occipitotemporal region in the ventral visual stream (see cross hairs in Figure 21) using a linear correlation threshold of $r(46) = 0.60$, $p < .0001$, with the exception words and pseudohomophones showing the greatest area of activation. The pseudohomophones activated a region more anterior and medial in the right temporal lobe, and the dual meaning words activated a region in the right posterior occipital area. Moreover, the exception words also activated a region of the right frontal lobe, which is likely the homologue region of Broca's area (Figure 22). The exception words and dual meaning words also activated temporal regions of the left hemisphere, which were close to, but posterior to the planned resection line (Figure 23).

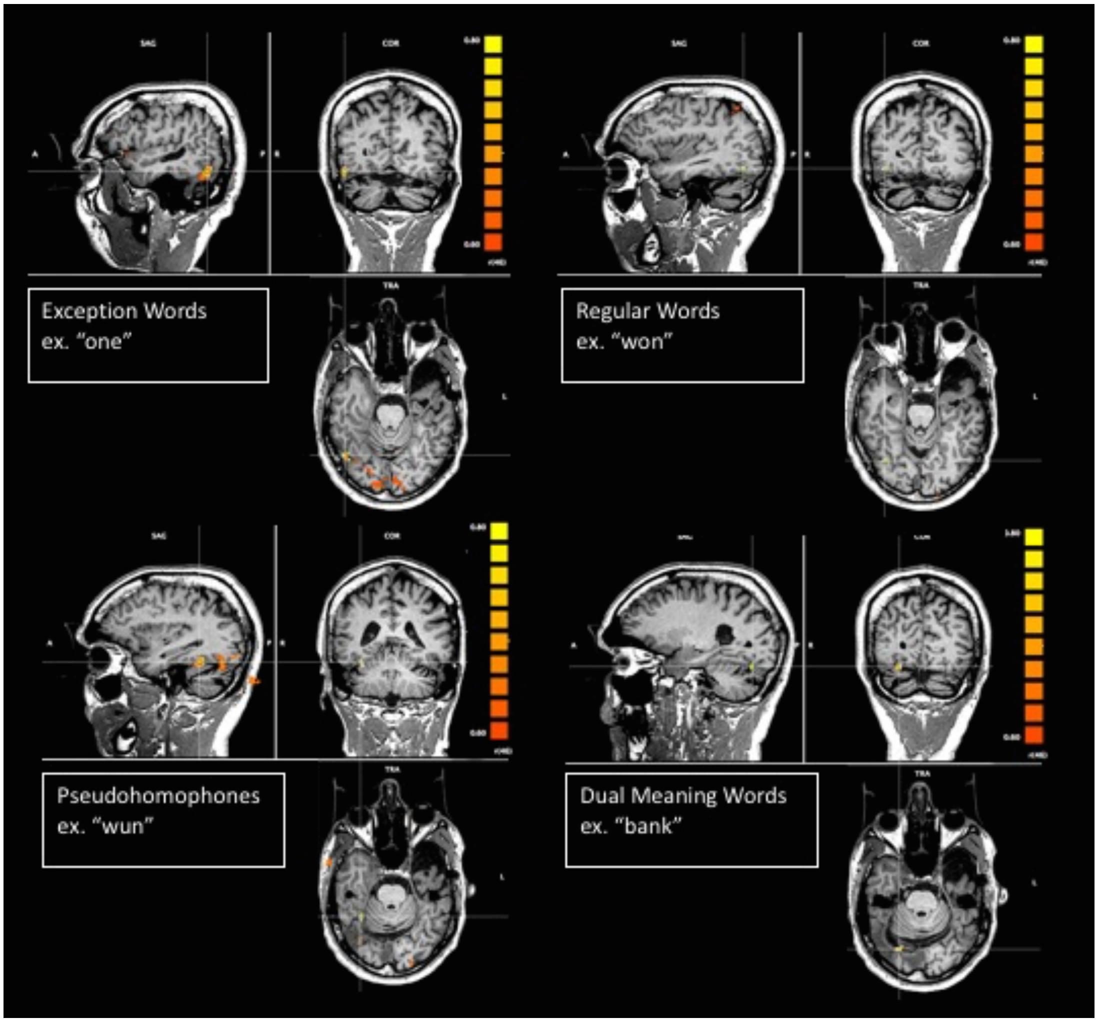

Figure 21: Anatomical T1 images as underlays, and functional T2* images as functional overlays for regions of BOLD activation for task > rest for exception words, regular words, pseudohomophones, and dual meaning words, $r(46) = .60$, $p < .0001$.

