NEURAL UNDERPINNINGS OF ORTHOGRAPHY IN FIRST AND SECOND

LANGUAGE READERS

by

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Abstract

Reading success in a second language (L2) is crucial for billions of people worldwide, but it is well known that it remains difficult for L2 learners to automatize the L2 processing in general. I investigated how long-term reading experience in a first language (L1) might change the neural L1 orthographic processing, and if these results can be generalized to L2 orthographic processing. I recruited adult monolingual English readers and adult Mandarin readers with latelanguage learning of English. By contrasting single-letters with pseudoletter visual stimuli (a pseudoletter effect) in L1, the reaction time data showed that reading experience makes letter processing faster than in pseudoletter processing. The electroencephalogram data showed that the L1 pseudoletter effect was manifested in a left-dominant oscillatory activity and network dynamics. The electroencephalogram data also showed that the L1 pseudoletter effect was robust, regardless of the level of attention paid; letters elicited more of left-lateralized neural connectivity desynchronization than did pseudoletters. Additionally, the data from L2 showed that the magnitude of the L2 pseudoletter effect in the N170 in the left hemisphere was correlated with L2 proficiency. Taken together, I concluded that with reading experience, the brain has automatized orthographic processing, which is evidenced by being (1) more specific by shifting the processing demands to different neural regions within visual processing networks-left dominant for well experienced orthographies, (2) being more obligatory, at least, at the singleletter level, and (3) faster by completing the process of differentiating letters from pseudoletters at fairly early stages of visual processing. Further, I concluded that some of the above changes appear to be ready throughout adulthood; orthographic development appears to be free from the fossilization or critical period hypotheses.

Lay Summary

Reading success in a second language (L2) is crucial for billions of people worldwide. Yet, late L2 readers continue to struggle with L2 processing being slow and effortful, compared to first language (L1) processing being fast and effortless. I investigated how single alphabet letters and Chinese characters were processed for adult monolingual English readers and adult Mandarin readers with late-language learning of English. What changes does L1 reading bring? Are these changes limited in early in life? The results of my research indicate that the brain has built a system for L1 processing which is faster, more specific and efficient than processing unfamiliar visual symbols. The results also indicate that such changes continue to take place throughout adulthood. Thus, while late L2 readers might continue to struggle with L2 language processing (e.g., vocabulary and grammar), visual single-letter processing appears to be an area that L2 readers can keep improving.

Preface

I was a co-lead investigator for the study in Chapters 2, where I was responsible for data analyses, results interpretation, and major portion of the manuscript composition. Dr. Anthony Herdman was the supervisory author on this project and was involved throughout the project in concept formation and manuscript composition.

A version of Chapter 3 was published in an open-access journal [Herdman, A. T., & Takai, O. (2013). Paying attention to orthography: A visual evoked potential study. Frontiers in Human Neuroscience, 7, 1-12.]. I was a co-lead investigator responsible for data analyses, results interpretation, and major portion of the manuscript composition. Dr. Anthony Herdman was the supervisory author on this project and was involved throughout the project in concept formation and manuscript composition.

I was the lead investigator for the study in Chapters 4, where I was responsible for data analyses, results interpretation, and major portion of the manuscript composition. Dr. Anthony Herdman was the supervisory author on this project and was involved throughout the project in concept formation and manuscript composition.

I was the lead investigator for the study in Chapter 5, responsible for all major areas of concept formation, data collection and analyses, as well as manuscript composition. Drs. Jeff Small and Anthony Herdman were co-supervisory authors on this project and were involved throughout the project in concept formation and manuscript composition.

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List of Abbreviations

AAC (anterior cingulate cortex) aFuG (anterior fusiform gyrus) ALU (abstract letter units) ANOVA (analyses of variance) BOLD (blood-oxygenation level dependent) EEG (electroencephalography) EP (evoked potential) ERD (event-related desynchronized) ERF (event-related field) ERP (event-related potential) ERS (event-related synchronization) ER-SAM (event-related synthetic-aperture magnetometry) FDR (false-discovery rate) FL (feature level) fMRI (functional magnetic resonance imaging) fNIRS (functional near-infrared spectroscopy) GFP (global field power) IOG (inferior occipital gyrus) L1 (first language) L2 (second languageL2) LGN (lateral geniculate nuclei) MCMV (multi-constrained minimum variance) MEG (magnetoencephalography) MER (multi-source event-related beamformer) MTG (middle temporal gyrus) PET (positron emission tomography) pFuG (posterior fusiform gyrus) PL (pattern level) PLV (phase-locking value) SN (selection negativity) SPM (statistical parametric mapping) STG (superior temporal gyrus) TFR (time-frequency response) TOCFL (test of Chinese as a foreign language) V1 (primary visual cortex) V2 (secondary visual cortices) VWFA (visual word form area) WS (working space)

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Dedication

To my daughters and to all of the learners of an additional language

Chapter 1: Introduction

Reading remains a major form of communication and is an expected skill to be able to adequately function in today's society. Approximately 84% of the world's population (15 years or older) is literate (UNESCO, 2012). Particularly in Western societies, everyone is expected to be able to read (National Reading Council, 1998). Yet, of those who can read, many struggle to read sufficiently. About 40% of the literate population in Canada reads (English or French) at a level that is lower than what is needed to function at work and home (Employment and Social Development Canada, 2013; OECD, Statistics Canada, 2011). Such low literacy competency is correlated with lower levels of health, safety, finance, and participation in society (Life Literacy Canada, 2005). Canada is known to have a large immigrant population who are learning to read English or French as a second language (L2). About 20% of adult Canadians are immigrants, of which 99% have a first language (L1) other than English or French (Statistics Canada, 2011). The literacy competency of these immigrants is even lower. About 60% of adult Canadian immigrants read below the functionally expected reading level (Statistics Canada, 2011). Because adults learning a new language after puberty have greater challenges than learning before puberty (Abrahamsson, 2012; Birdsong, 2009; Johnson & Newport, 1989; Long, 1990), it would be important to understand how late-language learners learn to read in such immigrant populations. Thus, investigating L2 reading acquisition in late-language learners could provide insights into how to improve literacy competency among adult Canadians.

In addition, globalization in business, education, and other sectors highly encourages L2 reading acquisition (particularly in English) (Bernhardt, 1993, 2011; Grabe, 2009). Consequently, L2 reading is a practically important skill for numerous people worldwide. Potential impacts of the research findings in this area are substantial. Understanding the brain mechanisms involved in both L1 and L2 readers should lead to a greater understanding of the neural and behavioural complexities involved in L2 reading acquisition and how we might intervene to improve L2 reading proficiency. Because the initial stages of learning to read typically involves letter and word recognition, my thesis mainly focused on understanding the neural mechanisms involved in letter and word processing in English L1 and L2 adult readers.

1.1 Importance of L2 Reading Acquisition

English has been a popular L2 worldwide, and this popularity appears to be increasing. For example, in 2001, about 10% of the world's population used English, and of these English users, over 80% were L2 learners (Crystal, 2011). A report by The University of Winchester "English Project" (2013) announced that about one third of the world's population uses English and that L2 users are about 75% of them. The world's population in 2018 was estimated to be ~7.6 billion (Worldpopdata, 2018). Consequently, over 1.7 billion people are estimated to be L2 English users. Recall that reading in L2 is a socially and practically important skill in today's multilingual world. Thus, understanding how L2 reading acquisition takes place in late language learners will have broad and substantial impacts on many lives worldwide. My thesis provides some insight into a couple of these issues.

1.2 Issues to Consider about L2 Reading Acquisition

At least four important issues can be considered with respect to L2 reading acquisition: automaticity, fossilization, speech primacy, and learning stages of reading. My thesis aimed at providing neuroimaging evidence regarding automaticity (Chapters 2, 3, and 4) and fossilization (Chapter 5). In order to limit the scope of my thesis, I did not design and conduct studies to investigate the third and fourth issues.

The *first issue* to consider with respect to L1 and L2 reading is the concept of **automaticity** of language perception. A consensus on the definition of automaticity (or automatized processing) is still lacking. For example, automatic processing of stimuli was initially described as being fast and requiring no attentional resources (Posner & Boies, 1971; Shiffrin, Dumais, & Schneider, 1981), but Navon and Gopher (1979) and Paap and Ogden (1981) argued that automatic processing still consumed some attentional resources, even for mature L1 readers. Meanwhile, automatic processing has been viewed as being obligatory – "processing while attention is directed elsewhere" (LaBerge & Samuels, 1974, p295) – and ballistic – "difficult to inhibit" (Logan, 1985, p318). Segalowitz and Segalowitz (1993) operationalized the preciseness of automatic processing. They created a coefficient of variation of lexical decision reaction time. They observed that this statistic became smaller as the participants gained greater proficiency in L2. As a result, automaticity is "one issue of interest to most SLA [Second Language Acquisition] researchers [that] cuts across all levels of analysis" (Segalowitz, 2007, p181). Word-recognition processing in L2 reading is no exception. The only available model of L2 reading (Bernhardt, 1993, 2011) suggests that to reach the ultimate goal of reading (i.e., efficient text comprehension), highly automatized word-recognition is required. Drawing upon contemporary reading models in L1, Grabe (1991, 2009) suggested that automatic word-recognition is necessary for successful reading comprehension in L2. With these several criteria for automatic processing, Logan (1985) concluded that automaticity is not a binary concept that is either automatic or not. Rather automaticity falls on a continuum, from less automatic to more automatic. The assessment of this more-or-less automatic processing also requires examining multiple characteristics of automaticity. Based on the aforementioned views, I define automatic processing of highly-familiar stimuli as being faster, cheaper on attentional

resources, more precise, more obligatory, and more ballistic as compared to processing of less familiar stimuli.

A second issue is that L2 proficiency has a protracted or plateaued development in late language learners (Abrahamsson, 2012; Birdsong, 2009; DeKeyser, 2013; Long, 1990). L2 learning is considerably more challenging than L1 learning, especially when L2 learning occurs after puberty (Abrahamsson, 2012; Birdsong, 2009; Johnson & Newport, 1989; Long, 1990). A term, "fossilization", was coined to capture those late L2 learners whose L2 development appeared to reach a plateau (Selinker, 1972). The observation of these phenomena and others led to the suggestion of critical (Lenneberg, 1967; Penfield & Roberts, 1959) and sensitive (e.g., Oyama, 1979; Schachter, 1996) periods for L2 acquisition. These periods are when our sensitivity for linguistic input for language acquisition is particularly heightened; after these periods, we become resistant to learning with age. A critical period indicates that our resistance to learning is absolute and that the onset of the resistance is abrupt, while a sensitive period means that the resistance remains malleable and that the onset of the resistance is gradual (Knudsen, 2004; Oyama, 1979). Recently, a notion of an optimal period has been suggested (Werker & Tees, 2005). This period is a type of a sensitive period but it consists of multiple sensitive periods, meaning that the learning in the earlier period (e.g., phonological category acquisition) contributes to the learning in the later periods (e.g., Lexical-semantic item acquisition and reading acquisition) in a cascading manner.

Lenneberg (1967) suggested that the critical period for language acquisition ends by puberty (at around 13 years old). Also, although he did not explicitly define which domains of language the critical period speaks to, later work on the critical period exclusively focused on the implicit knowledge, such as phonology (pronunciation), morphology, and syntax (Long, 1990).

The onset and offset of such maturational constraint can vary across language domains and research studies. For example, the offset has been suggested to be approximately at 6 years of age for phonological development and 15 years for semantic and morphosyntactic development (Long, 1990; Oyama, 1976). Yet for phonological development, some other research groups suggest that the offset begins at 6 years old and ends at 12 years old, implying a sensitive period (Birdsong, 2009; Granena & Long, 2013; Long, 1990).

Auditory perception in L2 acquisition also exhibits a maturational constraint. Initially by six months of age, infants are sensitive to most of the phonetic categories in many languages in the world, without exposure to these sound categories in their environment (Grieser & Kuhl, 1989; Maye, Werker & Gerken, 2002; McMurray & Aslin, 2005; Werker & Lalonde, 1988). Yet, by 10 to 12 months of age, most of their sound sensitivity becomes tuned to the phonemes of their home language, although some phonetic categories can maintain their categorical boundaries into adulthood (Werker & Tees, 1984, 2005). The resistance to acquiring L2 phonemes starts showing its effects by 6 years old and becomes absolute by 13 years of age (Abrahamsson, 2012). Also, comprehension of spoken sentences in noise was comparable with native speakers, only if L2 learners began their learning before the age of eleven (Oyama, 1978). Moreover, auditory training of mature adults for L2 phonemic categories can be effective (Werker, 1994; Ylinen et al., 2010), but the effect of the training is restricted to the context of the training (Pisoni, Lively, & Logan, 1994). Overall, the auditory perception of late L2 adults consistently falls short of the level of native speakers of a language (Bomba, Choly, & Pang, 2011; Brandmeyer, Desain, & McQueen, 2012; Polka, 1992; Takata & Nabelek, 1990; Ylinen et al., 2010).

In summary, the level of L2 language performance for late L2 learners is most likely limited in some capacity (but not fully "fossilized") as compared to the level that L1 learners and early-childhood L2 learners can attain. The exact time range for such maturational constraints varies across language domains. L2 proficiency (i.e., the level of language performance in L2) is an important variable that the starting age of L2 learning can determine.

A *third issue* is that late L2 readers starting to learn how to read an L2 likely have not adequately learned L2 phonology before reading instruction begins (Bernhardt, 1993, 2011; Grabe, 2009). This is in contrast to L1 reading acquisition where L1 phonology is typically acquired before reading instruction begins. A consequence of this lack of **speech primacy** in L2 reading development likely affects how L2 reading acquisition occurs within the brain as compared with L1 reading acquisition (Green, 2003; Werker & Tees, 2005). For instance, L1 reading acquisition can be conceptualized as introducing a written form of particular speech tokens, however, L2 reading acquisition cannot do so because the learners do not yet possess the speech in L2. A question that remains is whether or not L2 learners will ever be able to become proficient in their perception of speech tokens to allow for proficient associations between L2 speech and written text?

A *fourth issue* to consider is the type of instruction and **learning stages** that give rise to the L2 reading proficiency. For L1 reading acquisition in typical young learners, there are several stages that have been defined as logographic, alphabetic, orthographic, and automatic (Kamhi & Catts, 2012), which summarized previously proposed stage theories of reading (Chall, 1983; Ehri, 1991, 2005; Frith, 1985). The logographic stage is where beginning readers can decipher the text only by salient graphic or contextual cues (e.g., They read "Xepsi" as "Pepsi" if it is in a Pepsi logo). The alphabetic stage is when beginning readers have an epiphany that the written symbols in fact represent phonemes, but also when they read by processing letter-sound correspondences. The orthographic stage is when readers read visually by letter sequences (graphemes, morphemes, and whole words), not necessarily translating the sequences to corresponding sounds. Although empirical observation tells us that the progress that readers make is not always in a clear-cut stage-by-stage manner (Ehri, 2005; Share & Stanovich, 1995), these stages at least give us guidance to how reading in L2 might progress.

Unfortunately, there is paucity of literature with respect to defining such reading acquisition stages for late L2 learners. I speculate, though, that they most likely begin at the alphabetic stage. For instance, late L2 learners are most likely already literate in their L1. Therefore, they already know that the written text in L2 represents L2 speech, skipping the logographic stage. Still, many L2 readers must learn alphabets if their L1 orthography is not a roman alphabetic script, such as Chinese, Japanese, and Korean. Even if their L1 orthography is a roman alphabetic script, such as German and Spanish, the correspondence of the roman letters with L1 phonemes is different from that with L2 phonemes. As a result, investigating how late L2 learners acquire single-letter knowledge (i.e., orthographic and phonologic knowledge) would be of particular interest to understanding how the brains' of L2 learners begin to associate speech to text.

1.3 Importance of Single-Letter Knowledge in L1 and L2 Reading

Letter knowledge is an important beginning stage of L1 reading acquisition (Adams, 1994; Chall, 1983; Ehri, 1991, 2005; Frith, 1985). All contemporary models of L1 word-recognition acknowledge that single-letter processing is an important element of word-recognition (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Jacobs, Ray, Ziegler, & Grainger, 1998; McClelland, & Rumelhart, 1981; Perry, Ziegler, & Zorzi, 2007; Seidenberg, &

McClelland, 1989). The L1 literature provides evidence that letter knowledge, such as letter naming, predicts reading development in initial stages of reading acquisition (Bond & Dykstra, 1967; Chall, 1967, 1983; Share, Jorm, Maclean, & Matthews, 1984). Beginning readers use their knowledge of letter names in order to learn and master letter-sound correspondences (Barnes, 1991; Chall, 1983; Treiman, 1993). Then, phonological awareness predicts reading development in the later stages (Bentin, Hammer, & Cahan, 1991; Bradley & Bryant, 1983; Gottardo, Stanovich, & Siegel, 1996; Lundberg, Olofsson, & Wall, 1980; Perfetti, Beck, Bell, & Hughes, 1987; Shankweiler, Lundquist, Dreyer, & Dickinson, 1996; Share, 1995; Siegel, & Ryan, 1988; Stanovich, & Siegel, 1994). Because phonological awareness in L2 learners likely has a protracted, or possibly a fossilized, developmental trajectory, it might not be a good predictor of L2 reading acquisition in later stages. Thus, knowledge of and perception of letter names might have some predictive power and thus it is an area of interest to investigate orthographic processing in L1 adults and late-L2 learners.

1.4 Neural Models of Reading

The following subsections briefly overview the neural models of reading. My thesis does not aim to validate or verify these models; therefore, I'm only introducing some relevant neural models of reading to contextualize my thesis work and provide some background regarding where letter perception fits within reading models. I am not providing exhaustive description of the models because that is beyond the scope of my thesis. Most of the models presented below have principles that follow modularity and/or connectionist perspectives of how the brain operates. Modularity perspectives tend to associate discrete perceptual or cognitive functions within distinct regions of the brain, sometimes referred to as region-specific models. On the other end of the spectrum, connectionists' perspectives typically propose that perceptual or cognitive functions are an emergent property of neural networks that have multiple feed-forward and feedback connections among several brain regions; in other words, no one region can be solely responsible for a specific function. Early neurological models usually take more of a brain modularity perspective whereas current models usually take a connectionist perspective. However, a hybrid of these models is generally more accepted because of the wealth of neuroimaging evidence demonstrating that brain regions do perform specific operations but they require reciprocal connections to other regions, forming a network, in order to perform perceptual and cognitive functions.

1.4.1 Neurological/lesion models

One of the earliest neural models of reading was proposed back in 1892 by Déjerine and later followed up by Geschwind in 1965. It was based on a lesion study of an alexic patient, Mr. C, who selectivity lost his ability to recognize single letters or words while still being able to recognize and name faces and other visual objects, such as numbers. Interestingly, Mr. C also retained his ability to fluently write but he was unable to read what he or others wrote. Thus, overall language was not impaired in his case. This and other aspects of Mr. C's case led Déjerine to conclude that Mr. C had selective deficit in letter recognition, which he termed "verbal blindness" – now referred to as alexia. About 70 years later, Geschwind (1965) revisited Déjerine's case report and autopsy of Mr. C's brain and proposed one of the first brain models for reading (Figure 1.1). This model proposed that visual features of letters are initially processed in visual centres that then send information to the visual imagery brain area for identifying letters. Letter/word identity is then sent to an auditory imagery area to identify letters/words. From there letter/word information is sent to frontal areas for motor imagery to generate motor commands for speech, which are then finally sent to motor output areas. Mr. C's lesion was

primarily restricted to the visual processing centers in the occipital and inferior temporal gyri. Déjerine proposed that visual information regarding letters was either not being processed in the lesioned area or was disconnected from the rest of the system. Geschwind (1965) later concurred with Déjerine's early supposition that the visual centres might be disconnected from the visual imagery area of letters. Although this model was strictly a feed-forward model, it does demonstrate properties of modularity and network connections. Follow-up research looking at lesion sites in stroke patients who had occipital and inferior temporal lobe infarcts with and without alexia (Cohen et al., 2004) revealed that the middle portion of inferior temporal cortices (predominantly in left hemisphere) is involved in letter processing and word reading. This area has been referred to as the "visual-word form area (VWFA)" for the past few decades but is now referred to as the "letterbox area" by some researchers (see Dehaene, 2005 Chapter 2). This shift in terminology is mainly due to a reconsideration of the neurological (Dejerine, 1892; Geschwind, 1965; Cohen et al., 2004) and neuroimaging findings (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Allison, Puce, Spencer, & McCarthy, 1999; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Haxby, Hoffman, & Gobbini, 2000; Haxby et al., 2001; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Nobre, Allison, & McCarthy, 1994) with respect to this region's specificity of being mostly active when perceiving unpronounceable or pronounceable letter strings and words as compared to other visual stimuli, such as faces, places, and objects.



1.4.2 Dual-route model of reading

Coltheart and his colleagues proposed a "Dual-Route" model of reading that was predominantly based on behavioural measures of reading in individuals with and without different forms of alexia and dyslexia (Coltheart, 1981; Coltheart, Curtis, Atkins, & Haller, 1993; Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). Even though debate among modelers remains, the dual-route model has similar global features akin to those in the neurological and connectionists' models of reading. The dual-route model proposed that visual input is extracted within visual feature processing units, that have feed-forward and feedback connections to higher centers, called "abstract-letter units", that identify letters. From here the information is sent along two different routes; the lexical route and the non-lexical route (Figure 1.2). Although, Coltheart et al. (1993) did not formally provide evidence of where these routes are located within the brain, other researchers have provided evidence for different brain regions that might be associated with these routes (see meta-analyses by Taylor, Rastle, & Davis, 2013). The lexical route receives the information from the abstract letter units and rapidly identifies that the letter strings are consistent with a word form in the orthographic lexicon and a word is recognized quickly and efficiently. Because of strong connections to the semantic system and the phonological lexicon, semantic information and/or phonology can be quickly accessed depending on the task demands. If the task is to repeat the written word aloud then the phoneme system and motor speech units are activated to generate speech. The lexical route is proposed to be used for reading highly familiar words regardless of whether they follow the language's typical grapheme-phoneme conversion rules (i.e., familiar regular- or irregular- spelled words; e.g., "yard" or "yacht").

The non-lexical route, however, requires that the phoneme system and motor speech units be activated only after the sound of each letter (or bigram = two letters) is sequentially processed within the grapheme-phoneme rule system in order to sound out the written word. This route will be slower than the lexical route because of the sequential "sounding-out" of the word and is proposed to be used by readers to read unfamiliar but pronounceable words (e.g., "yaib").



locations of the model's boxes are not specifically localized to the underling brain regions but they are generally placed near associated brain regions where such operations may occur (see Taylor et al., 2013).

1.4.3 Network Connection Models of Reading

One of the first network connection models of reading was proposed at a conference in 1959 by Oliver Selfridge. He proposed the **Pandemonium model** of learning in that there are many demons (i.e., neuronal populations) within the brain that process information and pass that information onto the next demon. What was interesting about this model with respect to reading was that each demon was selectively excited by an image (i.e., "image demons"), a specific visual feature of the image (i.e., "feature demons"), or identity of the visual object (i.e., "cognitive demons"). These demons were placed in a sequential-processing network whereby an "image demon" would tell the "feature demons" about the image features. The features that are present within the image would most excite specific "feature demons". The excited feature demons would then yell loudly to a few "cognitive demons" that they are excited. The loudness of a cognitive demon's yell would depend on the number and loudness of yells from the lower feature demons that are connected to him. He would then yell to a final "decision demon". If his yell is louder than all other yells coming from the other cognitive demons, then the decision demon would select that "cognitive demon" as being the correct identity of the visual image that fell on the retina. This was an insightful model and provided a basis upon which many other network models were built upon.

One model that expanded on such early models of Selfridge's is the **Interactive** Activation Model (IAM) proposed by McClelland and Rumelhart (1981). In its simplest form, the IAM is very similar in general structure to most of the early neurological and dual-route models in that there are sequential levels of feature, letter, and word processing. The major difference is that the IAM model proposed that the overall interactions among all neural populations within the visual system are a requisite for identifying the visual object (e.g., a written word). These interactions are complex networks of functional and structural connections that will selectively be activated dependent on the inputs and outputs of each level. Similar to the Pandemonium model, the local neural-network that codes for a specific word wins out over all others if it has the largest activation. In addition to this model being able to explain many of the reading functions, it was also able to explain many findings from visual priming studies of letters and words (Grainger & Jacobs, 1994). Thus, this has become a prevailing model of reading and is continually being modified to aid in explaining new research findings. For example, Grainger and colleagues (Grainger, Rey, & Dufau, 2008), revisited the IAM and Pandemonium models placing them in context with the growing evidence from neurological and neuroimaging studies. For a detailed discussion of these models, see reviews by Dehaene (2005) and Grainger et al. (2008).

In his book, Dehaene (2005) presented a compelling revision to the IAM model of reading, which he called the **Neural Recycling Hypothesis**. The hypothesis is that the human visual

cortices have evolved for rapid visual feature extraction and that the reading process has hijacked (or recycled) this system in order to perform fast processing of orthographic objects. Because the invention of reading was only a few thousand years ago, there has been insufficient time, in evolutionary terms, for selective adaptations to create brain regions/networks that are only specific for the reading process. Thus, a more parsimonious explanation is that human socio-cultural advancements have co-opted the previously evolved visual system to operate as a "reading brain". A possible reason for this socio-cultural influence is that information in the form of written text can be more efficiently communicated among people, across space, and across time; thereby giving readers a selective socio-cultural advantage of finding, seizing, storing, and using resources.

Visual processes involved in object recognition have been extensively studied over the past several decades. Much of that information has been incorporated into the models of reading with respect to where and when different operations are occurring (see Figure 1 in Dehaene, Sigman, & Vinckier, 2005). In brief, when photons of light hit the retina they activate different on- visual-field receptors that send that information into the central visual system via the optic nerve. At the level of the lateral geniculate nuclei (LGN), local contours (i.e., a visual feature) are extracted from the visual input and are sent on to the primary visual cortex (V1) where neurons integrate such information and code for line orientations. Higher centres in the secondary visual cortices (V2) receive and integrate the oriented line information to form more local contours and rudimentary line forms. These line forms are then used to construct letter shapes in the next visual level (likely in V4) but they still retain the retinal spatial information and thus are not considered abstract letter yet. The next level up (possibly V8) is involved in extracting the letter identity information only and is thus believed to house the "abstract-letter units". From there the

information about the abstract letters is sent to even higher centres for further combinatorial processing to form bigrams and words. These later levels are believed to be involved in lexical retrieval, which possibly resides in a network involving predominantly left occipital temporal and inferior temporal regions. For simplicity, I described the model from a feed-forward perspective, however, keep in mind that all IAM models have feedback and re-entrant loops within and among all levels. Thus, there is constant checking and modification of lower visual centres by higher centers. The key term in these models, "interactive", means the processing of the incoming information occurs within and among many brain areas and levels.

1.4.4 Temporal Model of Lexical Processing

Most of the neural models of reading focus on the spatial distribution of information processing within the human brain and only a few present the timing and dynamics of information flow. Below describes the time courses of general neural processes that are typically presented in neural models: visual, sublexical, and lexical (Figure 1.3) with respect to their likely timings. Such categorical descriptions might imply that these types of processes are sequential, but a general consensus in the literature is that word recognition is a result of cascading processes that substantially overlap and interact with each other across space and time (Barber & Kutas, 2007; Grainger & Holcomb, 2009; McClelland, & Rumelhart, 1981; Pulvermüller, Shtyrov, & Hauk, 2009; Sereno & Rayner, 2003). Maximally at around 100 ms post stimulus onset, the occipital lobe is processing visual stimuli, but it does not appear to differentiate lexical stimuli from faces (Tarkiainen, Cornelissen, & Salmelin, 2002) nor pseudoletters (Herdman, 2011). Thus, this early phase of neural processing does not appear to be truly lexical, but rather general visual processing.
Sublexical processing follows the above mentioned general visual processing, from 100 to 250 ms (Holcomb & Grainger, 2006). Sublexical processing consists of orthographic and phonological processing. A general agreement in the literature on visual word recognition has been that orthographic and phonological processing are distinct and that orthographic processing precedes phonological processing by about 50 ms (Ferrand & Grainger, 1993; Grainger, Kiyonaga, & Holcomb, 2006; Holcomb & Grainger, 2006; Perfetti & Tan, 1998). Yet, these studies examined data from orthographies that are opaque only (i.e., the association between the orthographic depth hypothesis (Frost, 2005; Katz & Feldman, 1983), the above mentioned consensus is challenged. The distinction between orthographic and phonological processing might be a product of opaque orthographies because phonological processing becomes less relevant in a transparent orthography (i.e., the association between the orthographic symbol and its pronunciable) (Zeguers, Snellings, Huizenga, & van der Molen, 2014).

Lastly, semantic processing follows sublexical processing from about 300 ms until 400 ms (Dehaene, 1995; Grainger & Holcomb, 2009; Holcomb & Grainger, 2006). However, it is possible that the onset of semantic processing can take place even earlier, for example before 200 ms (Hauk, Davis, Ford, Pulvermuller, & Marslen-Wilson, 2006; Hauk, Coutout, Holden & Chen, 2012; Sereno & Rayner, 2003).

Much of **my thesis focused on** investigating sublexical **orthographic processing**; therefore, most of my studies were limited to investigating differences in electrophysiological responses within the time interval of 0 to 250 ms. Some of my studies provide results with respect to phonological and semantic processes involved in viewing letters and words, but specifically investigating these were beyond the scope of my thesis.



interactions.

