

**Neural correlates of bilingual reading:
Effects of orthographic depth and age of
acquisition of a second language in brain
function and structure.**

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BASQUE CENTER
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AND LANGUAGE



Universidad del País Vasco Euskal Herriko Unibertsitatea

**Neural correlates of bilingual reading:
Effects of orthographic depth and age of
acquisition of a second language in brain function
and structure.**

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Esta tesis narra la historia de cómo los caminos cerebrales se forman y transforman según nuestras experiencias vitales (ej., aprender una lengua en edades tempranas o tardías). Ya lo decía el poeta Antonio Machado (1912):

*“Caminante, son tus huellas
el camino, y nada más;
caminante, no hay camino,
se hace camino al andar...”*

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Resumen en Castellano

El lenguaje forma parte de la esencia del ser humano. Es nuestra herramienta más poderosa para comunicarnos, para compartir nuestro conocimiento, sentimientos y emociones. La comunicación permite tanto nuestro desarrollo personal como profesional y social, imprescindible en nuestra interacción con el ambiente. El poder del lenguaje es tan grande que incluso las lenguas están relacionadas con la adquisición de la propia identidad, y está, a su vez, está ligada a la etnicidad. Una habilidad íntimamente vinculada con el lenguaje es la lectura. La lectura permite que el conocimiento pueda ser compartido sin que ambos interlocutores estén físicamente en el mismo lugar. Además, las nuevas tecnologías permiten que las noticias, los artículos y los libros escritos estén a nuestra disposición como nunca antes lo habían estado.

El poder de la lectura se refleja en su capacidad para transportar al lector a otro lugar y conocer al momento las noticias y sucesos del mismo (p.ej., leyendo el periódico en internet) o incluso trasladarnos a otro mundo completamente ficticio (p.ej., leyendo el libro titulado El maravilloso mago de Oz). Además, la lectura también es relevante en contextos de educación formal ya que, una parte importante de la metodología empleada en colegios y universidades, se difunde a través de libros de texto y artículos. De hecho, en los últimos años ha aumentado el número de universidades y centros superiores que permiten el seguimiento de su formación *online*, únicamente a través de material escrito sin apenas interacción cara a cara con el profesorado. Todo esto hace que la lectura sea una de las formas de comunicación más populares del siglo XXI.

Es importante tener en cuenta que en muchos lugares se habla y se lee en más de una lengua. Países como España, Suiza y Bélgica son ejemplos de ello. Además, vivimos en un mundo de migrantes que deben adaptarse a un ambiente nuevo y en muchas ocasiones, dicha habituación requiere el aprendizaje de una nueva lengua. Esto hace que el bilingüismo se encuentre en todas partes del mundo, en cualquier nivel social y en todos los grupos de edad (Grosjean, 2010). La importancia del bilingüismo se ve reflejada en la educación, orientada tanto a niños como a adultos, la cual se encamina cada vez más hacia la formación de personas que manejen más de una lengua.

Sin embargo, para diseñar o evaluar un programa de educación bilingüe es necesario analizar las diferentes variables que intervienen en el bilingüismo (p.ej., las propiedades de la ortografía de una lengua). Una manera novedosa que puede aportar información desde otro punto de vista, es examinar dichas variables a través de la neurociencia cognitiva. Este campo del conocimiento se ocupa del estudio científico de los mecanismos cerebrales subyacentes a la cognición. Así, el objetivo de la presente tesis es: examinar, a través de dos experimentos, cómo dos variables principales del bilingüismo, como son 1) la ortografía de la lengua y 2) la edad de adquisición de la segunda lengua, influyen en la modulación de las redes neurales de la lectura en bilingües. Entender, por un lado, las bases cognitivas y cerebrales de la lectura en bilingües y, por otro, cómo estas bases se pueden ver influenciadas por las diferentes variables del bilingüismo, tiene importantes implicaciones para comprender cómo lee el cerebro bilingüe. Esta tesis doctoral tiene el potencial de proporcionar un marco científico que dote de soluciones a las técnicas de enseñanza que buscan optimizar la lectura en bilingües. A continuación se detallan los dos experimentos llevados a cabo en el presente trabajo.

Por un lado, en el **Experimento 1** se examinaron los correlatos neurales de la lectura en bilingües en función de la ortografía de la lengua. La lectura requiere relacionar las letras (grafemas) con sus correspondientes sonidos (fonemas) y acceder a su significado (semántica). Sin embargo, las lenguas están compuestas por diferentes sistemas de escritura y, no siempre, la relación entre grafema y fonema es consistente. Las lenguas transparentes, como el español o el euskera, tienen una fuerte correspondencia grafema-fonema, es decir, la mayoría de letras equivalen a un sonido y, en general, cada letra tiene un solo sonido. En cambio, las lenguas opacas, como el inglés, presentan una menor consistencia en la relación grafema-fonema. En otras palabras, una misma letra puede ser asociada con diferentes sonidos (p.ej., en inglés, el sonido de la letra “i” en la palabra *pint* (/paɪnt/) o *mint* (/mɪnt/)). Aparentemente, los mecanismos lectores y las regiones cerebrales involucradas en la lectura, varían en función de si la lengua es transparente u opaca. Las lenguas transparentes se sirven en mayor medida de mecanismos fonológicos, relacionados con regiones cerebrales dorsales (Paulesu et al., 2000). En cambio, para las lenguas opacas los mecanismos fonológicos no son suficientes y dependen de mecanismos léxicos, llevados a cabo principalmente por regiones cerebrales ventrales (Meschyan & Hernandez, 2006). La consiguiente cuestión es, por tanto, cómo varían las estrategias y las redes neurales de la lectura en bilingües de dos lenguas con ortografías diferentes. Este podría ser el caso de, por ejemplo, bilingües español (transparente) e inglés (opaca). Para contestar a dicha pregunta se llevó a cabo el Experimento 1.

En el **Experimento 1** se reunió a dos grupos de bilingües tardíos. En ambos casos su lengua nativa (L1) era el español, pero diferían en su segunda lengua (L2). Un grupo tenía como L2 el euskera y el otro grupo el inglés. Todos los sujetos adquirieron la L2 después de los 6 años de edad y eran muy competentes tanto en la L1 como en la L2. Además, ambos grupos fueron

igualados en edad, periodo o edad de adquisición de la segunda lengua, nivel de competencia y exposición a la L1 y a la L2. Por tanto, la única diferencia entre ambos grupos era la ortografía de la L2; transparente en el caso del euskera y opaca en el del inglés. Los participantes de ambos grupos realizaron dos tareas de lectura dentro de la resonancia magnética: una perceptual y una semántica. En ambas tareas los participantes veían palabras, pseudopalabras y cadenas de consonantes. En la tarea perceptual debían apretar un botón cuando veían una letra en un color (p.ej., cam*i*on), en cambio, en la tarea semántica tenían que apretar un botón cuando veían una palabra referida a un animal (p.ej., perro). Ambas tareas se realizaron en las dos lenguas (L1 y L2).

Los resultados mostraron la activación de la misma red neural de lectura (ventral y dorsal) en ambos grupos para las dos lenguas y tareas. Sin embargo, dicha red neural reveló modulaciones en activación y en conectividad funcional según las demandas de la lengua (L1 vs. L2), de la ortografía de la L2 (transparente vs. opaca) y de la tarea (semántica vs. perceptual). Con respecto a las demandas de la lengua, ambos grupos mostraron mayor activación en la red neural de lectura durante la L2 en comparación con la L1, lo cual puede estar relacionado con un mayor esfuerzo durante la lectura en la lengua menos dominante (L2). A su vez, los análisis de activación y conectividad funcional mostraron diferencias entre grupos debido a la ortografía de la lengua de la L2. Específicamente, el grupo español-euskera presentó una mayor dependencia y conectividad funcional en regiones cerebrales dorsales, involucradas principalmente en la codificación fonológica. En cambio, el grupo español-inglés exhibió mayor activación y una fuerte conectividad funcional entre las regiones ventrales, implicadas en procesar demandas léxico-semánticas. En relación con la tarea, ambos grupos mostraron mayor activación en la red ventral que en la dorsal para la tarea semántica. Dichos resultados fueron replicados en los

análisis de conectividad funcional, los cuales revelaron una conectividad más fuerte entre las regiones ventrales ante demandas semánticas. En cambio, las regiones de la red dorsal mostraron una mayor activación para demandas fonológicas.

En resumen, los resultados del Experimento 1 demuestran la importancia de varios factores relevantes: lengua (L1 vs. L2), ortografía de la lengua (transparente vs. opaco) y tarea (semántica vs. perceptual), que modulan la actividad de las regiones críticas involucradas en la lectura en bilingües, así como la dinámica entre dichas regiones. El presente estudio es de especial importancia ya que la ortografía de la lengua es una variable de creciente interés. Sin embargo hasta el momento, hay escasa evidencia empírica sobre su papel en la modulación neuronal de la lectura en bilingües. Nuestros datos arrojan nueva información sobre la mayor implicación de regiones dorsales-fonológicas y ventrales-semánticas en la lectura de lenguas transparentes y opacas respectivamente. Estos hallazgos tienen implicaciones para la enseñanza de la lectura en una segunda lengua, en sintonía con estudios previos que han destacado la importancia de tener en cuenta las particularidades de los idiomas, como la ortografía de la lengua, en las prácticas educativas (Ziegler et al., 2010).

Por otro lado, el objetivo del **Experimento 2** fue investigar los correlatos neurales de la lectura dependiendo de la edad de adquisición de la L2. Algunas perspectivas sugieren que la adquisición de una segunda lengua en edades tempranas es más beneficiosa a la hora de alcanzar un mayor nivel de competencia en la L2 (Lenneberg, 1967). Esto se debe, al parecer, a que durante la niñez, el cerebro presenta una mayor plasticidad cerebral. La plasticidad cerebral se refiere a la habilidad del cerebro para adaptarse a nuevas experiencias, como el aprendizaje de nuevas lenguas. Aparentemente, después de este periodo, la habilidad para aprender nuevas lenguas decrece (Flege et al., 2006). Perspectivas como ésta desmotivan el aprendizaje de nuevas

lenguas en la edad adulta, por la preocupación de no poder conseguir una competencia media/alta en la L2. Sin embargo, la evidencia empírica ha demostrado que dicha plasticidad cerebral continua durante la edad adulta, y que se puede alcanzar un nivel alto, similar al de un nativo, en la L2 (Martensson et al., 2012). Entonces, ¿en qué medida la edad de adquisición de la L2 modula la función y la estructura cerebral asociadas con la lectura? Responder a esta pregunta es el objetivo del Experimento 2: investigar, mediante el empleo de medidas funcionales y estructurales de resonancia magnética, la influencia de la edad de adquisición de la L2 en las redes cerebrales de la lectura.