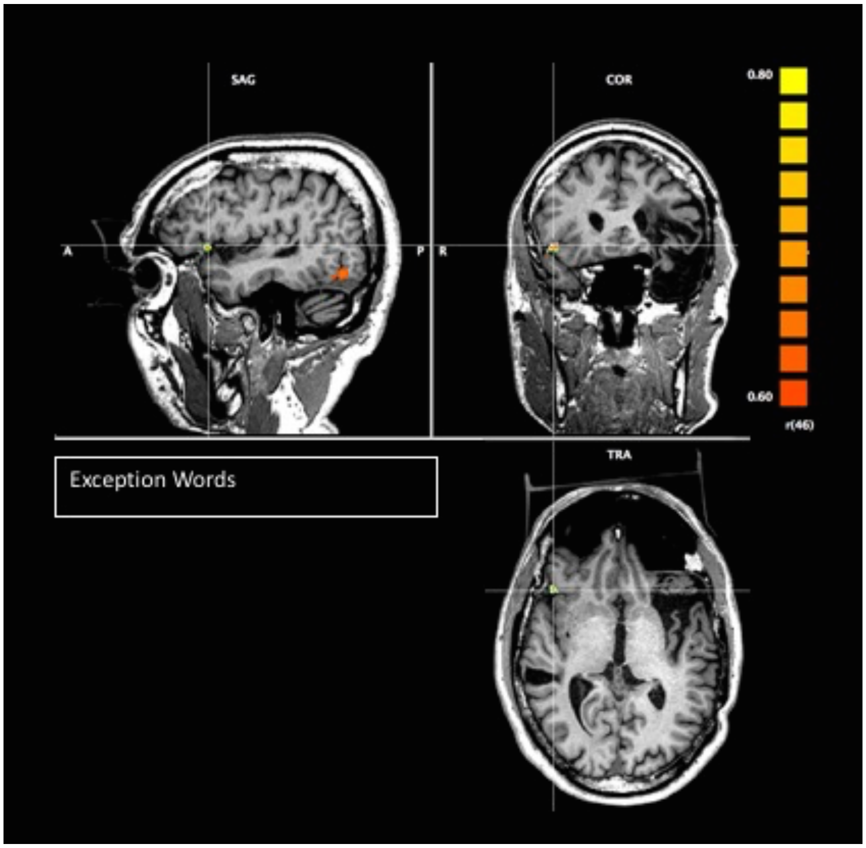

Figure 22: T1 images as underlays, and T2* images as functional overlays for regions of BOLD activation for task > rest for exception words, $r(46) = .60$, $p < .0001$.

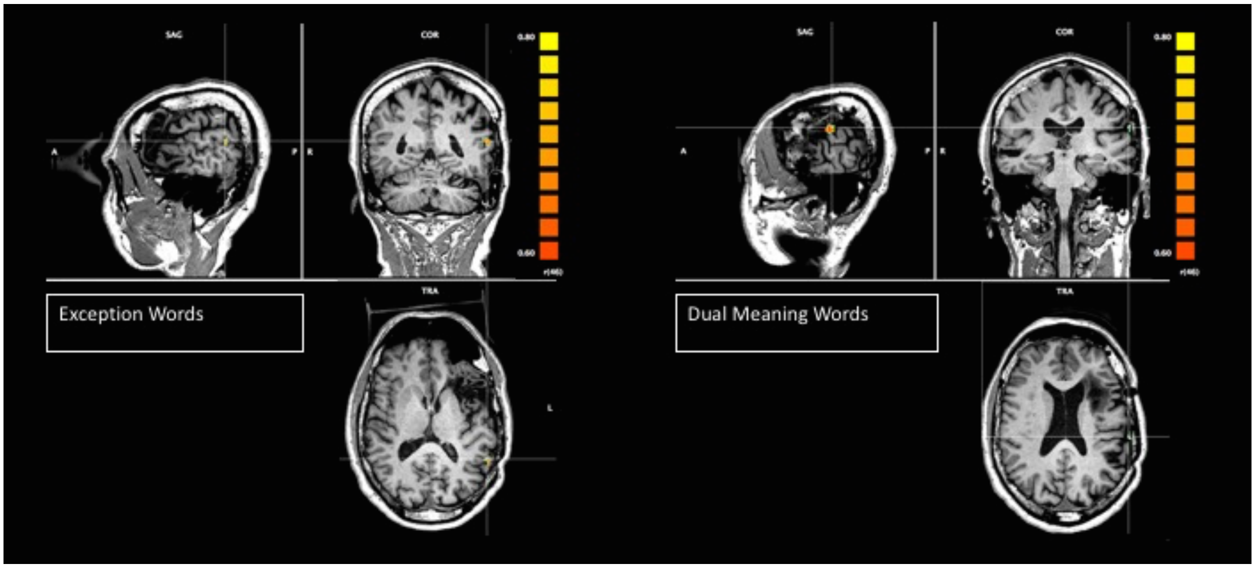

Figure 23: T1 images as underlays, and T2* images as functional overlays for regions of BOLD activation for task > rest for exception words and dual meaning words, $r(46) = .60$, $p < .0001$.

4.14 Surgical Procedure

A left temporal lobectomy was performed using neuronavigation with the STEALTH system, with intraoperative EEG and awake speech mapping using the same reading stimuli as used during fMRI. After exposure of the temporal lobe surface, speech was mapped using an Ojemann stimulator, and the absence of speech arrest was confirmed over the entirety of the planned resection area. Surface grids were placed over the left temporal lobe and intraoperative EEG used to identify areas of abnormal seizure activity. The anterior left temporal lobe was excised, opening the temporal horn of the lateral ventricle and exposing the hippocampal head, which was in turn removed. Removal of the seizure focus was confirmed by intraoperative EEG after completion of the resection, followed by hemostasis and closure.