1.5 Orthography

The term "orthography" has been treated differently, narrowly, or broadly across disciplines. Orthography is viewed narrowly in Linguistics. The orthography is a writing system that is intended for use in a particular language (Sebba, 2007). A writing system can employ a particular set of visual symbols, but an orthography is certain conventional rules to order these symbols to make up a word, depending on the languages. For instance, the English and the German languages both employ the Roman writing system but "Friday" in English is "Freitag" in German. In contrast, orthography is viewed broadly in the literature of visual processing. The orthographic stimuli that this line of research considers, range from words (e.g., Dehaene, 1995), pronounceable nonwords (e.g., Holcomb & Grainger, 2006), bigrams (e.g., Dehaene & Cohen, 2011), single letters (e.g., Tarkiainen, Cornelissen & Salmelin, 2002) to single characters (e.g., Wong, Gauthier, Woroch, Debuse, & Curran, 2005). The Linguistic view of orthography can accept only the first three types of these stimuli. An alternative view is that orthography in visual processing is all of the visual symbols used in a writing system, and this is the definition of orthography in the present thesis. My thesis focused on understanding the neural underpinning of orthographic processing in L1 and L2 adult readers thus, the following sections are limited in scope in this regard. Moreover, the following sections only briefly introduce the concepts in order to minimize redundancy in writing because each chapter provides an introduction to its relevant concepts and findings.

1.6 Neural Processing Underlying L1 Orthography

There are several types of neuroimaging devices that can be used to measure neurophysiological changes that occur during brain activity. Functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) can provide excellent spatial resolution (mm) for locating changes in blood oxygenation and metabolic activity, respectively. However, these methods are limited in temporal resolution because the minimal time that fMRI and PET and detect changes in blood oxygenation and metabolic uptake is about 1 sec. Much of the perceptual and cognitive processes involved in viewing/reading letters and words is over by about 400 ms. Another technique that is becoming more commonly used in neuroimaging is functional near-infrared spectroscopy (fNIRS). Like fMRI and PET, it measure blood flow and also has limitations with temporal resolution. Electroencephalography (EEG) and magnetoencephalography (MEG) are two commonly used methods for measuring the temporal dynamics of neural activity on a millisecond time scale. However, both methods are limited with respect to spatial resolution of precisely locating where in the brain neural populations are active. The spatial resolution of MEG (5-10 mm) is slightly better than whole-head dense-array EEG recording (10-20mm). Considering this, MEG might be considered the better methodology, however, MEG is less sensitive to neural activity that is radially-oriented to the scalp surface (i.e., neural populations within gyri). EEG on the other hand picks up both radially- and tangentially-oriented neural sources (i.e., gyri and sulci). But, EEG has a limitation compared to MEG in that electrical fields easily conducts across the scalp so that a signal in the occipital cortex can be recorded at the nose, simply by volume conduction. This causes challenges with locating sources using neuroimaging analyses. Thus, MEG and EEG are generally considered to be complimentary techniques and are often used to measure neural signals generated by processes involved in reading. Such neural signals are discussed below in greater detail. Note, EEG and MEG signals are commonly denoted with an "N" for EEG and an "M" for MEG followed by a number that corresponds either to the ms timing of the response (e.g., P100, N170, P200 or M100, M170, M200) or the sequent listing of the peak responses (e.g., P1, N1, P2).

1.6.1 N170/M170 Effect

Orthographic processing activates the inferior-temporal cortices within 200 ms, which is manifested in the N170/M170 (Allison, Puce, Spencer, & McCarthy, 1999; Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006; Pernet et al., 2003; Tagamets, Novick, Chalmers, & Friedman, 2000; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). For instance, intracranial recordings around the inferior-temporal cortices revealed that word stimuli elicited activation at about 180 ms (Allison, et al., 1999). An MEG study further provided support by using single-letter stimuli (Tarkiainen et al., 1999). Meanwhile, fMRI studies have repeatedly identified the activation in the inferior-

temporal cortex for letter processing, although the exact location (Flowers et al., 2004; James et al., 2005; Joseph et al., 2006; Pernet et al., 2003) and the laterality (Tagamets et al., 2000) varied across studies.

Although the validity of using the N170 as a marker for orthographic processing of single-letters is promising, some limitations exist. While the source of and the stimulus category that elicits the N170 are clear, a limitation in our understanding of the N170 is the true nature of this event-related potential. There are two major controversies in the literature surrounding the N170 response to single-letters. One of the controversies appears to lie within the reported changes in the N170 to familiar letters versus unfamiliar pseudoletters (or unfamiliar L2 characters). One group of studies showed larger N170 amplitudes to letters than pseudoletters, particularly over left scalp regions (e.g., Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013; Wong, Gauthier, Woroch, Debuse, & Curran, 2005; Xue, Jiang, Chen, & Dong, 2008). These researchers suggested that a larger N170 reflects an expertise effect that is enhancing the neural processing related to familiar letter stimuli. Contrarily, other research has found that a primary difference in ERPs between letters and pseudoletters occurred as a delay or broadening of N170 response to pseudoletters compared to letters (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013; Takai & Herdman, 2013; Figure 1.4). These findings likely indicate that familiar letters are processed faster (and possibly more automatically) than pseudoletters. N170 amplitudes for letters and pseudoletters were not different yet the timing of the response created apparent amplitude differences. In addition, reaction times to letters are about 15 ms faster than to pseudoletters (Herdman, 2011; LaBerge & Samuels, 1974). This led researchers to suggest that letter expertise was reflected more by an increased speed of neural processing and greater network synchronicity than by a modulation of

a single neural event. A possible reason for these discrepant findings and interpretations is that the authors analyzed and reported their findings differently. For example, the studies that reported enhanced N170 amplitudes to letters only evaluated such differences at the peak of the N170 response and provided no ERP difference waveforms (i.e., letters vs. pseudoletters). Thus, waveform differences that might exist due to slightly shifted responses between letters and pseudoletters may have largely gone unnoticed in their reports. For the other studies that reported difference waveforms, a clearer view of the timings and modulations of the responses to letters and pseudoletters were evident. As a result, these studies hold opposing interpretations of the N170 effects related to letter and pseudoletter processing.



Figure 1.4 Grand-mean (n=13) ERPs to letters (blue) and pseudoletters (green) recorded at electrode PO7. Difference waveform (letter-pseudoletter) is presented as grey line with significant differences overlaid as colour amplitudes corresponding to the false-discovery corrected p-values. See Chapter 3 for more details.

Another relevant finding in the ERP literature on visual processing is the inversion effect.

The broader and more delayed N170 to pseudoletters ressembles the well-known object-

inversion effect. A highly-experienced visual object, such as a face, has been consistently shown to elicit a smaller and earlier peaking N170 than the inverted version of the object (Gauthier & Tarr, 2002; Gauthier, Williams, Tarr, & Tanaka, 1998; Tanaka, 2001; Tanaka & Taylor, 1991). Researchers explained this inverted image effect in terms of the difference in the nature of the processing. Experts are so used to the object of expertise, and as a result, their processing of this object is automatic and holistic. On the other hand, the inverted object breaks the holistic processing and elicits analytic processing, which results in a larger or delayed N170. A recent study also showed that attention increased the negativity of the N170 in single-word processing (Proverbio & Adorni, 2009), which well fits with this automatic and holistic processing account on the N170.

Another controversy exists with respect to the N170 and its relation to learning experience. Intervention studies on visual objects have shown that the amplitude of the N170 became more negative after training (Gauthier, Williams, Tarr, & Tanaka, 1998; Maurer, Blau, Yoncheva, & Mccandliss, 2010; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002). In applying these results to single-letter processing, the N170 might be more negative with increasing reading proficiency. Meanwhile, if we take an automatic and holistic processing point of view, the N170 might become less negative but faster in latency with increasing reading proficiency. Thus, I propose to investigate whether greater expertise (i.e., L2 proficiency) is reflected in an enhanced N170 amplitude difference (expertise hypothesis) or by an earlier peaking N170 (automaticity/holistic processing hypothesis). This leads to another aim of my research (Chapter 5) that investigated the relationship between the N170 for single-letter processing and L2 reading proficiency.

An L2 learning effect on the N170 might also be manifested in the hemispheric laterality of brain activity associated with language and literacy functions. In the single-letter domain, the results of hemispheric laterality are mixed. On the one hand, some reports showed that the N170 amplitude differences between letters and pseudoletters are more left-lateralized (Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013). This observation perfectly fits evidence in the single-word domain that increased language experience shifts the hemispheric laterality to the left (Maurer, Brandeis, & McCandliss, 2005; Maurer, Zevin, & McCandliss, 2008). A caution here is that these studies all employed a one-back matching task, and thus the effects might be more associated with hemispheric shifts in working memory functions. Conversely, letter identification tasks that demand much less working memory updating and retrieval reported more bilateral or even right-lateralized processing of letters and pseudoletter differences (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013). Again, the choice of the task appears to influence the interpretation of the N170. More research is needed to understand these discrepant findings between tasks, however, this is beyond the scope of my proposed studies.

To summarize, the L1 literature reports that the inferior-temporal cortices are involved in single-letter processing. This region becomes activated at around the latency of the N170, which EEG researchers have used as a marker for letter processing. These researchers often use pseudoletters as their control stimuli, but the problem is that the N170 elicited by these pseudoletters can be more or less negative than the single-letters depending on the study). To make matters worse, the literature on visual object expertise provides supporting evidence for both opposing types of observation. By focusing on the task employed, the controversy might be resolved. The use of one-back tasks supports the visual expertise account, the observation that

letters elicit more negative N170 than pseudoletters. On the other hand, the use of other tasks generally supports the automatic and holistic account, which explains the observation that letters elicit a less negative N170 than pseudoletters. This task effect is also manifested in the laterality of the N170. The one-back task observed a more left-lateralized N170, while other tasks showed a more right-lateralized N170. Lastly, no studies to my knowledge have examined single-letter processing across different L2 proficiency levels. Such studies could help answer the question of whether the N170 is a manifestation of expertise or automatic processing.

1.6.2 P2 Effect

Following the N170, letters and pseudoletters show another divergence in their neural responses between 200-250ms, and this divergence is recorded over parietal-occipital scalp regions, pseudoletters being more positive than letters (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Herdman, 2011; Park, Chiang, Brannon, & Woldorff, 2014; Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013). This evidence supports the view that processing of unfamiliar objects requires additional neural processing than do familiar objects (Appelbaum et al., 2009; Herdman, 2011).

A question then arose, "Why do unfamiliar objects require more neural processing than familiar objects?" In an fMRI study, Vinckier et al. (2007) proposed that it might be due to attention. These researchers observed that words affected a signal change in the left inferior temporal regions but false-font strings did in the right inferior temporal regions and suggested that false-font strings might require additional attentional processing in the right inferior temporal regions. Whether or not attention modulates a pseudoletter effect requires investigation. Thus, the study presented in Chapter 3 aimed to reveal attentional effects on letter and pseudoletter processing.

1.6.3 Hemispheric Laterality

Unfortunately, the hemispheric laterality of responses evoked by single letter and pseudoletter stimuli has produced inconsistent results in the literature. Several event-related potential (ERP) or event-related field (ERF) studies reported that the divergence between letters and pseudoletters in the N170 (or M170) range was left-hemispheric dominant (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Eulitz et al., 2000; Miller & Wood, 1995; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Wong, Gauthier, Woroch, Debuse, & Curran, 2005). Allison, Puce, Spencer, & McCarthy (1999) reported that this N170 signal was mainly located in the inferior temporal regions (i.e., letter-box area), and positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies also observed increased activations in this region for word processing (Cohen et al., 2000; Fiez & Petersen 1998; Petersen, Fox, Snyder, & Raichle, 1990; Price, 2000; Price & Devlin, 2003; Price et al., 2003; Turkeltaub, Eden, Jones, & Zeffiro, 2002). Thus, the left inferior temporal gyrus has been suggested to play a prominent role in visual processing of orthographic stimuli.

In contrast to these findings, several other studies reported a right-hemispheric dominant response to pseudoletters than letters. An fMRI study observed widespread bilateral activation by pseudoletters as compared to letters (Tagamets, Novick, Chalmers, & Friedman, 2000), and a PET study showed right-lateralized activations for pseudoletter strings (Liotti, Gay, & Fox, 1994). In addition, two EEG studies and one MEG study showed right lateralized pseudoletter effects (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Herdman, 2011). The studies throughout my thesis provide further evidence for the hemispheric laterality of letter and pseudoletter processing, specifically tested in Chapters 4 and 5.

1.7 Neural Processing Underlying L2 Orthography

Only a few neuroimaging studies exist with respect to single-letter visual perception in late L2 learners (Wong, Gauthier, Woroch, Debuse, & Curran, 2005; Ihara & Kakigi, 2006; Xue, Jiang, Chen, & Dong, 2008). Wong et al. (2005) compared three types of stimuli across two different language groups. The three types of stimuli were single alphabet letters, single Chinese characters, and single alphabetic pseudoletters. The language groups were L2 English (Chinese as L1) at a moderate proficiency level and L1 English. For the L2 group, the amplitude of the N170 was the most negative for Chinese characters and the second most negative for alphabet letters. In contrast for the L1 group, the N170 was more negative for alphabet letters than for Chinese characters and pseudoletters. Wong et al. (2005) concluded that the more expertise you have with a visual object (such as a letter), the more negative the N170 becomes. However, they did not have L2 learners of different L2 proficiency levels. Thus, their findings can only be generalized to differences in brain processes between L1 and L2 learners.

Xue et al. (2008), using a similar stimulus comparison and L2 participant group, replicated the same findings. L2 participants showed that their N170 was more negative for alphabet letters than for another set of alphabetic letters in an unfamiliar script. Meanwhile, Ihara and Kakigi (2006) examined Korean learners of Japanese at a very beginning level. Their MEG data showed that the oscillatory activity in the left inferior-temporal cortex was more sensitive to L2 character processing, compared to the L1character processing.

Collectively, these findings indicate that single-letter processing in L2 learners is different than that in L1 learners. However, the concept that the more expertise a person has in an L2 cannot be fully elucidated from these aforementioned studies because only one group of L2 learners with similar proficiencies/expertise was compared to L1 learners. Thus, a specific aim of my research in Chapter 5 was to evaluate how the N170 for single-letter processing might vary as a function of L2 reading proficiency.

1.8 Overview of Chapters with Studies.

This thesis is a compilation of stand-alone manuscripts that are: published, to be resubmitted, or to be submitted. Below is a brief overview of the aims of the studies within each chapter.

Overview of Chapter 2: "Brain regions involved in single-letter and word processing" (publication status: to be submitted). Experience with visual stimuli, such as letters and words, likely modifies the visual perceptual system to become more efficient at identifying such objects. The aim of the study in Chapter 2 was to explore differences in brain responses to familiar visual stimuli (letters, symbols, and words) as compared to unfamiliar visual stimuli (pseudoletters) in adult L1 readers. We performed beamforming analyses of the magnetoencephalographic (MEG) data to reveal a distributed network of activity within the visual perceptual system related to orthographic (letters and words) and non-orthographic (pseudoletters and symbols) processing. A left-lateralized network for word processing was evidenced by significantly larger responses at 188 and 254 ms in the left fusiform gyrus and at 206 ms and 226 ms in the left cuneus and right middle occipital gyrus. Additionally, reaction times to word stimuli were significantly faster to words than to any other stimuli. Results also showed a right-lateralized processing difference between orthographic and non-orthographic stimuli occurring between 180 to 220 ms in the right fusiform and middle temporal gyri. Collectively, these results indicate that experience with text shifts the processing demands to different regions in the neural network depending on the level of abstraction required. I discuss the findings within the context of reading and visual perception models and aspects of automaticity.

Overview of Chapter 3: "Paying attention to orthography: A visual evoked potential study" (published Herdman & Takai, 2013). In adult readers, letters and words are rapidly identified within visual networks to allow for efficient reading abilities. Neuroimaging studies of orthography have mostly used words and letter strings that recruit many hierarchical levels in reading. Understanding how single letters are processed could provide further insight into orthographic processing. The present study investigated orthographic processing using single letters and pseudoletters when adults were encouraged to pay attention to or away from orthographic features. We measured evoked potentials (EPs) to single letters and pseudoletters from adults while they performed an orthographic-discrimination task (letters vs. pseudoletters), a colour-discrimination task (red vs. blue), and a target-detection task (respond to #1 and #2). Larger and later peaking N1 responses (~170 ms) and larger P2 responses (~250 ms) occurred to pseudoletters as compared to letters. This reflected greater visual processing for pseudoletters. Dipole analyses localized this effect to bilateral fusiform and inferior temporal cortices. Moreover, this letter-pseudoletter difference was not modulated by task and thus indicates that directing attention to or away from orthographic features did not affect early visual processing of single letters or pseudoletters within extrastriate regions. Paying attention to orthography or colour as compared to disregarding the stimuli (target-detection task) elicited selection negativities at about 175 ms, which were followed by a classical N2-P3 complex. This indicated that the tasks sufficiently drew participant's attention to and away from the stimuli. Together these findings revealed that visual processing of single letters and pseudoletters, in adults,

appeared to be sensory-contingent and independent of paying attention to stimulus features (e.g., orthography or colour).

Overview of Chapter 4: "Brain oscillations and functional connectivity involved in single letter processing" (publication status: to be submitted). Understanding how the spectral- and spatial-temporal dynamics of neural activity and information transfer among brain regions is an important goal in knowing how visual and orthographic information is processed and transferred throughout the human brain. The study in Chapter 4 aimed at understanding these dynamics for letter processing by investigating oscillatory and functional connectivity in the L1 adult brain. We used a new multi-source beamforming method for EEG source modeling of the event-related potentials to single letter and pseudoletter stimuli in order to minimize findings of false connections. Time-frequency analyses were performed using wavelet analyses of the electrode and source waveforms. Event-related enhanced power within the theta band (4-8 Hz) was significantly different between letters and pseudoletters within the 0-300 ms, but removing the evoked response contributions mostly abolished this effect. More event-related depressed power was seen for letters than pseudoletters within the alpha band (9-15 Hz). Wavelet analyses also provided the phase information for calculating the phase-locking value (PLV) connectivity among selected brain regions. PLV network connectivity results showed significantly greater connectivity within theta band for pseudoletters than letters within a posteriorly distributed network. Alpha-band connectivity was significantly more desynchronized among posterior brain regions for letters than pseudoletters between 85-400 ms. Overall connectivity, summed across time-frequency points, revealed similar amounts of synchronized connectivity for letters and pseudoletters but predominantly more desynchronized connectivity for letters than pseudoletters. In addition, the overall network was more left-lateralized for both synchronized and

desynchronized connections, regardless of stimulus condition (letters and pseudoletters). These results indicated that visual processing of letters and pseudoletters occur within a widely distributed left-dominant network with significant differences in oscillatory activity and network dynamics between letters and pseudoletters. Because differences occurred early (~85 ms), these findings provide evidence that familiar objects (i.e., letters) are coded at fairly early stages of visual processing for L1 adults.

Overview of Chapter 5: "Second-language reading proficiency and event-related potentials to single-letters" (publication status: submitted 10/2017, revised, to be submitted). Proficient reading in a second language (L2) requires efficient processing of its orthographic symbols. We examined the relationship between a reader's proficiency in English and electrophysiological markers of efficiency while processing English and Chinese orthographies. We recruited 49 adult late Chinese learners of English at different proficiency levels, and 32 native English speakers/readers, who participated in an implicit single-letter processing task (alphabet letters vs. pseudoletters) and a Chinese character processing task (characters vs. pseudocharacters) while an electroencephalogram measured their evoked potentials. The difference between letters and pseudoletters was manifested in the N170 and P2 ranges in a posterior-occipital distribution for both Chinese L2 and native English readers, but the difference between characters and pseudocharacters was manifested only for Chinese readers. Further, the N170 pseudoletter effect in the left hemisphere correlated with L2 proficiency. We concluded that single-letter processing in L2 continues to gain efficiency with experience. Future cross-linguistic investigations are necessary to determine whether this L2 effect generalizes to other L2 populations.

Chapter 2: "Brain regions involved in single-letter and word processing"

2.1 Introduction

At first sight, letters and words are meaningless to a child or an adult learning to read a new language in a different script. The exposure to unfamiliar text placed within situations that associate these initially nonsensical visual objects with a sound and/or meaning is an initial stage of learning to read, orthographic-to-phonological association. This constitutes part of the encoding phase for letters and words whereby modifications of the visual neural networks involved in object processing lay down long-term representations of such visual objects with their associated phonology. As described by McClelland and Rumelhart (1981) and many subsequent models (see Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001; Dehaene, Cohen, Sigman, & Vinckier, 2005; Grainger, Rey, Dufau, 2008; McCandliss & Noble, 2003), features of letters are bound together in the initial visual processing stages, followed by comparisons with existing abstract-letter representations that are associated with phonology, and then by comparisons within higher centers containing existing word forms. Continued experience with text leads to a perceptual expertise for letters and words within a given language and gives rise to our human ability to understand language in a written form.

Research has continued to develop more detailed descriptions of the global levels of processing presented in the aforementioned reading models. Investigations are continually expanding on these models to provide a better understanding of the complexities at each of the processing levels that give rise to letter and word recognition. For instance, findings from basic perceptual research and animal neurophysiological studies have lead researchers to expand on visual feature analysis levels in reading models (Dehaene, Cohen, Sigman, & Vinckier, 2005; Grainger, Rey, Dufau, 2008). A growing body of research using neuroimaging techniques is

providing additional insights into the neural substrates underlying these postulated multi-stage processing modules responsible for letter and word recognition. Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies have revealed regions within the ventral visual stream that are possibly specialized for word processing (Cohen et al., 2000; Fiez & Petersen, 1998; Petersen, Fox, Snyder, & Raichle, 1990; Price, 2000; Price & Devlin, 2003; Price et al., 2003; Turkeltaub, Eden, Jones, & Zeffiro, 2002). The middle portion of the left fusiform gyrus has been labeled the visual-word form area (VWFA) because it shows preferentially larger activity when processing letter strings than other non-orthographic stimuli, such as inanimate objects and faces (Cohen et al., 2000; Cohen & Dehaene, 2004; Dehaene, Le Clec'H, Poline, Le Bihan, & Cohen, 2002; for review see McCandliss & Noble, 2003). This designation, however, has been debated (Price & Devlin, 2003). Furthermore, other fMRI results indicated that there is a specialized region for single letter perception residing within the left fusiform gyrus near but distinct from the VWFA (Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006; Pernet et al., 2003). These findings provided evidence that the left fusiform gyrus is highly involved in orthographic processing and indicated a left hemispheric dominance for processing words and letters as compared to symbols or unfamiliar pseudoletters.

Findings from studies measuring event-related potentials (ERP) or fields (ERF) have provided insights into the temporal dynamics underlying orthographic processing (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Eulitz et al., 2000; Miller & Wood, 1995; Herdman, 2011; Bann & Herdman, 2016; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Wong, Gauthier, Woroch, Debuse, & Curran, 2005). A major finding from such studies is that an evoked response peaking between 130-190 ms (N170/M170) is larger when participants view letters than symbols or pseudoletters. This effect is typically lateralized in the left hemisphere and interpreted as larger neural activity resulting from more experience with letters than symbols or pseudoletters. Along with larger N170 amplitudes, Wong et al. (2005) reported significantly shorter N170 latencies to letters than pseudoletters in bilingual participants. Eulitz et al., also reported a tendency of shorter M170 peak latencies to letter strings than pseudoletter strings (Eulitz et al., 2000). Although Tarkiainen and others (Tarkiainen et al., 1999; Tarkiainen, Cornelissen, Salmelin, 2002) did not formally assess latency differences, their results showed that two participants' M145 responses were delayed to symbols and letter-like symbols (strings of rotated letters) as compared to M145 responses to words (see Figure 6 in Tarkiainen et al., 1999). A more recent article by Park and colleagues showed later and broader peaking N170 responses to pseudoletter strings than letter strings (Park, Chiang, Brannon, & Woldorff, 2014). These findings are consistent with the concept that experience modifies neural networks to increase processing speed for familiar visual objects, such as words and letters, as compared to less familiar objects, such as symbols and pseudoletters. Shorter latencies of earlyevoked responses, such as the N170/M170, might reflect automatic visual object processing and categorization of letters or words by abstract letter units or word form units (Coltheart, 1981; Dehaene, Cohen, Sigman, & Vinckier, 2005; Grainger, Rey, & Dufau, 2008; McCandliss & Noble, 2003).

A not so widely emphasized finding in the literature is a right-hemispheric dominant response to the pseudoletters (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Herdman, 2011; Liotti, Gay, & Fox, 1994; Tagamets, Novick, Chalmers, & Friedman, 2000). Tagamets et al. (2000) proposed that their fMRI results reflect that the visual system responsible for orthographic processing encompasses a widespread bilateral network that is differentially

tuned to the amount of experience it has had with a visual stimulus. They suggested that the visual ventral stream doesn't contain isolated regions coding for specific stimuli, such as that proposed for the VWFA, but that there are progressive shifts in the amount of processing within given areas of the network. For example, highly familiar stimuli (words) shift the activations to a more left lateralized network whereas less familiar stimuli (pseudoletters) recruit a more rightlateralized network (see Figure 2B in Tagamets et al., 2000). Liotti and colleagues (Liotti, Gay, & Fox 1994) showed that results from the seminal PET study (Petersen, Fox, Snyder, & Raichle, 1990) had right-lateralized activations to pseudoletter strings and left-lateralized activations to words. Further support for a right-lateralized network when processing non-orthographic stimuli comes from an ERP study by Bentin and colleagues (Bentin et al., 1999). They showed a larger N170 over the right posterior hemisphere (electrode T6) to non-orthographic than to orthographic stimuli and a larger N170 over the left posterior hemisphere (electrode T5) to orthographic than non-orthographic stimuli. A more recent ERP study by Appelbaum, Liotti, Perez, Fox, and Woldorff (2009) showed that an ERP peaking at about 180 ms (N170) was larger over the right hemisphere to pseudoletter strings (i.e., pseudoletter strings) than to words. They also showed that the N145 ERP component peaking at about 140 ms (N145) was larger over the left hemisphere to words than to pseudoletter strings. The 180 ms difference response was localized to the right occipital temporal cortex using discrete dipole source modeling procedures. The authors suggested that the right-lateralized 180 ms ERP to pseudoletter strings could reflect prolonged activation needed to determine the meaning of these unfamiliar stimuli. In other words, their results could provide evidence that a more left-lateralized occipital network is used to more rapidly identify familiar stimuli (words) and a more right lateralized network is used to identify unfamiliar stimuli (pseudoletters). However, we have found that the ERP difference

between letters and pseudoletters was bilaterally distributed over the scalp (Bann & Herdman, 2016) and localized to bilateral fusiform gyri (Herdman & Takai, 2013). What was apparent in these studies was that the N170 was significantly more delayed and broader to pseudoletters than letters and likely reflects a slowing of cortical processing for the inexperienced pseudoletters. Further, such difference at the N170 was even correlated with reading skills (see Chapter 5). Discrepancies within the literature might be related to stimuli features, and thus in this study we designed a task that incorporated stimuli of different character types and lengths (letters, pseudoletters, symbols, and words).

A basic question of many studies within the visual perception literature is how does experience modify the neural codes to form long-lasting representations of visual objects? The current study's objective was to gain insight into the underlying neural substrates of experiencedbased neuroplasticity for visual perception of text by comparing neural responses amongst highly-experienced (letters/words), moderately-experienced (symbols), and inexperienced (pseudoletters) stimuli. In order to investigate this we measured magnetoencephalography (MEG) from participants performing a mixed-trial category judgment task of letters, pseudoletters, and symbols. We performed event-related beamforming on the ERFs and compared the source waveforms across stimulus category (letters/words, symbols, and pseudoletters). Results from this study are discussed in the context of previously presented models of visual perception and reading.

2.2 Materials and Methods

2.2.1 Participants

Fifteen right-handed adults (5 males; 19 to 36 years of age) with normal or corrected vision and normal neurological histories participated in this study. All participants spoke English

as a first language. Three participants had head movements in the MEG dewar that exceeded our tolerance level and two participants had insufficient number of trials after artifact rejection to provide adequate signal-to-noise ratios; therefore, their data were excluded from further analyses. Ten participant datasets were thus admitted for further analyses. Informed consent was obtained from all participants after a full description of the experiment was provided. Ethics review boards from The University of British Columbia and Simon Fraser University approved this study.

2.2.2 Stimulus Procedure

Visual stimuli were white letter, symbol, or pseudoletter characters presented alone or as three-character strings on a black background. Single letter stimuli were 13 uppercase letters: A, B, D, E, G, H, J, N, P, R, T, U, and Y (Figure 2.1). The letters were selected because their line forms could be manipulated to for pseudoletters. Single pseudoletter stimuli were created by segmenting and rearranging the line forms of the letter stimuli in order to reduce the differences in the physical properties between letter and pseudoletter stimuli. Single symbol stimuli were 13 symbols: *, =, %, $\sqrt{}$, \div , \oplus , ", \oplus , \oplus , \oplus , \oplus , *, and #. Letter string stimuli were 13 monosyllabic words. Words were chosen based on the bank of single letters (word frequency % from Google Ngram Viewer): BOY (.0094%), CAR (.0093%), DAY (.0511%), GAS (.0055%), HAT (.0028%), HEN (.0004%), JOY (.0005%), LIP (.0011%), PIE (.0007%), RUN(.0125%), SEA(.0093%), SUN(.00074%), and ZOO(.0002%). Pseudoletter strings were random mixtures of the pseudoletter counterparts of the letters used to create the word stimuli. Symbol string stimuli were a random mixture of the 13 single symbol stimuli. Character strings only contained characters from one stimulus category.



Each stimulus was presented through an LCD projector onto a rear projection screen at a distance of 65 cm from the participant's eyes. A single character covered about 2-3 degrees of vertical and horizontal visual angle with 0.25 degrees between characters. Stimuli were presented for 500 ms at centre fixation followed by a cross hair that remained on the screen for a random duration between 2250 to 2750 ms. The thirteen stimuli for each of the six stimulus categories (letter, symbol, pseudoletter, word, symbol string, and pseudoletter string) were randomly presented in six blocks consisting of 130 trials in each block. This yielded a total of 780 trials; 130 trials per stimulus category. A rest screen was presented between blocks at the same time as the head localization was performed. A session lasted about 30 minutes.

Participants were asked to identify, as quickly and accurately as possible, the visual stimuli as a letter, pseudoletter, or symbol by pressing one of three buttons with their right index, middle, or ring finger. The finger-to-stimulus category mappings were randomly assigned across participants. A 30-stimulus practice block was given in order to familiarize the participants with the pseudoletter stimuli and the experimental procedure.