Una de las posibles razones de las inconsistencias en los resultados de estudios que han investigado los efectos de la edad de adquisición puede ser la influencia de otros factores, como el nivel de competencia o exposición a la L2. Por esta razón, en el Experimento 2 se prestó especial atención a controlar dichos factores para así, separar de una manera más eficiente y eficaz el rol específico de la edad de adquisición de la L2 a nivel cerebral. Con este fin, incluimos en nuestra muestra dos grupos de bilingües de español-euskera altamente competentes en las dos lenguas. Ambos grupos vivían en el mismo contexto bilingüe y además, fueron igualados en la cantidad de exposición diaria a sus respectivas L1 y L2. Su exposición a otros idiomas era mínima. La diferencia entre estos grupos reside en la edad de adquisición de la L2. Los bilingües tempranos habían adquirido su L2 antes de los 3 años de edad. En cambio, los bilingües tardíos la aprendieron después de los 6 años. Ambos grupos realizaron dos tareas de lectura en cada lengua (L1, L2) dentro de la resonancia magnética: una perceptual y una semántica. Además, se recogieron distintas medidas estructurales para analizar las diferencias anatómicas entre grupos.

Los resultados de dicho estudio revelaron que las regiones *pars triangularis* izquierdo y derecho fueron las únicas que mostraron diferencias en función de la edad de adquisición. La evidencia empírica ha demostrado la participación de ambas regiones en tareas de lectura, recuperación léxica y semántica (Menenti, et al., 2009; Price, 2012). Debido a esto se analizó de forma más exhaustiva el patrón estructural y de conectividad (estructural y funcional), entre dichas regiones. Los análisis demostraron que la región *pars triangularis* izquierda presenta mayor grosor cortical en los bilingües tempranos que en los bilingües tardíos. Por otro lado, los resultados de conectividad demostraron que los bilingües tempranos, comparados con los bilingües tardíos, presentan también mayor conectividad estructural y funcional entre la región *pars triangularis* izquierdo y derecho, y que la mayor conectividad funcional entre estos grupos ocurría únicamente durante la lectura en la L1.

En general, los resultados del Experimento 2 sugieren que la adquisición de una L2 durante o después de la primera infancia puede ser impulsada por diversos procesos que conducen a diferencias en los patrones de activación y conectividad entre regiones clave para la lectura, como el *pars triangularis*. Este resultado es consistente con estudios estructurales previos que sugieren una red de lenguaje inter-hemisférica más extensa en bilingües (Schlegel et al., 2012), y con investigaciones que muestran una mayor conectividad en reposo entre el giro frontal inferior izquierdo y derecho (Berken et al., 2016). Lo novedoso de la presente investigación no es sólo su acercamiento analítico multimodal y la consistencia en el resultado de las diferencias entre bilingües tempranos y tardíos en estas regiones a través de varias medidas, sino también que dichas diferencias son principalmente debidas al procesamiento de la L1. Este resultado se puede explicar por la edad de adquisición. Así, cuando el aprendizaje de dos lenguas se da en las primeras etapas de la vida, como en el caso de los bilingües tempranos, el

procesamiento del lenguaje se produce de una forma más bilateral, en lugar de ser dominante en el hemisferio izquierdo. Esta bilateralidad podría ser un mecanismo cerebral más eficiente para lidiar con dos lenguas al mismo tiempo en etapas tempranas (Feng et al., 2015). En cambio, en los bilingües tardíos, su L1 sigue el desarrollo cerebral típico observado ya en monolingües, presentando mayor lateralización izquierda (Shaywitz et al., 2003). Esto explicaría que la diferencia entre bilingües tempranos y tardíos se encuentre en la L1 ya que, en los bilingües tempranos, el procesamiento es más bilateral y, en los tardíos, está más lateralizado a la izquierda.

En resumen, los hallazgos de la presente tesis doctoral proporcionan evidencia del rol crucial de factores como la ortografía y la edad de adquisición de la lengua, en la modulación de las regiones cerebrales involucradas en la lectura en bilingües. Hasta ahora ningún estudio ha investigado el papel conjunto de estos dos factores de forma sistemática a nivel cerebral, teniendo en cuenta variables claves que influyen en la lectura bilingüe, como la competencia y la exposición de la L2. Además, el presente trabajo demuestra cómo la dinámica cerebral a nivel funcional y estructural se modifica en función de dichos factores manipulados no solo en regiones típicamente investigadas del hemisferio izquierdo, sino también en el hemisferio derecho. Estos resultados revelan el rol de ambos hemisferios en la lectura bilingüe. Además, en el presente trabajo se emplea un método multimodal mediante el uso de técnicas innovadoras de neuroimagen. Esto permite añadir un factor novedoso e importante para lograr avances científicos, permitiendo contrastar los resultados con el uso de diferentes técnicas y análisis, lo cual verifica los resultados obtenidos. La presente tesis doctoral proporciona nuevos conocimientos para la comprensión de la plasticidad neural en el aprendizaje de segundas lenguas, tiene implicaciones para las teorías y debates actuales en el campo de la neurobiología

del lenguaje y lectura, y proporciona nuevos conocimientos sobre cómo el cerebro bilingüe lee, una cuestión de creciente interés teórico y aplicado, especialmente teniendo en cuenta que el bilingüismo es cada vez más común en el mundo actual.

Chapter 1. Introduction

The primary research goal of this doctoral dissertation is to unravel the impact of learning to read in a second language on the organization of the brain reading networks. This chapter is aimed at underlining the importance of second language acquisition in today's world and understanding the critical factors that can influence reading performance in bilinguals.

We live in a world of language. Whatever else people do when they meet together (walk, exercise, cook and so on), they talk. Furthermore, learning a second language is a critical ability, not only for someone like me who was born and raised in different bilingual environments, but for most of the world population. In the 125th anniversary Special Issue of Science (Kennedy & Norman, 2005), age of acquisition in second language learning was included in a list of 100 important science questions to be addressed in the next few decades. Why second language acquisition is such a relevant matter?

It is generally believed that over half of the world's population is bilingual (Grosjean, 2010). For instance, in Spain four different languages are co-official with Spanish. In Europe, the percentage of citizens who know at least one foreign language increased from 47% in 2001 to 56% in 2005 (Eurobarometer, 2012). In the US and Canada, 20% of the population speaks a language other than English at home. Furthermore, besides the countries and regions where two or more languages are already spoken, as globalization advances, more people are becoming bilingual. Indeed, in the globalization era, where more people can use the Internet to connect

with someone else across the globe and where migrations result in multilingual and multicultural societies, the need of speaking more than one language becomes critical.

Thus, bilingualism is a reality in today's world and therefore educational strategies must adapt to this reality. The requirement of this adaptation comes from the fact that the process of globalization brings many advantages but also many challenges. One of these challenges is that, not only adults, but also children, find themselves in educational programs where they must acquire a language they do not speak at home. In 2009, on average 10% of 15-year-old students in the countries within the Convention on the Organization for Economic Co-operation and Development (OECD) (see Figure 1 for OECD countries) had an immigrant background (as second- and first-generation students). Children immersed in bilingual educational programs grow up facing numerous challenges for reading in different languages with different writing and phonological systems; in other words, reading in different language orthographies. The PISA 2009 assessment shows that in most OECD countries, except Australia, Israel and Hungary, children with an immigrant background perform less well in reading than their non-immigrant peers (44 score-point difference) (Figure 1). In fact, these children are twice as likely as being identified as having reading disabilities, which contributes to low educational attainment (Co-operation & Development, 2010)

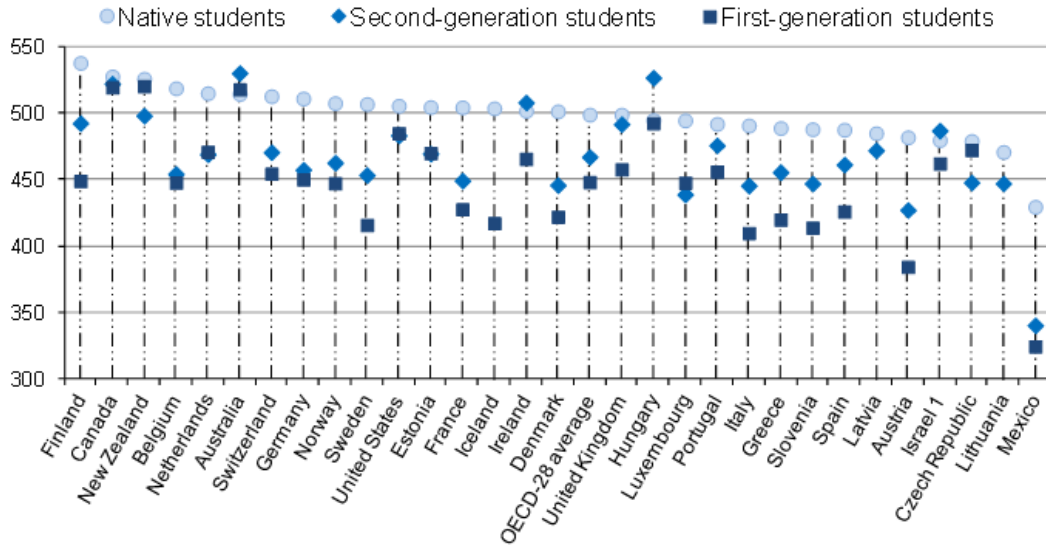


Figure 1. Students’ performance in reading scores as a function of immigrant background, PISA 2009. Source: Co-operation, O. f. E., & Development. (2010). PISA 2009 results: overcoming social background: equity in learning opportunities and outcomes (volume II): OECD, Paris, France.

The critical factors that seem to influence lower performance on the PISA report are language orthography (i.e., orthographic distance between the native and second language) and the age of acquisition (AoA) of the second language (L2). Therefore, the research goal of the present work is to measure the impact of these two factors on bilingual reading networks using the latest neuroimaging tools to examine brain function and structure (i.e., functional activation and connectivity, cortical thickness, diffusion tensor imaging). This multimodal approach is a novel manner to shed further light on the cognitive processes and brain representations involved in bilingual reading through Cognitive Neuroscience. Cognitive Neuroscience is a discipline involving the study of brain function and structure and their associations with different cognitive functions.

Then, what do we already know about the two main factors that are examined in this work and that seem to influence reading in bilinguals (i.e., language orthography and AoA)? Concerning

language orthography, languages can be classified according to their grapheme to phoneme mapping or language orthography. Transparent languages (e.g., Spanish, Basque) have a more consistent grapheme to phoneme mapping compared to opaque languages (e.g., English). Conversely, in opaque languages, the same letter can be associated with more than one sound (e.g., the letter 'i' in pint/mint). Apparently, reading strategies and also the brain regions involved in reading are modulated by language orthography (Paulesu et al., 2000). However, a question that has not been answered yet is to what extent reading strategies in bilinguals, and the brain reading networks supporting them, vary as a function of the native language (L1) versus non-native language (L2) and as a function of the L2 orthographic depth (e.g., Spanish-English bilinguals or Spanish-Basque bilinguals). The Experiment 1 of the present doctoral dissertation specifically addresses this research question.