4.15 Discussion

The results of Case Study 2 demonstrate that fMRI of reading processing, as used here, can be helpful in identifying the language-dominant hemisphere in an individual patient with epilepsy. In addition to aiding global localization, our fMRI protocol lateralized particular language regions, such as the homologue region of Broca’s area. As the surgery involved the resection of the hippocampus, amygdala, and remaining neocortical tissue of the left temporal lobe, which can be critical in language processing, the tasks included reading words, decoding pseudohomophones, and semantic retrieval (by asking the patient to also think about another word that is associated with the dual meaning words). It was found that BOLD fMRI signal consistently activated the right temporal lobe across four reading-aloud tasks (see Figure 22).

In this case, the neurologist had suspected right language dominance because of the patient’s intact speech during seizures. The fMRI supported right language dominance, and that there was minimal activation near the planned resection, and thus minimal eloquent cortex to avoid during surgery. These findings suggest a redistribution of language function in the brain that may have occurred due to recurrent ictal activity in the left hemisphere language areas. An alternative explanation is reorganization may have occurred following the earlier remote partial left temporal lobectomy with a shift of language areas to the right hemisphere.

4.16 Conclusions

In summary, Case Study 2 demonstrated that fMRI of reading processes is a useful clinical tool for language localization and lateralization presurgically in TLE cases. Moreover, the results suggest that protocols similar to the one used here including different stimulus types (e.g., exception and regular words, pseudohomophones, dual meaning words) are valuable for pre-surgical cortical localization of language function in epilepsy patients. These findings will inform future pre-surgical localization of eloquent cortex in temporal lobe resection cases, and provide further insights into the functional reorganization in patients with long-standing TLE.

CHAPTER 5

GENERAL DISCUSSION

A Summary of Findings from Chapters 2 to 4

The aim of this dissertation was to provide a comprehensive examination of the reading aloud task, as well as the interaction of processing between musical and speech rhythm by using newly developed stimulus sets and rhythm priming reading paradigms, as well as demonstrate the utility of the reading aloud task to patient applications (i.e., 'bench to bedside'). The results provide a novel set of findings about this connection, and are consistent with the idea that musical rhythm can affect speech production and that these processes share at least partly overlapping brain regions. Furthermore, the results provide directions to explore in future research.

The overall aim of Chapter 2 was to provide a behavioural and neuroanatomical examination of the effect of rhythmic priming on reading aloud using target words, as well as the corresponding PHs, which placed the stress on either the first or second syllable (e.g., *prac*tice vs. po*lice* and *prak*tis vs. po*leese*), and the rhythm prime either matched or mismatched the metric stress of the target letter string. The results from Experiment 1 demonstrated that naming RTs were faster for PHs when the rhythmic prime was congruent with the syllabic stress, and slower when the rhythmic prime was incongruent. Moreover, there was an interaction between congruency by stimulus type, whereby significant congruency effects were found with PHs, but not with words. The interaction was taken to suggest that congruency and stimulus type reflect at least one common stage of processing, most likely grapheme-to-phoneme translation. Overall, the results indicated that a rhythmic prime matched to the syllabic stress of a letter string requiring phonetic decoding aids sublexical reading. The lack of rhythm priming effects on word stimuli in this experiment may partly reflect a floor effect (i.e., relatively fast RTs in both congruent and incongruent rhythm priming conditions), and thus, Experiment 2b aimed to extend the findings of Experiment 1 to test whether a significant effect would emerge for words when these stimuli were presented at a slower pace, as is typical in an fMRI experiment. The results from Experiment 2b revealed that naming RTs for both words and PHs were indeed faster when preceded by a rhythmic prime that was congruent with the syllable stress of the letter string compared to when the rhythmic prime was incongruent. The results of Experiment 2b demonstrated that the rhythm priming effect does extend to real words when trials are presented at the slower pace necessary in the MRI environment, thereby suggesting that the lexical reading pathway is also affected by rhythm.