2.2.3 Measurement

Magnetic fields were recorded over a participant's head using a 151-channel whole-head CTF MEG system (VSM MedTech Ltd.) located in a magnetically shielded room at the Down Syndrome Research Foundation, Burnaby, Canada. MEG sensors were configured as axial gradiometers and had a noise level of less than 10 fT/ \sqrt{Hz} above 1 Hz. MEG was collected at a rate of 600 Hz with an online bandpass filter of 0-200 Hz. Participants sat comfortably with their heads in the MEG dewar that housed the 151 sensors. Three small coils were placed on a participant's nasion and left and right preauricular points in order to locate a participant's head within the dewar and to monitor head movement from the beginning to the end of a recording block. Blocks that had head movements exceeding 8 mm were excluded from further analyses. Video monitoring was used to assess that a participant was alert and on task.

We obtained each participant's head shape by digitizing at least 1000 points covering the surface of the participant's scalp using a digitizing system (Polhemus Inc., Vermont, USA). This procedure took approximately 20 minutes. Each participant's head shape was then used to best match head shapes created from an MRI database in order to obtain best-fitted anatomical information for spatial normalization procedures used in SPM. This procedure is similar to that used by Barnes and Hillebrand (Barnes & Hillebrand, 2003).

2.2.4 Data Analyses

Behavioural. Behavioural reaction times were calculated as the time difference from the onset of the stimulus to the button press. Accuracies were calculated as the percent correct for each stimulus category. Analyses of Variance (ANOVAs) were performed on reaction times and accuracies across the two character lengths (1 and 3) and three stimulus categories (letter, pseudoletter, and symbol). ANOVA results were considered significant if p < .05. Newman-

Keuls Post-hoc tests were performed on significant ANOVA results and were considered significant if p < .01.

MEG. Trials contaminated by muscle or blink artefacts were manually rejected after careful inspection of the individual data. Trials without artefacts were baseline corrected relative to a 250 ms prestimulus interval and used for further analyses. We used the event-related SAM (ER-SAM) method to estimate the spatiotemporal dynamics of the evoked responses to the six stimulus categories (Cheyne, Bakhtazad, & Gaetz, 2006; Herdman, Pang, Ressel, Gaetz, & Cheyne, 2007). We calculated weighting factors between each sensor and each point source located at 5 x 5 x 5 mm voxel in a volume determined by the participant's head shape. The participant's head shapes were then co-registered with head shapes obtained from an in-house database of MRIs. The ER-SAM weighting factors are based on the single-state, pseudo-Z SAM spatial filter for the single-trial data between -500 and 1500 ms across 0-30 Hz for all stimulus conditions combined. We then applied these weighting factors to the averaged trial data from -200 to 800 ms for each stimulus condition and created ER-SAM spatiotemporal maps for each sample point. The ER-SAM maps co-registered to head shape-matched MRIs were normalized into common MNI anatomical space using SPM99 (Barnes and Hillebrand 2003). We then obtained group-averaged ER-SAM maps by averaging the spatially normalized ER-SAM maps across participants. In addition, we performed subtractions of the ER-SAM spatiotemporal maps for the following contrasts: letter minus pseudoletter; letter minus symbol; word minus pseudoletter string; and word minus symbol string. The ER-SAM maps were overlaid onto the MNI template brain for visualization.

Statistical analyses were performed on the ER-SAM maps to define confidence intervals of significant evoked activity. A null distribution was estimated by bootstrap sampling 8192

times the samples within a prestimulus interval (-200 to 0 ms) across all voxels and all participants. Confidence intervals of 99.9% were determined from the null distribution and used as significant thresholds for the ER-SAM maps. To find the peak response in this spatiotemporal data, we searched for a maximum of the pseudo-Z values that exceeded threshold within 15 x 15 x 15 mm volumes. This procedure was performed across time by combining the maxima found for each time sample and then performing a second spatial search. This was done in order to determine the peak of the evoked activity that occurs across space and time. Once these spatiotemporal peaks were found, we then extracted the time courses for each peak. The same statistic as described above was used to determine significant activity or differences in activity because a waveform of an ER-SAM peak is simply a temporal representation of the ER-SAM maps at one voxel location. Thus, the statistics are likely conservative when applied to the peak ER-SAM waveforms because they are based on the noise across all voxels and not the noise just at the peak locations.

2.3 Results

2.3.1 Behavioural

Participants showed high levels of accuracies across all conditions with an average of 95.5 ± 4.2 % correct. We found a main effect of character length in that stimuli with 3 characters (94.8 %) were identified more accurately by 1.3 % than stimuli with 1 character (96.1%; *F* = 6.346; *df* = 1,9; *p* = .033). We found no evidence for a significant main effect of stimulus category (*F* = 0.132; *df* = 2,18; *p* = .877) or an interaction (*F* = 0.619; *df* = 2,18; *p* = .877).

Reaction times are graphically shown in Figure 2.2. We found evidence for significant main effects and an interaction for reaction times (F = 3.748; df = 2,18; p = .044). Post-hoc analyses performed on the significant interaction showed that reaction times to word stimuli were significantly faster by 56 ms, on average, than to any other stimulus (p < .01). No other significant differences existed amongst character length and stimulus category (p > .01). Thus, the main effects of character length (F = 19.057; df = 1,9; p = .002) and stimulus category (F = 3.935; df = 2,18; p = .038) was driven by the significantly faster reaction times to words than to any other stimuli.



2.3.2 MEG

Sensor Space. Topographies for the group-averaged M125 ERF and the M200 ERF differences are depicted in Figure 2.3A. They show large ERFs entering and exiting over the posterior regions of the head. Two sensors (MLO32 and MRO21) over the occipital cortices

showed large differences around 200 ms amongst stimulus categories and were therefore selected in order to visualize the temporal dynamics. All six stimuli (letter, pseudoletter, symbol, word, pseudoletter string, and symbol string) produced robust visual ERFs, which are labeled as the M80, M125, M170, M200, and M250 (Figure 2.3B). Note that the ERFs in the left sensor (MLO32) are the inverted pattern of those in the right sensor (MRO21) because the likely neural generators in bilateral visual cortices are oriented in opposite directions causing fields to exit and enter the left and right posterior regions of the head, respectively. For example, the M125 response has an outgoing ERF (black) at MLO32 and an ingoing ERF (white) at MRO21.

A prominent ERF difference amongst stimuli is an additional or delayed ERF between 160-220 ms in the left hemisphere (MLO32) for words versus pseudoletters and symbol strings (see difference waveforms in Figure 2.3B). This pattern is reversed in the right hemisphere (MRO21) where pseudoletters and symbols (regardless of character length) show an additional or delayed ERF as compared to letter or word stimuli. Although, the differences appear to be the same modification in each hemisphere, as shown by the difference waveforms (bottom plots), they are likely reflecting separate processes. The ERFs to words in MLO32 are larger or prolonged, in what could be classified as an M170, as compared to ERFs to pseudoletter or symbol strings. The reverse difference is seen in the right hemisphere where ERFs to pseudoletters and symbol stimuli (single- and three-characters) show prolonged responses (possibly an M170) as compared to words or letters. Moreover, no ERF differences around 170 ms are evident in the left hemisphere amongst the single-character stimuli (letter, pseudoletter, and symbol); whereas ERF differences amongst these stimuli clearly exist in the right hemisphere. Furthermore, note the high-degree to which the waveforms for pseudoletter and symbol stimuli overlap for the early ERFs; demonstrating highly replicable responses. Another

noticeable response difference amongst stimuli is a larger ERF peaking between 240 to 290 ms for word and letter stimuli as compared to pseudoletter and symbol stimuli. The M250 effects for

character string stimuli (Word-Pseudoletter String and Word-Symbol String) are more prominent in the right than left hemisphere.



Figure 2.3 (A) Topographies of the grand-averaged (n = 11) event-related fields (ERFs) for the six stimulus types at 125 ms and difference topographies at 200 ms. Cold (blue-white) and hot (red-yellow) hues represent ingoing and outgoing magnetic fields, respectively. Grey dots represent each sensor. Anterior sensors are at the top and left hemispheric sensors are on the left of each map. (B) ERFs at selected sensors that had large ingoing and outgoing fields at 125 ms over the left (MLO32) and right (MRO21) occipital regions, respectively. From top to bottom: first set of waveforms are ERFs to single-character stimuli (letter, pseudoletter, and symbol); second set are single-character differences (letter minus pseudoletter; letter minus symbol); third set are to character strings (word, pseudoletter string, and symbol string); and the fourth set are character string differences (word minus pseudoletter string; word minus symbol symbol). ERF peaks (M80, M125, M170, M200, and M250) are designated by arrows. Note that the ERFs in the right occipital sensor are the inverted versions of ERFs in the left occipital sensor.



Figure 2.4 (A) Statistically significant (p < .001) grand-averaged ER-SAM maps projected to the surface of a 3D MRI to word stimuli displayed at 26 ms intervals from 90 to 480 ms (labeled in white text above each map). Pseudo Z-values represent the ratio of signal-to-noise power of the evoked response. (B) ER-SAM difference maps of word minus pseudo string subtractions at latencies with maximal pseudo Z-value differences between 90 and 500 ms. Hot and cool colours represent greater activity for words and pseudoletter strings, respectively. Source peaks are consecutively labeled from 1 to 14 and correspond to the source waveforms in Figures 2.5 and 2.6. Note that the right frontal hemisphere for the 302 ms map has been cut away to reveal the anterior cingulate source 12.

2.3.3 Source Space

The ER-SAM spatiotemporal maps for word stimuli show a typical visual response pattern with activity in the cuneus occurring at about 90 ms, extending antero-laterally and ventrally between 120 to 180 ms, followed by right hemispheric dominant activity within posterior middle temporal regions between 180 and 400 ms, and then bilateral frontal responses between 400 to 500 ms (Figure 2.4A). This spatiotemporal profile of activity from cuneus to fusiform to inferior frontal gyrus/insula follows the processing stream for object recognition in the ventral visual pathway. The activation patterns for pseudoletters and symbols are similar to the pattern for words but with some differences that are difficult to see when visually comparing amongst single-state maps. Thus, the more informative difference maps for words minus pseudoletter strings are presented below.

Difference activity. We found 14 areas with significant (p < .001) response differences between words and pseudoletter strings from 125 to 500 ms (Figure 2.4B). There were similar significant spatiotemporal differences between letter and pseudoletter or symbol stimuli in locations near to sources 4 and 6 in Figure 2.4B (Talaraich coordinates = 27 -56 -10 and 43 -51 0 mm). We have thus only showed the difference maps for word versus pseudoletter strings. To determine the spatiotemporal dynamics associated with orthographic experience we compared letters/words to pseudoletters/symbols for single- and three-character stimuli.

Sublexical effects. The difference map at 188 ms (Figure 2.4B) shows larger responses to pseudoletter strings than to words in the left inferior occipital gyrus (IOG; source 3), right posterior fusiform gyrus (pFuG; source 4), right anterior fusiform gyrus (aFuG; source 5), and middle temporal gyrus (MTG; source 6). This response difference appears to be caused by prolonged responses to pseudoletter strings and pseudoletters as compared to words and letters in

bilateral ventral visual regions (sources 3 to 5), but an additional response peak to pseudoletters in right MTG (source 6) at approximately 206 ms (Figures 2.5 and 2.6). Response differences in sources 3 to 5 occur at approximately 188 ms and precede the extra response peak in source 6 at 206 ms. A similar trend can be seen in waveforms contrasting letter and symbol stimuli where protracted activations occur in sources 3 to 5 at about 188 ms and an additional response occurs at about 206 ms in source 6 (Figures 2.5 and 2.6). At 268, responses in the right superior temporal gyrus (STG; source 9) to pseudoletter strings are significantly greater than to words. Additionally, at 302 ms responses to pseudoletter and symbol stings were significantly larger than responses to words in the left lingual (source 10) and right MOG (source 11). These differences persisted until about 550 ms but they were just under the statistical threshold (p<.001). Such long-latency differences are also noticeable in source 3 to 6 and source 14 for the string stimuli (Figure 2.5) and single-character stimuli (Figure 2.6), but again they are just below statistical threshold.

Word effects. We found no evidence that single letters produced larger responses than responses to single pseudoletters or symbols. However, we found significantly greater response to words than to pseudoletters or symbol strings at 126 ms in the left cuneus. This was evident in the difference waveforms for sources 1 and 7 (Figure 2.5). At 188 ms, the left fusiform gyrus had larger responses to words than to any other stimulus category (source 2; Figures 2.5 and 2.6). Activity in the left cuneus (source 7) and right MOG (source 8) had larger responses to words than to any other stimuli between 200 and 230 ms. We also unexpectedly found a larger response to words than to any other stimuli within the anterior cingulate (source 11; Figure 2.4B). A left frontal source (left insula; source 13) showed larger responses to words than to pseudoletter and symbol strings peaking at about 430 ms.



Figure 2.4B. Difference waveforms are plotted below the single-state waveforms for each source: word minus pseudoletter string (solid red line) and word minus symbol string (solid black line). The solid horizontal black dotted lines are the statistical significance thresholds for the difference waveforms at *p* < .001. Talaraich labels and coordinates (in mm) are displayed above each plot. The number in the upper left corner of each plot corresponds to the source number in Figure 2.4B.



2.4 Discussion

In this study, we investigated the brain responses to highly experienced visual stimuli (i.e., words and single letters) as compared to inexperienced visual stimuli (i.e., pseudoletters and symbols). We found two main effects, a right-lateralized sublexical effect and a left-lateralized word effect. These are discussed in the context of previously presented models of reading and visual perception (Dehaene, Cohen, Sigman, & Vinckier, 2005; Di Lollo, Enns, & Rensink, 2000; Grainger, Rey, & Dufau 2008; McCandliss, Cohen, & Dehaene, 2003; McClelland & Rumelhart, 1981; McClelland & Rumelhart, 1981; Rey, Dufau, Massol, & Grainger, 2009).

Figure 2.7 depicts our generalized conceptual model of letter perception based on these previous models. Retinal input is coded as features within the visual cortex, here depicted as the feature level (FL). For our purpose, in order to perform the task of identifying letters, pseudoletters and symbols, the line forms are the most relevant visual features of the stimuli. Neurons in bilateral primary and secondary visual cortices that code for these local line contours send information through excitatory, feed-forward connections (designated as lines ending with arrows) to more complex-feature and composite neurons that integrate the stimulus features to form object shapes. In our example, the two parallel vertical lines for the stimulus "H" will activate the feature integration cells that code for the object shapes "H", "N", and "M". The neurons coding of the letter shape "H" will also receive input from neurons coding for the horizontal line, whereas little to no activation will come from neurons coding for slanted line features in "N" and "M". Thus, greater activation will occur within the neurons integrating the features for the object shape "H" than for "N" or "M". Such feature integration is suspected to occur bilaterally in neural populations within the lateral occipital complex (possibly areas V4 and V8; for review see Dehaene, Cohen, Sigman, & Vinckier, 2005).



The pattern level (PL) in this model will receive the output of each object shape population in a feed-forward manner as well as the re-entrant signals of reconstructed object shapes from the working space (WS). For the initial feed-forward sweep, the re-entrant signals from the WS will be null. This is because object hypotheses have not been formulated yet; therefore, no comparison will be performed between the FL and WS outputs. Instead, the output of each FL channel will activate the PL neurons that code for letter identities (i.e., abstract letter units; ALUs), which have been associated with these object shapes through visual experience. The anatomical location(s) for an ALU pattern level is(are) yet to be confirmed. A few fMRI studies, however, have shown enhanced BOLD signals to letters as compared to pseudoletters in the left inferior temporal cortex, anterior to the visual word form area (Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Cerullo, Farley, Steinmetz, & Mier,
2006). In a study of McClelland and Rumelhart's interactive-activation model, Rey and colleagues showed that their computational models of ERP results support an inclusion of lateral inhibition within the abstract letter level (Rey, Dufau, Massol, & Grainger, 2009). Thus, we include lateral inhibition between ALUs within the PL, depicted in Figure 2.7 as lines ending with a filled circle. Lateral inhibition in the PL will further separate the functional distance amongst the ALUs coding for different letter identities. For example, the largest amount of inhibition to surrounding letter identities will come from the ALU coding for "H" because it was the most activated by the FL neurons. Thus, the ALU coding for "H" will have predominantly greater activity than any other ALU. Nevertheless, other competing ALUs might also maintain a high level of activity and remain as possible letter identity hypotheses. This pattern level is conceptually similar to the pattern recognition layer of the re-entrant model proposed by Di Lollo and colleagues (Di Lollo, Enns, & Rensink, 2000).

In this model, we also included a working space (WS) that is similar to that in Di Lollo et al.'s re-entrant model (Di Lollo, Enns, & Rensink, 2000). Within the WS, the hypotheses of probable letter identities sent from the PL are translated back to a high spatial resolution version of the object-shape information. The reconstructed object-shape information is then sent via reentrant pathways back to the PL in order to compare it to the information output from the FL. In our example, the WS reconstructed object-shape signal output for hypothesis h_1 (i.e., letter "H") will activate the same receptive fields in the PL as did the FL object shape signal for the letter "H". As a result of this overlap in receptive field activation, the ALU coding for the letter "H" in the PL will receive a boost in excitation as compared to reduced signals from the FL and WS for hypotheses h_2 and h_3 . Iterations through this loop can thus be used to tune the output of the PL and reduce uncertainty or ambiguity of the object's identity (i.e., reducing the number of competing hypotheses). Once uncertainty is reduced by limiting competing hypotheses, the WS will output the most probable hypothesis of the object's identity (e.g., letter "H"). The criterion for determining the uncertainty threshold is likely set by the task demands via top-down executive processes (e.g., a lower uncertainty threshold might be set when accuracy is more important, whereas a higher uncertainty threshold might be set when reaction speed is more important).

2.4.1 Right-Lateralized Sublexical Effect

Because pseudoletters have similar stimulus characteristics as compared to letters, we assume that early visual response differences between these stimulus categories are mainly an effect of experience. A sublexical effect of experience was evident in our results as additional activity occurred between 170-230 ms to pseudoletters than to letters in bilateral occipital cortices (sources 3 to 6; Figure 2.4B), regardless of whether they were presented as single- or three-character stimuli. Given that sources 3 to 6 show a significant expertise effect, we suggest that they constitute part of the neural network involved in object recognition (i.e., the ALU in the PL, Figure 2.7). The greater source magnitude to pseudoletter stimuli appears to be due to a prolonged response, or an additional response component (a lateralized M170?), or possibly both. Sources 3 to 5 (Figure 2.5 and 2.6) show prolonged responses yielding greater source magnitude that peaks at approximately 188 ms for pseudoletters, whereas source 6 shows an additional response for pseudoletters peaking at about 206 ms. This is consistent with our previous MEG findings for letter versus pseudoletter processing (Herdman, 2011). In accordance with our generalized IA model, we suspect that reverberations within the re-entrant loop that are needed to reduce the number of competing hypotheses creates this additional source activity for pseudoletters between 180-210 ms. For letters, only one loop is likely required to check the

limited number of competing hypotheses as described above in our adapted IA model for the letter "H", because experience will have modified the neural network to reduce competing hypotheses via strong lateral inhibition amongst ALUs in the PL (Rey, Dufau, Massol, & Grainger, 2009). For less familiar stimuli (pseudoletters and symbols), however, multiple iterations through the re-entrant loop might be required to disqualify competing hypotheses of letters and other pseudoletters/symbols that have similar features to the currently viewed stimulus. This is because limited experience with pseudoletters/symbols would not have created strong lateral inhibition among neural populations coding for the competing object representations in the PL. The need for more iterations would create more reactivations of the network and would thus show up as prolonged responses (i.e., in source 3 to 5) or additional responses (i.e., in source 6) associated with object recognition. Additionally, we showed that the extra processing for pseudoletters and symbols begins within the ventral visual cortices (sources 3 to 5) followed by a right MTG (source 6) possibly reflecting subsequent pattern recognition analyses. The ventral visual sources could represent regions responsible for comparing the outputs of the FL and WS that then pass its computation to object recognition units in the right MTG. A competing explanation is that the interplay among the left IOG (source 3) and the right extrastriate complex (sources 4 to 6) constitutes object recognition in the PL and that there isn't a region solely specialized for letter or object identity. An ALU could be represented by the communication within this distributed neural network and not by activation in a single region, such as the left anteriolateral fusiform gyrus suggested by previous fMRI research (Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006). We suspect that the left fusiform gyrus is also involved in such a network, however, we only found the differential activity within the left IOG. The lower spatial resolution of MEG

and higher coregistration error as compared to fMRI might account for this inconsistency but given that our other source locations (e.g., cuneus) do not have a large discrepancy in their expected locations, we believe that our left IOG source is distinct from that found in the fMRI literature. Another possible caveat to our right-lateralized finding is that MEG is less sensitive to neural activations that have their dendrosomatic axes radially-oriented with respect to the MEG axial sensors. Future multi-modal neuroimaging research using fMRI, EEG, and MEG measurements of letters, pseudoletters, symbols, and words could help elucidate these discrepancies among studies.

Even though there are discrepancies among studies, our results do expand on previously reported EEG and MEG studies of letter perception (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Eulitz et al., 2000; Herdman, 2011; Herdman & Takai, 2013; Miller & Wood, 1995; Park, Chiang, Brannon, & Woldorff, 2014; Park, van den Berg, Chiang, Woldorff, & Brannon, 2018; Pernet, Celsis, Demonet, 2005; Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Tarkiainen, Cornelissen, Salmelin, 2002; Wong, Gauthier, Woroch, Debuse, & Curran, 2005). Our results are consistent with most of these studies in that evoked responses to letters and pseudoletters show significant differences between 150-210 ms. Bentin and colleagues (Bentin et al., 1999) showed larger N170 responses to non-orthographic than orthographic stimuli over the right posterior scalp and the opposite effect over the left posterior scalp. They demonstrated a right-lateralized N170 to nonorthographic stimuli and a left-lateralized N170 to orthographic stimuli. Our findings are in direct agreement to the Bentin et al.'s (1999) results, in that we found significantly larger responses in the left fusiform gyrus to words than to any other stimuli at about 180 ms and larger

responses in the right hemisphere to non-orthographic stimuli (pseudoletters and symbols) than to orthographic stimuli at around 200 ms (Bentin et al., 1999). Unfortunately, Bentin et al. (1999) did not report their difference waveforms and their statistical analyses were only performed on the peaks of the N170 responses. We are; therefore, unable to directly compare our difference waveforms with theirs. From their figures however, divergence between orthographic and nonorthographic stimuli appears to continue past the N170 response into the P2 responses. Additionally, ERP studies (Park et al., 2018; Rey, Dufau, Massol, & Grainger, 2009; Stevens et al., 2013; Wong et al., 2005) showed larger ERPs at 200 ms recorded from central scalp sites to pseudoletters than to letters. Difference waves were again not reported, thus it is difficult to determine the timing of the peak of the response difference between letter and pseudoletter stimuli, however, the ERPs at central sites begin to clearly diverge at about 180 ms and persist until at least 250 ms. Although topographical differences between letter and pseudoletter stimuli suggest involvement of bilateral inferior temporal cortices, source localization was not performed in these studies. We have previously performed source modeling of MEG (Herdman, 2011) and EEG (Herdman & Takai, 2013) responses to letter and pseudoletter stimuli. We found that the main ERF (MEG) difference between letters and pseudoletters surrounding the M170 resided in the right inferior temporal cortex (Herdman, 2011). However, in a subsequent EEG study, we found such N170 differences to be localized bilaterally in the inferior temporal cortices. Thus, these findings suggest that MEG might not be sensitive to capturing all the source activity as compared to EEG because MEG mostly measures magnetic fields that are tangentially-oriented to the scalp surface.

James, James, Jobard, Wong, and Gauthier, (2005) conducted an fMRI study using a similar paradigm to ours and found larger fMRI signals to letter than pseudoletter stimuli within

the left fusiform cortex, which is consistent with the topographies of their ERP findings. MEG source modeling by Tarkiainen, Helenius, Hansen, Cornelissen, and Salmelin (1999) showed larger evoked responses to letters than letter-like symbols (rotated letters) occurred near the temporal-occipital junction, with predominantly more dipole sources localized within the left hemisphere. Interestingly, the source waveforms for their letter-like symbols showed prolonged and even delayed responses (see Figure 2.6 of Tarkiainen et al., 1999) as compared to letter stimuli. Park et al., (2018), also found prolonged N170s to pseudoletters strings as compared to letter strings. Such results are consistent with our findings (Herdman, 2011; Herdman & Takai, 2013; present results). Taken together, these findings are consistent with the IA model in that the object shape from the FL (see Figure 2.7) doesn't match an upright experience-based ALU in the PL.

Furthermore, Pernet and colleagues showed ERP effects of categorization occurred between 220 to 280 ms evidenced by delayed P2 latencies at about 220ms followed by reduced N2 amplitudes at about 280 ms for inexperienced (Asiatic letters) as compared to experienced (Latin letters) visual stimuli (Pernet, Celsis, & Demonet, 2005). Difference waves and source analyses were not provided thus it is difficult to assess if the P2 latency and N2 amplitude effects reflect a common underlying neural process. Pernet and colleagues attributed these effects to an effect on category judgment and suggested that they reflect additional processing time needed to resolve the category judgment for unfamiliar as compared to familiar stimuli (Pernet et al., 2005). This is in-line with our results in that we also found response differences about 200 ms between experienced (letter and word stimuli) and inexperienced (pseudoletter stimuli) stimuli (present study, Herdman & Takai, 2013). This P2 effect could reflect extra processing time for pseudoletters which might also be associated with prolonged gamma-band activity to pseudoletters as compared to letters (Herdman, 2011). Pernet et al. (2003) did not specify what type of extra processing was being performed, but their interpretation is in line with our proposal that inexperienced objects (pseudoletters or Asiatic letters) require additional loops through reentrant pathways to resolve conflicting hypotheses.

Our source modeling results of the differences between letter and pseudoletter stimuli within 180-300 ms showed an active neural network that consists of the inferior temporal, middle temporal, and middle occipital gyri. With the exception of the Bentin et al. study (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999), our results are in contrast to the former ERP studies (Eulitz et al., 2000; Herdman & Takai, 2013; Miller & Wood, 1995; Park, van den Berg, Chiang, Woldorff, & Brannon, 2018; Pernet, Celsis, & Demonet, 2005; Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Tarkiainen, Cornelissen, & Salmelin, 2002; Wong, Gauthier, Woroch, Debuse, & Curran, 2005) in that we showed larger evoked responses to pseudoletter stimuli than letter stimuli mainly in the right occipital cortices (present study; Herdman, 2011). Previous research has showed larger N170/M170 peak amplitudes to letters than pseudoletters. We are unable, at this time, to clearly establish the reason for these discrepant findings but can suggest at least three possibilities. One possibility is that most of the previous literature analysed only the peak N170 amplitude differences and did not provide difference waveforms between letters and pseudoletters, thus assuming that the effects are at the peak N170. As can be seen in the current study's results and from previous studies, the main ERP differences between letters and pseudoletters occurred slightly later than the peak of the N170 response (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013; Takai & Herdman, 2013). Another possibility is that MEG is less sensitive to measuring

radial sources, which might be generating a portion of the N170 responses seen in the ERP studies. Another possibility is that paradigm differences might cause recruitment of different neural networks. For example, previous ERP studies used a one-back matching task to evaluate experience effects on letter perception (Stevens et al., 2013; Wong et al., 2005). The letter stimuli are most likely being named on each trial and thus recruiting phonology whereas pseudoletter stimuli are most likely being processed at a feature level for storage and subsequent retrieval. A one-back task asks participants to memorize each letter for subsequent retrieval and comparison. In doing so, participants most likely name each letter because this would be a very easy and efficient way to complete a one-back task. This effectively recruits phonological processing only for the letters and not the pseudoletters (which are typically presented in a separate block). Participants are, therefore, in a phonological state for the letter block and a visual feature-discrimination state for the pseudoletter block. By comparing between these blocks, ERP differences are most likely reflecting differences between phonological processing and feature-discrimination and less likely reflecting orthographic processing differences between letters and pseudoletters. Our task required participants to judge stimuli based on previously experienced categories of letters, symbols, and pseudoletters; therefore, incoming stimuli would be compared to object category representations. Our task would be expectedly less dependent on phonological processing and more based on orthographic processing, however, this would need to be verified in future work. In any case, the increasing literature on sublexical (i.e., letter) perception is providing further evidence that experience-based plasticity appears to be molding the cortical responses involved in the early stages of perceptual processing.

2.4.2 Left-Lateralized Word Effect

We found significantly larger responses in the left fusiform gyrus (source 2 in Figure 2.5 and 2.6) between 170 to 250 ms to words than to any other stimulus category. This is consistent with many other fMRI, MEG, and EEG studies that investigated word reading and showed greater activity within the left fusiform gyrus (i.e., the putative VWFA) for word reading as compared to viewing character strings (for discussions see Cohen et al., 2000; Cohen & Dehaene, 2004; Price & Devlin, 2003; Price et al., 2003). An interesting aspect of our finding is that the task did not require explicit word reading. Instead, participants only had to identify if a letter, symbol, or pseudoletter was present in the stimulus. This could easily be accomplished by judging a single character within the string while ignoring the others. We found, however, a significant behavioural word effect that indicates that participants were either actively reading all characters on the screen or that viewing words, in this situation, obligatorily activates areas responsible for word reading.

Our findings suggest that part of the network involved in reading words is unavoidably engaged in addition to feature-based analyses of letter detection required for our task. This could help explain our behavioural results which show significantly faster reaction times to words as compared to all other stimuli. We did not find support for the possibility that flanking characters of same category could enhance reaction times because there were no significant reaction time differences between single- and three-character stimuli, with the exception of that for words. Importantly, these results indicate that letter detection is faster for words than for single letters and is akin to the well documented word-superiority effect (Reicher, 1969). Taken together, our neuroimaging word effect and our behavioural word-superiority effect further supports Rumelhart and McClelland's IA model of reading in that letter detection would be enhanced by

combined activation of word and letter detectors when a stimulus is a word compared to only activation of letter detectors when a stimulus is a letter.