Regarding *AoA*, some perspectives suggest that after early childhood there is a reduction in brain plasticity or in the ability to adapt to new experiences including learning new language. Then, after this period the ability to learn a new language decreases considerably. In fact, *AoA* has been previously considered as the primary predictor for some aspects of second language performance, such as pronunciation accuracy and proficiency level (Flege et al., 2006). In contrast, other perspective argues that the brain plasticity continues well into adulthood; therefore, reaching native-level in a L2 learned after early childhood is possible (Steinhauer et al., 2009). One possible reason for these inconsistencies between studies might be that *AoA* is typically confounded with other variables, such as language exposure and proficiency. In Experiment 2 of the present work, we will examine the functional and structural correlates of bilingual reading in groups of early and late bilinguals who either acquired their L2 before age 3 (i.e., early bilingual) or after age 6 (i.e., late bilinguals), while controlling for these potential

confounding variables (i.e., exposure and proficiency). This will allow us to better disentangle the specific effects of AoA in the bilingual brain.

The results of this doctoral dissertation can provide new insights on critical factors related to L2 acquisition and reading that we know may determine bilingual brain function and structure, giving additional relevant and useful information to current debates in the fields of Neurobiology of Language and Bilingualism. Furthermore, findings from the present work can also have implications for educational policies regarding L2 reading teaching and acquisition, providing information that can be useful to decide when to introduce a foreign language into the school system and also in line with studies that have stressed the importance of taking into account the specificities of languages in education reading practices (Share, 2008).

Next, Chapter 2 presents an overview of the current main theoretical approaches on reading and reviews previous neuroimaging studies examining the neural correlates of reading. Chapter 3 describes and reviews in detail the results from previous neuroimaging studies examining the neural correlates of bilingual reading and the main bilingual factors that modulate neural reading networks. Chapter 4 describes the main Magnetic Resonance Imaging (MRI) functional and structural measures used in the present work to examine the neural correlates of reading. Following that, two experiments that constitute the original research conducted for this doctoral dissertation are described. Chapter 5 presents Experiment 1 intended to examine the neural bases of reading in bilinguals as a function of language orthography, and Chapter 6 presents Experiment 2 that sought to investigate the role of L2 AoA on the bilingual brain reading networks. Both chapters give a detailed description of the purpose of the experiments, methodology, analyses carried out, results and specific discussions. Finally, in the last chapter

the reader will find a general discussion on the main questions addressed in this doctoral dissertation, conclusions and implications (Chapter 7).

Chapter 2: Reading and neural correlates underlying reading

This chapter is divided in two different sections. In section 2.1, a brief introduction will be given about why language, and more specifically reading, is relevant for humans within an evolutionary framework. Following that, reading processes will be discussed from two different theoretical accounts. In section 2.2, the reader will find a detailed review of the neural regions and networks involved in reading based on previous neuroimaging studies.

2.1 Reading

Language is a powerful representational system and one of the major “ways” of human communication. If there is one thing that distinguishes humans from other animals, it is our ability to use language. Researchers have long debated when humans started talking to each other. Although there is not a clear answer, estimates range wildly from as late as 50.000 years ago. Specifically, when modern humans entered Europe (about 45.000-42.000 years ago), Neanderthals were already there. How humans outpaced Neanderthals is still a mystery, but fossil evidence has left some clues. Some scholars believe that speech was the primary advantage of modern humans over Neanderthals. This was based on studies focused on skull differences in the basicranial line, nasopharynx and upper vocal cavity (Donald, 1991).

Compared to oral communication, writing and reading come more recently in the history of human evolution, approximately about 5.000-4.000 years ago. The first known systems of writing were pictographs and counting methods, which were used in commerce between 4.000

and 3.000 BC, such as Sumerian cuneiform. In contrast, Egyptian hieroglyphics date from 2.000 to 1.500 BC. Importantly, the first phonetic written systems, which began to bridge the gap between speech and external symbols, started around 1.700 BC (Figure 2).



Figure 2. Evolution of writing. A) Sumerian Cuneiform from Shuruppak, Iraq, circa 2500 BC. B) Egyptian Hieroglyphs 1800 BC (British Museum, London). C) Cippus Perusinus, Etruscan writing, 3rd/2nd century BC (Museo archeologico di Perugia, Italy)

In addition to the evolution of written symbols, social expectations and assumptions about reading correspondingly evolved (Finkelstein & McCleery, 2012). In this regard, those individuals who could read held considerable economic and social importance (Moorhead, 2011). This made reading not only a very useful activity, but also an important social ability that probably contributed to its expansion. Currently, reading has become an elementary part of Western societies, where we are continually approached by written messages in almost any media (e.g., television, advertising messages on the street, etc.) and also, by new technologies (e.g., computers, mobile phones). This makes reading and writing one of the most popular ways of communication in the XXI century.

Nonetheless, reading is not a trivial activity; it requires the visual recognition of a word and the awareness that spoken words can be decomposed into its phonologic constituents. This

awareness allows the reader to connect letter strings (i.e., orthography) to the corresponding units of speech (i.e., phonology). In other words, the reader is required to represent the links between the components of printed words and the components of spoken words. Moreover, reading requires accessing the meaning of those words (i.e., semantics). Thus, reading lead to a progressive interaction between visual, orthographic, phonologic and semantic systems.

Theoretical models of reading

Based on empirical evidence, different theoretical models have been proposed to explain reading processes. Two main models of reading have emerged: the parallel distributed processing (PDP) model (Harm & Seidenberg, 1999; Plaut et al., 1996; Seidenberg & McClelland, 1989) and the dual route cascaded (DRC) model (Coltheart et al., 2001; Figure 3). These models differ, among other things, in the number of non-semantic routes available for performing phonological computations based on orthography.

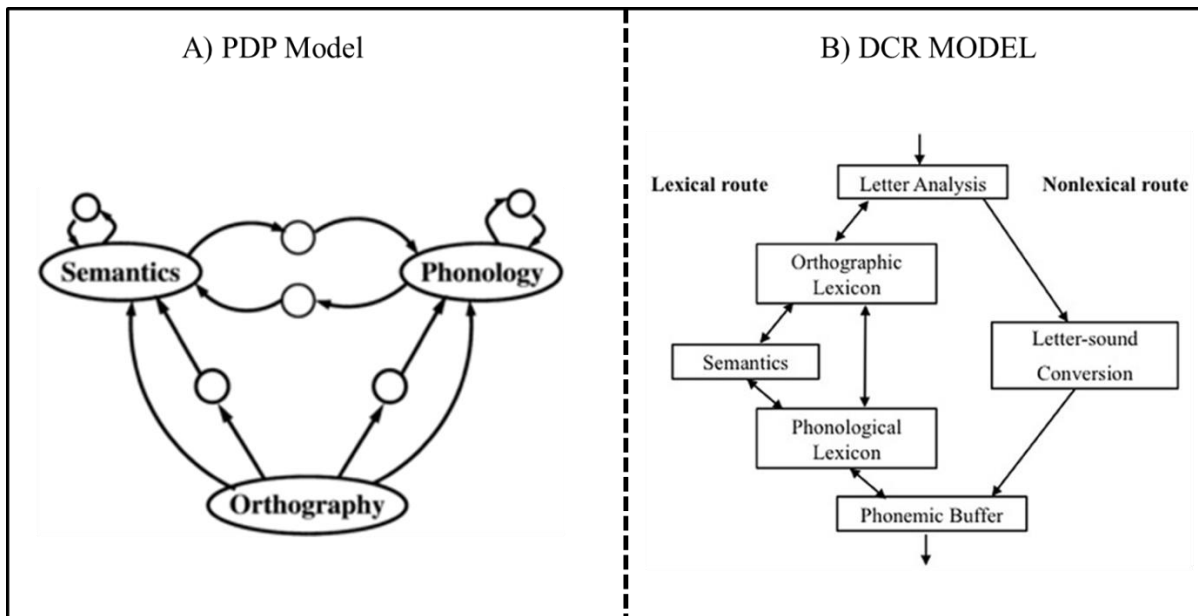


Figure 3. Theoretical models of reading. A) PDP model (Seidenberg & McClelland, 1989) and B) The DCR model of visual word recognition and reading aloud (Coltheart et al., 2001)

In the *PDP model*, distributed orthographic representations map onto distributed phonological representations by a single-route model. This model claims that a single mechanism embedded in a parallel-distributed processing model is sufficient to account for both semantic and lexical processing. Initially, when a printed word is not known, it cannot be decoded into its corresponding sound. Learning to read involves modifying the connections between the letters and the sounds in response to reading exposure. This model proposes that the same set of connections, operating in parallel, can handle both familiar words and novel words, and that exposure to print words is responsible for these changes in the letter-to-sound connections. In contrast, the *DRC model* argues that there are two distinct and independent modes of processing printed words: one that relies on their visual-orthographic properties (lexical) and one that recovers their phonological structure (sublexical). According to this model, skilled readers read words via both lexical and sublexical routes. The lexical route looks up a word in the mental representation of that word or mental lexicon, and if this representation is found, accesses its pronunciation. If the representation is not found, readers are able to perform correct reading of the word using the sublexical route. In the sublexical route, readers reach the pronunciation using rules that relate units of spelling to sounds. Specifically, in the learning process, readers rely on the sublexical route, and when a word is already known, the lexical route is the predominant one (Coltheart et al., 2001).

These theoretical frameworks explain which are the specific systems required to read and how those system process the information. They allow researchers to explore the properties of the reading system and develop empirical research studies (Friederici et al., 2012). However, there is extant debate regarding which is the best model describing the reading process and many are the controversies and criticism for each of these models (Harm & Seidenberg, 2004;

Borowsky & Bersner, 2006; Seidenberg & Plaut, 2006). Indeed, recent evidence support the importance of integrating evidence from various methodological approaches in order to fully understand word reading (Carreiras et al., 2014). Recently, the availability of techniques such as functional magnetic resonance imaging (fMRI) have provided new opportunities to ask precise question regarding where in the brain is reading processed. Given the architectural constraints of the brain, the “where” information tell us relevant information about what types of representation are activated (Pugh et al., 2001). Neither the PDP nor the DCR make predictions at the neural level. In fact, empirical support for these models (Jobard et al., 2003) often include neural regions that perform multiple functions, adding to the difficulty of validating these models (Mechelli et al., 2004). To identify the neural systems underlying reading represents a priority for Cognitive Neuroscience, having profound implications for understanding the brain mechanisms supporting typical reading, as well as for extending our knowledge of reading disorders and atypical reading. In the next section, therefore, I review the neural regions and networks involved in reading.