The goal of Experiment 2a was to use fMRI to examine the brain regions associated with the effect of congruency between rhythmic stress and syllabic stress on reading aloud. The study involved elucidating the neural mechanisms underlying the effect of rhythmic priming on reading aloud, and particularly the putamen's involvement given recent research suggesting its role in phonetic decoding. The results revealed that separate brain regions, including regions within the putamen, are associated with congruent compared to incongruent conditions. Furthermore, there was both shared and unique regions of activation for words and PHs. Importantly, activation was found in the left anterior putamen was activated for PHs, which is consistent with previous reports that this region is involved in sublexical grapheme-to-phoneme conversion (Oberhuber et al., 2012) and the initiation of unskilled, difficult movements (Okuma & Yanagisawa, 2008; Aramaki et al., 2011). The other regions of activation showing greater activation for PHs compared to words (i.e., midbrain, superior occipital gyrus, precuneus, precentral gyrus, and cingulate gyrus) may represent levels of processing beyond orthography, such as grapheme-to-phoneme conversion or phonological retrieval (e.g., Borowsky et al., 2006, 2012). The regions of shared activation between words and PHs, including the cerebellum, occipital lobe, middle occipital gyrus, thalamus, IFG, putamen, precentral gyrus, and SMA, are consistent with previous literature that has implicated these regions in language related tasks (see also Price, 2012 for review). The consistent activation in the cerebellum for the rhythm and reading tasks for both words and PHs is in line with previous research that implicates the cerebellum with the encoding of time intervals (Irvy & Keele, 1993; Grube et al., 2010ab), early sequence learning of language processes (Doyon, Penhune, & Ungerleider, 2009), and the timing of irregular sound sequences (Teki, Grube, Kumar, & Griffiths, 2011). The results of the brain-behavioural analyses revealed significant correlations between the number of active voxels and activation intensity in the anterior putamen and naming RTs for congruent PHs, indicating that in conditions where entrainment is occurring there is a positive relationship between RT and activation within the putamen.

The goal of Chapter 3 was to provide a behavioural and neuroanatomical examination of the effect of rhythm on reading noun-verb homographs (i.e., ISDNs), which provided a stronger within-stimulus comparison of syllabic stress, and allowed for a more tightly-controlled examination of the influence of rhythmic priming on speech production. Additionally, the use of

ISDNs also provided an opportunity to explore how the brain processes nouns and verbs, and whether shared or unique brain regions are involved in noun-verb processing. The results from Experiments 4 and 6 provided converging evidence that target letter strings whose syllabic stress conformed to the temporal structure of the rhythm prime result in faster naming RTs compared to when a target letter strings do not conform to the temporal structure of the prime. The aim of Experiment 4a was to identify brain regions associated with the effect of rhythm on reading aloud using noun-verb homographs. The fMRI results demonstrated that many distinct brain regions are involved in processing congruent versus incongruent rhythm and reading conditions, especially within the ROI of the putamen. This difference was taken to reflect the putamen's involvement in extracting temporal regularity in stimuli (Fujii & Wan, 2014; Grahn & Rowe, 2009), which is thought to be heightened in conditions where the syllabic stress of the word or PH matches with the stress of the rhythmic prime. These findings support the notion that the putamen is involved in predicting upcoming events, which leads to improved speech processing (Rothermich & Kotz, 2013). The fMRI results also revealed that the vast majority of activation was shared by both noun and verbs across both the ventral and dorsal visual processing streams, which supports the notion that the cerebral circuits underlying noun and verb processing are shared across the streams.

Lastly, the goal of Chapter 4 was to provide a behavioural and neuroanatomical examination of reading aloud processes in two types of patients. Namely, Case Study 1 used fMRI and behavioral measures to examine the effect of rhythm priming on reading aloud in a patient with PD, given that dysfunctions of the basal ganglia, and especially the putamen, are frequently associated with impairments in the timing of motor functions. The behavioural results demonstrated that the patient with PD showed a benefit from reading aloud letter strings that were congruent rhythm primes compared to incongruent. The fMRI results revealed greater activation for words than PHs in the left anterior putamen, and fewer brain regions for PHs compared to words overall, which may reflect hierarchical specialized function (Ogden, 1996) or the 'crowding hypothesis' for language processing (Lansdell, 1969). Taken together, these results have implications for the future development of a speech rehabilitation technique that uses entrainment via rhythmic priming cues. Specifically, the short-term effects described above could be tested in long-term interventions, such as over several weeks, months, or even years to investigate whether the benefit observed for congruent rhythmic primes (in comparison to the incongruent primes) actually represents a benefit in reading for individuals with speech impairments such as children with SLI and dyslexia.

Case Study 2 used fMRI to localize brain regions associated with speech production near the surgical resection plane in a patient undergoing brain surgery for TLE. The fMRI results demonstrated that reading aloud activated regions of the right posterior occipitotemporal lobe, supporting the notion that a redistribution of language function in the brain that may have occurred due to recurrent ictal activity in the left hemisphere language areas. Together, the results from Chapter 4 reveal the utility of using fMRI to map eloquent cortex associated with reading aloud processes in patient applications.