Most other EEG and MEG studies reported differences between words and pseudoletter strings or symbol strings at the peak of the N170/M170 (Eulitz et al., 2000; Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Wong, Gauthier, Woroch, Debuse, & Curran, 2005); however this might not be where the largest response difference occurs. We showed that there are at least two peaks in the difference waveforms in the left fusiform gyrus (source 2 in Figure 2.5). Thus, we believe that these differences reflect additional responses that override the N170/M170 response and might change the M170 onset latencies depending on task demands. Furthermore, the double peaks in the difference waveform in the left fusiform taken with the peak response difference in bilateral occipital cortices (sources 7 and 8) might indicate a re-entrant loop of response checking. The first peak difference at about 188 ms in the left fusiform might represent the first processing step of formulating hypotheses about possible word forms (i.e., lexical retrieval), whereas there are limited or no competing hypotheses of word forms for pseudoletter strings, single pseudoletters, or single letters because these stimuli are being obligatorily processed like words. The iterations through the loop of the IA model (Figure 2.7) can be conceptualized in much the same way as that for letters but replacing ALUs with word form units. Output of the left fusiform is sent via re-entrant pathways back to the lateral occipital cortices (sources 7 and 8) for reactivation of the feature level at approximately 220 ms, which then is sent back to the left fusiform gyrus at about 250 ms for final lexical retrieval. The final output is then sent forward to higher centers in the reading network for further retrieval of associations and computations. For example, at about 430 ms, the left inferior frontal gyrus/insula (source 13 in Figure 2.5) shows a larger response to

words than to any other stimuli, which might reflect semantic retrieval/rehearsal. This is consistent with the classical language models of reading (see Fiez and Petersen, 1998; Price, 2000).

A perplexing finding in the present study was a larger activation at about 300 ms in the anterior cingulate cortex (ACC) for word stimuli as compared to all other stimuli. This was completely unexpected and difficult to interpret given the current literature on ACC function. Our first impression was this difference was related to an eye-blink or eye-movement artefacts, but all blinks and eye-movements were removed during this time interval prior to source modeling. Moreover, beamformer results for eye artefacts are fairly precise in localizing them within or near the orbits. Our second thought was that the ACC activation resulted from difference in the beamformer calculations across conditions, but the beamformer weights were based on all stimulus trials regardless of stimulus category. Furthermore, responses to all other stimulus categories have highly replicable waveforms in the ACC. Our current conjecture is that the ACC is involved in conflict monitoring between the local letter features to be detected and the global features of the word. In other words, the internal representation defines that the stimulus is a word but the response judgment for this task is that the stimulus needs to be judged as a letter; thus, internal conflict ensues. ACC activation hasn't been reported in previous MEG studies of word reading (Barnes & Hillebrand, 2003; Cornelissen et al., 2009; Herdman, Pang, Ressel, Gaetz, Cheyne, 2007; Herdman, 2011); therefore, we suspect that our ACC activation is purely dependent on our task used and is not directly involved in letter/word perception.

In conclusion, our results are consistent with the IA model proposed by Rumelhart and McClelland in that there are multiple stages of perceptual processing of words and letters that are molded by experience. We believe that these stages are represented within neural networks

spanning many brain regions across the hemispheres. Our results indicate that the bilateral activations in the visual ventral stream are left lateralized when processing words and right lateralized when processing non-orthographic stimuli, such as pseudoletters and symbols. Our results further show that long-term experience of viewing letters and words modifies a portion of the network responsible for visual perception at early (125 ms), mid (180-210 ms), and late (260-500 ms) processing stages.

Chapter 3: Chapter 3: "Paying attention to orthography: A visual evoked potential study" (published Herdman & Takai, 2013)

Abstract

In adult readers, letters and words are rapidly identified within visual networks to allow for efficient reading abilities. Neuroimaging studies of orthography have mostly used words and letter strings that recruit many hierarchical levels in reading. Understanding how single letters are processed could provide further insight into orthographic processing. The present study investigated orthographic processing using single letters and pseudoletters when adults were encouraged to pay attention to or away from orthographic features. We measured evoked potentials (EPs) to single letters and pseudoletters from adults while they performed an orthographic-discrimination task (letters vs. pseudoletters), a colour-discrimination task (red vs. blue), and a target-detection task (respond to #1 and #2). Larger and later peaking N1 responses (~170ms) and larger P2 responses (~250 ms) occurred to pseudoletters as compared to letters. This reflected greater visual processing for pseudoletters. Dipole analyses localized this effect to bilateral fusiform and inferior temporal cortices. Moreover, this letter-pseudoletter difference was not modulated by task and thus indicates that directing attention to or away from orthographic features didn't affect early visual processing of single letters or pseudoletters within extrastriate regions. Paying attention to orthography or colour as compared to disregarding the stimuli (target-detection task) elicited selection negativities at about 175 ms, which were followed by a classical N2-P3 complex. This indicated that the tasks sufficiently drew participant's attention to and away from the stimuli. Together these findings revealed that visual processing of single letters and pseudoletters, in adults, appeared to be sensory-contingent and independent of paying attention to stimulus features (e.g., orthography or colour).

3.1 Introduction

Single-letter perception is a prerequisite to word perception and research is starting to unravel the mystery of how the brain processes such basic building blocks of literacy. Reaction times to letters are faster than to symbols or pseudoletters indicating that somewhere along the visual processing stream familiar letters are processed faster (Herdman, 2011; LaBerge, 1973). This might be caused by increased neural activity to letters or faster responding neural ensembles. Evidence for increased neural activity comes from previous neuroimaging research that showed visual evoked responses between 140-190 ms were larger to letters as compared to symbols or pseudoletters (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Eulitz et al., 1996; Maurer, Brandeis, & McCandliss, 2005; Maurer, Zevin, & McCandliss, 2008; Miller & Wood, 1995; Pernet et al., 2003; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Wong, Gauthier, Woroch, Debuse, & Curran, 2005). A negative response recorded from left inferior temporal cortices, termed the N200, has also been shown to be larger for words than for faces or objects (Nobre, Allison, & McCarthy, 1994). However, later responses between 200-400 ms were shown to be greater for pseudoletters than letters (Herdman, 2011; Miller & Wood, 1995; Wong et al., 2005). Such processing advantages for letters have been suggested to be a result of language-dominant networks within the left inferior temporal cortices used for word reading (Cohen & Dehaene, 2004; Eulitz et al., 1996; Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006; Maurer, Brandeis, & McCandliss, 2005; Maurer, Zevin, & McCandliss, 2008; McCandliss, Cohen, & Dehaene, 2003; Miller & Wood, 1995; Pernet et al., 2003; Pernet, Celsis, & Démonet, 2005; Tarkiainen et al., 1999; Wong et al., 2005). Conversely, a few other studies showed consistently early visual processing differences between letters and pseudoletters across bilateral visual cortices with a

possible right-hemispheric dominance (Appelbaum et al., 2009; Herdman, 2011). This provides evidence that orthographic processing is recruiting more bilateral networks, as has been previously proposed (Tagamets, Novick, Chalmers, & Friedman, 2000). Correspondingly, an fMRI study contrasting false-font strings with words or word-like characters showed a greater signal change in the left inferior temporal regions to words than false-font strings but conversely greater signal change in the right hemisphere to false-font strings than words (Vinckier et al., 2007). The authors suggested that false-font strings might capture greater attention because they are unfamiliar objects and thus recruit more resources within extrastriate regions. This is in line with our previous proposal that pseudoletters elicit prolonged processing within the right extrastriate regions (Herdman, 2011). Furthermore, modulation of neural activity associated with orthographic processing is consistent with findings from Ruz and Nobre (2008) showing that attention to orthography modulated early N200 to words more so than attention to phonology or semantics. However, the attention-related modulation of ERP differences between words and false-font strings were not reported in that study and thus it is difficult to interpret how attention might modulate processing differences between letters and pseudoletters. The current study addressed this issue by manipulating attention towards or away from orthographic features of single letters and pseudoletters.

As compared to the neuroimaging literature on word processing (for reviews see Cohen & Dehaene, 2004; Dehaene, Cohen, Sigman, & Vinckier, 2005; Grainger, Rey, & Dufau, 2008; Maurer, Brandeis, & McCandliss, 2005; Maurer, Brandeis, & McCandliss, 2008; McCandliss, Cohen, & Dehaene, 2003; Price, 2000; Price & Delvin, 2003), the literature on single-letter processing is less well-developed (e.g., Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Grainger et al., 2008; Herdman, 2011; James, James, Jobard, Wong, & Gauthier, 2005; Miller & Wood, 1995; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Wong, Gauthier, Woroch, Debuse, & Curran, 2005). Initial stages of reading acquisition are dependent on singleletter recognition (e.g., grapheme-to-phoneme encoding) and thus it is important to understand how the human brain processes individual letters. Interpretations of low-level orthographic processing have mainly been inferred from studies investigating orthography in tasks involving word and letter-string recognition (Grainger et al., 2008). These tasks likely prime neural networks associated with word recognition, such as the visual word form system that could potentially recruit additional processes beyond low-level orthographic processes. For instance, participants are faster at identifying letters in words than when presented alone, commonly known as the word superiority effect (McClelland & Rumelhart, 1981; Reicher, 1969). Thus, tasks that compare words to letter strings might be recruiting hierarchical processes beyond that of single-letter processing. Evidence for extra processing can be seen in ERP recordings to words or letter strings as compared to single letters in that character strings elicited broader N1 responses as compared to single characters (Wong et al., 2005). Measuring neural responses to single-letters would provide further information about the underpinnings of low-level orthographic processing.

The inconsistent findings for orthographic-related processing within the literature might be due to differences in attention demands on stimulus features as driven by task set or stimulus familiarity (letters vs. pseudoletters). For instance, target-detection tasks that asked participants only to respond after a target (e.g., Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009) might have minimally activated the networks responsible for orthographic processing as compared to tasks that asked participants to discriminate between letters and pseudoletters on a trial-by-trial basis (e.g., Herdman, 2011). Attention is likely less focused on the orthographic stimuli during target-detection tasks than orthographic-discrimination tasks. Reduced attention to a stimulus feature, such as colour, is known to modulate early visual processing as evidenced by an early selection negativity (SN) between 140 to 180 ms when attending to stimulus colour (Hillyard & Anllo-Vento, 1998). Whether such attention to stimulus feature modulates early orthographic processing differences needs further research. Thus, we investigated the hypothesis that tasks encouraging participants to directly pay attention to orthographic features would enhance early orthographic processing differences between letters and pseudoletters (Herdman, 2011), as compared to tasks that did not encourage recruitment of orthographic networks, such as a colour discrimination task or a non-orthographic target-detection task. Contrarily, letters become highly consolidated and relevant for adults who have gained a large amount of experience with these familiar visual objects. Thus, early orthographic processing within the lower-visual centers might be automatic and not task dependent. If this alternative hypothesis is correct then there will be little, if any, change in the early orthographic processing differences between letters and pseudoletters due to attention to or away from orthographic features. We used evidence from visual evoked potentials among three tasks (orthography discrimination, colour discrimination, and target detection) to determine whether early visual processing of letters and pseudoletters are modulated by paying attention to orthographic features.

3.2 Material and Methods

3.2.1 Participants

Fifteen right-handed participants (age 18-28 years; 8 female) volunteered for this study. Participant's handedness was determined by Edinburgh Handedness Inventory (Oldfield, 1971). Due to insufficient ERP trials (< 40) after artifact rejection of EEG artefacts, datasets from four participants were excluded from this study. All participants disclosed that they had no known sensory or cognitive impairments. Participants were screened for normal 20-20 visual acuity (with corrected lenses) and for colourblindness. Informed consent was signed by all participants. This study was approved by the Research Ethics Board at Simon Fraser University, Canada. The experiment lasted for approximately 50 minutes, consisting of 15-20 minutes for electrode set-up and 30 minutes for ERP recording. Participants received a \$10 honorarium.

3.2.2 Stimuli and Task

Visual stimuli were upper-case, roman-alphabetic letters (A, B, D, E, G, H, J, N, P, R, T, U, and Y), pseudoletters (mixed line forms of the letters: A, B, D, E, G, H, J, N, P, R, T, U, and Y), and numbers (1 and 2) presented as red or blue characters on a grey background (Figure 3.1). Stimuli covered 60 x 60 pixels at the centre of a 19" inch VGA monitor with a resolution of 600 x 800 pixels situated approximately 70 cm in front of the participant's eyes. Stimuli were randomly presented for a duration of 500 ms in the central visual field. Stimuli were followed by a black fixation dot on the grey background shown for a random duration between 1500-2000



ms. Presentation software (NeuroBehavioral Systems Inc., Albany, CA) was synchronized to the VGA monitor's refresh rate in order to accurately synchronize the stimulus onset with the trigger pulse that was sent to the EEG recording computer.

Participants performed three tasks in separate randomly-assigned blocks. A participant was asked to press one of two

buttons with his/her right hand to discriminate between letters and pseudoletters (Orthography

Task), to discriminate between red and blue stimuli (Colour Task), and to detect target numbers 1 and 2 (Target Task). For the Orthography and Colour tasks, 200 letters and 200 pseudoletters were randomly presented across three blocks of 133, 133, and 134 trials with each block lasting about five minutes. Participants were given approximately 30 seconds of rest between blocks. For the Target task, 200 letters, 200 pseudoletters, and 50 targets (25 number "1" and 25 number "2") were randomly presented across three blocks of 150 trials with each block lasting about five minutes. Participants were given approximately 30 seconds of rest between blocks. For the Target task, 200 letters, 200 pseudoletters, and 50 targets (25 number "1" and 25 number "2") were randomly presented across three blocks of 150 trials with each block lasting about five minutes. Participants were given approximately 30 seconds of rest between blocks. For the Target task, participants were asked to detect when a number 1 or 2 appeared on the screen by pressing only one button and ignore the other stimuli (i.e., letters and pseudoletters). Participants were asked to press buttons as accurately and as fast as possible. This allowed us to collect behavioural response accuracy and reaction times to stimuli when button presses were required.

3.2.3 Data Acquisition

EEG was collected using a 136-channel BIOSEMI system (BIOSEMI, www.biosemi.com). Scalp electrodes (128 channels) were situated within a cap in a modified 10-5 configuration with two additional mastoid electrodes (M1 and M2), two inferior occipital electrodes (SI3 and SI4), and four electrooculogram electrodes (SO1, IO1, LO1, and LO2). EEG was amplified and sampled at a rate of 1024 Hz with a band-pass filter of 0.16 to 256 Hz. For online collection, the 136-electrodes were referenced to a common electrode placed between CPz and CP2. For offline analyses, the 132 scalp-electrodes (excluding electrooculogram channels) were re-referenced to their average reference.

3.2.4 Data Analyses

Behavioural. Behavioural accuracy and reaction times were determined from the participants' button presses for each task. Trials with correct button presses within the post-

stimulus interval of 100 to 1500 ms were used to calculate accuracy and reaction times. Correct responses (hits) were correct button presses to corresponding stimulus type (letters and pseudoletters) for the Orthography task, correct button presses to stimulus colour (red and blue) for the Colour task, and correct button presses to numbers (1 or 2) for the target task. False alarms were considered as incorrect button responses and misses were considered as no button responses when participants should have pressed a button. We performed one-way analysis of variances (ANOVAs) on accuracy (hits, false alarms, and misses) and reaction times among stimulus types (letter, pseudoletter, red, blue, target). Tukey-Kramer post-hoc tests were performed on significant ANOVA effects. Statistical results were considered significant at p<.05.

Event-related potentials (ERPs). ERPs were time locked to each stimulus onset and epoched to yield trials of -500 to 1500 ms. Trials with ERPs exceeding ±100 microV between -350 to 850 ms were rejected from further analyses. We subsequently performed a principle component artefact reduction procedure with a principle component threshold of ±100 microV between -500 to 1500 ms in order to reduce the rising and falling edges of artefacts that might remain within the interval of -350 to 850 ms window (Picton et al., 2000). This ensured that the artefacts did not contaminate the prestimulus interval during baseline correction between -200 to 0 ms. The mean, standard deviation, and range (in parentheses) for artefact-free trials for each Task-Stimulus type are as follow: Orthography-Letters = 125 ± 36 (42-172); Orthography-Pseudoletters = 125 ± 35 (44-159); Colour-Letters = 117 ± 41 (45-158); Colour-Pseudoletters = 130 ± 49 (43-182); Target-Letters = 122 ± 26 (42-153); Target-Pseudoletters = 125 ± 17 (87-145); and Target-Targets = 47 ± 13 (20-69). Artefact-free trials were averaged across trials and filtered using a 30-Hz low-pass filter to obtain evoked potentials (EPs) for each stimulus type (letters and pseudoletters) within each task condition (Orthography, Colour, and Target). For the purpose of this study, we only investigated the EPs to letters and pseudoletters among tasks. Target stimuli (numbers 1 and 2) were excluded from our analyses and results. We also calculated the global field power (GFP) as the root-mean-squared values of the EPs averaged across the scalp electrodes (excluding the electrooculogram electrodes) for each sample.

We performed two-way ANOVAs on the EP and GFP waveforms averaged over 25 ms intervals spanning from -100 to 600 ms across Tasks (Orthography, Colour, and Target) and Stimulus type (letter and pseudoletter). Main effects and interactions were considered significant at p<.05. Tukey-Kramer post-hoc tests were performed on significant ANOVA main effects of Task. Post-hoc results were considered significant at p<.05. We also evaluated ANOVA and post-hoc results at significance levels of p<.01 and p<.001.

In addition to statistical testing across samples, we performed statistical analyses on the P1, N1, and P2 peak amplitudes and latencies at electrodes PO9h, PO10h, P7 and P8. These electrode sites were chosen because they had significant Stimulus effects from the two-way ANOVA analyses described above. An experienced rater manually identified peak responses with a maximum between 50-100 ms as P1, a first minimum between 50-250ms as N1, and a maximum between 150-300 ms as P2 for electrodes PO9h, PO10h, P7, and P8. In addition, P3 peaks were identified in electrode Pz as a maximum between 200-600 ms. Three-way ANOVAs were performed for peak amplitudes and latencies for the P1, N1, P2, and P3 peaks across stimulus type (letter and pseudoletter), tasks (Orthography, Colour, and Target) and hemisphere (left hemisphere = averaged PO9h and P7; right hemisphere = averaged PO10h and P8).

Dipole Modeling. Dipole modeling using BESA software (BESA GmbH; www.besa.de) was performed post-hoc on EP difference waveforms for significant main effects of Task (Orthography, Colour, Target) and Stimulus (letter vs. pseudoletter). This was done to determine the possible source locations of processing differences between Tasks and Stimulus types. For the Task-effects model, a pair of symmetrically-constrained dipoles was fitted to significant differences that occurred between 175-200 ms for the Orthography versus Target and Colour versus Target contrasts (i.e., a selection negativity component). A third dipole was fitted to the significant differences between 225-250 ms for the Colour versus Target contrast (i.e., an N2 component). A fourth dipole was fitted to the significant differences between 300-500 ms for the Orthography versus Target and Colour versus Target contrasts (i.e., a P3 component). Residual variances for the source modeling of the difference waves were less than 10% for all intervals. Talairach locations for these dipoles were $x = \pm 45.5$, y = -56.0, z = -17.2 mm (left/right fusiform gyri); x = 4.1, y = 2.9, z = 49.9 mm (medial frontal gyrus); and x = -3.6, y = -61.0, z = 5.3 mm (lyngual gyrus). For the Stimulus-effects model, two pairs of symmetrically constrained dipoles were used to model the significant differences occurring between 150-200 ms (around the N1 peak) and between 225-300 ms (around the P2 peak). Residual variances for the source modeling of the difference waves (letter minus pseudoletter) were less than 10% for both intervals. Talairach locations for these dipoles were $x = \pm 42.6$, y = -72.4, and z = -14.4 mm (left/right fusiform gyri) $x = \pm 41.4$, y = -62.1, and z = -0.6 mm (left/right inferior temporal gyri).

Similar to the statistical analyses used for the EP waveforms, we performed two-way ANOVAs on the dipole waveforms averaged over 25 ms intervals spanning from -100 to 600 ms across Tasks (Orthography, Colour, and target) and Stimulus type (letter and pseudoletter). This was done for both the dipole models of EP difference waveforms for the Task and Stimulus effects. Tukey-Kramer post-hoc tests were performed on the significant ANOVA main effects of Task. ANOVA and post-hoc *t*-test results were considered significant at p < .05. We also evaluated ANOVA and post-hoc results at significance levels of p < .01 and p < .001.

3.3 Results

3.3.1 Behavioural Responses

Behavioural responses showed participants were highly accurate at discriminating among stimuli and detecting targets (see Table 3.1). However, ANOVA and Tukey-Kramer post-hoc testing revealed that participants were less accurate at pressing the correct button to red stimuli in the Colour task than to any other stimuli across tasks (see Table 1 for means; F = 7.2; df = 4,50; p = .0001). This was a result of making more false alarms to red stimuli as compared to other stimuli (see Table 1 for means; F = 14.1; df = 4,50; p < .0001) and not misses (F = 0.56; df = 4,50; p = .6897). ANOVA results for RTs did not support significant differences in RTs among stimulus type (letter, pseudoletter, red, blue, target) (see Table 1 for means; F = 2.52; df = 4,50; p = .0526). Although the ANOVA results for RTs were close to significance, this was driven by reaction times to targets being most delayed as compared to the other stimulus types (see Table 1).

	Ortho	Orthography		Color	
	Letter	Pseudoletter	Red	Blue	Numbers
Hits (%)	94.9 ± 3.5	94.7 ± 3.1	90.3 ± 2.7	97.1 ± 3.4	97.4 ± 4.7
False Alarms (%)	3.2 ± 1.5	3.6 ± 2.5	8.3 ± 3.0	2.2 ± 2.2	0.4 ± 0.5
Misses (%)	1.9 ± 3.1	1.6 ± 3.4	1.3 ± 2.0	0.8 ± 1.5	2.6 ± 4.7
Reaction Times (ms)	474 ± 69	482 ± 71	452 ± 106	446 ± 101	552 ± 98

Table 3.1 Behaviorual Results

3.3.2 GFP and EP Waveforms

GFP waveforms showed typical responses patterns of P1, N1, P2, and P3 peaks to visual stimuli (Figure 3.2, top graph). Comparison across Task (Orthography, Colour, and Target)

revealed that GFPs between 175-200 ms were significantly (p < .05) greater for Colour versus Target task and close to being significantly greater (p = .089) for the Orthography versus Target task. GFPs between 375-600 ms were significantly greater for the Orthography task as compared to the Colour and Target tasks. GFPs between 450-525 ms were significantly greater for the Colour task as compared to the Target task. For the Stimulus effects, GFPs between 150-200 ms, 225-275 ms, and 450-500 ms were significantly greater for Pseudoletter than Letter stimuli (Figure 3.2, middle graph). There were no significant interactions of Task by Stimulus on GFP (Figure 3.2, bottom graph).

EP waveforms showed typical P1-N1-P2 responses to the letter and pseudoletter stimuli (Figure 3.3 and 3.4). Because participants were asked to attend to and press buttons to letter and pseudoletter stimuli in Orthography and Colour tasks, additional attention-related EP responses (N2, and P3) occurred as compared to the Target task in which participants disregarded the letter and pseudoletter stimuli. In addition, Orthography and Colour tasks evoked a significantly greater negative response between 175-200 ms (around the N1) as compared to the Target task at POz (Figure 3.3, top graph). Topographies of the differences among Tasks revealed that the greater negativity has a posterior scalp distribution for the Orthography versus Target and Colour versus Target contrasts. This has a similar posterior scalp distribution and timing as an SN response that has been previously reported (Hillyard & Anllo-Vento, 1998). At central electrode sites (e.g., FCCh1), EPs were significantly greater between 225-250 ms for Colour versus Target task (Figure 3.3, middle graph). Scalp topography for this contrast revealed a central distribution of this negativity, stereotypical of an N2b component. Although the Orthography versus Target contrast didn't reach statistical significance at p<.05, p-value for this contrast between 225-250 ms was .09 and its topography was strikingly similar to the Colour versus Target topography.

Significant EPs differences among Tasks were evident at Pz spanning 300-550 ms (Figure 3.3, bottom graph).

Similar to the GFP results, EPs at Pz in this interval were greatest for the Orthography task, next for the Colour task, and then for the Target task. The topographies between 425-450 ms among the Task contrasts showed typical P3 scalp distributions with peak responses occurring over parietal regions (Figure 3.3, bottom topographies).



Figure 3.2 Global field power of evoked potentials for Task effects (top plots), Stimulus effects (middle plots), and Interaction of Task by Stimulus (bottom plots). Waveforms for the Task effect are averaged across stimulus type (letters and pseudoletters) and waveforms for the Stimulus effect are averaged across tasks (Orthography, Colour, and Target). Waveforms for the Interaction are plotted as the differences between letter and pseudoletters for each task (Orthography, Colour, and Target). Peaks in the waveforms reflect P1, N1, P2, and P3 responses of the evoked potentials. Bars above the waveforms designate intervals of significant main effects at p < .05, p < .01, and p < .001.

Stimulus comparison results showed that pseudoletters evoked greater and later peaking N1 waves between 100-200 ms than did letters (Figure 3.4). The significant difference in the 100-125 ms interval appeared to result from a delayed N1 onset to pseudoletters than to letters. In addition to these differences in the N1 interval, P2 responses peaking around 250 ms were greater to pseudoletters than to letters over parietal sites (e.g., P6), with a right hemispheric dominance. Topographies revealed that the significant N1 and P2 differences were mainly recorded over the parieto-occipital scalp.

Contrary to our hypothesis that the N1 and P2 responses differences between letters and pseudoletters would be reduced when attention was drawn away from categorizing stimuli, we found no statistical support for interactions of Task by Stimulus at electrode sites (PO10h, PO9h, and POz), which clearly showed significant main effects of Task or Stimulus (Figure 3.5). All tasks showed the same difference waves between letters and pseudoletters. Additionally, none of the other scalp recordings revealed significant interactions (data not shown). To further support these findings we calculated peak amplitudes and latencies for the P1, N1, P2, and P3 responses. These are shown in Table 2 and 3 and presented below with ANOVA results.

P1 peak responses. Peak P1 amplitudes averaged across tasks and stimulus types were significantly larger in the right hemisphere (averaged across P8 and PO10h electrodes; $3.61 \pm 2.11 \mu$ V) than the left hemisphere (averaged across P7 and PO9h electrodes; $2.11 \pm 1.83 \mu$ V) (*F* = 16.96; *df* = 1,112; *p* < .0001). No other ANOVA effects or interactions for P1 amplitudes were found to be significant (*p* > .20). A significant ANOVA hemispheric effect for P1 latencies revealed P1 peaked earlier in the right (96 ± 10 ms) than left hemisphere (100 ± 9 ms) (*F* = 4.59; *df* = 1,112; *p* = .0343). No other ANOVA effects or interactions for P1 latencies were found to be significant (*p* > .17).

N1 peak responses. Peak N1 responses were significantly larger to pseudoletters (-6.66 ± 2.92 µV) than to letters (-5.47 ± 3.07 µV) (F = 5.213; df = 1,112; p = .0243). ANOVA results also revealed a significant hemispheric effect whereby N1 amplitudes were larger in the left (-7.06 ± 2.83 µV) than right hemisphere (-5.08 ± 2.95 µV) (F = 14.475; df = 1,112; p = .00023). No other ANOVA effects or interactions for N1 amplitudes were found to be significant (p > .15). N1 responses peaked significantly earlier to letters (150 ± 17 ms) than pseudoletters (165 ± 13 ms) (F = 29.419; df = 1,112; p < .00001)

P2 peak responses. Peak P2 responses were significantly larger to pseudoletters (5.75 \pm 3.64 µV) than to letters (4.21 \pm 3.38 µV) (*F* = 5.801; *df* = 1,112; *p* = .0177). No other ANOVA effects or interactions for P2 amplitudes were found to be significant (*p* > .2). Peak P2 latencies were not found to show any significant effects or interactions among task, stimulus type, and hemisphere (*p* > .06).

P3 peak responses. Peak P3 responses were significantly larger for the Orthography (6.41 $\pm 3.19 \mu$ V) and Colour (6.06 $\pm 3.54 \mu$ V) tasks as separately compared to target task (3.1 $\pm 2.66 \mu$ V) (*F* = 5.801; *df* = 1,112; *p* = .0177). No other ANOVA effects or interactions for P3 amplitudes were found to be significant (*p* > .60). ANOVA and post-hoc testing revealed that P3 responses peaked significantly later for the Orthography task (394 \pm 50 ms) as separately compared to the Colour (333 \pm 38 ms) and Target (344 \pm 34 ms) tasks (*F* = 12.447; *df* = 2,56; *p* < .0001). No other ANOVA effects or interactions for P3 latencies were found to be significant (*p* > .87).







Figure 3.4 Grand-mean evoked potentials for Stimulus effects averaged across tasks (Orthography, Colour, and Target) at electrodes PO10h, PO9h, and P6. Bars above the waveforms designate intervals of significant differences between letters and pseudoletters at p<.05, p<.01, and p<.001. Scalp topographies plotted under the waveforms reflect difference waveforms averaged across the designated intervals shown for left, posterior, and right views. The grey dots in the topographies reflect the electrode location for the waveforms plotted above.



PO10h, and PO9h that showed significant Task or Stimulus effects (see Figures 3.3 & 3.4). Waveforms are plotted as the differences between letter and pseudoletters for each task (Orthography, Colour, and Target). No statistical evidence of significant interactions were found at these electrodes or at any other scalp electrodes (data not shown) at p < .05, p < .01, and p < .001.