2.2 Neural correlates underlying reading

Learning to read induces changes on both brain activation and brain structure, requiring a reorganization of the brain (Carreiras et al., 2009; Dehaene et al., 2010). Empirical evidence has evinced that reading is mediated by a dedicated cortical network, located along the perisylvian areas of the left hemisphere (Jobard et al., 2003). The dual-stream hypothesis proposes a brain-based model of reading with a differential involvement of ventral and dorsal routes (Pugh et al., 2001; Schlaggar & McCandliss, 2007). This hypothesis is supported by neuroimaging studies that found different patterns of activation within regions along the ventral and dorsal pathways allowing the speculation of their roles (Saur et al., 2008). According to the dual-stream

hypothesis, the ventral pathway, including left ventral occipitotemporal (vOT) and anterior inferior frontal gyrus (IFG) regions (*pars orbitalis* and *pars triangularis*), supports mapping orthographic-lexical stimuli onto semantic representations (Sandak et al., 2004). On the other hand, the dorsal pathway, encompassing parietal lobe, superior temporal gyrus (STG) and posterior IFG (*pars opercularis*), is thought to subserve phonological processing. Learning a word would involve the ventral system, while recognizing a word that already pertains to our lexicon would be dependent on the dorsal system (Jamal et al., 2012). A specific description of the reading process and previous research on the neural correlates of reading is discussed next.

The gateway from vision to language is proposed to be in the vOT area, where visual word recognition occurs prior to accessing nonvisual information (Twomey et al., 2011). However, important debates exist about its specific functional role. Some theoretical accounts highlight its involvement in bottom-up prelexical computation processes of visual word forms (Cohen et al., 2000), while others underline its implication in integrating visuospatial features abstracted from sensory inputs with higher-level associations *via* bottom-up and top-down connections (Price & Devlin, 2011).

To investigate visual word recognition allows establishing links between the processing of visual features with semantic and phonological processing on ventral and dorsal regions, respectively. Evidence regarding the semantic and phonological reliance of ventral and dorsal pathway regions comes from studies revealing a specific modulation of these two pathways based on the type of stimuli and reading demands. Regarding the type of stimuli, ventral regions typically show greater engagement for high-frequency words than for pseudowords (Jobard et al., 2003; Vigneau et al., 2005), which suggests that ventral regions are recruited for well-learned words and are involved in a more automatic word identification. In contrast, dorsal regions

typically show stronger activation during reading pseudowords and low-frequency words (Borowsky & Besner, 2006; Mechelli et al., 2003; Tagamets et al., 2000). The increased activation for pseudowords in regions along the dorsal stream reflects the demands on accessing phonology from sublexical orthographic codes (Carreiras et al., 2014a; Price, 2012). Concerning reading demands, ventral regions appear to be more strongly activated by semantic than phonological reading tasks (Price & Mechelli, 2005). In contrast, the opposite pattern is found in dorsal regions, which are typically more activated for phonological than semantic reading-related decisions (Paulesu et al., 1993; Zatorre et al., 1992).

A crucial region within the ventral and dorsal network for reading is the IFG. This region is divided into its anterior parts (*pars orbitalis* and *pars triangularis*) at the ventral pathway, and its posterior part (*pars opercularis*) at the dorsal pathway. This ventral and dorsal subdivision is based on cellular and neuroanatomical studies. One of the first cytoarchitectonic differentiation of the anterior and posterior IFG parts was proposed by Brodmann (1909) based on the presence of particular cell types therein. Specifically, he found variations between anterior and posterior IFG in size and packing density of cell bodies over the layers of the cortical sheet. Other parameters were added successively to this initial topological classification, such as the distribution and amount of intracortical myelinated fibers (Vogt, 1910) or the density of certain neurotransmitters receptors (Zilles et al., 2004). Consistently, recent neuroimaging studies on reading have also found a differential functional involvement of anterior and posterior IFG regions (Price, 2012). Specifically, the anterior IFG is more strongly activated in studies using semantic reading tasks and when word retrieval during the reading task is semantically demanding, such as retrieving narratives (Badre & Wagner, 2002; 2004; de Zubicaray et al., 2001; Wagner et al., 2001). In contrast, when stronger phonological demands are required by the

task, stronger posterior IFG engagement is typically found (Bitan et al., 2005; Gabrieli et al., 1998; Poldrack et al., 1999).

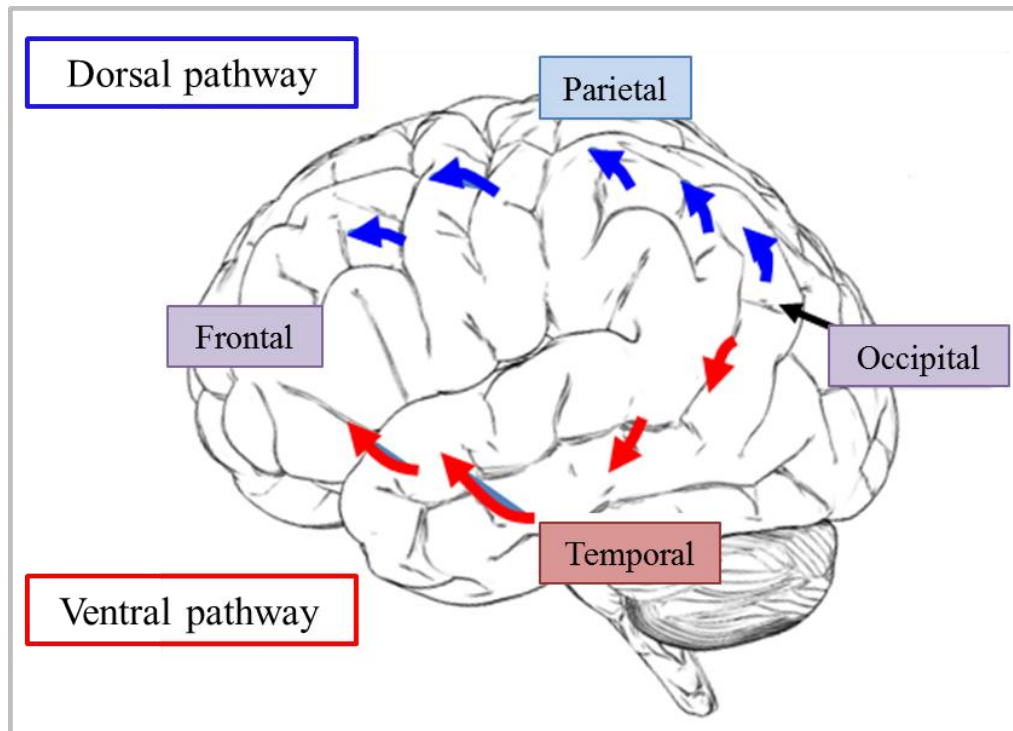


Figure 4. Ventral and Dorsal reading pathways based on Pugh et al., (2001)

As previously described, the modulation of the ventral and dorsal pathways depends on the reading demands posed by the task and stimuli. Importantly, different languages present different writing systems, and therefore reading demands may differ depending on the characteristics of a given language. Neuroimaging studies revealed a different modulation of these ventral and dorsal reading pathways upon the orthography of the language (Paulesu et al., 2000). Languages can be classified according to their grapheme to phoneme mapping or language orthography. Transparent orthographies, such as Spanish or Basque, have a quick letter-to-sound correspondence. Opaque orthographies, such as English, have a more complex

grapheme to phoneme mapping. Given that transparent orthographies have relatively simple, consistent and complete connections between letters and phonemes, it is easier for readers to recover the phonology of the printed words prelexically by assembling letter-to-phoneme correspondences. In other words, the phonology of transparent orthographies directly support word recognition processes. In contrast, in opaque orthographies the reader must process printed words by referring to their morphology via the visual-orthographic structure of the printed words.

Neuroimaging evidence showed that whereas transparent languages rely more on phonological areas within the dorsal pathway, opaque orthographies rely more on ventral pathway regions; consistent with the graphemic analysis to resolve ambiguities with pronunciation (Meschyan & Hernandez, 2006; Paulesu et al., 2000; Rueckl et al., 2015). However, the opposite pattern was also found in other study (Jamal et al., 2012), suggesting that if fewer phonological processing is needed, as would be expected in transparent languages, there may be less use of the phonological (dorsal) pathway and greater use of the semantic (ventral) pathway. In contrast, in opaque languages greater activation of the dorsal route would be found. Further studies on language orthography are needed to resolve these mixed findings.

In sum, empirical evidence seems to suggest the involvement of two different routes in reading: a ventral lexico-semantic route and a dorsal route linking orthography and phonology. This division is supported by a large number of functional studies and metanalytic reviews (Jobard et al., 2003). However, understanding the structural organization of the cortex is critical for the study of brain function, considering that structure support function. Then, what are the structures that support the different computations carried out by ventral and dorsal streams? Evidence from studies using diffusion tensor imaging (DTI), which allow the identification of

white-matter (WM) structural connections between brain regions, showed that structural connections between temporal and frontal regions are mediated by different ventral and dorsal fiber tracts, in line with the dual-stream hypothesis (Friederici, 2012; Saur et al., 2008; Figure 10). More specifically, Saur et al. (2008) used a deterministic fiber tracking approach with the two end points of the connection predefined on the basis of functional data. This study showed that within the ventral pathway, the extreme fiber capsule system (EFCS), which connects temporal cortex with the *pars triangularis* and *pars orbitalis*, supports sound-to-meaning mapping. On the other hand, this study defines the structural dorsal pathway as going from the temporal lobe to the premotor cortex and continuing to the *pars opercularis*, via the arcuate and superior longitudinal fascicle supporting sensory-motor mapping of sound-to-articulation. These findings suggest that the different types of decoding required during the reading process found in fMRI studies on the ventral and dorsal functional pathways, are also supported by white-matter microstructure.