The Effect of External Auditory Rhythm on Reading Aloud

One potential account of the consistent effect of rhythm priming on reading aloud throughout the present research is that it is occurring via entrainment. As previously mentioned, entrainment refers to the process of synchronizing oscillators to external beats in auditory stimuli. Although entrainment studies typically use stimuli of a longer duration, we are inclined to speculate that entrainment may be at work here even with this very brief tone pair stimulus given that we obtained significant priming effects. Previous research has shown that neural oscillations entrain to the temporal rate of a perceived stimulus (Giraud & Poeppel, 2012) and further, that auditory rhythmic patterns may have an effect on motor entrainment (Thaut, Kenyon, Schauer, & McIntosh, 1999). In addition, it has been shown that low frequency synchronization between regions of the basal ganglia and the cortex may provide the basis for which higher frequency oscillations across cortex can become entrained to external stimuli (Saalmann, Pinsk, Wang, & Kastner, 2012). Further support for this notion comes from observations in attentional studies, such that there are increases in higher frequency synchrony among cortical areas along with an increase in low frequency synchrony between regions of the pulvinar and the cortex (Saalmann, Pinsk, Wang, & Kastner, 2012). Saalmann et al. propose that these low frequencies may provide the basis for which higher frequency oscillations across the cortex can become entrained to external stimuli. These oscillations between regions in the basal ganglia and other regions of the cortex provide a viable explanation for the synchronization between speech and musical rhythm as in the studies described above. Relatedly, Giraud and Poeppel (2012) proposed that neural oscillations are engaged by quasi-rhythmic properties of speech and are fundamental in speech and language processing by parsing and decoding speech, as well as ‘packaging’ information into the appropriate temporal structure. In other words, cortical oscillations provide ways to temporally organize incoming speech signals. These oscillations between regions in the basal ganglia and other regions of the cortex may provide a potential explanation for the synchronization between speech and musical rhythm.

Additional studies regarding motor synchronization have also investigated whether or not speech motor movement could be entrained by external auditory rhythmic stimuli. For example, LaGasse (2013) aimed to determine whether an external auditory stimulus could facilitate speech motor entrainment in children and adults while repeating the bilabial syllable /pa/ with or without an external auditory stimulus. She found that an external auditory stimulus appeared to positively influence speech motor synchronization, despite the children's underdevelopment of motor coordination in comparison to adults. These results support the use of external auditory cues as a strategy to facilitate speech motor synchronization.

The finding that the congruency of a rhythmic prime has an effect on speech production while reading words and PHs suggests that external auditory stimuli entrain motor production (i.e., naming), thereby producing faster RTs in the congruent condition where the word stress is "in phase" with the expected stress initiated by the rhythmic pattern. In other words, it may be the case that faster RTs for the congruent conditions were induced by a rhythmic prime, via entrainment, through an implicit temporal expectation about the stress of the word.

Underlying Cognitive Systems Involving Rhythm and Speech during Reading

Interpreting these results in terms of underlying cognitive systems can be aided through applying the Additive Factors Method (Sternberg, 1969, 1998; Gould et al., 2012). The additive factors method posits that if two variables are affecting a temporally common cognitive system, this would result in an overadditive interaction pattern on RT, whereas if two variables are affecting separate systems then this situation would result in an additivite pattern on RT. The results from Experiment 1 revealed an ideal example of an overadditive interaction between Stimulus Type and Congruency, which was interpreted as these two factors influencing at least one common system in time. Through the use of real words and PHs, we were able to control for reading strategy, as PHs must be phonetically decoded, whereas real words would typically be read via lexical access. In this cognitive model of reading (Figure 24 below), stimulus type is assumed to have its effect early in the cognitive architecture, specifically at the inputs to the grapheme-to-phoneme conversion system and the orthographic lexical system, as correct identification of PHs will rely more on phonetic decoding, whereas word identification would rely more on orthographic lexical access. The results illustrated that sublexical reading was more affected by a rhythmic prime than lexical reading, which was shown in the form of an interaction. This was interpreted to indicate that rhythm and speech production are interacting at a common cognitive system at the level of the grapheme-to-phoneme conversion system. The results from Experiments 3 and 5 revealed an additive pattern on RT between Stimulus Type and Congruency, whereby the rhythm prime affected both words and PHs when trials are presented at the slower pace in the MRI environment. Together, these results extended the findings of Experiment 1, and suggest that both the lexical and sublexical reading pathways are affected by rhythm priming.

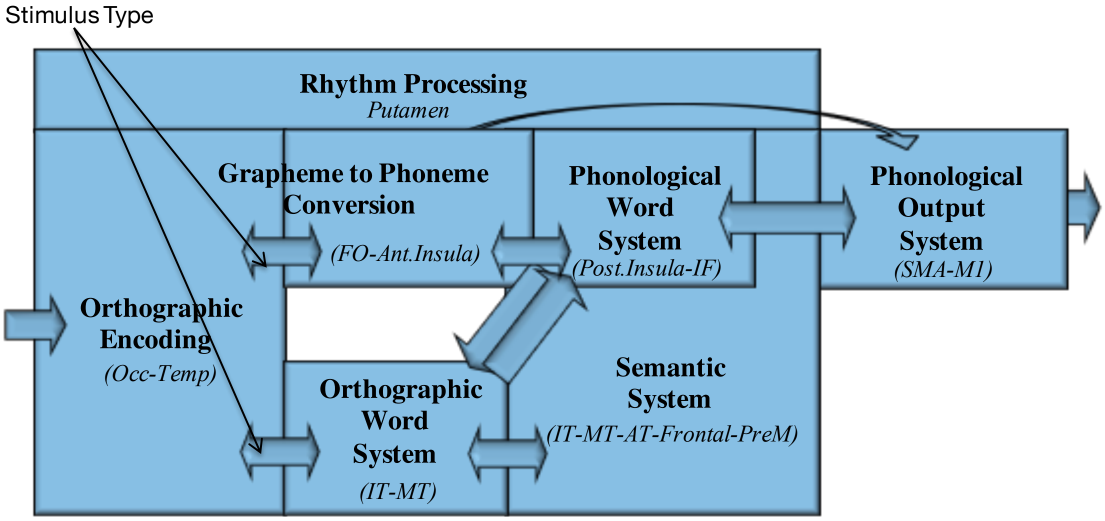

Figure 24: Example of a dual-stream, ventral-lexical, dorsal-sublexical, cascaded processing framework for basic reading processes extended to account for the effects of rhythm priming entrainment.