Table 3.2 Peak EP amplitudes

ERP peak	Orthography task		Color task		Target task	
	Letter	Pseudoletter	Letter	Pseudoletter	Letter	Pseudoletter
P1 LH	2.18±1.91	2.51 ± 2.18	1.97 ± 1.46	1.56 ± 2.51	1.84 ± 1.19	2.55 ± 1.60
P1 RH	4.17 ± 2.3	4.03 ± 2.58	2.66 ± 1.52	3.56 ± 1.59	3.20 ± 2.35	3.91 ± 2.19
N1 LH	-6.87 ± 2.97	-7.93 ± 2.98	-7.06 ± 2.73	-8.12 ± 2.90	-5.61 ± 2.88	-6.69 ± 2.38
N1 RH	-4.90 ± 3.13	-6.14 ± 3.11	-4.48 ± 2.48	-5.85 ± 2.63	-3.84 ± 3.41	-5.18 ± 2.90
P2 LH	4.04 ± 4.22	4.92 ± 3.45	3.51 ± 2.92	5.14 ± 3.95	4.25 ± 2.85	5.54 ± 3.03
P2 RH	5.11 ± 4.03	6.18 ± 3.37	4.17 ± 3.85	6.76 ± 5.13	4.08 ± 2.54	6.02 ± 3.20
P3 @ Pz	6.28 ± 3.36	6.83 ± 2.99	5.78 ± 3.7	6.39 ± 3.51	3.12 ± 2.73	3.28 ± 2.67

Table 3 | Peak EP latencies.

ERP peak	Orthography task		Color task		Target task	
	Letter	Pseudoletter	Letter	Pseudoletter	Letter	Pseudoletter
P1 LH	96±8	99±8	99 ± 11	101 ± 12	102 ± 14	102 ± 8
P1 RH	94 ± 6	96 ± 8	93 ± 6	97 ± 7	96 ± 9	101 ± 14
N1 LH	153 ± 17	163 ± 12	152 ± 15	165 ± 15	152 ± 19	164 ± 14
N1RH	146 ± 15	163 ± 11	148 ± 18	166 ± 12	150 ± 19	169 ± 14
P2 LH	239 ± 34	252 ± 26	239 ± 29	250 ± 26	250 ± 39	254 ± 33
P2 RH	249 ± 44	263 ± 37	239 ± 27	254 ± 24	260 ± 40	272 ± 36
P3 @ Pz	385 ± 55	409 ± 55	336 ± 37	331 ± 23	352 ± 69	331 ± 64

3.3.3 Dipole Waveforms

Dipole-source waveforms showed effects in the Task-effects and Stimulus-effects models (Figure 3.6-3.9) similar to those seen in the EP waveforms (Figures 3.3-3.5). The source model for Task effects (Figure 3.6) had significantly larger N1 responses in the right fusiform gyrus (dipole 1L) for the Orthography and Colour tasks as compared to the Target task. Although this effect was not significant (p > .15) in the right fusiform gyrus (dipole 1R) the waveforms showed the same larger N1 responses, as seen in the left fusiform gyrus, for the Orthography and Colour tasks as compared to the Target task. The N2 effect was localized to the medial frontal gyrus (dipole 2), which showed significant N2 differences among all task contrasts. This source had a large and prolonged N2 response for the Orthography task, a smaller and narrower N2 for the Colour task, and a minimally evident N2 for the Target task. Because of the prolonged nature of the N2 for the Orthography task, it was significantly larger than the N2 for the Colour task. The P3 effect was localized to the midline of the lingual gyrus (dipole 4). This dipole had its large

responses for the Orthography and Colour tasks and minimal responses for the Target task. Task contrasts revealed that the P3 response were significantly prolonged, extending out to about 500 ms, for the Orthography task as compared to P3 response for the Colour Task that peaked around 330 ms. Source waveforms for the differences between Letters and Pseudoletters for the Task-effects dipole model showed little, if any, disparity among tasks (Figure 3.7). Moreover, the statistical interaction of Task by Stimulus revealed no evidence that tasks modulated the responses differences between letters and pseudoletters (Figure 3.7).



< .01, and p < .001. Vertical axis scale for waveform plots is in nAmp.



model (inset) with bilateral dipoles in the fusiform gyri (dipoles 1L and 1R), medial frontal gyrus (dipole 2), and medial lingual gyrus (dipole 3). Waveforms are plotted as the differences between letter and pseudoletters for each task (Orthography, Colour, and Target). No statistical evidence of significant interactions were found in these source waveforms at p < .05, p < .01, and p < .001. Vertical axis scale for waveform plots is in nAmp.

The Stimulus-effects model localized the EP differences between letters and pseudoletter to bilateral fusiform gyri (Figure 3.8). Source waveforms showed that bilateral fusiform gyri generated significantly larger N1 responses (between 150-200 ms) to pseudoletters than to letters. This is consistent with the EP results shown in Figure 4. This model further revealed that the right inferior temporal region (dipole 2R) had significantly larger P2 responses (225-325 ms) to pseudoletters than to letters. This result is consistent with the Stimulus effect shown at the P6 electrode (see Figure 3.4). We found no statistical evidence to support significant stimulus type differences in P2 responses in left hemispheric source (dipole 2L). In addition, dipole 2R had significantly larger responses to pseudoletters than to letters between 350-475 ms. Interactions of Task by Stimulus, yet again, showed that difference waveforms (letters minus pseudoletters) showed little, if any, differences among tasks. We found no statistical evidence (i.e., no interaction of Task by Stimulus) to support the hypothesis that task modulated the differences between letters and pseudoletters (Figure 3.9).



Figure 3.8 Grand-mean source waveforms for Stimulus effects averaged across tasks (Orthography, Colour, and Target) for the Stimulus-effects model (inset) with bilateral dipoles in the fusiform gyri (dipoles 1L and 1R) and bilateral inferior temporal gyri (dipoles 2L and 2R). Bars above the waveforms designate intervals of significant differences between letters and pseudoletters at p < .05, p < .01, and p < .001. Vertical axis scale for waveform plots is in nAmp.



Figure 3.9 Grand-mean source waveforms for the Interaction of Task by Stimulus for the Stimulus-effects model (inset) with bilateral dipoles in the fusiform gyri (dipoles 1L and 1R) and bilateral inferior temporal gyri (dipoles 2L and 2R). Waveforms are plotted as the differences between letter and pseudoletters for each task (Orthography, Colour, and Target). No statistical evidence of significant interactions were found in these source waveforms at p < .05, p < .01, and p < .001. Vertical axis scale for waveform plots is in nAmp.

3.4 Discussion

A main finding from this study was that the early response differences between letters and pseudoletters occurring around 170 ms were not affected by task demands that encouraged attention to be directed toward (Orthography task) or away from (Colour and Target tasks) orthographic stimulus features. This provides evidence that early orthographic processing of single letters is not largely influenced by selective attention to stimulus features, at least with respect to the task demands used within this study. In addition, attention didn't affect the P2 differences seen in the right hemisphere. Thus, our results are in opposition to previous findings that showed attention to orthography of word stimuli enhanced early (N200) responses as compared to attention to phonology and semantics of words, which modulated later EP components (Ruz & Nobre, 2008). One explanation for our discrepant findings is that we used single character stimuli; whereas Ruz and Nobre (2008) used words and character strings. Thus, stimulus complexity and lexical retrieval might recruit higher levels of visual processes that might be influenced by top-down attention. Another difference between studies is that we used a block design for task manipulation that could have resulted in participants paying attention to letters and pseudoletters to the same degree for all tasks. However, we attempted to control for such order effects by randomly assigning task-block order across participants. Moreover, participants' attention appeared to be successfully manipulated across tasks as expected because selection negativities (SN) and N2 responses were apparent for the Orthography and Colour tasks but not for the Target task (see Figures 3.3 and 3.6). The selection negativities associated with paying attention to a stimulus feature (Orthography or Colour) that occurred between 175-200 ms had a similar scalp topography and source locations as to those shown previously (Hillyard & Anllo-Vento, 1998). In addition, the N2 following the SN had a typical topography

of an attention-related N2b response, also referred to as the anterior N2 (Folstein & Van Petten, 2008). Further indication that this study's tasks modulated participants' attention was that P3 responses increased in amplitude with increasing task demands on directing attention to orthography and colour (Orthography-task P3 > Colour-task P3 > Target-task P3). In contrast to our study, Ruz and Nobre (2008) used a trial-to-trial cueing paradigm for drawing participants' attention to orthographic, phonologic, or semantic stimulus features. Thus, task procedures and sensory-to-motor mapping were required to be maintained throughout the block and could have recruited networks associated with perceptual and motor processes in which attention could modulate activity. Furthermore, attention effects in their study were only provided for the word stimuli and thus differences in orthographic processing between words and false-font strings are not available for comparison to the present study's results.

Another main result from this study is that we further replicated the findings that the N1 peaked earlier to letters than pseudoletters and that P2 responses are greater to pseudoletters than letters (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman, 2011). These findings add support to the notion that letters are processed faster and to a lesser degree than pseudoletters. This makes sense because adult participants had many years of consolidating visual templates for familiar letters as compared to unfamiliar pseudoletters; thus template matching for letter recognition should be fairly automatic and require minimal processing. This is in line with many models of reading (e.g., Grainger, Rey, & Dufau, 2008; McClelland & Rumelhart, 1981; Price, 2000). Contrary to our original hypothesis, task demands appeared not to affect either the early or later stages of letter and pseudoletter processing. Thus, these processes appear to be resistant to the attention demands we placed on the participants in this study and signify that letter-pseudoletter effects are most likely sensory-contingent processes, at least in adults.

Interestingly, the N1 responses and difference waveforms between letters and pseudoletters were largest in the left as compared to the right visual cortices. This is consistent with a left-lateralized language model for reading (Cohen & Dehaene, 2004; Dehaene, Cohen, Sigman, & Vinckier, 2005; Price et al., 2003) and could be akin to the N200 effects (Nobre et al., 1994; Ruz & Nobre, 2008). However, this laterality is in opposition to a right-dominant effect showing greater processing for pseudoletters that we and others previously reported (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman, 2011). Given similarities in timing, topography, and source locations across studies for the N1 letter-pseudoletter effect indicates that these are likely analogous processing effects. However, at this point we cannot explain the discrepant findings among these studies. Task differences among studies are unlikely because the current experiment found no evidence for task effects for similar tasks and stimuli to those previously used in the literature. More research is thus warranted to determine laterality of these early visual processing differences between letters and pseudoletters.

Possible explanations for the larger and later peaking N1 and the larger P2 to pseudoletters than letters is that extra processing of unfamiliar objects occurs in order to identify and categorize the unfamiliar pseudoletters (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman, 2011) or that pseudoletters capture attention to a greater extent and thus modulate early visual processing (Ruz & Nobre, 2008; Vinckier et al., 2007). However, this later possibility is less likely because we found no change in this letter-pseudoletter processing differences among the tasks that manipulated attention to or away from orthographic stimulus features. It appears that the different levels of attention paid to stimulus features did not alter the broader N1 and larger P2 responses to pseudoletters. Thus, the results indicate that the greater responses to pseudoletters appear to be sensory-contingent and are not under the control of
attentional focus. This further leads us to believe that the N1 and P2 enhancements are likely related to the initial processing stages that are molded by experience to become more rapid and efficient at identifying letters than pseudoletters. In this case, bigger or broader is not better. Bigger responses here reveal more processing of the stimulus attributes, which requires more energy and poorer efficiency. The EPs to letters peaking earlier and with reduced neural responses, points toward consolidation of letter templates within neural ensembles to allow for rapid and accurate identification of these highly familiar letters. The finding that the behavioural reaction times are faster to letters than pseudoletters (Herdman, 2011; LaBerge, 1973; also in present study but not significant) further supports a more efficient system for processing familiar letters than unfamiliar pseudoletters.

EPs can peak later because of deconstructive addition upon averaging. Two reasons for this deconstructive addition is that there is greater variability in the timing by which neural populations are synchronously evoked by stimuli (i.e., less overlapping components of the N1) or there is greater trial-to-trial latency jitter of the EP. These would also reduce the EP amplitudes. We found that the N1 was larger and peaked later to pseudoletters than letters. Thus, a more likely alternate explanation for this later and larger N1 is a greater recruitment of neural ensembles. Because pseudoletters are less familiar and had very limited time to create wellformed templates within the visual networks, the brain likely attempts to first match the pseudoletters to letter templates. This could take a few template-matching iterations within the network and thus cause greater neural discharges over time as compared to more automatic template matching that would occur for letters. Such a notion fits with many reading models describing the early stages of orthographic processing (e.g., Dehaene, Cohen, Sigman, & Vinckier, 2005; Grainger, Rey, & Dufau, 2008). Our behavioural results were largely unremarkable. They showed that participants were fairly engaged in performing all tasks (> 90% accuracy). Interestingly though we didn't find statistical evidence for faster reaction times to letters than pseudoletters as previously reported; however the difference was in the right direction, about 8 ms faster to letters than pseudoletters (Herdman, 2011; LaBerge, 1973). This might have been due to statistical power issues of having a limited number of participants. We did, however, find an unexpected result in that participants made more false alarms to red than blue stimuli. This could be a result of an ecological effect in that red stimuli are commonly associated with the concept of "stop" and possibly this association is interacting with participants ability to discriminate and press the buttons (Elliot, Maier, Moller, Friedman, & Meinhardt, 2007). Reaction times were similar between red and blue stimuli; thus motor-response inhibition is unlikely. In hindsight, we should have used colour stimuli that are not commonly associated with motor commands. We did not include false-alarm trials within the EP analyses so this unexpected result likely had little or no effect on our EP differences between letters and pseudoletters.

In conclusion, the present study's results provided further evidence that single letters are processed faster and with less neural activity than pseudoletters. Tasks encouraging participants to direct attention towards and away from orthographic stimulus features did not change the early (N1 at ~170 ms) and late (P2 at ~250 ms) processing differences between letters and pseudoletters. Thus, visual processing of single orthographic or non-orthographic characters appeared to be sensory-contingent and independent of top-down control of directing attention towards or away from orthographic stimulus features.

Chapter 4: "Brain oscillations and functional connectivity involved in single-letter processing"

4.1 Introduction

Single letters are the building blocks of words in most languages and are typically learned first in order to become fluent readers. Thus, letters become highly-experienced visual stimuli after years of reading. This experience is suggested to modify the visual processing networks to provide fast and accurate identification of letters and words that occurs during reading. Most brain imaging research investigating single-letter perception has been aimed at identifying the specific timing (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013; Takai & Herdman, *2013;* Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013; Wong, Gauthier, Woroch, Debuse, & Curran, 2005; Xue, Jiang, Chen, & Dong, 2008) and/or spatial distribution (Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006; Pernet et al., 2003; Tagamets, Novick, Chalmers, & Friedman, 2000) of single-letter perception. These findings have provided excellent insight into when and where large groups of neurons are active during specified periods of perceptual processing.

The fMRI and neurological/lesion literatures have provided evidence that single-letters are bilaterally processed within visual cortices but with more dominant responses in the left inferior temporal gyrus when comparing across stimulus categories (letters, pseudoletters, numbers, objects) (Flowers et al., 2004; James, James, Jobard, Wong, & Gauthier, 2005; Joseph, Cerullo, Farley, Steinmetz, & Mier, 2006; Pernet et al., 2003; Dehaene, & Cohen, 2011). This region is contemporarily referred to as the letter-box area and previously referred to as the visual-word form area (Dehaene, & Cohen, 2011; James, James, Jobard, Wong, & Gauthier, 2005). The letter-box area is also very close to studies that have localized the sources of the N170/M170 (EEG/MEG) components for orthographic processing (Herdman & Takai 2013; Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier et al. 1999; Eulitz et al. 2000; Miller & Wood 1995; Tarkiainen et al. 1999; Wong et al. 2005). The N170/M170 is an evoked response that has been shown to be modulated by the type of visual stimulus (e.g., letters, pseudoletter, symbols, numbers) (Bentin et al. 1999; Eulitz et al. 2000; Miller and Wood 1995; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Wong, Gauthier, Woroch, Debuse, & Curran, 2005).

Another key finding from the EEG and MEG evoked studies was that the response differences between letters and the other visual stimuli appear to extend from 50 to 500 ms. This demonstrated the complexity in timing of visual computations underlying orthographic processing, which likely involved several brain regions being active across several time intervals. In addition, neural responses recorded over the scalp (EEG and MEG) were believed to be a reflection of oscillations of interacting neural ensembles within different frequency bands. Thus, our recorded signals at the scalp reflected spatial-spectral-temporal neural activity. A recent study of single-letter perception by Park and colleagues (Park, van den Berg, Chiang, Woldorff, & Brannon, 2018) showed significant differences in event-related oscillations between letters and pseudoletters in theta and alpha bands. The main time-frequency results showed greater theta-band (4-7 Hz) and beta-band (15-20 Hz) power for pseudoletters than letters for adults but when the evoked power was subtracted from total power (i.e., induced power), only the beta-band power differences remained significant. These differences were seen at the electrode level that reflects a combination of underlying brain source activity. Thus, the current study

investigated differences in brain oscillations between letters and pseudoletters at the electrode level as well as the brain source level. We also extended the previous findings to include functional connectivity analyses to evaluate the brain network connectivity dynamics.

Understanding the spatial-temporal and spectral dynamics of neural activity and information transfer among brain regions is an important goal in knowing how visual and orthographic information is processed and transferred throughout the human brain. Coordinated neural activity of synchronized and desynchronized oscillations among visual regions is believed to be the mechanism for integrating information across perceptual and cognitive processes (Eckhorn et al., 1988; Gray & Singer, 1989; Gray et al., 1989; Fries et al., 1997; Vaerla, 1995). The intent of the current study was to investigate the oscillatory activity and functional connectivity in the adult brain with respect to processing highly-experienced (familiar) single letters and inexperienced (unfamiliar) pseudoletters. Based on our previous evoked and oscillatory findings (Bann & Herdman, 2016; Herdman 2011; Herdman & Takai, 2013), we hypothesized that the neural networks responsible for processing letters will show earlier, stronger, and a greater number of functionally connected regions than the neural network responsible for processing pseudoletters. In addition, we hypothesized that this early difference in connectivity will be followed by a reverse pattern (pseudoletters > letters) in later time intervals. We tested these main hypotheses by measuring EEG from L1(English) adults and estimating the oscillatory activity and functional connectivity among brain regions as a function of frequency and time.

4.2 Material and Methods

This paper used data previously reported in Herdman and Takai (2013). The study design and general methods are briefly repeated here with the addition of the methods for analyzing functional connectivity (see Chapter 3 for more details).

4.2.1 Participants

Fifteen right-handed participants (age 18-28 years; 8 female) volunteered for this study. Participant's handedness was determined by Edinburgh Handedness Inventory (Oldfield, 1971). Due to insufficient ERP trials (< 40) after artifact rejection of EEG artefacts, datasets from four participants were excluded from this study. All participants disclosed that they had no known sensory or cognitive impairments. Participants were screened for normal 20-20 visual acuity (with corrected lenses) using Snellen Chart placed a 6-meter viewing distance and for colourblindness using Ishihara pseudoisochromatic plates.

4.2.2 Stimuli and Task

Visual stimuli were upper-case, roman-alphabetic letters (A, B, D, E, G, H, J, N, P, R, T, U, and Y), pseudoletters (mixed line forms of the letters: A, B, D, E, G, H, J, N, P, R, T, U, and Y), and numbers (1 and 2) presented as red or blue characters on a grey background (Figure 1). Stimuli covered 60 x 60 pixels at the centre of a 19-inch VGA monitor with a resolution of 600 x 800 pixels situated approximately 70 cm in front of the participant's eyes. Stimuli were randomly presented for a duration of 500 ms in the central visual field. Stimuli were followed by a black fixation dot on the grey background shown for a random duration between 1500-2000 ms. Presentation software (NeuroBehavioral Systems Inc., Albany, CA) was synchronized to the VGA monitor's refresh rate in order to accurately synchronize the stimulus onset with the trigger pulse that was sent to the EEG recording computer.

Participants performed three tasks in separate randomly-assigned blocks as described previously (Herdman & Takai, 2013). For the purpose of this study, we only used the data from the Orthography Task. Future studies will investigate functional connectivity in the other tasks (Colour and Target) and compare among all tasks. For the Orthography task, a participant was asked to press one of two buttons with his/her right hand to discriminate between letters and pseudoletters (Orthography Task). A total of 200 letters and 200 pseudoletters were randomly presented across three blocks of 133, 133, and 134 trials with each block lasting about five minutes. Participants were given approximately 30 seconds of rest between blocks. Participants were asked to press buttons as accurately and as fast as possible. This allowed us to collect behavioural response accuracy and reaction times to stimuli when button presses were required (see Herdman & Takai 2013; Chapter 3 for behavioural analyses and results).

4.2.3 Data Acquisition

EEG was collected using a 136-channel BIOSEMI system (BIOSEMI, www.biosemi.com). Scalp electrodes (128 channels) were situated within a cap in a modified 10-5 configuration with two additional mastoid electrodes (M1 and M2), two inferior occipital electrodes (SI3 and SI4), and four electrooculogram electrodes (SO1, IO1, LO1, and LO2). EEG was amplified and sampled at a rate of 1024 Hz with a band-pass filter of 0.16 to 256 Hz. For online collection, the 136-electrodes were referenced to a common electrode placed between CPz and CP2. For offline analyses, data were down sampled to 512 Hz and the 132 scalp-electrodes (the four electrooculogram channels excluded) were re-referenced to their average reference.

4.2.4 Data Analyses

4.2.4.1 Electrode Level

Event-related potentials (ERPs). ERPs were time locked to each stimulus onset and epoched to yield trials of -2000 to 2000 ms. Trials with ERPs exceeding ± 100 microV between -500 to 500 ms were rejected from further analyses. Artefact-free trials were averaged across trials and filtered using a Finite-Element Response filter with a band-pass of 1 to 50-Hz for each stimulus category (letters and pseudoletters). For the purpose of this study, we only investigated the event-related potentials (ERPs) to letters and pseudoletters in the Orthography Task.

Time-Frequency Response (TFR) analyses. We applied a continuous 1D wavelet transform with L1 normalization using matlab's "cwt.m" function to the ERP data in order to obtain the TFR results for each trial of the four electrode channels (FCC1h; POOz; PO10h; and PO9h) reported in our previous paper Herdman and Takai (2013). The wavelet transform was a 'morse' wavelet with the symmetry parameter (gamma) equal to 3 and the time-bandwidth product equal to 60. This wavelet transform yielded 73 frequency bins, which were reduced to 53 frequency bins with centre frequencies that spanned from 4 to 50 Hz. Because the wavelet outputs coefficients that are complex values, we were able to extract the amplitude and phase for each sample for each frequency and trial. The amplitudes were determined for each trial by taking the absolute value of each trial's wavelet coefficients. We then averaged these values across trials to yield averaged "trial" TFR amplitudes [channels x frequency x samples]. Because neural oscillations are believed to come from evoked and induced activities, we also calculated the induced TFR amplitudes by averaging the ERP data across trials, applying the wavelet transform to this average to get the "evoked" wavelet coefficients, and then subtracted each trial's wavelet coefficients by the evoked wavelet coefficients. This returned the "induced"

wavelet coefficients, whereby we took the absolute values and averaged across trials to obtain averaged "induced" TFR amplitudes. Essentially, the "evoked" and "induced" TFR amplitudes reflect the oscillatory activities that are phase-locked (evoked) and not phase-locked (induced) to the stimulus onset. One reason to do this is to get results that can inform us about the changes in event-related oscillations that are separate from the frequency content of evoked responses.

Statistical analyses were performed on the "trial" and "induced" TFR amplitudes using Student t-tests of the differences between the letter and pseudoletter condition for each source for each time-frequency sample between 4-50 Hz and 0 to 500 ms [4 channels x 53 frequencies x 256 samples]. The resulting p-values were then collated across all channels, frequencies, and samples (total t-test = 4x53x256) and adjusted for family-wise error by conducting a falsediscovery-rate (FDR) correction on these *p*-values (Benjamini & Hochberg, 1995). The FDR corrected p-values were then reshaped to form the same indices as the TFR response matrix of [4 channels x 53 frequencies x 256 samples]. TFR amplitude differences were considered significant if the corresponding FDR-corrected *p*-values were < .05. The TFR data were plotted as surface plots with the significant time-frequency intervals overlaid as white contours.

4.2.4.2 Brain Source Level

The ERPs [channels x samples x trials] were used for modeling of source waveforms in order to perform time-frequency and functional connectivity analyses in brain space. To generate source waveforms, we generated a head model, calculated leadfields, identified source locations, and signal-space projected the ERP data into the source locations. These preprocessing steps are described below.

Head Model. We used openMEEG software to generate one head model with 8803 dipole locations (5 x 5 x 5 mm grid) bounded by the cortical surface of the Colin27 default MRI

from Brainstorm2 (Tadel, Baillet, Mosher, Pantazis, & Leahy, 2011). The head model was constructed using 130 EEG channel locations based on a slightly modified 10-10 system (Herdman & Takai, 2013). A boundary-element model was used and had scalp, skull, and brain conductivity ratios equal to 1, 0.0125, and 1, respectively.

Seeded Source Locations. Whole-brain (voxel-to-voxel) connectivity has been shown to generate many false-connections (Palva & Palva, 2007; Herdman, Moiseev, & Ribary, 2017) thus we did not take this approach for this study. Instead, we opted for using a seeded approach whereby brain areas were pre-selected based on previous literature (Herdman & Takai, 2013; see chapter 3; Dehaene, Cohen, Sigman, & Vinckier, 2005; Hillyard & Anllo-Vento, 1998). These seeded locations were then used to determine the signal-to-source weights for signal-space projection (see next section below). There were a total of 13 dipoles placed in the brain volume (Figure 4.1). Based on the existing literature for brain regions involved in orthographic processing, we selected voxel locations as seeds in bilateral medial occipital cortices (voxels 1 and 2), bilateral middle occipital cortices (voxels 3 and 4), bilateral lateral occipital cortices (voxels 5 and 6), bilateral inferior temporal cortices (voxels 7 and 8), bilateral inferior frontal cortices (voxels 9 and 10), anterior cingulate cortex (voxel 11), and bilateral motor cortices (voxels 12 and 13). Voxels 1 to 6 and voxel 11 were selected based on our previous findings of significant orthographic effects within these areas (Herdman & Takai, 2013). The two voxels within inferior temporal cortices (voxels 7 and 8) were based on the neuroimaging literature localizing the letter-box area. The two voxels in inferior frontal cortices were visually selected from the anatomical features of reconstructed template MRI. The two voxels in bilateral motor areas were also placed based on anatomical features defining the motor hand regions on the template MRI because participants were engaged in pressing a button during this task. These 13

voxel locations acted as seeded-source locations on which the collected EEG signals were projected to obtain source waveforms for connectivity analyses.



Source waveforms. Source waveforms were created by signal-space projecting the EEG data into seeded voxel locations using weights that were calculated from our multi-source minimum variance (MCMV) event-related beamformer (MER) (Herdman, Moiseev, & Ribary, 2018; Moiseev, Gaspar, Schneider, & Herdman, 2011; Moiseev & Herdman, 2013). We chose to use MCMV beamforming because the calculated signal-to-source weights are mathematically independent among the seeded source locations (Moiseev et al., 2011; Moiseev & Herdman, 2013). This reduces source leakage among sources, which often leads to findings of false connectivity (Palva & Palva, 2007). MCMV beamforming was used to find the source orientations which were then used to calculate signal-to-source weights [channels x source location], based on the forward leadfields (see Moiseev et al., 2011 for mathematical derivations). The seeded sources' orientations were solved using a eigen-value decomposition based on the signal-to-signal [channel x channel covariance matrices for an active interval (0 to

500 ms) compared to the control interval (-500 to 0 ms) (see Moiseev et al., 2011 for mathematical derivations). Once the source orientations are found for each seeded source, the signal-to-source weights were calculated by multiplying the source orientations by their leadfield matrix. This generated signal-to-source weights for each seeded source. Signal-space projection was then performed by multiplying the ERPs [channels x samples x trials] by the signal-tosource weights [channels x source locations] to yield the projected event-related source waveforms [source locations x samples x trials] (Hamalainen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993; Herdman, Moiseev, & Ribary, 2018). These event-related source waveforms were then used to for time-frequency response (TFR) and functional-connectivity analyses.

Time-Frequency Response (TFR) analyses. We used the exact same procedures for calculating TFR and performing the statistical analyses for the source waveforms as those used for the electrode-level analyses (see above). Thus, we obtained "trial" and "induced" TFR amplitudes for the 13 sources [sources x frequency x samples].

Functional connectivity analyses. We calculated functional connectivity from the "trial" TFR wavelet coefficients for the voxel-to-voxel comparisons among all 13 seeded sources (78 unique comparisons). To do this, we extracted the phase data from the "trial" TFR coefficients by taking the "imaginary" component of the complex value yielding a phase matrix [source locations x frequency x samples x trials]. We passed the phase matrices sequentially for each source location and frequency into our phase-locking value (PLV) functions to calculate the phase-locking. Phase-locking values (PLVs) were calculated using the formula presented by Lachaux, Rodriguez, Martinerie, and Varela (1999) and then baselined to a prestimulus interval (-350 to -50 ms) so that we could visualize the event-related changes in PLV. Ten surrogated PLVs (surgPLVs) were calculated by randomly mixing the trial order between channels before

calculating the PLV. This provided an estimate of the consistency in phases between two virtual channels that likely occur due to evoked responses (i.e., phase-locked to the stimulus onset). Therefore, the surgPLVs are conceptually akin to evoked responses.

Statistical analyses were performed on the PLV data by subtracting the surgPLV from the PLV for each condition, so that we could determine when and where induced changes in PLV were greater than those for evoked changes in PLV. We also subtracted the PLVs for pseudoletters from the PLVs for letters to determine the differences in network connectivity between conditions. These PLV differences were evaluated for significance by using Student t-tests for each time-frequency sample between 4-50 Hz and 0 to 500 ms [78 comparisons x 53 frequencies x 256 samples]. The resulting *p*-values from the *t*-tests were collated across all comparisons, frequencies, and samples (total *t*-test = 78 x 53 x 256 = 1,058,304) and adjusted for family-wise error by conducting a false-discovery-rate (FDR) correction (Benjamini & Hochberg, 1995). The FDR corrected *p*-values were then reshaped to reform the same indices as the PLV matrix of [78 comparisons x 53 frequencies x 256 samples] and used as a significant mask so that insignificant PLVs were substituted as "nan" (not-a-number) and thereby had no further contribution in the analyses. PLV differences were considered significant if the corresponding FDR-corrected *p*-values were < .05.