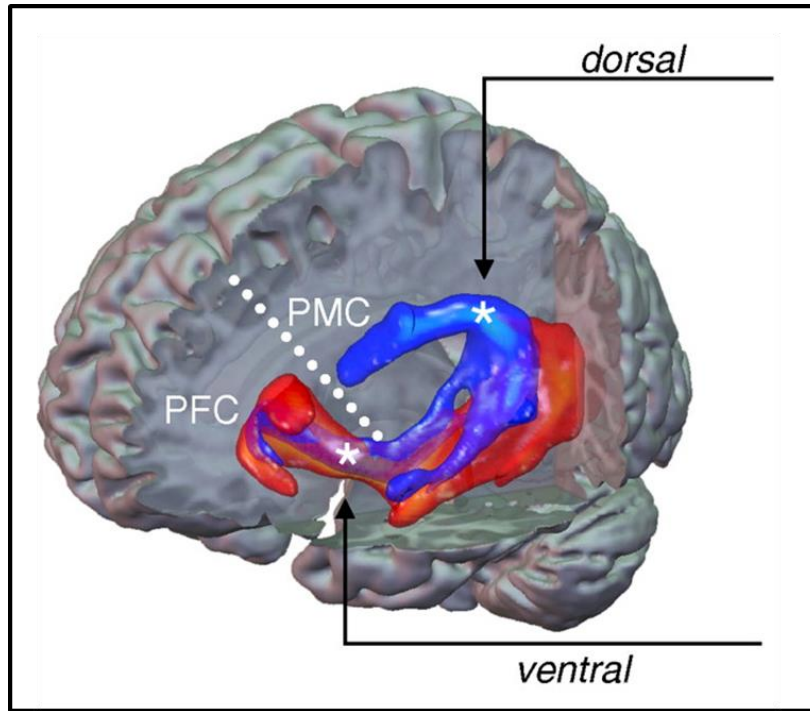


Figure 5. Ventral and Dorsal anatomical pathways (Saur et al., 2008)

The crucial role of the structural WM pathways on reading was also determined by previous studies with children, and also with adults. Specifically, empirical evidence showed the development of WM connectivity in line with reading acquisition in children and their predictive value of future reading performance (Yeatman et al., 2012, 2013). Importantly, structural changes have also been observed in adult illiterates who have learned to read for the first time during the adulthood (de Schotten et al., 2012). These studies highlight that reading acquisition induces structural changes that can be observed in neuroimaging studies. These changes can also occur during the adulthood, overturning the classical view that structural change is limited to critical or sensitive periods (Lenneberg, 1967).

To sum up, in this section I have described the reading process at the brain level and how the different reading demands, such as, stimuli, task and language orthography modulates the activation of the ventral and dorsal reading networks. Furthermore, the reading networks seem to be supported by structural scaffolding, which appear to be modulated during reading acquisition during childhood and even during adulthood. Overall, this evidence highlights that functional and structural brain modulation occur as a result of environmental demands. A relevant demand in today's world is the need to speak more than one language. The rapid rise of bilingualisms and multilingualism in modern societies encourages a significant proportion of individuals to learn new languages over childhood and adulthood years. How does the brain accomplish such a feat? How language is organized in individuals who know more than one language? The following chapter provides a description regarding this relevant matter.

Chapter 3: Bilingualism and neural correlates underlying bilingual reading

This chapter is divided in two different sections. In section 3.1, a brief description of the importance of bilingualism in today's world will be given. Following that, the second section (3.2) pays particular attention to the factors that seems to influence bilingual reading, such as, AoA, language exposure, language proficiency, and language orthography, and I describe how these factors modulate the neural correlates underlying bilingual reading.

3.1 Relevance of bilingualism

Over half of the world's population is already bilingual (Grosjean, 2010). Just in Europe, 19% of the population is bilingual, 25% trilingual and 10% speak four or more languages (Eurobarometer, 2012; Figure 4). Monolingual Europeans are now in minority. Also, of interest, 98% of Europeans think that learning at least one foreign language it is important for the future of their children (Eurobarometer, 2012). This belief seems to be similar in other countries outside Europe. As a matter of fact, in the last years, substantial efforts have been made to implement bilingual education programs at schools in predominantly monolingual societies. In the US for example, 317 dual immersion programs were operating in elementary schools in 10 different languages (Center for Applied Linguistics, 2005).

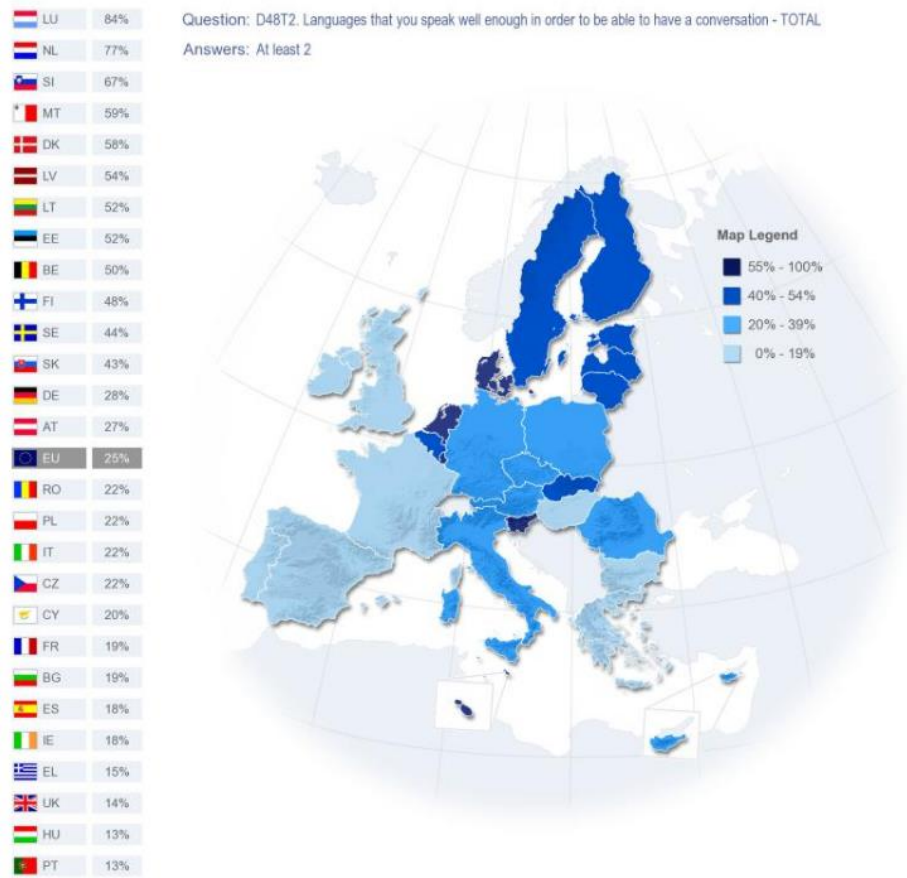


Figure 6. Percentage of Europeans who speak two or more languages (Eurobarometer, 2012).

Bilingualism is, thus, both a reality and a desired situation in today's world. However, there are many questions still unanswered about how bilinguals process reading, such as, is there an age-related window of opportunity at the offset of which language acquisition becomes qualitatively different? To what extent is reading in the L1 and in the L2 supported by the same processes? The responses to these questions are relevant, not only to inform current models on bilingual reading, but also because of their implications and the impact that they may have on current educational programs. For example, some perspectives support that children are somehow harmed by early bilingual exposure and need to establish the native language first

(Crawford, 1999). Based on this account, some bilingual families withhold one of the two languages in their child's early life to better establish one language and avoid confusing the child (Petitto et al., 2001). Next, I review the empirical evidence regarding bilingual reading at the brain level.

3.2 Neural correlates underlying bilingual reading

For people who speak two languages, understanding tens of thousands of words in either of the two languages is an exceptional accomplishment of their cognitive and neural systems. One of the main issues that are generating heated debates is to what extent bilinguals share or not the same neural networks for their L1 and L2 (Parker, Jones et al., 2012; Price, 2012; Schlaggar & McCandliss, 2007). Neuropsychological evidence has showed that injuries in bilinguals Broca's area can produce deficits in language production (i.e., expressive aphasia) in their L1, but not necessarily in their L2 (Wolf et al., 1999). In contrast, neuroimaging research has showed mixed results in this regard, with some studies revealing differential regional activation in L1 relative to L2 processing (Kim et al., 1997) and, other studies showing extensive overlap among the regions being recruited for L1 and L2 processing (Friederici et al., 2002; Musso et al., 2003). However, there are some relevant factors that are known to influence functional and structural correlates of reading networks, such as AoA, proficiency level and exposure to the L2 and language orthography (Jamal et al., 2012; Mechelli et al., 2004; Perani et al., 2003; Wartenburger et al., 2003), that can determine these inconsistencies found in neuroimaging research in regard to the overlap or the lack of overlap between L1 and L2 regions and networks involved in bilingual. A detailed description of the functional and structural findings regarding these factors is discussed next.

Age-of-acquisition

AoA refers to the age at which exposure to the L2 begins. The “critical period” hypothesis suggests that there is a brain maturational period when the infant brain is more flexible and plastic (Lenneberg, 1967). During this period, the brain adapts more easily to any new experience, including language acquisition. According to this hypothesis, the earlier the AoA of the L2, the more probable it is to achieve a native-like proficiency in this L2. The brain plasticity theory is supported by studies that revealed that language recovery in aphasics is considered to be excellent if occurs in early infancy, while older children show more adult-like aphasic patterns and poorer recovery (Bates et al., 2001). Thus, the changes in plasticity may explain the advantage of children versus adults to learn a new language. The critical period hypothesis has also been supported by different studies showing that late learners of an L2 diverge from native speakers at the lexico-grammatical (Hyltenstam & Abrahamsson, 2000) and phonological levels (MacKay et al., 2001; Scovell, 2006), including degree of accent, production and comprehension of morphology and syntax, grammaticality judgment for morphology and syntax, and syntactic processing speed and accuracy (Neville et al., 1998). Findings from these studies revealed that individuals exposed to an L2 during middle childhood and during the adulthood are likely to end up speaking the L2 with a non-native accent. There is not a common agreement about when the optimum period for language acquisition ends. Penfield & Roberts (1959), proposed after age 9 as the offset point for the critical period. Lenneberg (1967), in contrast, proposed puberty as the offset point. Others have suggested that language-learning mechanisms progressively deteriorate from birth on and that for this reason “native-like proficiency in an L2 is unattainable” (Abrahamsson & Hyltenstam, 2009). More recently, there has been increased consensus among researchers about the critical period ending progressively

over a number of years, starting around age 6 (Perani et al., 2003; Pinker, 1994). Nevertheless, the critical period hypothesis has been challenged by studies finding no qualitative changes in learning outcomes at the end of the critical period (Hakuta, 1999). Empirical evidence suggests that late L2 beginners attained native-like levels of L2 proficiency based on reading performance and other language aspects, such as, vocabulary, grammatical knowledge and semantic comprehension (Bongaerts et al., 2000; Singleton, 2012; Singleton & Muñoz, 2011). According to this line of research, AoA does not influence all aspects of language learning equally. AoA effects appear to be present in the formal properties of language, but not in the processing of meaning. Then, late learners acquire the basic word order and vocabulary of a language relatively well, but more complex aspects of grammar show strong effects of late acquisition (Gillon-Dowens et al., 2010; Neville et al., 1992). Neuroimaging evidence support this interpretation revealing that AoA mainly affected the cortical representation of grammatical processes compare to semantic judgments (Wartenburger et al., 2003).