Applications of Rhythmic Priming Speech Techniques for Patient Populations

The results from these experiments may also be of clinical significance for numerous patient types. There is evidence that rhythmic therapies may elicit functional and structural reorganization in the neural networks underlying communication for various patient populations (see Fujii & Wan, 2014 for review). For example, rhythm-based rehabilitation methods have been shown to be effective for treating speech deficits in patients with PD, such as improving vocal loudness and speech prosody (Liotti et al., 2003; Ramig, Fox, & Sapir, 2004, 2007; Ramig, Sapir, Fox, & Countryman, 2001; Sackley et al., 2014; Sapir, Ramig, & Fox, 2011, see Fujii & Wan, 2014 for review). Furthermore, rhythm-based therapy techniques using rhythmic cueing have been shown to be efficacious for individuals who stutter (e.g., Toyomura, Fujii, & Kuriki, 2011), as well as patients with aphasia (Stahl et al., 2011; Stahl, Henseler, Turner, Geyer, & Kotz, 2013), whereby rhythm provides a timing cue to facilitate oral-motor production and coordination. Contrary to the idea that singing may be the key aspect in rehabilitation in non-fluent aphasics, where rehabilitation is often attributed to melodic intonation, Stahl, Kotz, Henseler, Turner, and Geyer (2011) instead proposed that rhythm may be the critical aspect in rehabilitation of speech, particularly for patients with lesions in areas such as the basal ganglia. Their findings indicate that benefits typically attributed to melodic intonation actually have their roots in rhythm and, importantly, point to a crucial contribution of the basal ganglia for rhythmic segmentation in speech production. Moreover, previous research has shown that reading following regular primes compared to irregular primes is improved in children with dyslexia and speech language impairments (Schön & Tillmann, 2015). Moreover, Cason, Hidalgo, Isoard, Roman, and Schön (2014) found that musical rhythmic priming can enhance phonological production in hearing impaired children via an enhanced perception of the target sentence. Our results show that rhythm priming may also be helpful for basic reading processes and thus may be useful for reading remediation purposes, particularly for phonological dyslexia, in which individuals exemplify lower-than-normal accuracy in sublexical reading (e.g., McDougall, Borowsky, MacKinnon, & Hymel, 2005; and see Goswami, 2011 for a model of dyslexia involving temporal sampling deficits in the syllabic theta-band range, and Giraud & Poeppel, 2012 for a description of a temporal sampling deficit in the phonemic low-gamma band range). Taken together, these studies promote the use of musical primes to boost language processing, and that such a technique may have great potential for rehabilitative purposes and for stimulating language development in atypical populations.

Directions for Future Research

One direction for research is to use event-related potentials to determine whether entrainment is occurring between the rhythmic primes and reading aloud, and to elucidate the source of the effect. Surface-based event-related potentials may be particularly well-suited for this given the lower-frequencies at which basal ganglia structures are thought to entrain to external stimuli (particularly in the theta bandwidth, which corresponds to the rate at which rhythmic beats were presented in our experiment; Saalmann & Kastner, 2011) and that the skull's low-pass filter characteristics might not interfere with the measurement of such low frequencies.

Additional research could also use diffusion tensor imaging (DTI) to examine the connections between various brain regions associated with speech entrainment, and highlight the structure of a potential cortical network that supports speech entrainment. For example, one could create probabilistic maps of the white matter connections between each of the activated areas and examine the integrity of each of the white matter tracts connecting those regions of activation. It would be predicted that interhemispheric connections between the left and right ITG, MTG, and STG would connect via the splenium of the corpus callosum, whereas connections between the left and right insula, and IFG would connect via the genu of the corpus callosum. Furthermore, there should be intrahemispheric connection between the anterior portions of the ITG/MTG to the IFG/insula following a ventral pathway that extends from the temporal lobe into the frontal lobe via the inferior longitudinal fasciculus and the uncinate fasciculus, and the posterior portions of the ITG/MTG should connect to the IFG via the inferior fronto-occipital fasciculus. Activation in the MTG/STG should connect to the IFG via a dorsal pathway that extends from the temporal lobe into the frontal lobe via the superior longitudinal fasciculus and the arcuate fasciculus. Further, the ITG and MTG should connect to the primary motor cortex via the internal capsule and corona radiata. Lastly, intrahemispheric connections should also be observed between the thalamus and putamen via the internal capsule. The integrity of these tracts could also be correlated with behavioural RT for reading tasks to investigate the connection between white matter tracts and reading aloud (e.g., Cummine, Dai, Borowsky, Gould, Rollans, & Boliek, 2013).