We evaluated the degree of network connectivity across time and frequency by setting all significant connections to a value of 1 and summing all the significant connections across the 78 possible connections. We then chose a few time-frequency points from these connectivity degree maps in order to visualize the underlying significant network connections across the conditions (letter, pseudoletter, and letter-pseudoletter). In addition, we generated an overall connectivity degree map by summing up all the degree maps for synchronized (PLV > 0) and desynchronized

(PLV < 0) time-frequency points between 4-50 Hz and 0-500 ms. The summed degree maps were then divided by the total number of possible connections (78 x 53 x 256) and multiplied by 100 to yield a percentage of total degree of connectivity. This gave us overall connectivity maps for synchronized (ERS) and desynchronized (ERD) connections for letters and pseudoletters. We also subtracted overall connectivity degree maps between letters and pseudoletters to determine which condition had a greater number of significant connections. To evaluate network laterality, we summed the percent of connections for sources within the left hemisphere and for sources within right hemisphere. Voxel 11 (midline of anterior cingulate cortex) was not included as part of either the left or right hemisphere, but its connections to the left and right sources were included in the calculations.

4.3 Results

4.3.1 TFR Power

TFR results at the electrode level showed prototypical visual time-frequency patterns of event-related spectral power increases within theta (4-8 Hz) band and event-related spectral power decreases within alpha (9-15 Hz) and beta-bands (16-24 Hz). Compared to letters, pseudoletters produced larger positive total power (induced + evoked) within the theta bands over most of the analyzed scalp electrodes (Figure 4.2). However, this effect disappeared after subtracting out the evoked component, which indicates that this theta-band difference is likely driven mostly by the pseudoletter evoked responses as previously demonstrated for these data in Herdman and Takai (2013; chapter 3). What remained as significant after removing the evoked contributions was significantly more negative spectral power for letters than pseudoletters between 100-300 ms at FCC1h and POO2 electrodes. Surprisingly, this effect was not evident within PO10h and PO9h electrodes and might be due to how the generators of such an effect are oriented so that they point toward the frontal and posterior midline electrodes. The main significant results seen in electrode PO10h (left) was a significantly more negative beta-band power for letters than pseudoletters. In electrode PO9h, there was a significantly more negative power to pseudoletters than letters between 320-500 ms.



For the sources, TFR plots showed similar prototypical visual patterns within voxels 2, 3

and 4 as that seen at the sensor level (Figure 4.3). Voxel 9 did not show this same pattern

because it is located within the left inferior frontal region and not likely involved with visual

sensory processing of the letter and pseudoletter stimuli. We found that the voxels within posterior visual cortices (voxels 2-4) had similarly significant TFR results as those seen at the electrode level. There was significantly more positive total power for pseudoletters than letters within the theta band for the voxels 3 and 4, which was mostly abolished in the induced plots. Again, this likely indicated that the theta effect is reflecting the evoked response effect seen previously. Significantly more negative alpha-band power between 0-325 ms was also seen for these visual sources. Interestingly, the right visual source had more spectral power within the beta-band for letters than pseudoletters between 50-200 ms; whereas voxel 2 (medial occipital source) had significantly more negative power to letters than pseudoletters within the beta-band between 250-350 ms. The left inferior frontal source (voxel 9) also showed this greater negativity within the beta band but it occurred slightly earlier between 180-240 ms. This source also had significantly more positive power to letters than pseudoletters within the theta band.



Figure 4.3 Time-frequency plots total power and induced power (i.e., evoked responses removed) for Letter, Pseudoletter, and Letter-Pseudoletter conditions for selected brain sources 2, 3, 4, and 9 (see left scalp/brain plot for locations). Hot colours indicate event-related enhanced power (EREP) relative to prestimulus baseline and cool colours indicate event-related depressed power (ERDP). The white contour lines indicate significant differences between letters and pseudoletters (p < .05 FDR corrected) and are plotted on each graph for visualization. Note the scales for the letter and pseudoletter plots are larger (±2 dB) than the difference plots (±1 dB).

4.3.2 Functional Connectivity Results

Network dynamics rapidly shift across time and frequency and it is difficult to summarize such dynamics by averaging across frequency and time intervals because effects often get washed out. Thus, we took a different approach whereby we plotted the percentage of significant connections across time and frequency and selected time-frequency points with a large number of connections. We then plotted connectivity maps for these points of interest to visualize the network dynamics (Figure 4.4). These connectivity maps revealed three major features. First, there was significantly greater ERS connectivity (hot colored lines) for pseudoletters than letters

(bottom panel) in the theta-band (7Hz) across most of the time interval (85-400 ms). Most of these connections were among posterior sources with the addition of the ACC voxel (#11) whereby there was greater ERS connectivity for letters than pseudoletters until about 300 ms. After this, significant connections were more distributed throughout the frontal sources. This likely reflects the early theta-band (evoked and induced) activity seen within the TFR plots for the occipital sources and later theta-band activity seen in the frontal sources. Overall, theta-band connectivity was larger for pseudoletters than letters with the posterior to frontal spatial shift in network connectivity as processing continued in time.

We also saw significant differences in network dynamics between letters and pseudoletters within the alpha band (12 Hz; Figure 4.4 top panel). Letters produced early ERD (85 ms) within a posteriorly distributed network, whereas pseudoletters produced ERS within a posterior-frontal network. This double dissociation in spatial distribution and type of phase locking (ERS vs. ERD) is seen as significant negative connections within the network maps for letter-pseudoletters. This pattern of more ERD for letters than pseudoletters persisted throughout much of the time interval between 85-400 ms with the same posterior to frontal shift in connectivity as time passed.



conditions (i.e., summed of the number of significant PLV connections compared to surrogate PLV connections at p < .05 FDR corrected). **Bottom Panels**: PLV connectivity maps for Letter, Pseudoletter, and Letter-Pseudoletter conditions corresponding to the selected time-frequency points (7 and 12 Hz; 85, 170, 230, and 390 ms; at crossings of the magenta hashed lines in the top panels). Connections with hot colours indicate significant event-related synchronized (ERS) connections and connections with cool colours indicate event-related desynchronization (ERD; p

If we assume that the significant connections reflect the amount of information transfer within the network, then the overall (total) connectedness of the network across the timefrequency intervals can provide some indication of which regions are responsible for the overall processing of the stimuli. From figure 4.5A, we see that the overall connectedness of the synchronized regions appeared to be greater for letters than pseudoletters in frontal regions and greater for pseudoletters than letters in posterior visual regions. The connectedness difference between letters and pseudoletters (Letter-Pseudoletter map) further demonstrates this distinction, with positive connections (red lines) showing larger number of connections for letters than pseudoletters among frontal regions and negative connections (blue lines) showing larger number of connections for pseudoletters than letters among posterior regions. In contrast, desynchronized connections are more prominent for letters than pseudoletters among the posterior regions, with the exception that for letters they appear to be connected within and not across hemispheres as compared to pseudoletters that had more interhemispheric connections (red color lines within letter-pseudoletter plot).

A left-hemispheric dominance in network connectivity was also evident from looking at both ERS and ERD connectivity maps for letters and pseudoletter. For clarity, we summarized this by taking the percentages of significant connections (relative to total possible connections) for sources located in left and right hemispheres (Figure 4.5B). There was a larger percentage of connections in left than right hemisphere for both synchronized (ERS) and desynchronized (ERD) networks regardless of stimulus condition (letters or pseudoletters). The difference in number of connections between letters and pseudoletters was similar for left and right hemispheres for the ERS network, but for the ERD network, there were a greater number of connections for the letters than pseudoletters in the left hemisphere. This indicated that sources within the left hemisphere had a greater number of desynchronizing communications with other sources in the network. Overall, this network appeared to be left-hemispheric dominant when processing letters and pseudoletters.



Figure 4.5 (A) Network connectivity maps for synchronized and desynchronized connections presented as a percent of significant connections summed across the time and frequency intervals of 0-500 ms and 4-50 Hz. Letter-Pseudoletter maps show the difference between the % of connections within the Letter and Pseudoletter maps. (B) Laterality of the summed Letter and Pseudoletter network connections in (A) for the summed connections for left- (LH) and right-hemispheric (RH) sources. The Letter-Pseudoletter condition is the absolute differences between % of connection between Letters and Pseudoletters.

4.4 Discussion

The main aims of this study were to evaluate the network spatial-spectral-temporal dynamics of oscillatory activity within a connected network involved in processing familiar (i.e., letters) and unfamiliar (i.e., pseudoletters) visual stimuli.

4.4.1 Theta-Band TFR Power

A main finding from our study is that there was more positive theta total power between 0-250 ms within occipital cortices for pseudoletters than letters that became insignificant once the evoked responses were removed (i.e., induced power). This is consistent with the fact that the evoked visual responses have a prominent theta power spectrum within this time interval and the evoked visual responses are known to be larger for pseudoletters than letters (Herdman & Takai, 2013; Park, van den Berg, Chiang, Woldorff, & Brannon, 2018; Maurer, Zevin, & McCandliss, 2008). This effect was also evident at the electrode level as well with significant theta power differences existing in electrodes POOz, PO10, and PO9h. We also found this effect in a frontal electrode (FCCh1) but not in frontal sources, which likely indicates that the effect is mainly generated within occipital cortices, and their generators are oriented in a frontal-posterior manner so that their field distributions can be recorded over the frontal scalp regions. Thus, it is important to conduct source modeling to get a better understanding of the underlying brain networks because field spread and volume conduction make it difficult to interpret which parts of the brain are responsible for the effects if the interpretation is solely based on electrode-level effects. Thus, our findings extend some of the previous literature on TFR to letters and pseudoletters by evaluating these effects within brain space. For instance, our TFR findings were consistent with results of Park et al., (2018) who showed that adults had significantly greater ERP power (8-14 Hz) for letters than pseudoletters between 200-500 ms over bilateral posterior

scalp regions (PO7/PO8 and PO9/PO10), but we only found this effect to be significant over the right hemisphere (PO9h) even though it was evident (but not significant) in the left (PO10h). Because this effect was only found for the right occipital source (see voxel 4; Figure 4.3) and it occurred within the reaction time interval (see Herdman & Takai, 2013 Chapter 3), the effect could be likely related to visual perceptual updating with respect to motor-response selection.

4.4.2 Alpha-Band TFR Power

Alpha-band power is postulated to be inversely related to increased attention and cognitive processing in that the more power depression the more engaged that cortical area is in processing the stimulus information (Jensen & Mazaheri, 2010; van den Berg, Appelbaum, Clark, Lorist, & Woldorff, 2016). Considering this concept along with our findings of greater alpha-band power depression within occipital source (voxels 2, 3, and 4) for letter than pseudoletters between 0-300 ms, we surmise that attention may, in part, be shifted to a greater degree to letters than pseudoletter early on in the visual processing of familiar visual stimuli. This is in contrast to our null findings of attentional effects on evoked responses between letters and pseudoletters (Herdman & Takai, 2013; Chapter 3). This might not be discrepant but simply another view into how attention is affecting the underlying neural processing of familiar versus unfamiliar stimuli. Our previous work on attention evaluated evoked responses, but attention might alter neural oscillations and connectivity that are not apparent in evoked activity. Thus, future work investigating attention effects for oscillatory activity is warranted.

4.4.3 Beta-Band TFR Power

Another interesting finding was the greater negative beta-band power for letters than pseudoletters within the left inferior frontal (voxel 9) and medial occipital (voxel 2) sources. Given that the beta-band activity may be involved in visual attention (Gola, Magnuski, Szumska, & Wróbel, 2013) and that the left inferior frontal source power differences occurred around 180 ms and then in primary visual regions (voxel 2) around 250 ms. This might indicate a communication of attentional allocation from frontal areas back to posterior visual regions. Future studies will be required to determine the modulatory effects of attention on TFR to letters and pseudoletters, with a particular focus on alpha- and beta-band oscillations.

4.4.4 Network Connectivity

We found a posterior theta-band network that had greater synchronized PLV connectivity for pseudoletters than letters. Because the PLVs for the networks were tested against the evoked PLV (i.e., surgPLVs), we interpret these networks to reflect connectivity that is not strictly a result of difference in stimulus phase-locked activity that we and others have previously reported for evoked potentials (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013: Park, Chiang, Brannon, & Woldorff, 2018). Thus, pseudoletters appeared to induce greater connectivity within occipital networks than did letters. This might be related to greater processing required for the pseudoletters in an attempt to match unfamiliar visual patterns with an existing letter template. For letters this process likely occurs early and is highly automatic, therefore, requiring little processing.

Moreover, the alpha-band network expectedly had early (85 ms) desynchronized connections within occipital sources for letters as compared to pseudoletters which had more occipital to frontal synchronized connections. This early alpha-band desynchronization within occipital regions supports the idea that the visual processing network is shifting from a "readiness" state (high alpha-synchronization within the pre-stimulus interval) to an "analysis" state much earlier after stimulus onset for letters than pseudoletters. This fits well with the concept that familiar letters are processed much more rapidly than unfamiliar pseudoletters

because there are existing visual templates within these networks that can easily detect letters (i.e., abstract letter units), whereas several loops through the network might be required to reconcile the conflicting hypothesis about which abstract-letter template is the correct match for a pseudoletter.

Another main result from the network connectivity analyses was that we found a left lateralized network for total percent of connections within the network regardless of stimulus category (letters or pseudoletters), which is consistent with a left-lateralized language model for reading (Cohen & Dehaene, 2004; Dehaene, Cohen, Sigman, & Vinckier, 2005; Price et al., 2003). However, this laterality is in opposition to a right-dominant effect showing greater processing for pseudoletters that we and others previously reported for evoked responses (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman, 2011). It could be that fMRI studies, which often find left-lateralized brain regions for processing letter-based stimuli, are measuring more oscillatory activity than evoked activity. This is consistent with findings from Logothesis, Pauls, Augath, Trinath, & Oeltermann (2001) that revealed that neural oscillations, and not evoked responses, are highly correlated with fMRI signal changes. Thus, the evoked EEG/MEG results that we and others have reported are likely reflecting only part of the underlying neural signals responsible for familiar (letters) and unfamiliar (pseudoletters) processing. Thus, the current study's results provide some indication that the network is more left-hemispheric dominant when processing visual stimuli that appear to be orthographic in nature.

4.5 Conclusion

This study used brain oscillations and network connectivity to provide further evidence that single letters are processed earlier and with less neural activity than pseudoletters. The

interplay among the spatial, spectral, and temporal dimensions of cortical network involvement for processing familiar (i.e., letters) and unfamiliar (pseudoletters) visual stimuli is highly complex and requires multiple perspectives to be able to unravel its intricate form of information processing and communication. We conclude that our findings demonstrate that there was an earlier disengagement of "readiness" (alpha-band) network for visual processing of familiar letters and a greater engagement of the visual "analysis" (theta-band) network for unfamiliar pseudoletters. In addition, we conclude that this visual processing network is, in general, leftlateralized when processing orthographic-like stimuli (letters or pseudoletters). Chapter 5: "Second-language reading proficiency and event-related potentials to singleletters"

5.1 General Introduction

For beginning readers, the script of their target language is initially encountered as a set of meaningless symbols. However, as the readers gain reading experience, processing of these symbols becomes more efficient (Polk & Farah, 1998; LaBerge & Samuels, 1974; Jonides & Gleitman, 1972). For example, reaction times to letters are much faster than those to pseudoletters (LaBerge, 1973; Herdman, 2011), and the reaction times to pseudoletters become faster after training on these symbols (LaBerge, 1973). In the brain, our neural perceptual system undergoes a functional specialization through extensive training in order to achieve such efficiency (Dehaene & Cohen, 2007).

The neural specialization for orthographic symbols is hypothesized to be manifested in the formation of a neural template, which allows perceptual processing of these symbols to be much faster and accurate with experience (Goldstone, 1998). This hypothesis has been supported by several reading models (Dehaene, Cohen, Sigman, & Vinckier, 2005; Grainger, Rey, & Dufau, 2008; McCandliss, Cohen, & Dehaene, 2003; McClelland & Rumelhart, 1981).

A particular brain region of interest to reading is the inferior occipital-temporal cortex. Intracranial studies observed that neural populations in this region respond particularly stronger around 170 ms to certain visual categories, such as words, whose activation is more leftlateralized (Allison, McCarthy, Nobre, Puce & Belger, 1994; Nobre, Allison & McCarthy, 1994). These findings have been supported by subsequent MEG research (Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). Furthermore, the N170, an event-related potential (ERP) measured at the lateral posterior region of the scalp, follows a similar pattern. Letters and words evoke an N170 bilaterally, but it is usually more negative in the left hemisphere than in the right hemisphere (Daffner, Alperin, Mott, & Holcomb, 2014; Maurer, Brandeis, & McCandliss, 2005; Park, Chiang, Brannon, & Woldorff, 2014; Wong, Gauthier, Woroch, Debuse, & Curran, 2005 but see Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013) and the N170 amplitude is different across visual categories (e.g., words, objects, faces; Joyce & Rossion, 2005; Rossion, Joyce, Cottrell, & Tarr, 2003; Tanaka, Luu, Weisbrod, & Kiefer, 1999).

Several researchers have explored how the functional specialization driven by reading experiences would modify the activity at the inferior occipital-temporal region. Illiterate individuals show only minimal activation in this region in the left hemisphere (Dehaene et al., 2010). In monozygotic twins, the same region in the left hemisphere appears to be sensitive to the contribution of their reading experience, compared to the contribution of their genes (Park, Park, & Polk, 2012). Although word-like stimuli elicit activation at the inferior occipitaltemporal region in both hemispheres, it is the left side that is more sensitive to reading experience (Dehaene et al., 2010; Park et al., 2012).

In order to determine the neural efficiency of single-letter processing, researchers have investigated the N170 in terms of the dissociation between letter-processing and pseudoletterprocessing while the participants detect trials with a target symbol or number (e.g., '#" or a "1") intermixed with trials of letter and pseudoletter stimuli (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Chapter 3 – Herdman & Takai, 2013; Park, Chiang, Brannon, & Woldorff, 2014; Pernet et al., 2003; Xue, Jiang, Chen, & Dong, 2008). Findings indicate that the process of differentiating letters from pseudoletters for mature readers is so efficient that it appears not to require their attention to process the orthography of letters. In passive viewing or target detection paradigms, pseudoletters consistently evoke a more negative N170/M170 than do

letters (Appelbaum et al., 2009; Chapter 2; Chapter 3 – Herdman & Takai, 2013; Park et al., 2014; Pernet et al., 2003). A general consensus among researchers as to why N170/M170s are larger for pseudoletters than letters is that pseudoletters require additional neural processing (Appelbaum et al., 2009) due to a lack of their template (Park et al., 2014), which might lead to re-entrant loops for searching for a possible template (Chapter 2 an Chapter 3 – Herdman & Takai, 2013). In other words, letter processing is more efficient than pseudoletter processing due to readers' experience with each type of character.

Another evoked potential that has not been widely emphasized is the P2 because much of the research was focussed on the N170 findings. The P2 to visual stimuli is a positive-going potential at around 220 ms recorded over parietal-occipital scalp regions. Pseudoletters have consistently evoked a larger P2 as compared to letters (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Chapter 2 an Chapter 3 – Herdman & Takai, 2013; Herdman, 2011; Park, Chiang, Brannon, & Woldorff, 2014; Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013). This P2 effect supports the idea that unfamiliar objects require an additional amount of neural processing compared to familiar objects (Appelbaum et al., 2009; Bann & Herdman, 2016; Herdman, 2011; Chapter 2 and Chapter 3 – Herdman & Takai, 2013).

An inconsistent finding in the literature of the pseudoletter effect at the N170 in passiveviewing paradigms is whether the pseudoletter effect is larger in the right hemisphere (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009) or is bilaterally distributed (Herdman & Takai, 2013). Such inconsistency might be due to methodological issues. Neural activities elicited by visual stimuli dynamically change; visually evoked potentials typically emerge with a P1, N170, and P2 in the posterior region of the brain. Both of the above mentioned studies

evaluated the laterality of the pseudoletter effect at the N170 only, possibly missing any manifestation of the laterality at a later ERP.

In the present study, we aimed to extend our understanding of the involuntary neuralprocessing differences between letter recognition and pseudoletter recognition in late second language acquisition. We recruited three participant groups: monolingual English speakers (L1), and Mandarin learners of English, who were divided into high or low levels based on their English proficiency (L2high and L2low). In Experiment 1, we examined how differing levels of English proficiency might be manifested in the difference between letter- and pseudoletterelicited N170. In Experiment 2, we aimed to confirm that the absence of the knowledge of the stimuli (i.e., monolingual English speakers viewing of Chinese characters) would result in no perceptual difference between Chinese characters and pseudocharacters.

5.2 Experiment 1

5.2.1 Introduction: Experiment 1

One of the main objectives of Experiment 1 was to investigate whether or not the N170 pseudoletter effect in a target detection task could be generalized to late (>18 years old) second-language acquisition. Another main purpose was to examine how different proficiency levels in English might be manifested in the N170 pseudoletter effect. We addressed the following research hypotheses in Experiment 1.

- Hypothesis 1: Pseudoletters will evoke larger N170 and P2 responses than letters for all of the participant groups, replicating past research that employed the same task (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman & Takai, 2013).
- Hypothesis 2: The N170/P2 differences between letters and pseudoletters will be larger for the L2high group than for the L2low group (i.e., L2 pseudoletter-proficiency effect).

- Hypothesis 3: The L2 pseudoletter effect in the N170 range in the left hemisphere will correlate with L2 proficiency such that a greater effect will be associated with more advanced L2 proficiency.
- Hypothesis 4: The magnitude of the pseudoletter effect will be larger for the lefthemisphere recordings (at PO7 electrode) than the right-hemisphere recordings (at PO8 electrode) because of a left-hemispheric language dominance.

5.2.2 Methods: Experiment 1

5.2.2.1 Participants

Recruitment. Forty nine Chinese participants were recruited (*Mdn_{age}* = 22 years, range = [18, 39], 34 females). All of the L2 English learners were born and grew up in mainland China until at least their completion of high school. They spoke Mandarin as their native language (L1) and learned English solely as a foreign language throughout the standard formal education curriculum in China. Their age of immersion to natural English was at least 18 years old. Since their arrival to Canada, they have been actively using both Mandarin and English. Their reading skills in simplified Chinese were examined on the "Test of Chinese as a Foreign Language (TOCFL)" (http://www.sc-top.org.tw/mocktest_e.php), and their accuracy scores ranged from 86 to 100%, with a median of 95%. None of the Chinese participants were fluent in a third language. The recruitment further specified the following two criteria: their length of residence in English-speaking environments (either shorter than one year or longer than four years) and their English proficiency on their latest official test, if available.

There were 23 L2 learners, who had lived in an English environment for less than one year, and whose self-reported test proficiency had not met the entry level for the university

education required by the University of British Columbia (i.e., 6.5 on IELTS, and 90 on TOEFL). The majority of this group were exchange students from Chinese universities.

The remaining 26 L2 learners had lived in an English environment for longer than four years. Their self-reported test proficiency was above the entry level for university education, and they were at least in the third year of an undergraduate degree at English-speaking universities or equivalent. The members of this group consisted mostly of graduate students at UBC and workers in the community holding a bachelor's degree from North American universities.

Because some of the L2 participants had not taken formal English proficiency tests that are internationally recognized, and other L2 participants' official scores were outdated (e.g., 12 years ago), we assessed all participants' current English proficiency on six subtests of the *Woodcock Johnson III Diagnostic Reading Battery*: passage comprehension, reading vocabulary, reading fluency, sound awareness oral vocabulary, and oral comprehension (Woodcock, Mather & Schrank, 2004). Participants' mean value on the age equivalence of these tests was used to group these L2 learners based on their current proficiency in English.



the L2 learners. Top: The L2 learners whose length of residence (LOR) is longer than four years. Middle: The L2 learners whose LOR is shorter than one year. Bottom: The results of splitting the L2 learners at the median score. Those whose English proficiency is low (L2low, in green) vs. high (L2high, in red). The vertical axes are the number of participants per bin.

Our visual inspection of these mean scores whose length of residence was either short or long suggested that, as a whole, they were distributed bimodally with some overlap, and the distribution was skewed to the right (Figure 5.1). We excluded two participants from further analyses because their mean scores were identified as outliers: their deviation from the third quartile was larger than 1.5 times of the interquartile range (Hoaglin & Iglewicz, 1987; Wilcox, 2001). By taking the median split of the rest of the mean scores, we obtained two groups that are divided by their English proficiency: L2low and L2high.

A third participant group was the control group, who spoke English as their L1 (n = 32, $Mdn_{age} = 23$ years, range = [18, 33], 24 females). They were fluent only in English and had no exposure to Mandarin, Cantonese, or Japanese. The majority of this group were undergraduate students. In this L1 group, we excluded participants whose mean age-equivalent score on the

Woodcock Johnson III Diagnostic Reading Battery was below their chronological age by at least three years. One participant met this exclusion criterion.

Table 5.1 shows the summary of demographic information and English proficiency information for all three groups after the exclusion based on their English proficiency. On visual inspection, the distribution of the data sets for these groups was mostly skewed; the Shapiro-Wilk test consistently resulted in a p value smaller than .001 (24 out of 34 data sets). Thus, we reported the median value for each group and conducted the Wilcoxon signed rank sum test to infer the group differences at the alpha level of .05 (FDR corrected).

	L2low	L2high	L1
Sample size (female)	24 (16)	23 (17)	31 (23)
Age in years ~^	20 (18, 24)	24 (19, 39)	23 (18, 33)
Age when studying English as	7 (6, 12)	9 (6, 14)	n/a
a foreign language started in			
years			
Age of arrival in years	19.1 (18.0, 23)	19.5 (18.0, 26.9)	n/a
Length of residence in years [~]	0.4 (0.1, 4.3)	5.0 (0.2, 15)	n/a
Length of English learning [~] in	12 (7, 18)	16 (11, 27)	n/a
years			
English use per day in %~	35 (6, 80)	64 (44, 90)	n/a
Overall English proficiency:	8.9 (6.7, 10.7)	13.3 (11.7, 22.8)	26.0 (18.0, 33.8)
Mean of WJ III subtests*			
Passage Comprehension*	8.2 (7.2, 13.10)	11.10 (9.1, 24)	>31 (9.11, >31)
Reading Vocabulary*	11.0 (7.7, 13.11)	14.9 (12.5, >56)	26 (14.9, >56)
Reading Fluency*	12.0 (8.9, 16.6)	15.11 (13.9, >23)	>23 (15.8, >23)
Sound Awareness*	6.9 (5.1, 12.1)	12.1 (6.3, 19)	19 (12.1, >24)
Oral Vocabulary*	9.1 (6.3, 12.11)	12.11 (8.6, >46)	>46 (12.11, >46)
Oral Comprehension*	6.5 (2.11, 11.9)	13.3 (9.5, 20)	>23 (12.5, >23)

Table 5.1 Participant Information and Age-Equivalence for all Three Groups

Note. The median (min, max) was reported because the distribution of the data was often skewed and because some of the data showed a ceiling effect.

Note. Proficiency scores represent age-equivalence.

Note. The Wilcoxon signed rank sum test was statistically significant, p < .05 (FDR corrected), between L2low and L2high[~], L2low and L1[^], and all three groups^{*}.

L2low and L2high groups were comparable on their age when they started to learn English as a foreign language (U = 792, p = .292) and their age of arrival (U = 542.5, p = .467). On the other hand, the L2low group showed a statistically significant smaller value than the L2high group on their chronological age (U = 743.5, p < .0001), their length of residence in an English-speaking environment (U = 784, p < .0001), their length of English learning (U = 744.5, p < .0001), and English use per day (U = 747.5, p < .0001). The L1 group age was comparable with the L2high group (U = 792, p < .292) but older than the L2low group (U = 1063, p < .0001).

In terms of English proficiency, the L2low group was significantly lower than the L2high group (U = 852, p < .0001), which was lower than the L1 group (U = 1226, p < .0001) in the overall scores. A similar relationship was observed in all of the subtests and this relationship was statistically significant, p < .05 (FDR corrected).

Participants were recruited through advertisements distributed across the university and in the community. All of the participants were right-handed on the Edinburgh inventory (Oldfield, 1971). Their (corrected) vision was 20/20 based on testing using a Snellen chart placed 6 m away. Participants' hearing thresholds were evaluated using pure-tone audiometry and all thresholds were below normal levels of 20 dB SPL for 500, 1000, 2000, and 4000 Hz pure tones. Participants had no self-reported history of psychiatric challenges or speech and language disorders. This study was approved by the Behavioral Research Ethics Board at the University of British Columbia.

5.2.2.2 Stimuli

Two kinds of visual stimuli were used: alphabet letters and pseudoletters. Stimuli were white characters presented on a black background. Single alphabet letters were six uppercase letters: B, D, F, M, N, and S. Six pseudoletters were created by segmenting and rearranging

parts of each of the six alphabet letters. This was done to equate the number of pixels and thus luminance between letters and pseudoletters. Each stimulus was presented on a 19-inch LCD monitor (DELL/1908FPC) at a distance of 70 cm from the participant's eyes. A single stimulus covered approximately 2.5 degrees of vertical and horizontal visual angle. The duration of the stimulus presentation was 500 ms. Before and after the stimulus, a white dot, whose duration ranged from 1250 to 1750 ms, appeared at the center of the screen. This dot acted as a visual fixation point.

In the English condition, the alphabet letters and pseudoletters were presented in one single block, which consisted of 250 trials. The appearance of each of the letters and pseudoletters was random and equiprobable, except for the number key, *#*, which acted as a visual target. The target appeared randomly on 10% of the trials.

Participants performed a target detection task while their EEG signals were measured. The participants were instructed to respond by pressing a button with their right hand when they saw the target (#). They were also informed that the stimuli that were to be passively viewed consisted of real (e.g., alphabet letters) and meaningless (e.g., pseudoletters) characters.