Despite of debates on the existence of a critical period and its precise offset, AoA has a central role in L1 and L2 processing. Learning an L2 early in childhood or after substantial first language development typically entails different outcomes and also impacts the way in which L1 and L2 are processed at the neural level. In the first situation, both languages are acquired as part of a continuing developmental process, however, in the second situation, language development has already occurred. Research studies on L2 AoA suggest that in early bilinguals L1 and L2 are processed by common orthographic and phonological neural systems. In contrast, in late bilinguals different processes are engaged for each language (Kim et al., 1997). Specifically, neuroimaging studies have found extensive overlap in left-perisylvian regions for L1 and L2 reading in early bilinguals, but not in late bilinguals (Kim et al., 1997; Wartenburger et al.,

2003). In particular, Kim et al.'s (1997) study revealed that separate but adjacent tissue of Broca's area, at the IFG, was activated for L1 and L2 in late bilinguals, whereas stronger overlap within this region was found in early bilinguals for L1 and L2 processing. More recently, similar results were observed in reading studies with bilinguals (Wartenburger et al., 2003), and also in studies focused on different language-related processing, such as syntax (Mahendra et al., 2003) and lexical aspects (Isel & Shen, 2011). Neuroimaging evidence also show that neural organization for late-learned languages tend to be less lateralized (Berken et al., 2016). This evidence indicates that the later an L2 is acquired, less overlap will be observed in cortical representations for L1 and L2. This can be determined by further need of additional resources in late bilinguals to achieve a comparable native-like performance in their L2. In contrast, early bilinguals learn both languages in parallel and appear to show stronger overlap in brain regions for processing L1 and L2 (Hernandez & Li, 2007).

The effect of L2 AoA was also investigated at the structural level. Empirical evidence suggests that the earlier bilinguals begin L2 learning, the more grey matter (GM) density in the left inferior parietal cortex (Mechelli et al., 2004). The structural changes in this region are described as reflecting an explicit learning strategy for linking new words to concepts (Richardson et al., 2011), a process that is implicit when learning languages natively. Furthermore, differences in WM were found as a function of the AoA. Early bilinguals relative to late bilinguals exhibited higher fractional anisotropy (FA) values in the left inferior-frontal occipital fasciculus (IFOF), which has been suggested to play a role in semantic processing (Mohades et al., 2012). Higher FA values may be related to increase structural connectivity between reading related regions, such as among the regions that the IFOF connects, due to greater language experience or automaticity (Mohades et al., 2012; Schlegel et al., 2012).

Recently, one study suggested that later acquisition of L2 is associated with thicker cortex in the left IFG, a crucial region within the reading network (Klein et al., 2014) which is interpreted to be due to less synaptic pruning in this region as a result of acquiring L2 later in development. Overall, the bulk of the evidence suggests that acquiring an L2 as a new skill earlier or later over childhood induces different functional and anatomical changes in reading and language related regions.

Language Proficiency

Proficiency refers to the competence level achieved in a given language. High-proficient bilinguals are described as people who can function equally well in their L1 and L2. In contrast, in low-proficient bilinguals, the competence in the L2 may be weaker than in the L1. Empirical evidence found that low-proficient bilinguals showed greater reaction times and less accuracy during L2 reading (Chee et al., 2001) and L2 verbal fluency (Blumenfeld et al., 2016). Also, there is evidence indicating that the reading strategies differ depending on the proficiency level. Specifically, it has been suggested that in later proficiency stages (i.e., high-proficient bilinguals), reading becomes more concept mediated without translation. In contrast, in low-proficient bilinguals, L2 reading is processed by direct translation from their L1 (Dufour & Kroll, 1995; Perani et al., 2003). Then, as proficiency in L2 increases, L2 reading strategies become more native like (Kotz & Elston-Güttler, 2004).

Some studies have pointed out to proficiency as the main factor determining differences in the recruitment of neural regions for reading in L1 and L2. Neuroimaging studies have showed that lower proficiency in the L2 is associated with greater IFG (BA 47) activation during reading (Chee et al., 2001). Convergent evidence showing hyperactivation in participants with lower

versus high proficiency was found in studies examining other language-related tasks, such as verbal fluency (Vingerhoets, 2003), semantic and syntactic judgments (Wartenburger et al., 2003), and naming tasks (Hernandez et al., 2001). This hyperactivation during L2 reading and other L2 language-related processes may be due to a lower degree of automaticity because of the lower proficiency in L2. In line with this interpretation, when L2 and L1 proficiency are equated, early and late bilinguals tend to exhibit strikingly similar neural responses for processing both the L1 and L2 (Abutalebi et al., 2001; Chee et al., 2001; Frenck-Mestre et al., 2005; Klein et al., 2006). Thus, as L2 proficiency increases, differences in the neural correlates of reading in L1 versus L2 decrease. Then, AoA effects might be diminished when early and late learners are equated on proficiency.

Furthermore, L2 proficiency seems to induce changes also in structural measures. L2 proficiency correlates with increased GM in a variety of reading related regions, such as, left IPC (Mechelli et al., 2004), left IFG (Grogan et al., 2009; Stein et al., 2012) and left STG (Martensson et al., 2012). Additionally, increases in WM connectivity between left hemispheric perisylvian regions and their right homologs regions (IFG, caudate nucleus, STG) are related to the level of L2 proficiency in English learners of Chinese (Schlegel et al., 2012). In sum, it is possible to affirm that, in general, higher L2 proficiency is associated with a larger GM density or larger structural increases in GM and also increased WM connectivity in reading related fiber tracts.

Language Exposure

L2 exposure has also been identified as an important factor that predicts performance on a second language (De Angelis, 2014), but also on a third language (De Angelis, 2015).

Specifically, empirical research has showed that students in total immersion programs generally acquire higher levels of proficiency in the L2 than students in partial immersion programs (Cenoz et al., 1998). Other studies found a direct correlation between the amount of L2 exposure and the level of L2 achievement (Bhatia & Ritchie, 2004). Specifically, Yelland et al., (1993) compared high-L2 exposed grade school students relative to low-L2 exposed. The results reveal greater L2 and also L1 reading development in high-L2 exposed compared to their low-L2 exposed counterparts. The level of exposure to L1 and L2 has also been implicated in the modulation on the neural correlates of reading processes in bilinguals (Tu et al., 2015). Even when the degree of proficiency is kept constant, differential exposure seems to be associated with a differential engagement of reading related regions (Vingerhoets et al., 2013). Similar results have been observed in studies using language-related tasks, other than reading. For example, Perani et al.'s (2003) study compared two groups of high-proficient bilinguals that differ in their L2 exposure on a word generation task. Participants with high L2 exposure exhibited reduced activation in left prefrontal cortex relative to those with lower L2 exposure. Thus, experience and practice on the L2 may result in a decrease of neural activation, suggesting more automaticity and less effort or resources needed for L2 processing (Abutalebi et al., 2007). Recent evidence also suggests that even brief 30-days periods of differential exposure to a given language may induce significant neural changes in areas responsible for language processing (Tu et al., 2015). Furthermore, the influence of one language on another due to differential exposure has also been previously examined. Neuroimaging studies have proposed that L2 exposure can even replace L1 when bilinguals are no longer exposed to their native language (Pallier et al., 2003). Thus, exposure to a second language is thought to be a potential predictor of L2 proficiency development. The role of L2 exposure was also investigated in a few structural

studies that found correlations between L2 exposure and GM density in language related regions, such as the bilateral posterior putamen (Pliatsikas et al., 2014). Based on these findings, the amount of language exposure seems to affect the functional and structural neural responses involved in L2 processing.

Language Orthography

Orthographies vary across languages in their grapheme to phoneme correspondence (Paulesu et al., 2001). The degree of orthographic distance between the L1 and the L2 can also play an important role during reading. McDonald, (2000) found that Spanish native speakers who started acquiring English before age 5 were able to perform at native levels on an English grammaticality judgment test. In contrast, Vietnamese speakers who also started to be exposed to English before age 5 were not able to perform at native levels on that same test. The authors of this study concluded that these differences may be due to the closer grammatical similarity between English and Spanish than between English and Vietnamese. This evidence suggests that the language that one was first taught to read can facilitate L2 reading.

Furthermore, in line with this evidence, it was also suggested that the strategies used to read in L1 might be transferred to L2 reading and vice-versa, even if the orthography between L1 and L2 differs. Specifically, readers of a transparent L1 use more phonological strategies for L2 reading relative to readers of an opaque L1 (Tan et al., 2003; Wang et al., 2005). Regarding the “reverse” transfer or the influence of L2 into L1, empirical evidence reveals that L2 training shows an improvement in L1 reading and writing, measured by syntactic complexity (Kecskes & Papp, 2000) and an increase in L1 vocabulary (Cunningham & Graham, 2000). The common

claim from these studies is that languages influence each other; which suggest that there should be an overlap between the brain systems used for different languages.

The language orthography differences lead to variations in the involvement of the functional reading networks (Paulesu et al., 2001; see previous 1.1 section). Disparities in the activation of the reading networks may be even more extensive for bilinguals with two different language orthographies (e.g., Spanish-English bilinguals). In fact, Meschyan and Hernandez (2006) reported differences in activation profiles for early Spanish-English bilinguals during L1 and L2 reading. More specifically, in this study Spanish reading elicited greater activation in the right supplementary motor area, right putamen, right insula and left STG. In contrast, English reading elicited greater activation in the inferior parietal cortex and along regions in the occipito-parietal vicinity. However, subjects in this study differed in proficiency, consequently, it is not clear if these differences were due to proficiency or to language orthography per se. A more recent study of Spanish-English late bilinguals matched in proficiency, revealed functional differences in the reading network as a function of language orthography (Jamal et al., 2012). In contrast, another study with early and late Hindi-English bilinguals, did not found divergent activation based on language orthography in late bilinguals, but differences were found in early bilinguals (Das et al., 2011). The results of this study suggest that early, but not late, exposure to reading distinct orthographies results in orthography-specific plasticity that persists through adulthood (Rueckl et al., 2015). Altogether this evidence suggests that bilinguals show adjustments to the typical neural representations of reading upon language orthography. However, it is still not clear which specific neural representations are expected as a function of the orthography and if this divergent activation is confounded with other variables such as AoA.

In sum, based on the research evidence reviewed in this chapter, it is possible to conclude that the brain has an extraordinary ability to functionally and structurally change in response to environmental stimulus, cognitive demands, or experiences. Specifically, the task and stimuli demands, AoA, language proficiency and exposure and language orthography are crucial factors that can affect the brain representations of each language in bilingual reading. Despite of the recent advances in Cognitive Neuroscience regarding bilingual reading, the results on functional and structural studies with bilingual populations are still sparse and inconsistent. Future studies should take into account the influence of the variables here reviewed (i.e., AoA, proficiency, exposure, language orthography) and the importance of either controlling or manipulating them within the same study. Importantly, there is also increasing evidence that individual differences in functional activation are related to the underlying brain structure. Therefore, future investigations can shed further light on the neural basis of bilingual reading by combining structural and functional data in the same study.