Additionally, these results show that rhythm priming may be helpful for remediating speech in patients with speech and language impairments, and thus there may be potential for developing a rhythm priming reading task for rehabilitative purposes. Additional studies that examine the effect of rhythmic priming on speech production in patients, particularly those with PD, on a larger scale with a wider range of deficits is warranted. Nevertheless, these experiments provide promising support for the use of rhythm as an effective rehabilitation tool for speech timing impairments. Future studies that examine the improvement of speech motor timing in long-term music training programs with rhythmic auditory cueing would also be useful for determining the efficacy of rhythmic priming therapies for speech impairments.

Another clinical application of the rhythm priming paradigms could be to help aim electrode stimulation in patients with PD who are undergoing deep brain stimulation (DBS). DBS is a technique that delivers a neural brain structure continuous electrical stimulation through chronically implanted electrodes connected to an internalized neuropacemaker or stimulator. DBS was first used at high frequency to replace thalamotomy (i.e., brain surgery in which the thalamus is ablated) for treating tremors in patients with PD, and has subsequently been applied to regions of the basal ganglia. High frequency chronic stimulation has been found to inhibit activity within the target region and thus suppress symptoms of PD. The mechanism of action may involve a functional disruption of the abnormal neural messages associated with PD (see Benabid, 2003 for review). In the abovementioned experiments, the consistent activation of the putamen in the rhythm and reading aloud tasks support the idea that these tasks could be used to help guide placement of the electrodes in patients undergoing DBS for PD. Moreover, our finding that specific regions of the putamen are involved in certain tasks, such as the anterior putamen's role in sublexical reading, may also help with placement of the electrodes in specific regions of the putamen. Previous work from our lab has demonstrated the utility of using fMRI activation to help guide the placement of deep brain electrodes into the subgenual anterior cingulate cortex in patients with major depressive disorder (Lorentz, Mickleborough, Mendez, Gould, Ekstrand, Ellchuk, & Borowsky, 2016).

Furthermore, recent experimental studies have begun to investigate the efficacy of transplantation of stem cells (i.e., embryonic mesencephalic tissue) to the striatum (which serves as the primary input to the basal ganlia) for improving symptoms of PD (see Lindvall & Kokaia, 2009 for review). Given that the rhythm priming and reading tasks described above showed consistent activation within the basal ganglia network, it is postulated that these tasks could also be used to help guide the injections of stem cells in cases of patients undergoing this treatment.

Limitations

The research discussed in this dissertation sought to provide a comprehensive examination of reading aloud, and particularly the effect of rhythmic priming on speech production. Nonetheless, there are some limitations to the research that should be acknowledged. First, a potential limitation of the present study is the use of a 50/50 split between first and second syllable stress words, as well as loud-soft and soft-loud rhythmic primes. Given that English is a "strong-weak" language in general (stress tends to fall on initial syllable in English; Cutler & Carter, 1987; Schreuder & Baayen, 1994), a 50/50 split may not represent the linguistic reality of English speakers. A future experiment could vary the proportion of loud-soft and soft-loud primes and first- and second-syllable stressed words (e.g., 80% loud-soft/first syllable stress versus 20% soft-loud/second syllable stress and vise versa). It would also be interesting to compare English to languages that are last syllable stress dominant, such as French or Turkish. In addition, future experiments could manipulate the proportions of congruent versus incongruent conditions to examine whether the effects would be enhanced by higher congruency contexts as they have been shown in other priming paradigms (e.g., Stolz & Neely, 1995). Moreover, future studies could manipulate the amount of times that the rhythm prime tones repeat, which would change whether the primes were predictive or non-predictive, and thus provide an indication to the extent of automaticity in these processes.

With regard to Case Study 1, the results are qualified by the case study methodology with one PD patient. Further, the patient was in the early stages of PD and on medication, which may have mitigated any underlying deficit to a certain extent. It is possible that the resulting brain activity may reflect the effects of pharmacological treatment or successful compensatory mechanisms. It is also important to acknowledge that other pathological factors may contribute to general PD deficits, such as noradrenergic, serotonergic and cholinergic deafferentation of the cortex (Agid, Javoy-Agid, & Ruberg, 1987) or differences in cortical Lewy bodies between the patient and normal healthy participants (Byrne, Lennox, Lowe, & Godwin-Austen, 1989).

Furthermore, regarding Case Study 2, great caution is always required when trying to interpret the absence of activation in fMRI and especially so in pre-surgical localization of relevant language processing. However, there was some reassurance in that both fMRI and direct cortical stimulation were consistent in this null finding, and moreover, the patient has no speech deficits and remains seizure free thus far (over one year) following the surgery.