5.2.2.3 Data Analysis

Behavioral. The accuracy of the behavioral responses was calculated as the percent correct for the target stimulus. For each of the participant groups, the distribution of the accuracy was skewed to the left and many of the data showed a ceiling effect. Thus, we reported the median value for each group and conducted the Wilcoxon signed rank sum test to infer the group differences at the alpha level of .05 (FDR corrected). The reaction time was defined as time elapsed since the stimulus onset. We reported the mean value for each group and conducted
Welch's *t*-test (Delacre, Lakens & Leys, 2017; Ruxton, 2006; Welch, 1951) at the alpha level of .05.

EEG. Participants were seated in a comfortable chair, located in a sound attenuatedbooth. The 64 electrodes with the 10-20 system were positioned on electrode caps, whose size matched the head circumference and the location of the nasion, inion, Fz, Pz, T8, and T9 electrodes for each of the participants. EEG signals were simultaneously recorded by an ActiView2 64-channel system (BioSemi, Netherlands), with output impedances less than 1 Ohm. These 64 channels were referenced to a common electrode between CPz and CP2; later we rereferenced the 64 channels to an averaged reference. Four additional bipolar electrodes were placed near the right and left outer canthi and infra- and supra-orbital margins, in order to record eye movements and blinks. EEG signals were amplified, sampled at a rate of 1024 Hz with a band-pass filter of 0.16-208 Hz, and digitized at a rate of 24-bit.

ERPs of -1000 to 1500 ms were time locked to the stimulus onset. We judged that trials with ERPs which exceeded ±100 microV between -350 to 850 ms contained artefacts and therefore rejected them from further analyses. Seven participants' data (three in L1, two in L2high, and two in L2low) resulted in having too few (< 50) trials remaining after rejection; thus, their data were excluded from further analyses. Artifact free trials were then down sampled to 512 Hz, averaged across four types of the stimuli and filtered at a 30-Hz low-pass filter to extract evoked potentials. We also calculated the global field power (GFP) of the evoked potentials for each condition, in order to inspect global field strength over the scalp (Lehmann & Skrandies, 1980; Murray, Brunet, & Michel, 2008; Skrandies, 1990).

For each of the participant groups, we performed *apriori* statistical analyses on the difference between the stimulus categories (i.e., letters vs. pseudoletters for the English

condition) at PO7 and PO8 across samples between 80 and 250 ms, which will encompass the P1 and N170 for evoked potentials (Bann & Herdman, 2016; Herdman & Takai, 2013). For these *apriori* analyses, we employed running *t*-tests at every sample point for the epoch (80 to 250 ms). We then performed further *apriori* running Welch's *t*-tests on the magnitude of the difference wave between the participant groups across the above samples.

For the P2, topographies showed that this evoked potential for letters and pseudoletters was maximal at P3 and P4 and thus we performed the above analyses *post-hoc* across samples between 80 and 350 ms. For these *post-hoc* analyses, we employed running t-tests at every sample point for the epoch (80 to 350 ms). The topographies for the difference waveform between letters and pseudoletters in the P2 range showed that the group comparisons between L1 and L2low and between L2high and L2 low were maximal at P07 and P08, while the comparison between L1 and L2high was maximal at P3 and P4. For these group comparisons, we performed further *post-hoc* running Welch's *t*-tests on the magnitude of the difference wave between the participant groups across the above samples.

Lastly, we calculated the envelope of the event-related potentials at each of PO7 and PO8 by use of the Hilbert transform, in order to capture the overall amplitude change of the wave form. We then applied a laterality index (Myslobodsky, Coppola, & Weinberger, 1991; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; van der Lubbe & Utzerath, 2013) to the envelope, in order to infer the laterality for the pseudoletter effect. We conducted running Welch's t-tests at every sample point for the epoch (80 to 350 ms). For all of these above mentioned analyses, we avoided conducting omnibus tests and irrelevant post-hoc pairwise comparisons in order to maintain the efficiency of the statistical tests and the overall balance between type I and type II errors (Howell, 2010; Wilcox, 1987).

In order to control for an alpha inflation, our significance level was modified by a False Discovery Rate (FDR) correction procedure (Benjamini & Hochberg, 1995; Benjamini & Yekutieli, 2001), unless specified. We treated *p* values to be statistically significant at the .05 FDR corrected significance level for *apriori* tests and .025 FDR corrected significance level for *post-hoc* tests. Also, in order to secure the reliability of the *p* values, we treated only *p* values that sequentially maintain the above significance level for at least 20 ms (20 samples).

For the duration where the group comparison between L2high and L2low (i.e., L2 proficiency effect) reached significance in the English condition, we examined the correlation between the mean magnitude of the pseudoletter effect at PO7 for each of the L2 participants and their overall proficiency in English (i.e., the mean of Woodcock Johnson subtests). The results of this *apriori* correlational analysis were considered significant at the alpha level of .05. When the correlation was significant, we added data from the L1 group to the L2 data. Then we examined the *post-hoc* correlation between an overall proficiency effect in English and the scores on the English proficiency across all groups (L1, L2high, L2low), with the significance level lowered to .025 (Bonferroni correction). As in Hypothesis 3, this study's primary aim is to look at the correlation between N170 pseudoletter effect and L2 proficiency. If we included the L1 group to begin with, we would run a risk of identifying an L2 proficiency effect whereby language transfer effects might mask L2 proficiency.

By employing this two-step procedure for correlations, we changed the degree of control over a potential influence of language transfer (Koda, 1989a, 2007; Wang, Koda, & Perfetti, 2003) from strict to loose, in order to infer the generalizability of the observed correlation. Also as post-hoc, because the L2low group was the youngest, we further examined a correlation

between age of the participants and the mean amplitude of the pseudoletter effect at PO7. For all of these correlational analyses, we performed the Spearman's rank correlation because the data appeared to violate the homoscedasticity assumption on visual inspection and because some of the proficiency scores contained a ceiling effect.

5.2.3 Results: Experiment 1

5.2.3.1 Behavioral Results

The median accuracy of the behavioral responses for the target detection task was 100% for each of the participant groups (Table 5.2). The Wilcoxon signed rank sum test on each of the pairwise comparisons did not reach statistical significance for L1 vs. L2low, U = 412, p = .747, L1 vs. L2high, U = 592, p = .505, and L2high vs. L2low, U = 412, p = .747.

 Table 5.2 Results of Behavioral Responses: Median (min, max)

	L2low	L2high	L1
Accuracy in %	100 (94.1, 100)	100 (97.0, 100)	100 (94.1, 100)
Reaction Times (ms)	491.5 (421.5, 595.2)	513.1 (436.7, 593.8)	488.1 (409.4, 593.0)

The mean latency of the behavioral responses for the target detection task for L2low, L2high and L1 groups was 491.5, 513.1, and 488.1 ms, respectively. The Welch's t tests did not reach statistical significance, for L1 vs. L2low, t(21.585) = -0.105, p = .918, L1 vs. L2high, t(43.696) = -0.761, p = .550, and L2high vs. L2low, t(21.908) = 0.658, p = .517.

5.2.3.2 Electrophysiological Results

Global field powers. For each of the three groups, grand mean GFPs for both the letter and pseudoletter conditions showed clear peaks that corresponded in latency to the visual evoked potentials (P1, N170, and P2) (Figure 5.2). The GFP for pseudoletters appeared to be larger than that for letters in the N170 range (170 to 210 ms) and in the P2 range (250 to 350 ms) for L1 and L2high groups. For the L2low group, the pseudoletter effect appeared to be present only in the P2 range (285 to 350 ms).



Evoked potentials: within-group. For each of the three groups, topographies for the letter and pseudoletter conditions showed clear positivity (80 to 130 ms), negativity (150 to 200 ms) and positivity (230+ ms) in a posterior-occipital distribution. They corresponded to the typical visual evoked potentials: P1, N170 and P2. Topographies in these latencies for the pseudoletter effect showed the effects on the N170 maximally at PO7 and PO8 (Figure 3) and on the P2 maximally at P3 and P4 (Figure 4); hereafter, we will refer to these effects as the N170 effect and the P2 effect.

For L1 and L2high groups, grand mean evoked potentials for the pseudoletter effect reached statistical significance in two time intervals: N170 (150 to 245 ms) (Figure 5.3) and P2

(250 to 350 ms) bilaterally (Figure 5.4). For the L2low group, the differences between the conditions reached statistical significance in two time intervals. The N170 response was significant in the right hemisphere (165 to 235 ms) (Figure 5.3) but not in the left (minimum p = .024 at 233ms). The P2 response was in both hemispheres but shorter at the P3 (300 to 330 ms) than at the P4 (280 to 355 ms) (Figure 5.4).

Evoked potentials: between-group. On visual inspection, the magnitude of the N170 pseudoletter effect appeared to be the largest for the L1 group, second largest for the L2high group, and the smallest for the L2low group (Figure 5.5). Meanwhile, the P2 pseudoletter effect appears the most negative for the L2low group, second negative for the L2high group and the least negative for the L1 group.

Topographies for the pairwise comparisons on the pseudoletter effect showed that the N170 effect had a posterior-occipital distribution. The P2 effect showed a similar distribution, except for the comparison between L1 and L2high, showing maximal group differences in a mid-posterior-occipital distribution (Figure 5.5).



below; the peak of the difference wave corresponds to the latency of the topography.



(second row with red lines), and L2low group (third row with green lines), for letters (dark), pseudoletters (light), and the P2 pseudoletter effect: letters minus pseudoletters (dotted boxes), at electrodes P3 (left column) and P4 (right column). Bars below the waveforms are intervals where the pseudoletter effect was statistically significant at p < .05 (light gray, FDR corrected) and p < .01 (dark gray, FDR corrected). Shaded columns (blue) correspond to the P2 effect shown below; the peak of the difference wave corresponds to the latency of the topography.



Figure 5.5 The P2 pseudoletter effect (i.e., grand-mean evoked potential differences between letters and pseudoletters) for L1 (blue), L2high (red), and L2low (green) at electrodes P3 and P4 (top); the N170 pseudoletter effect at PO7 and PO8 (bottom). Bars below the waveforms are intervals where the pseudoletter effect was statistically significant at p < .05 (light gray, FDR corrected) and p < .01 (dark gray, FDR corrected), for L1 vs. L2low (first row), L1 vs. L2high (second row), and L2high vs. L2low (bottom row), and for the N170 effect (left column) and the P2 effect (right column). Shaded columns (orange and light blue) correspond to the N170 and P2 effects; the peak of the difference wave between L2high and L2 low at PO7 for the N170 and P4 for P2 corresponds to the latency for the topography (middle).

Pairwise comparisons of the N170 effect at PO7 and PO8 showed that the L1 group was significantly larger than L2high and L2low groups (160 to 235 ms) (p < .05 FDR corrected). The N170 effect for the L2high group was larger than that for the L2low group at PO7 (160 to 235 ms) but not at PO8 (minimum p = .220 at 210 ms). Pairwise comparisons of the P2 effect at PO7 and PO8 as well as at P3 and P4 did not reach statistical significance, p > .10.

Laterality. The laterality index on the envelope of the pseudoletter effect tended to be lateralized to the right for the L1 group and bilateral for L2 groups (Figure 5.6). This right-lateralization reached statistical significance only for the L1 group (270 to 290 ms) (p < .05 FDR corrected), not for the L2high group, p > .18, or the L2low group, p > .15.



their difference (black), for L1 group (top), L2high group (middle), and L2low group (bottom). below the waveforms are intervals where the Laterality Index of the envelope difference was statistically significant at p < .05 (light gray, FDR corrected).

5.2.3.3 Correlations

We examined the correlation between the mean scores of Woodcock Johnson III and the mean amplitude of the N170 effect at PO7 between 160 and 235 ms for all of the L2 learners (Figure 5.7). One outlier was detected (Hoaglin & Iglewicz, 1987; Wilcox, 2001). The Spearman's rank correlation was significant, $\rho = .363$, p = .019. We then replaced the proficiency scores with the chronological age of the participants. The Spearman's rank correlation was not significant, $\rho = .281$, p = .075. Lastly, we added the data from the L1 group to the data from L2 groups in order to examine the relationship between English proficiency and the mean amplitude of the N170 effect at PO7. We found one outlier (Hoaglin & Iglewicz, 1987; Wilcox, 2001). The Spearman's rank correlation remained significant, $\rho = .369$, p < .002 (Bonferroni corrected).



Figure 5.7 Scatter plots showing a relationship between the magnitude of the N170 pseudoletter effect and participants' profiles (L2low in green, L2high in red, and L1 in blue). Top Left: Age equivalence English proficiency for L2 groups, $\rho = .36$, p = .019. Top Right: Age equivalence English proficiency for all three groups, $\rho = .37$, p = .002 Bottom Left: Chronological age of L2 participants, $\rho = .28$, p = .075. ^ indicates an outlier.

5.2.4 Discussion: Experiment 1

In summary, we observed that the pseudoletter effect in the N170 range was present bilaterally for the L1 and the L2high groups but only at the right hemisphere for the L2low group. In addition, the pseudoletter effect in the P2 range was robustly present bilaterally for all the groups, and the magnitude of this P2 effect was equal across groups. There was a small but significantly right-hemispheric laterality for the P2 in the L1 group, which might indicate greater processing in the right hemisphere for this task, this is consistent with Park et al. (2018) who also showed greater pseudoletter effect in right compared to the left hemisphere between 250-300 ms. Lastly, the magnitude of the N170 pseudoletter effect at the left hemisphere correlated with English proficiency for all of the participants.

5.2.4.1 N170 Pseudoletter Effect for L2high and L2low Groups

For the L1 group, pseudoletters evoked a more negative N170 than did letters between 140 and 250 ms in the posterior occipital regions bilaterally. This N170 pseudoletter effect replicated the results from past studies using the same experimental task (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman & Takai, 2013; Park, Chiang, Brannon, & Woldorff, 2014; Pernet, 2003) and provides support for the results from studies employing other experimental tasks (Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013).

For the L2high group, we observed an N170 pseudoletter effect with a latency and topographic distribution resembling those for the L1 group. For the L2low group, however, the N170 pseudoletter effect was barely present only in the right hemisphere or only later (e.g., the P2). We believe that this is evidence that unintentional processing for English orthography for the L2high group is closer to that of the L1 group; whereas the L2low group has less automatic processing for English orthography as compared to the L2high and L1 groups.

5.2.4.2 P2 Pseudoletter Effect for L2high and L2low Groups

For all three of the groups, pseudoletters evoked a larger P2 than did letters between 250 and 350 ms in the posterior occipital regions. This finding corroborates the P2 pseudoletter effect reported in past studies (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013; Park, Chiang, Brannon, & Woldorff, 2014; Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013).

5.2.4.3 L2 Proficiency Effect

Confirming hypothesis two, we observed an effect of L2 proficiency, not only at the participant group level but also at the individual level. For both levels of analysis, the effect was present in the left hemisphere. Our group comparison between L2high and L2low groups showed that this group difference manifested as an N170 effect between 160 and 200 ms maximally at PO7. Our correlational analysis further supported this observation. The mean amplitude of the N170 pseudoletter effect and English proficiency was correlated at PO7. Confirming our third hypothesis, the more superior English proficiency is, the larger the N170 pseudoletter effect observed.

The overall pattern of results fits with a point of view based on the re-entrant theory (Di Lollo, Enns, & Rensink, 2000). The finding that pseudoletters elicited a larger N170 is because they require additional neural processing for searching their neural templates via re-entrant loops among visual cortical areas. In other words, because the participants had learned letters, finding their match was much more efficient than trying to find a match for pseudoletters. More re-entrant loops would, therefore, be required when processing pseudoletters than letters. This could manifest as greater ERPs to pseudoletters than to letters as we observed in this study and others (Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013).

One limitation of our interpretations of the above results is the possibility that the N170 for the L2high group might be inherently more negative than for that for the L2low group, regardless of the amount of experience with the new language. This could be the case because the L2high group's brains have a greater propensity for learning new visual templates and languages as compared to the L2low group. Another limitation is that the N170 pseudoletter effect might have nothing to do with knowledge of *alphabet* letters specifically. This limitation is plausible because Experiment 1, as well as many past studies with a target detection task, did not have a control orthography condition whereby one group (e.g., L2high/L2low) is familiar with the test (e.g., English) and control (e.g., Chinese) orthographies and another group (e.g., L1) is only familiar with the test (e.g., English) orthography. Thus, in Experiment 1's pseudoletter effects would disappear for the L1 group to the Chinese orthography but would remain for L2 groups to the Chinese orthography.

5.2.4.4 Laterality

The magnitude of the pseudoletter effect was right-lateralized for the L1 group. Thus, at the macrolevel, the differences in ERPs between letters and pseudoletters surrounding the P2 intervals were larger in the right than left hemisphere. This observation does not support hypothesis four for the L1 group but is consistent with the findings from Appelbaum, Liotti, Perez, Fox, & Woldorff (2009). However, we found no evidence of hemispheric laterality for the L2 groups. By assuming that the pseudoletter effect is a manifestation of an overall gain in efficiency in letter processing (i.e., pseudoletters simulate letters at the beginning of learning of these letters, as in learning to read in the first language), our observation could indicate that the L1 group's brains are specialized within the right hemisphere for processing of single letter

features; whereby the L2 group's brains have yet to gain this specialization. Yet, this view does not fit well with the prevailing hypothesis of a left-lateralized orthographic neural network (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Cohen et al., 2003; Dehaene & Cohen, 2011; Leff et al., 2001; Nobre, Allison, & McCarthy, 1994; Price & Devlin, 2011). Alternatively, by assuming that the pseudoletter effect is a manifestation of a reaction of pseudoletters against previously established letter processing (i.e., pseudoletters simulate visual stimuli that challenge preexisting letter processing networks, as in learning to read in a foreign or late second language), our observation could indicate that the right hemisphere might be functioning as a reservoir of letter feature processing. Cases of pure alexia can support this interpretation. Due to a lesion in the left inferior-temporal area, patients with pure alexia experience difficulty in word reading, during which it is the right inferior-temporal area that shows activation (Cohen et al., 2004; Ino, Tokumoto, Usami, Kimura, Hashimoto, & Fukuyama, 2008; Pyun, Sohn, Jung, & Nam, 2007; Tsapkini, Vindiola, & Rapp, 2011). In addition, a recent longitudinal study showed that over the course of recovery, a patient with pure alexia increased activation in the right inferior-temporal area as well as the areas in the left hemisphere that are adjacent to the lesion (Cohen, Dehaene, McCormick, Durrant, & Zanker, 2016). The results of another case study observed that the functional role of the right inferior-temporal area can reflect functional reorganization of orthographic processing, which has been previously established in the left hemisphere (Fischer-Baum & Kajander, 2017). Taken together, for mature monolingual English readers in our study, their alphabet letter processing has already been well specialized and hemispheric lateralization has been established; the left hemispheric network is used for letter processing and the right hemispheric network is used for a reservoir of letter feature processing. Meanwhile for L2 learners, their letter processing is not yet so specialized, due to possibly their

lower proficiency in English and/or reading experiences in Mandarin. As a result, the hemispheric lateralization for letter processing is still being molded by experience with English text, and consequently, the pseudoletter effect is manifested bilaterally.

5.3 Experiment 2

5.3.1 Introduction: Experiment 2

The main purpose of Experiment 2 is to test our assumption that the pseudoletter effect in a target detection task reflects the participants' experience with the target language. Specifically, we expect ERPs elicited by Chinese characters and pseudocharacters to diverge only for Chinese participants but not for English L1 participants who have no experience with Mandarin or relevant Asian orthographies, such as Japanese. Also we expect that the magnitude of the pseudocharacter effect will be the same between L2low and L2high groups because their educational and language background in China were comparable.

In addition, we are aware of only one study that investigated a pseudocharacter effect for adult Chinese readers in a target detection task (Xue, Jiang, Chen, & Dong, 2008). These authors observed that characters elicited a more negative N170 than did pseudocharacters. Yet, Xue et al. (2008) did not appear to control the average luminance between characters and pseudocharacters. Because the luminance is known to affect the N170 (Bieniek, Frei, & Rousselet, 2013; Johannes, Munte, Heinze, & Mangun, 1995; Martinovic, Mordal, & Wuerger, 2011; Wijers, Lange, Mulder, & Mulder, 1997), it is difficult to interpret the results of Xue et al. (2008) with respect to differences in orthographic experience between these two types of visual stimuli. In experiments 1 and 2, we controlled for such a luminance confound by presenting the same number of equally luminant pixels for letters and pseudoletters. Lastly, there appears to be limited evidence on the P2 in the literature regarding late second-language literacy. Studies that compared characters and pseudocharacters employed tasks that are different from a target detection (Lin, Chen, Zhao, Li, He, & Weng, 2011; Wong, Gauthier, Woroch, Debuse, & Curran, 2005; Zhao, Li, Lin, Cao, He, & Weng, 2012). Although they did not formally analyze the P2, our visual inspection suggested that the P2 tended to be larger for pseudocharacters than for characters. The following were our research hypotheses in Experiment 2.

- Hypothesis 1: The L1 group (monolingual English) will show no pseudocharacter effect (i.e. no ERP differences between letters and pseudoletters between 0-250 ms).
- Hypothesis 2. The L2low and L2high groups will show a pseudocharacter effect in that the N170 and P2 will be larger for pseudocharacters than for characters, as shown in Experiment 1.
- Hypothesis 3: The L2low and L2high groups will show the same magnitude of a pseudocharacter effect.
- Hypothesis 4: The overall pseudocharacter effect in the L2 groups will be larger in magnitude for the left-hemisphere recordings (at PO7 electrode) than the righthemisphere recordings (at PO8 electrode) because of a left-hemispheric language dominance.

5.3.2 Methods: Experiment 2

5.3.2.1 Participants

The same participants as in Experiment 1 participated in Experiment 2. The order of the experiments 1 and 2 was counterbalanced across participants.

5.3.2.2 Stimuli

The same as Experiment 1, except that instead of alphabet letters and pseudoletters, we used Chinese characters and pseudocharacters. Chinese characters (pronunciation in Pinyin, [International Phonetic Alphabet (International Phonetic Association, 2015)], "meaning in English") were five nouns and one pronoun: 季 (ji4, [tɛî], "season"), 机 (ji1, [tɛí], "machine"), 客 (ke4, [k^hê], "guest"), 库 (ku4, [k^hû], "storehouse"), 他 (ta1, [t^há], "he"), and 皮 (pi2, [p^hĭ], skin). All of these characters were chosen out of the 5000 most frequent characters in the

Chinese lexicon (Xiao, Rayson, & McEnery, 2015). We created pseudocharacters out of Chinese characters in the same manner as we made pseudoletters out of alphabet letters.

5.3.2.3 Data Analysis

The same as Experiment 1, except that we did not examine any relationship between the magnitude of the pseudocharacter effect and proficiency in Mandarin among L2 participants. Also a pseudocharacter effect in the P2 range was maximal at PO7 for the L1 group, P3 and P4 for L2 groups, and all of the pairwise comparisons. Student's t-tests, as in Experiment 1, were conducted for the event-related potentials at these channels. Lastly, we calculated the laterality index for each of the participant groups as well as L2 group as a whole (L2combined).

5.3.3 Results: Experiment 2

5.3.3.1 Behavioral Results

The median accuracy of the behavioral responses for the target detection task was 100% for each of the participant groups (Table 5.3). The Wilcoxon signed rank sum test on each of the pairwise comparisons did not reach statistical significance for L1 vs. L2low, U = 404, p = .127, L1 vs. L2high, U = 640, p = .370, and L2high vs. L2low, U = 404, p = .127.

	L2low	L2high	L1
Accuracy in %	100 (94.1, 100)	100 (94.1, 100)	100 (97.0, 100)
Reaction Times in ms	512.7 (438.5, 622.8)	511.3 (435.6, 624.1)	495.4 (434.6, 613.4)

Table 5.3. Results of Behavioral Responses: Median (min, max)

The mean latency of the behavioral responses for the target detection task for L2low, L2high and L1 groups was 512.7, 511.3, and 495.4 ms, respectively. Welch's t test did not reach statistical significance, for L1 vs. L2low, t(23.078) = 0.041, p = .968, L1 vs. L2high, t(42.090) =-0.652, p = .519, and L2high vs. L2low, t(24.119) = 0.342, p = .735.

5.3.3.2 Electrophysiological Results

Global field powers. On visual inspection, characters and pseudocharacters both evoked clear peaks corresponding to the visual evoked potentials (P1, N170, and P2) for all participant groups (Figure 5.8). The difference wave for the L1 group was almost flat, while that for the L2 groups showed that pseudocharacters elicited a stronger potential field at around 200ms and 300ms, which corresponded to the pseudoletter effects in the N170 and the P2 intervals that we observed in Experiment 1.



Evoked potentials: within-group. On visual inspection, both characters and

pseudocharacters appeared to evoke the P1, N170, and P2 for all of the groups. Topographies

confirmed that the pseudocharacter effect was absent for the L1 group (Figure 5.9).

Topographies for L2 groups showed that the pseudocharacter effect was manifested in a

posterior-occipital distribution and maximally at PO7 and PO8. The two types of visual stimuli

diverged both in the N170 range (150 to 290 ms) (Figure 9) and in the P2 range (Figure 10) only

for the L2 groups.



(second row with red lines), and L2lowgroup (third row with green lines), for characters (dark), pseudocharacters (light), and the N170 pseudocharacter effect: characters minus pseudocharacters (dotted boxes), at electrodes PO7 (left column) and PO8 (right column). Bars below the waveforms are intervals where the pseudocharacter effect was statistically significant at p < .05 (light gray, FDR corrected) and p < .01 (dark gray, FDR corrected). Shaded columns (orange) correspond to the N170 effect shown below; the peak of the difference wave corresponds to the latency of the topography.



The differences of the grand mean evoked potentials by characters and pseudocharacters did not reach statistical significance for the L1 group, p > .10 at 202 ms. However, for the L2 groups, pseudocharacter effects (pseudocharacter > character) were significant in the N170 interval (180 to 280 ms) p < .05 FDR corrected) (Figure 5.9) and in the P2 interval (250 to 360 ms) (Figure 5.10) over both hemispheres. For the L2low group, the P2 pseudocharacter effect was significant at P4, but not at P3.

Evoked potentials: between-group. On visual inspection, the group difference on the pseudocharacter effect was present in the N170 range and P2 range bilaterally, except for within-L2group comparison in the P2 range (Figure 5.11). The pseudocharacter effect appeared to be the largest for L2high group, the second largest for the L2low group, and absent for the L1 group. Statistically, the group difference between L2high and L2low groups was not significant in the N170 range (minimum p = .170 at 209 ms at PO8) nor in the P2 range (minimum p = .023 at 320 ms at P4). The group differences between L1 and each of the L2 groups were significant bilaterally in the N170 range (200 to 260 ms) (p < .05 FDR corrected) and in the P2 range (270 to 330 ms).

Laterality. On visual inspection, the envelope of the pseudocharacter effect for the L1 group did not show any laterality while that for the L2 groups appeared to be right-lateralized (Figure 5.12). Statistically, the laterality index for the L1 group was not significant (minimum p = .087 at 284 ms). The laterality index for the L2high group was not significant (minimum p = .02 at 123 ms), but significantly right-lateralized for the L2low group (90 to 135 ms) (p < .05 FDR corrected) and for the L2combined (101 to 135 ms).



Figure 5.11 The P2 pseudocharacter effect (i.e., grand-mean evoked potential differences between characters and pseudocharacters) for L1 (blue), L2high (red), and L2low (green) at electrodes P3 and P4 (top); the N170 pseudocharacter effect at PO7 and PO8 (bottom). Bars below the waveforms are intervals where the pseudocharacter effect was statistically significant at p < .05 (light gray, FDR corrected) and p < .01 (dark gray, FDR corrected), for L1 vs. L2low (first row), L1 vs. L2high (second row), and L2high vs. L2low (bottom row), and for the N170 effect (left column) and the P2 effect (right column). Shaded columns (orange and light blue) correspond to the N170 and P2 effects; the peak of the difference wave between L2high and L2 low at PO7 for the N170 and P4 for P2 corresponds to the latency for the topography (middle).



5.3.4 Discussion: Experiment 2

In summary, while we found no evidence that the ERPs were different between

characters and pseudocharacters for the L1 group, we did find statistically significant differences

in ERPs in the L2 groups. We classify the ERP differences between characters and

pseudocharacters as the "pseudocharacter effect" in order to help isolate the findings from the

pseudoletter effect when discussing them across experiments, but the pseudocharacter and

pseudoletter effects appear to be the same effects just in different languages. As predicted, we

found that the magnitude of the pseudocharacter effect was comparable between L2low and L2high groups.

5.3.4.1 N170 Pseudocharacter Effect

Our observation of the absence of the pseudocharacter effect for the L1 group supports our first hypothesis and confirms our assumption that the presence or absence of the pseudocharacter/pseudoletter effects in a target-detection task corresponds to whether the participants know or do not know a language's orthography. In addition, our observation that the magnitude of the pseudocharacter effect was comparable between L2low and the L2high group supports our third hypothesis and provides evidence that our demographic data from these groups are comparable in terms of their educational and language history in Mandarin. Note, one potential confound for this comparison between L2 groups is that some of the L2 participants might have undergone first language attrition. We, however, judged that the effect of attrition is minimal for the present experiment because all of the L2 participants had been maintaining active use of Mandarin (Schmid, Köpke, Keijzer, & Weilemar, 2004).

In addition, our observation that pseudocharacters evoked a more negative ERP in the N170 range than did letters for the L2 groups fits our observations in Experiment 1. Similar to our interpretation in Experiment 1, we suggest that pseudocharacters appeared to require additional neural processing for the search of their template matching as compared to characters. These results support our second hypothesis.

5.3.4.2 P2 Pseudocharacter Effect

Our data showed a pseudocharacter effect in the P2 range, supporting our second hypothesis and lending support for past studies that employed different tasks (Lin, Chen, Zhao, Li, He, & Weng, 2011; Wong, Gauthier, Woroch, Debuse, & Curran, 2005; Zhao, Li, Lin, Cao,

He, & Weng, 2012). Interestingly, the group difference between L1 and L2 groups on the magnitude of the pseudocharacter effect was significant in the right hemisphere but not in the left hemisphere. The present study only compared groups that either know or do not know Chinese orthography. A future study that examines how proficiency in Mandarin will be manifested in a target-detection task will add valuable information to our observation on the P2 pseudocharacter effect.