One way for exploring the neural basis of language is using neuroimaging techniques, such as the MRI. The MRI is a non-invasive technique, useful for examining brain structure and function. This technique has a good spatial resolution, which means that is able to detect and represent different spatial locations in the brain precisely. Therefore, the MRI is the technique selected to conduct the main studies of the present doctoral dissertation. The next chapter is focused on providing the reader with an overview of the MRI technique and the main dependent measures that can be obtained with it to further examining the neural systems involved in reading processes.

Chapter 4: Magnetic Resonance Imaging

Over time, neuroanatomists have developed sophisticated ways of brain mapping, moving from dividing the brain into lobes and sulci to mapping cytoarchitectonic and connectivity features. The development of MRI methods over the last two decades has allowed us to measure many thousands of locations in the brain, and also doing so while subjects perform tasks through fMRI (Bandettini, 2012). The MRI technique has a high spatial resolution that is of the order of 2-3mm, which is used to inform us about "where" in the brain cognitive changes occur. MRI is the selected technique to reach the goal of this doctoral dissertation (to examine the neural networks involved in bilingual reading). The present chapter is intended to offer the reader a detailed description of functional and structural MRI, as well as the main measures examined in the analyses performed in the two experiments that constitutes the present work. For fMRI analyses we will examine voxel-wise, region-of-interest (ROIs) and functional connectivity analyses. Respect to structural MRI, we will look at cortical thickness (CT) and diffusion tensor imaging (DTI) measures.

Functional Magnetic Resonance Imaging

fMRI measures changes in the level of deoxygenated and oxygenated hemoglobin molecules presented in the blood. The ratio of deoxygenated (deoxyHb) and oxygenated hemoglobin (oxyHb) is called the blood-oxygen-level-dependent (BOLD) response (Ogawa et al., 1990). fMRI is able to detect changes in this response due to differences in paramagnetic properties of deoxyHb and oxyHb. DeoxyHb is paramagnetic and disturb the homogeneity of the magnetic field, whereas oxyHb is not, so has no effect on the local magnetic field. Large blood

fluctuations will result in BOLD signal changes, which makes possible to map changes in activity associated with a cognitive task (Raichle, 2009). Specifically, the increase in neural activity in a brain voxel results in an initial increase in oxygen consumption. After a delay of about 2 seconds, a large increase in localized cerebral blood flow is triggered, that over compensates the oxygen consumption. Therefore, localized increases in blood flow produce increments in blood oxygenation and, consequently, also reductions in deoxyHb. As a result, better visibility in fMRI images is thought to correlate with neural activity (Figure 5). The goal of an fMRI experiment is to examine the time series of brain voxels and to what extent a given manipulation produce BOLD signal changes in that voxel in response to some specific manipulations.

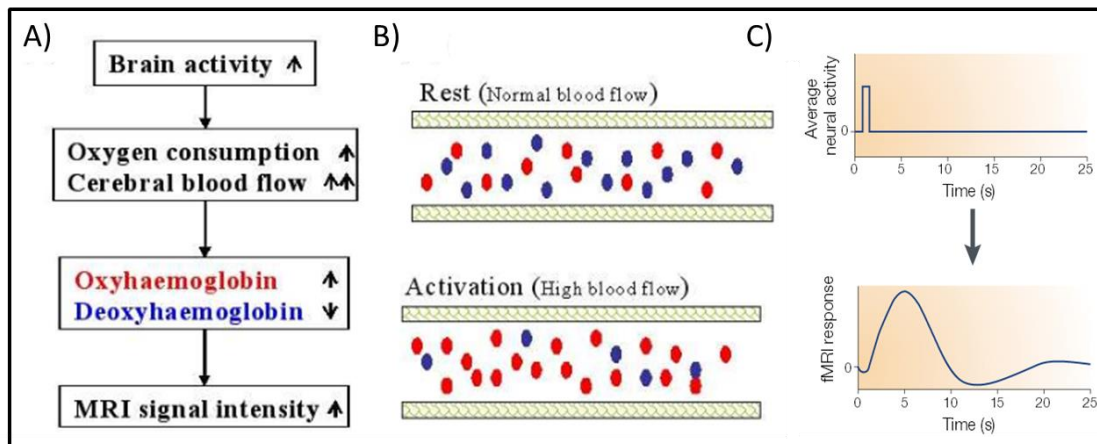


Figure 7. BOLD response in functional MRI. A) Blood-oxygen level-dependent signal mechanism in magnetic t imaging. B) oxyHb and deoxyHb blood flow during rest and activation. C) The standard hemodynamic response function in fMRI data; (Heeger & Ress, 2002)

The main issue analyzing fMRI images is comparing images or group of images in a statistically meaningful way. Several preprocessing steps are required before this statistical analysis can be performed. The main preprocessing steps typically include: *slice-timing* or

temporal interpolation, *realignment* or spatial interpolation, *normalization* and *smoothing* (see Figure 6A). The *slice timing* correction is used to compensate for slice acquisition delays, so that it would be equivalent to acquiring the whole brain image at a single time point. Because subjects may move in the scanner during data acquisition and consequently the location of every voxel might vary between scans, the realignment step help to correct to some extent these motion artifacts aligning as closely as possible the acquired functional images. During the *normalization* procedure subjects' brain images are warped into a standard stereotaxic space. Specifically, this procedure uses landmarks to adjust position, orientation and size of an individual brain to match the reference brain template. Almost all major analysis packages use templates based on the Talairach coordinates, also known as Talairach space, as a default for normalization. The Talairach space is a 3-dimension coordinate system or “atlas” of the human brain (Talairach & Tournoux, 1988). The normalization process is used to reduce inter-subject anatomical variability in human brain mapping studies, which allow averaging data across subjects by establishing spatial correspondence between brains. Additionally, the purpose of using the same space across studies and laboratories is that the research community can report results in a standard space, improving accuracy, comparability and reproducibility of the results across laboratories. Finally, during *smoothing* data points or voxels are averaged with their neighbors. Since the BOLD response is modulated by blood flow, the rate at which the signal changes, in an activated region, is limited. Therefore, smoothing each voxel with a filter of similar shape will improve the signal-to-noise ratio.

After preprocessing the images are ready for statistical analysis. The most widely tool used to fit and detect variations in BOLD response is the general lineal model (GLM; Friston et al., 1995). This model can be used for many different types of analysis including correlations,

one-sample t-tests, two sample t-tests, analyses of variance (ANOVA), and analyses of covariance (ANCOVA). Specifically, fMRI analyses are carried out in multiple stages. For example, in a two-sample t-test, the first-level involves modeling the data for each subject separately, estimating subject-specific differences upon the manipulation. The second-level model takes the subject-specific parameter and variance estimates from the first-level model. Then, the within-subject variance is estimated in the first-level and the between-subject variance in the second-level (Figure 6B). Finally, the model estimates a mean for each group and the contrast of interest to compare between groups (Poldrack, 2011). For an image composed of N voxels, there are several ways to decide if there are changes in the BOLD response: *voxel-level*, by testing each and every voxel in the brain or *cluster-level*, by examining specific clusters of activated voxels. Importantly, when comparing multiple voxels one must avoid “multiple testing problems”, such as Type I error, which refer to the change of one or more false positives. Different methods are available to avoid this problem, such as the False Discovery Rate (FDR) or the Family-wise error (FEW) rate that can be also applied at the voxel or cluster levels.

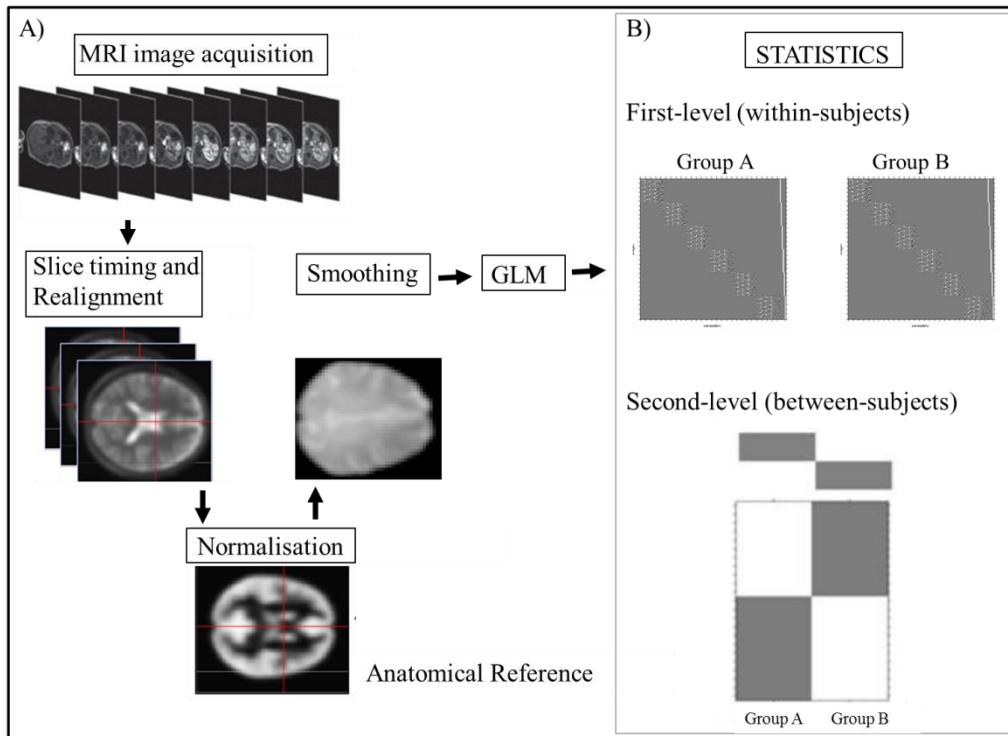


Figure 8. A) Overview of fMRI data preprocessing and B) statistical analysis. Adapted from SPM 8 Preprocessing, available on: www.fil.ion.ucl.ac.uk/spm/

One of the common objectives in fMRI analysis is localizing regions of the brain activated by a certain task or condition and determining the brain networks involved in specific cognitive functions. An approach that is specifically focused on the activation of specific brain regions or clusters is the ROI analysis. This approach involves the extraction of signal (i.e., parameter estimates) from specific brain regions of interest based on prior evidence suggesting the involvement of these brain regions in a specific cognitive function. If a study is focused on particular regions of the brain, based on prior evidence and the study hypotheses, it is possible to limit the search for different in activation to a given number of ROIs. There are different reasons to select this analysis. On the one hand, in complex designs, such as factorial designs with multiple levels, it can be difficult to discern the pattern of activity across conditions from an overall voxel-wise map; ROI analysis may illustrate more clearly this pattern. On the other hand,

by reducing the magnitude of correction needed for a large number of voxels, one can better control for Type I errors by limiting the number of statistical tests to a few ROIs (Poldrack, 2007).