Conclusions

The present results offer a window into reading aloud, and how congruency between rhythm and syllabic stress affect speech production and brain functioning, and may be translatable toward better understanding and possibly better interventions for patients with speech and language difficulties. Toward that goal, demonstrating the actual effectiveness of rhythm priming for helping speech impairments in patient populations, such as those with PD, stuttering, aphasia, or dyslexia, remains to be addressed in future studies. In general, these results indicate that a rhythmic prime matched to the syllabic stress of a letter string that requires phonetic decoding aids both lexical and sublexical reading processes. The functional neuroimaging results revealed that several brain regions, including the putamen, are involved in the rhythm priming effect on reading aloud, and that activation in the right putamen in congruent PH conditions correlates with mean RTs for those conditions, which is thought to reflect the entrainment of the congruent rhythm prime with the target. These results also have important implications for revealing the underlying neurobiological mechanisms of reading processes. Finally, the results also demonstrate examples of translational research for using reading aloud and fMRI to localize functional regions of eloquent cortex involved in neurological conditions such as PD and TLE.

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UNIVERSITY OF SASKATCHEWAN

Behavioural Research Ethics Board (Beh-REB)

Certificate of Re-Approval

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

INSTITUTION (S) WHERE RESEARCH WILL BE CARRIED OUT

SUB-INVESTIGATOR(S)

Paul Babyn, Marla Mickleborough

STUDENT RESEARCHER(S)

Chelsea Ekstrand, Layla Gould, Eric Lorentz, Joshua Neudorf, Sarah Wingerak

FUNDER(S)

NATURAL SCIENCES & ENGINEERING RESEARCH COUNCIL OF CANADA (NSERC)

SASKATCHEWAN HEALTH RESEARCH FOUNDATION (SHRF)

TITLE:

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

RE-APPROVED ON	EXPIRY DATE
06-Apr-2016	05-Apr-2017

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/

FOR

Vivian Ramsden, 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 Place
Saskatoon, SK S7N 4J8
Phone: (306) 966-2975 Fax: (306) 966-2069

UNIVERSITY OF
SASKATCHEWAN

Biomedical Research Ethics Board (Bio-REB)

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)
Paul Babyn, Marla Mickleborough, Jose F. Tellez-Zenteno, Adam Wu, Michael Kelly, Ivar Mendez

FUNDER(S)
NATURAL SCIENCES & ENGINEERING RESEARCH
COUNCIL OF CANADA (NSERC)
SASKATCHEWAN HEALTH RESEARCH FOUNDATION
(SHRF)

TITLE
Functional Magnetic Resonance Imaging (fMRI) and Electroencephalography (EEG)

RE-APPROVED ON	EXPIRY DATE
24-Mar-2016	23-Mar-2017

Delegated Review ☒ Full Board Meeting ☐

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 Part 4 of the Natural Health Products Regulations and 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. The University of Saskatchewan Biomedical Research Ethics Board has been approved by the Minister of Health, Province of Saskatchewan, to serve as a Research Ethics Board (REB) for research projects involving human subjects under section 29 of The Health Information Protection Act (HIPA).

Gordon McKay, PhD., Chair
University of Saskatchewan
Biomedical Research Ethics Board

Please send all correspondence to:

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Saskatoon, SK Canada S7N 4J8

Appendix A

Words			
First Syllable Stress	Second Syllable Stress	First Syllable Stress	Second Syllable Stress
always	about	awlwaiz	abowt
basic	above	baisik	abuv
biscuit	accept	biskit	aksept
blissful	ahead	blisphul	ahed
busy	allow	bizy	ahlao
china	around	chynah	arrownd
city	behind	sitie	beahynd
clever	complete	klevre	kumpleat
closest	convince	klosest	kunvince
college	defeat	kawledge	depheet
dinner	demand	dynner	dimanned
english	design	inglysh	deezine
happens	despite	kwestchun	dispyte
happy	discuss	hapins	dyskuss
hopeless	effect	happie	ephekt
kindness	embrace	hoeplis	imbrais
many	extent	kyndnes	ekstent
maybe	forgive	mennie	phorgiv
number	hotel	maibee	hoetelle
parent	include	numburr	inklued
picture	inside	pairent	innsyde
practice	machine	pikchur	masheen
question	mistake	praktis	mystaik
rhythm	police	rithm	poleese
seldom	regard	celldum	reegarde
slender	remain	slendurr	reemayn
student	success	stoodent	suksess
sunday	suppose	sundai	supoz
table	suspend	taybel	susspenned
tosses	today	tawssez	toodae

Appendix B

Words	Pseudohomophones
address	adjres
commune	desurt
conflict	eksport
console	eskortt
construct	implahnt
contract	insuhlt
convict	insurt
desert	invyte
escort	komyoun
export	konflikt
implant	konsole
insert	konstrukt
insult	kontrakt
invite	konvikt
object	objekt
permit	prezent
present	prodeuce
produce	proghress
progress	prohtest
project	projekt
protest	purmitt
rebel	rebhel
recall	refunned
record	rejekt
refund	rekall
reject	rekord
subject	subjekt
suspect	suspekt
transplant	tranzplant
upset	uhpset