5.3.4.3 Laterality

The L1 group did not show laterality. This result was reasonable because this group was a control group. The L2 groups as a whole (L2combined) showed that their pseudocharacter effect was right-lateralized. This observation does not support hypothesis four. Similar to the same pattern of observation and discussion in Experiment 1, it could mean that learning experiences in Chinese might alter neural orthographic processing in the right-hemisphere only or both hemispheres.

Given that the L2 groups did not show lateralization for the pseudoletter effect in Experiment 1, lateralization of pseudo effects (e.g., a pseudoletter effect for native English readers and a pseudocharacter effect for native Mandarin readers) appears to be consistently observable in the orthography of the first and dominant language. Cross-linguistic studies are valuable to understand whether this consistency is applicable to other types of orthographies (e.g., Korean and Arabic).

5.4 General Discussion

To the best of our knowledge, this study is the first to show that the pseudoletter effect in single-letter processing can be generalized from L1 to L2 groups. Moreover, the N170

pseudoletter effect correlated with behavioral scores on English proficiency (Experiment 1). Lastly, we eliminated two possibilities that both the pseudoletter effect and the proficiency effect might be spurious due to differences in stimulus features between letters/characters and pseudoletters/pseudocharacters or due to differences in the L2 group's native language proficiency (Experiment 2).

5.4.1 Pseudoletter Effect from L1 to L2

The pseudoletter and pseudocharacter effects examined in a target-detection task appear to be a manifestation of participants' reading experience with the tested language's orthography. We extended our current knowledge on this paradigm from first-language (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman & Takai, 2013; Park, Chiang, Brannon, & Woldorff, 2014; Pernet et al., 2003, but Xue, Jiang, Chen, & Dong, 2008) to late second-language acquisition. When participants have no experience with the orthography, their neural visual processing shows no distinction between real- and pseudo-orthographic stimuli (i.e., the L1 group with Chinese characters in Experiment 2). Learning this orthography as a foreign language, appears to cause these two types of visual stimuli to diverge in their visual processing within the N170 and at P2 time ranges. However, longitudinal studies of late second-language learners would be required to better evaluate this inference. Of particular interest, L2 proficiency in English correlated with the magnitude of the N170 pseudoletter effect in the left hemisphere. This indicates that the left-hemispheric network that underlies the N170/P2 responses might become more dominant for processing letters as people become more familiar with the language's orthography.

A potential caveat to our findings is the role of attention on the N170 (Hinojosa, Mercado, & Carretie, 2015; Ruz & Nobre, 2008; Strijkers, Bertrand, & Grainger, 2015). It could

be the case that each of the participant groups allocated a different amount of attention to each of the stimulus categories, affecting the magnitude of the pseudo effects in both Experiment 1 and Experiment 2. Although there might be potential impact of attention on each of the stimulus categories because the amplitude of the ERPs appeared to be different across the groups, we previously found evidence that the allocation of attention was similar between letters and pseudoletters and the N170/P2 pseudoletter effect remained under different allocations of attention towards or away from orthography (Herdman & Takai, 2013). The role of attention may be different when examined at the level of word recognition (Ruz & Nobre, 2008; Strijkers et al., 2015), however, these studies did not evaluate the attention effects on the difference waves as was done in Herdman and Takai (2013).

5.4.2 Pseudoletter Effect and English Proficiency

The N170 pseudoletter effect measured at PO7 correlated with English proficiency. This observation supports past studies showing the relationship between activation in the left inferior temporal region and literacy experience (Dehaene et al., 2010; Park, Park, & Polk, 2012). Our observation also fits with the literature on word-recognition, which indicates that longer-term L2 learning in adults results in changes in the N170 in the left hemisphere (Madec et al., 2016; Maurer, Blau, Yoncheva, & McCandliss, 2010).

Our research design, however, does not allow us to infer any causal relationship between the magnitude of the pseudoletter effect and L2 proficiency. It could be that learning to read in L2 induces changes in the generators of the N170 pseudoletter effect. If this learning effect is true, then it might indicate that L2low learners, who have been studying English for more than a four years, still have room for improvement in the efficiency for single-letter processing that could help them to improve their overall reading comprehension. Alternatively, it could be that

some individuals are already equipped with neural processing that can adapt to processing letters much more efficiently. Consequently, they are better positioned to acquire an L2 orthography. Regardless of which premise is true, future longitudinal investigations examining brain responses of late-L2 learners would be valuable.

Because our findings showed that the proficiency effect can be extended to the L1 group and that L2high and L2low groups did not differ in the magnitude of the pseudocharacter effect, the data seem to lend more support to a learning effect. It might be argued that directly comparing L2 groups and the L1 group on English proficiency might be confounded by other socio-cultural and linguistic differences between the two groups. However, our data showed that the more superior English proficiency is, the larger the N170 pseudoletter effect, regardless of language background. Whether single-letter processing for the L2high group can further improve, or has reached its maximum degree of efficiency, will be a theoretically important question for future investigation.

5.4.3 Expertise Research

We and other researchers have been consistently observing that a foreign/unfamiliar orthography evoked a more negative ERP in the N170 time range than a did native/familiar orthography in an target-detection task (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman & Takai, 2013; Park, Chiang, Brannon, & Woldorff, 2014; Pernet, Basan, Doyon, Cardebat, Demonet, & Celsis, 2003), and this phenomenon is in direct contrast with research findings from applications of the expertise research to single-letter processing (Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013; Wong, Gauthier, Woroch, Debuse, & Curran, 2005). It is important to note that Stevens et al. (2013) and Wong et al. (2005) both employed a one-back task. Along with encouraging phonological retrieval, a one-back task requires conscious manipulation of the visual stimuli in memory that might have increased the activity of the well-specified neural letter-processing compared to that in a passive target detection task (Park et al., 2014). Also, the one-back task necessitates block-wise presentation of the stimuli. Measuring brain activity in an English context and then in a foreign language context might entail more than differences in perceptual processing (Park et al., 2014; Strijkers, Bertrand, & Grainger, 2015). On the other hand, the target-detection task in the current study presents familiar and unfamiliar orthographies randomly in a single context. This will minimize potential context effects specific to each of the languages. Therefore, it is reasonable to think that the differences in the processing required between a known and a foreign orthography is not identical between a one-back task and a target-detection task. Rather, we suspect that evidence from these experiments likely provide complimentary evidence for multiple aspects of letterprocessing. Use of a one-back task is likely effective for elucidating the amount of knowledge and skills related to one's expertise and related to more phonological processing skills. Meanwhile, use of a target-detection task is likely effective in providing evidence for the familiarity of orthographic items.

5.4.4 Reading Development in Late L2 Learners

Our observation of the L2 proficiency effect for the N170 pseudoletter effect at PO7 suggests a possible developmental trajectory of learning English as a late second language for Mandarin speakers. After studying English as a foreign language for approximately 10 years, the distinction between letters and pseudoletters is reliably manifested only at the N170 range in the right hemisphere (e.g., PO8) and/or at a later ERP (e.g., P2). After an additional four or five years of second-language learning in English speaking environments, the neural distinction

between letters and pseudoletters in the left hemisphere in the N170 range emerges. Below we provide two possible interpretations of these results.

First, the L2low group is, in fact, distinguishing letters from pseudoletters unintentionally but visual templates have yet to be solidified in early visual areas for letters and thus processing around 170 ms remains similar to that for unfamiliar pseudoletters. As a result, the discrimination between letters and pseudoletters is delayed and is manifested in a later ERP, such as the P2. Even though they are equipped with efficient orthographic processing for their first language, their late second language processing appears to require additional processing time. A similar interpretation has been made in the literature on audio-visual association of single letters. For example, compared to normally developing readers, those with reading difficulties showed an audio-visual association effect at ERPs that were manifested much later (Froyen, Willems, & Blomert, 2011). It follows then that as late second language learners gain proficiency in English, their single-letter processing might become more efficient by relying more on earlier neural processing (e.g., from the P2 to the N170).

Second, differentiation of letters from pseudoletters might take place at multiple levels within the visual processing networks over the course of orthographic processing. The results of priming studies indicate that processing in the N170 range is at a visual-feature level, while processing in the P2 range is at a more abstract level (Mitra & Coch, 2009; Petit, Midgley, Holcomb, & Grainger, 2006). We observed that the magnitude of the P2 pseudocharacter effect was the same between L2 groups, and that of the P2 pseudoletter effect was the same across three participant groups with different English proficiency. Thus, our results support the idea that the L2low group might be unintentionally differentiating letters from pseudoletters at an abstract conceptual level but that the L2high group has an even more refined differentiating process level, which gets closer to that of the L1 group.

Future investigations on a potential functional dissociation between the N170 and P2 would be valuable for this line of research. For example, the N170 appears to be sensitive to the task employed (e.g., target-detection task vs. one-back task). A common observation using a target-detection task is that pseudoletters evoke larger negative ERPs within the N170 time range than do letters (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman & Takai, 2013; Park, Chiang, Brannon, & Woldorff, 2014; Pernet, Basan, Doyon, Cardebat, Demonet, & Celsis, 2003; Xue, Jiang, Chen, & Dong, 2008); whereas using a one-back task results in the opposite relationship between ERPs evoked by letters and pseudoletters (Stevens, McIlraith, Rusk, Niermeyer, & Waller, 2013; Wong, Gauthier, Woroch, Debuse, & Curran, 2005). Interestingly though, the P2 is always manifested as larger for pseudoletters than for letters, regardless of the task (Appelbaum et al., 2009; Bann & Herdman, 2016; Herdman, 2011; Herdman & Takai, 2013; Stevens et al., 2013; Wong et al., 2005). Attention during such tasks might account for the discrepancies among studies, but we found that attention towards or away from orthography did not modulate the pseudoletter effect within the N170 or P2 intervals (see Chapter 3).

Either of the above interpretations is plausible at the present moment, and experimental evidence is required to differentiate between them. One factor that is worth investigating is a potential cause of this possible emergence of the N170 pseudoletter effect in the left hemisphere as one develops L2 proficiency. Our L2high group, who showed this pseudoletter effect, was more proficient not only in reading skills but also in listening skills due to their longer exposure to natural English. Thus, perhaps the N170 pseudoletter effect in the left hemisphere is not only related to a higher level proficiency in reading in L2 but might also be related to phonological

development in L2. Future evidence from studies that recruit participants in their home country (i.e., before they expose themselves to natural English) will be particularly insightful in this regard. Also, investigations on the development of L2 phonological processing for these participants, and its relation to visual processing would be informative.

Overall, our findings indicate that single-letter processing for late L2 learners is likely more efficient as L2 learners have more experience with the L2 language. It follows that if a person's letter perception is inefficient, the word-recognition is most likely inefficient because letters constitute a basic unit of word-recognition (Coltheart, Rastle, Perry, Langdon & Ziegler, 2001; Davis, 2010; Forster, 2006; McClelland & Rumelhart, 1981; Perry, Ziegler, & Zorzi, 2007, 2010; Seidenberg & McClelland, 1989). Moreover, when word recognition is inefficient, more attention might be required for successful text comprehension by less advanced L2 readers (Grabe, 2009; Nassaji, 2014). This would lead to overall reduction in attentional capacity during higher-level reading and thus further reduce reading proficiency and comprehension. Future research addressing each stage of reading vis-à-vis L2 language proficiency could help map out changes in neural connectivity associated with each stage of the reading process.

Lastly, the research design of our study could not answer whether the observed L2 effect is universal (i.e., generalizable to other languages and L2 learners) or specific to the relationship between English and Chinese languages (e.g., from logographic to alphabetic orthography). Thus, further research is necessary that compares different language groups. The L2 acquisition literature has shown a language transfer phenomenon for specific types of language processing. For example, for L2 word-recognition, L2 learners employ a decoding strategy that has been useful for their L1 reading (Koda, 1989, 2007; Wang, Koda, & Perfetti, 2003). Also, when monolingual adults learn to read an artificial language, the types of instructional strategy during their training generate hemispheric differences in processing. When the training emphasizes grapheme-to-phoneme correspondences, as in English, the training effect is manifested in the N170 in the left hemisphere, whereas the whole-word reading training, as in Chinese, shows a change in the N170 in the right hemisphere (Yoncheva, Wise, & McCandliss, 2015). In line with this, our L2 participants appeared to continue to apply their L1 reading strategy, which manifests in the right hemisphere, while their L2 proficiency correlated with differences in the left hemisphere. Future investigations could explore whether this transfer is helping or burdening L2 reading development.

5.5 Limitations

There are several limitations of the current study. First, the English alphabet consists of 26 letters, from which we used only six. Future studies that involve more letters and/or examine the effect of the frequency of the letters in the English corpus would extend the external validity of the results of the present study. A similar argument can be made for the investigation of Chinese orthography. However, other studies show the same pseudoletter effects when using stimulus sets of more letters, different font types, and font cases. Second, our L2 learners spoke Mandarin as their L1 and read English as their late L2. Whether the results can be extended to other L1-L2 script relationships (e.g., French vs. Japanese or Italian vs. Hebrew) needs further investigation. Third, including a very advanced L2 group would have allowed us to see how close an L2 learner's ERPs can advance toward the L1's ERPs. Lastly, interpretations on "proficiency" in this study need some caution. For example, we defined proficiency in English as the mean of age-equivalence test scores for receptive language (i.e., listening and reading) only, but for some other research purposes, the inclusion of some measures of expressive language (e.g., speaking and writing) might add greater delineation among the L2 groups. As

another example, some of our L2 participants had a ceiling effect on their age-equivalence scores on our selected measure. Thus, we are unable to generalize our findings to L2 learners at the upper end of L2 reading proficiencies. Concerns for such ceiling effects have been raised in the literature (e.g., Newman, Tremblay, Nichols, Neville, & Ullman, 2012), and we find that these concerns are crucial when we consider the end-goal of late second language acquisition, which is to become as highly proficient as possible in a second language.

5.6 Conclusion

Because the N170 difference amplitudes between English letters and pseudoletters were different among groups (amplitude differences of L1 > L2high > L2low) and this effect was correlated with their reading proficiency, we conclude that L2 learner's neural networks become better organized to efficiently process the L2 orthography in order to improve reading proficiency. Longitudinal studies of late-L2 learners would be a next good step to further understanding how L2 learners' neural networks are modified to improve their L2 reading proficiency. Our results also provide support for the notion that L2 learners can modify earlystage visual networks responsible for processing visual objects, such as letters, and this might manifest as improved proficiency in reading a second language. In other words, L2 learners appear to be utilizing and modifying their first-language visual pathways as they learn to read a second language.
Chapter 6: General Thesis Discussion

Studies from my thesis provide evidence in regards to a few aspects of orthographic processing in L1 and L2 readers. In several of the chapters I provided a detailed discussion of each study's findings within the context of the relevant literature and for brevity these will not be recapitulated here. This chapter provides a general discussion of the main findings from all of my studies as they pertain to two main issues that were introduced in Chapter 1: automaticity and fossilization. In addition, I provide a brief discussion on hemispheric laterality.

6.1 Automaticity

Based on my interpretation of the literature on automatic processing, I defined automaticity as being faster, cheaper on attentional resources, more precise, more obligatory, and more ballistic for processing familiar versus unfamiliar stimuli. The following paragraphs provide a summary discussion of my thesis research as they relate to my interpretation of the meaning of automaticity.

Behavioural results from my thesis studies indicated that familiar (letters/words) stimuli were processed faster than unfamiliar (pseudoletter/pseudoletter strings). This was observed by significantly faster behavioural reaction times (56 ms) for identifying words compared to pseudoletter strings (section 2.3). Although not significant, we did find faster reaction times (10 ms) to single letter than single pseudoletter stimuli, which was consistent with previous significantly different reactions times of about 15 ms (Herdman, 2011; LaBerge & Samuels, 1974). Because behavioural reaction times measure the final output of all brain processing levels, these findings provide only a distal view with respect to speeded processing within the brain. Many perceptual and/or cognitive processes might be generating the findings of faster reaction

times; therefore, neurophysiological recordings can be helpful to hone in on the timing of when processing difference between familiar and unfamiliar stimuli occur.

Evoked and time-frequency response analyses of EEG and MEG provided evidence that letter stimuli are likely processed faster than pseudoletters. A major assumption here though is that I am interpreting the differences in evoked and time-frequency response amplitudes during specific time intervals to be an indicator of faster perceptual processing. An alternative interpretation is that the response differences reflect the amount of processing required and not faster processing. It is difficult to determine from my studies which interpretation is correct, but based on the visual processing models for reading, I interpret my findings to support the notion that familiar visual objects are processed quickly by an efficient neural network to provide rapid letter/word recognition. Even if the "greater processing" interpretation would be true, then based on the IAM (a modified Pandemonium) model the greater activity would likely activate higher centers to a greater extent and likely reach their threshold sooner thereby eventually speeding up object recognition. Thus, both "faster" and "greater" response interpretations would lead to the same outcome, at least based on our current models of visual processing involved in reading. For ease and clarity of discussion, I will interpret my results with respect to the idea that the early ERP differences reflect "faster" processing.

Visual processing has been well established to occur as early as 40 ms within the primary visual cortices, and the P1 component of visual evoked potentials that occurs between 50-100 ms typically reflects object feature processing (Hillyard & Anllo-Vento, 1998). I found no evidence from any of my studies to support that differences in the P1 amplitudes and latencies exist between letter (single or word) and pseudoletter (single or words) stimuli. However, I did find significant TFR differences within 0-200ms time interval for alpha-band power suppression and

desynchronized connectivity (see Figures 4.3 and 4.4). Letters produced more suppression and greater desynchronized connectivities than did pseudoletters as early as 20 ms. A caveat to this is that TFR analyses cause temporal smearing due to the wavelet transform so the timing isn't as precise as evoked responses analyses. The early 20 ms difference might be a smearing from a slightly later difference at around 100 ms. Regardless, these early changes in alpha-band activity fits with the idea that alpha-band reflects a disengagement of readiness network in order to release neural clusters to perform perceptual/cognitive computations. Alpha-band activity (ERS and ERD) has been implicated in visual object processing and visuospatial attention (Jesen & Mazaheri, 2010; Green & McDonald, 2010; Eckhorn et al., 1988; Gray & Singer, 1989; Gray, Konig, Engel, & Singer, 1989). The current understanding is that selectively directing attention to a visual object will cause more alpha-band power suppression and reduced synchronization (i.e., greater desynchronization) in occipital cortices contralateral to the attended location in order to process the visual object. Contrarily, the contralateral visual cortices will have increased alpha-band power and increased synchronization with other regions in order to suppress processing of distractor object located elsewhere (Jensen & Mazareti, 2010; Green & McDonald, 2010). Thus, if we assume that alpha-band suppression and desynchronization occur when visual objects are actively being processed then the results in chapter 4 that showed greater alpha power suppression and greater desynchronization within 0-200 ms for letters than pseudoletter likely reflect greater early shifts of attention or computational resources for processing letters than pseudoletters. Interestingly, this alpha activity difference was predominantly found in the left lateral occipital cortices whereas the right visual cortices showed alpha- and beta-band power enhancement between 0-100 ms for letters than pseudoletters. This difference in alpha-band laterality (negative power in left and positive power in right) might reflect a network shift in

activation so that the left visual cortices are predominantly used for processing the familiar letter stimuli while supressing activity in the right visual cortices that might be more used to process unfamiliar stimuli, as suggested by Park, van den Berg, Chiang, Woldorff, and Brannon (2018). Thus, these findings indicate that experience with letters causes shifts in brain networks that use less attentional resources by lateralizing processing to selective regions.

All of my studies of evoked responses showed that the N170 peaked earlier and with less amplitude to letters than pseudoletters. I interpreted this to be that letters were processed faster and used a lesser amount of neural resources than pseudoletters. Because viewing experience and letter-to-sound correspondence are the main categorical differences between letters and pseudoletters, I interpret this interval surrounding the N170 to mark the beginning of evoked differences between orthographic and non-orthographic processing. Results from Chapter 5 added to this evidence in that the N170 effect was greater in L2high proficiency group as compared with L2low proficiency group. Thus, experience with L2 script appears to modulate the N170 so that it peaks earlier and with a lesser amount of evoked activity with increased proficiency in L2 language. By evaluating the L2low group, I was able to extend the previous literature on the N170 in L2 learners by Wong, Gauthier, Woroch, Debuse, and Curran (2005) and provide evidence that the brain shifts from a novice L2 reader brain into more of an expertlike reader's brain and this can happen as early as 170 ms in the visual processing stream. This shift to early processing provides further evidence that orthographic objects likely become more automatically processed as one learns to read a new script.

Results from Chapter 3 provided evidence that the N170 letter effect is most likely obligatory because we manipulated attention during three tasks and did not find any significant differences in the N170 effect. Because the N170 effect was still robust and not different when

participants directed their attention towards or away from the orthographic characteristics of the stimuli, I interpret this to mean that the N170 differences between letters and pseudoletter are obligatory. A caveat to this obligatory orthographic/non-orthographic processing interpretation is that the N170 letter effect might be due to differences in attentional capture and that the N170 effect is really an N2 novelty-detection response to pseudoletters. However, this too would be an obligatory event because attention did not modify the evoked difference (see Figure 3.7). Thus, if the N170 pseudoletter effect is truly a novelty-detection N2-like effect, then it is a fairly automatic/reflexive shift of attention that is not under volitional control. Another retort to this being a possible N2 effect is that P3 responses typically follow N2 responses to novel stimuli (in my case pseudoletter). I did not observe large P3 responses to pseudoletters in any of my results; therefore, I suspect that this effect is unlikely due to an N2-novelty detection like event. In addition, pseudoletters are repeated regularly throughout the recording session, which means that they are not really infrequent "novel" events with respect ongoing stimulus presentation that are usually required to evoked large N2 responses. An interesting future investigation could look at altering the number of repetitions of pseudoletters within a stream of letters to see if this letter effect (possible N2 novelty effect) gets reduced as more repeats of pseudoletters occur.

TFR results within the 100-200 ms interval showed larger theta power and greater theta connectivity in posterior (visual) network for pseudoletters than letters. The TFR theta power effect was mostly a result of evoked power differences between letters and pseudoletters. Once the evoked power was removed (i.e., induced power), then the significant theta power effect disappeared. Connectivity results were also based on statistically testing PLV connections against surrogate (i.e., evoked) PLV connections, thus exposing induced connectivity changes to the stimuli. Chapter 4's results showed greater theta connectivity among visual processing

regions for letters as compared to pseudoletters, which indicates greater processing for pseudoletters than letters. These finding fit well with the IAM model (and our modified model) in that unfamiliar visual stimuli will require multiple iterations through the letter-template hypothesis space in an attempt to identify the visual object. Once plausible competing hypotheses of letter templates can no longer be distinguished and no unique solution exists then the object is recognized as "not a familiar object".

In addition to theta-band differences, alpha-band power continued to be suppressed between 100-200 ms for letters with desynchronized connections within posterior brain regions. In contrast pseudoletters had more synchronized connections predominantly between frontal and posterior regions. This difference in spatial distribution and connectivity type (synchronized and desynchronized) suggests that letters are being processed within a local posterior network; whereas pseudoletters might be recruiting frontal executive computational regions in an attempt to resolve the conflicting hypotheses of letter template activations. It might also be possible that this frontal recruitment is a feedforward projection of the information so that subsequent information from lower-processing regions can be checked and object recognition is determined at these later frontally-mediated stages of processing. Future research looking at ways to disentangle early visual processing and later executive processing of pseudoletters may provide a better understanding.

Results from the L2 studies also provide evidence regarding processing automaticity in that there was a larger pseudoletter effect within the N170 time intervals for high proficiency L2 readers than low proficiency L2 readers. I interpret this result to indicate that as a L2 reader becomes more experienced and familiar with her/his L2 language and script, the more automatic the brain processes become in recognizing the L2 letters. This interpretation is based on the

concept that the brain attempts to shift computationally- and resource-expensive processing to become more automatic. This fits well with Dehaene's (2005) neural recycling hypothesis for reading, whereby learning to read recycles efficient pre-existing processing units within the visual networks to accomplish reading tasks that requires fast and accurate (i.e., automatic) recognition of written script. The more practiced and familiar a person gets with an L2 script, the greater the shift from a computationally expensive cognitive network to a more automatized perceptual network.

Overall, these findings indicate that becoming more familiar with letters may be shifting brain networks involved in visual object recognition to be faster (reaction times and N170 effects), under minimal volitional attentional control and likely obligatory (no change in N170 effect with attention). This would make sense with respect to the automaticity that would be necessary to provide the human brain with the ability to identify letters/words to meet the rapid reading speeds of 2-3 words/second that humans can achieve.

6.2 Fossilization Hypothesis

The fact that the more proficient a reader is in an L2 language the greater the N170 difference between letters and pseudoletters (larger pseudoletter effect), signifies that even early visual processes can be modified by experience and thus fossilization (i.e., minimal ability to learn new languages) might not be as strong in adults as previously believed (Selinker, 1972). A caveat to this is that my L2 study was a cross sectional study of L2 learners and that the L2high group might have already had a network that could respond with a pseudoletter effect whereas as the L2low did not. Thus, the findings could be due to brain network formations at earlier ages, well before either group began learning to read English, and it is these network configurations

that are truly responsible for separating the groups into L2 high and L2 low proficiencies. Because this could be a possibility, I cannot fully conclude that my results provide evidence against fossilization. However, this leaves an alternative interpretation which would be that the results provide evidence that there are particular network configurations that are conducive (and not conducive) to learning to read in another language. This is an intriguing possibility and further research would be required to find out if these individuals are predisposed to learning to speak and read new languages even before late-language learning begins. Another theoretically important question for future investigation is whether or not single-letter processing for the L2high group can further improve, or has reached its maximum degree of efficiency? Longitudinal studies of late-L2 learners would be a next good step to further understanding how L2 learners' neural networks are modified to improve their L2 reading proficiency and what is the upper limit to their network modification.

6.3 Hemispheric Laterality

There are still conflicting results, even within my studies, regarding the laterality of orthographic processing. MEG results (Chapter 2) showed that the pseudoletter effect was more right-hemispheric dominant, which is consistent with some previous findings (Appelbaum, Liotti, Perez, Fox, & Woldorff, 2009; Herdman, 2011). However, EEG results from dipole source modeling of the N170 effect showed the effect to be bilateral. In addition, in chapter 5, I observed that the pseudoletter effect for English scripts in L1 and L2 readers was predominantly bilateral at N170 and P2, with a slight insignificant right-shifted dominance. Moreover, the pseudocharacter effect for Mandarin script was absent for the non-Mandarin readers (i.e., English L1 participants) but bilaterally distributed for readers of Mandarin (i.e., English L2

participants). If the left-hemisphere is sensitive to language proficiency and the right-hemisphere acts as a reservoir for the familiar orthographic processing, what is the nature of this reservoir processing? In my experiments, the pseudoletters and pseudocharacters share almost exactly the same visual features as the orthographic stimuli (letters and Mandarin characters). Thus, these results cannot be explained by visual feature extraction within the visual system but by a higher level of processing that reflects the differences in experience with such visual objects. Thus, the left- and right-hemispheric laterality discrepancy with single-letter versus word-level processing seen in my results and the literature might indicate that the experienced sub-lexical (orthographic) features of single-letters are processed within a bilaterally distributed network that later processing shifts to a left-lateralized network. Unfortunately, evoked response results remain inconclusive. One caution with interpreting the MEG finding alongside the EEG studies is that MEG might be missing some of the source activity because it mostly measures signal from sources that are tangentially-oriented to the scalp (i.e., within sulci), while EEG measures activity from both tangentially- and radically-oriented sources. A retort to this caution is that the study by Appelbaum et al. (2009) showed a right-lateralized N170 (i.e., EEG) pseudoletter effect. Thus, evoked responses are likely showing mixed results because they only measure the stimulus-locked changes in neural activity.

Given that the language processing network is believed to be left-hemispheric dominant (Cohen & Dehaene, 2004; Dehaene, Cohen, Sigman, & Vinckier, 2005; Price et al., 2003), a plausible explanation for my observation is that the right-hemispheric network is used for a reservoir of letter feature processing. Three research lines provide further supporting evidence for this reservoir explanation. First, developmental studies showed that letter processing shifts from right-lateralized processing to left-lateralized processing over the course of literacy experiences (Brem et al., 2013; Groen, Whitehouse, Badcock, & Bishop, 2012; van Setten, Maurits, & Maassen, 2018; Park, van den Berg, Chiang, Woldorff, and Brannon, 2018) and that such shift appears to be related to the correspondences of the orthographic processing and the phonological processing (Diehl et al., 2014; Emmorey, Midgley, Kohen, Sehyr, & Holcomb, 2017). Second, lesion studies showed that the right-hemisphere compensates for the lesion in the left-hemisphere (Cohen et al., 2004; Cohen, Dehaene, McCormick, Durrant, & Zanker, 2016; Ino, et al., 2008; Jung et al., 2007; Tsapkini, Vindiola, & Rapp, 2011). Third, adult training studies wherein adults learn an artificial script showed that a pseudoletter effect was rightlateralized (Maurer, Blau, Yoncheva, & McCandliss, 2010; Yoncheva, Wise, & McCandliss, 2015).

Taken together, neural orthographic processing appears to change its laterality over the course of learning an orthography as in second-language learning. The more learning of a given orthography in its relation to its corresponding phonology, the more its neural processing becomes increasingly specialized in the left-hemisphere and shows an effect for the proficiency in that language. This change does not mean that the right hemisphere stops processing all orthographies; rather the right-hemisphere is there as a reservoir to allow for the capacity to bind visual features of new orthographies that will then be shifted to the left hemisphere as a second-or third language is acquired. However, this is conjecture at this point and formal testing would be required.

6.4 Conclusion

In conclusion, results from my thesis studies showed that orthographic stimuli (particularly letters) are automatically processed at early-stages of visual perception within a posteriorly distributed brain network. Moreover, this early level of processing doesn't become fully fossilized and resistant to learning because as late-language learners become more proficient in reading English, their brain responses shift to be more like their native English counterparts. With respect to laterality of processing orthographic information, my studies provided conflicting results and thus the question of hemispheric laterality remains inconclusive.

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