More recently, the neuroscientist community has moved to the idea that the majority of functions are supported by coordinated activity between brain regions, so that the brain works in networks (Catani et al., 2003). Therefore, there is increasing interest in implementing analysis to better understand how various brain regions interact between each other. One approach to characterize these interactions is functional connectivity. Functional connectivity refers to the influence that one neural system exerts over another. This type of analysis typically compares correlations between regions of interest or between a “seed” region of interest and the rest of the voxels in the brain. This allows to discover patterns regarding which regions are coupled or work together in time, and to compare those patterns between networks (i.e., ventral versus dorsal network), between groups and or between experimental conditions (Friston, 2011).

One approach to estimate functional connectivity is the beta-series correlations developed by Jesse Rissman (Rissman et al., 2004). This is a multivariate method that capitalizes on trial-to-trial variability to characterize dynamic inter-regional interactions. The premise of this method is that if two areas of the brain are functionally interacting with each other during a particular cognitive task, then the amount of activity that the two areas exhibit during that stage should be correlated across trials. The beta-series correlation method has been widely used in event-related fMRI studies (e.g., Paz-Alonso et al., 2013). This specific analysis provides information about how different regions are functional connected and allows examining differences in functional connectivity at the whole-brain level (i.e., selecting a seed to examine coupling with this seed

throughout the brain voxels) and at the pairwise level (i.e., examine differences in the strength of functional connectivity between pairs of ROIs).

Structural MRI Measures

Neurons are organized within the brain forming GM and WM. GM consists of primarily neuronal cell bodies and is found in the surface of the brain. In contrast, WM consists of axons, which are the long strands of nerve cell extensions, and support cells (e.g., glia). In the WM, bundles of axons form the so-called fiber tracts that connect different cortical regions within the same hemisphere, between hemispheres or between cortical and subcortical structures. Thus, the axons carry information from one grey matter region to another. Additionally, the brain is filled with cerebrospinal fluid (CSF), which runs through the ventricles of the brain.

Cognitive neuroscientist had long dismissed the structural properties of GM and WM as an important value to further understand brain function. This view is now changing by studies examining the importance of actual changes in GM and WM brain structure in response to cognitive demands (Martensson et al., 2012). Structural MRI images allow studying GM and WM providing static information of qualitative and quantitative properties (i.e., size, shape). In the present work, we have examined structural brain differences using two different measures: CT, which allows examining GM properties and DTI to the study of WM micro-structural properties.

Regarding CT, the human cerebral cortex constitutes a highly folded sheet of neurons, which thickness varying on average between 1 and 4.5 mm depending of the region (Fischl & Dale, 2000). To perform CT analysis, voxels are first segmented into GM, WM or CSF, and

then, the boundaries between GM and WM, and between GM and the pia mater are delineated (Kabani et al., 2001; see Figure 7).

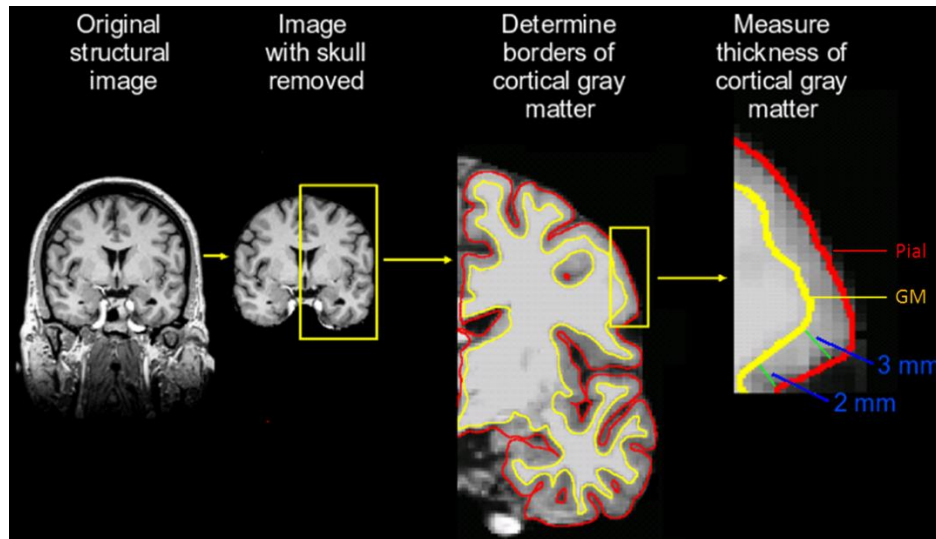


Figure 9. Main steps in CT analyses.

<http://surfer.nmr.mgh.harvard.edu/fswiki><http://surfer.nmr.mgh.harvard.edu/fswiki>.

The thickness of the cortex is of great of interest, and show marked changes over development (Sowell et al., 2003). During infancy and early childhood there is an initial overproduction of neurons and synaptic connections followed by activity dependent fine-tuning that lead to synaptic pruning that continues well into adolescence (Fuster, 2002; Shaw et al., 2008; Figure 8). Synaptic pruning refers to the fact that extra neurons and unused synaptic connections are eliminated in order to increase the efficiency of neuronal transmissions, leading to a decrease in cortical thickness (Paolicelli et al., 2011; Tamnes et al., 2010). Therefore, over development GM loss occurs as part of the ultimate sculpting of the brain into the fully functioning adult nervous system that results in cortical thinning (Courchesne et al., 2000; Raznahan et al., 2010; Shaw et al., 2008; Sowell et al., 2004);

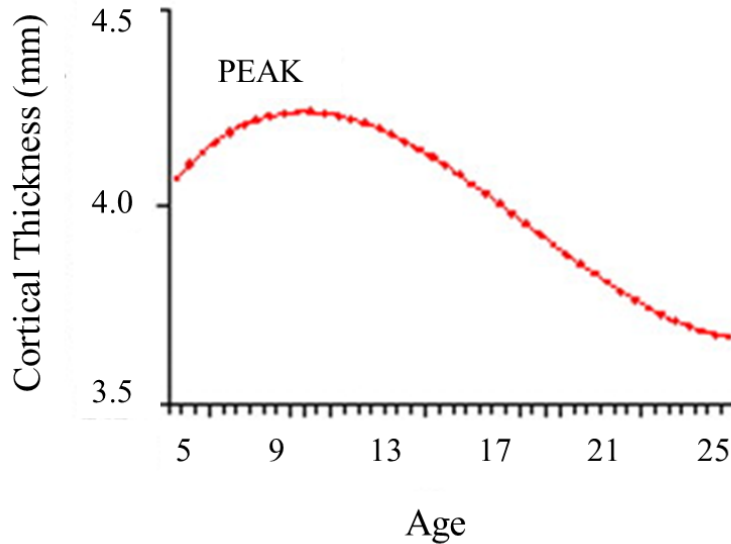


Figure 10. Age of attaining peak cortical thickness across the cerebral cortex (Shaw et al., 2008)

Empirical evidence has showed that left hemisphere decreases in cortical thickness were associated with increases in vocabulary size (Sowell et al., 2004). Similarly, it has been showed that L2 acquisition in different stages of development lead to differences in cortical thickness in left inferior frontal gyrus (Klein et al., 2014). In sum, CT can provide relevant information in relation to structural modulations in the form of neuronal loss and reduced size of neural cell bodies, which may be associated with performance in cognitive abilities and relevant factors associated with language acquisition.

Regarding DTI analysis, it provides a framework for acquisition, analysis and quantification of the diffusion properties of WM (Basser & Jones, 2002). In general, water molecules diffuse differently along the tissues depending of its type, integrity, architecture and presence of barriers. All these factors can give useful information about the orientation and diffusion properties of the main WM tracts in the brain. Specifically, the diffusion could be

isotropic, same in all directions, or anisotropic, varying with directions (Figure 8). Diffusion in WM tends to be anisotropic (directionally-dependent), whereas in GM is usually less anisotropic and in CSF is unrestricted or isotropic in all directions (Pierpaoli et al.,1996).

By knowing the diffusion orientation, one can infer the underlying tissue in each voxel and calculate several indices, such as FA, which provides information about WM tissue properties (Chenevert et al., 1990). FA is an index that provides a simple and robust indication to assess the degree of anisotropic diffusion occurring within a given tract. The FA will be high in regions heavily organized in terms of orientation (e.g., corpus callosum), intermediate in regions with some degree of organization (e.g., WM regions that have no strong predominant axon fiber axis orientation), and low in tissues where the predominant cell shapes are not specifically oriented (e.g., GM) (Pfefferbaum et al., 2000; Figure 9).

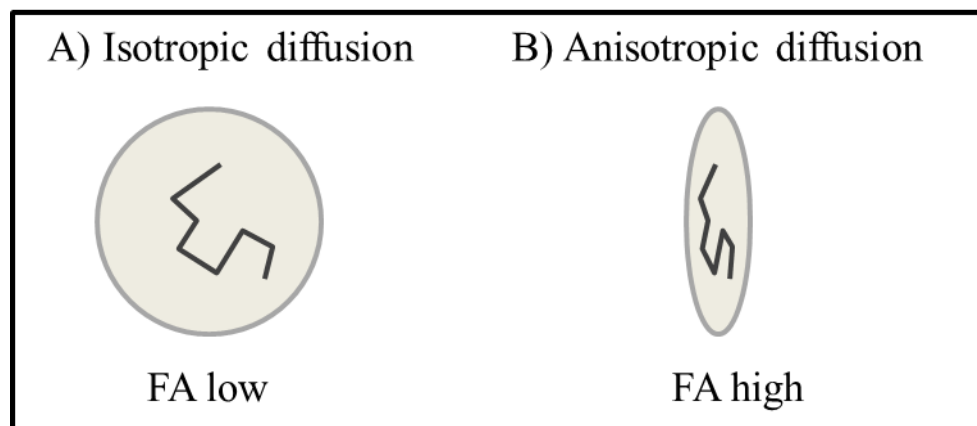


Figure 11. Diffusion sphere and ellipsoid. A) With isotropic diffusion, diffusion is equal in all directions and can be represented as a sphere. For isotropic diffusion FA is zero. B) Anisotropic diffusion can be visualized as an ellipsoid, and FA approaches the value of one as the diffusion becomes more and more ellipsoid in shape. Adapted from Beaulieu, 2002

Within the WM, higher FA values have been associated with increase variations in axon count, density of axonal packing and myelination. Myelination occurs more actively during

development but also in adulthood (Ishibashi et al., 2006), which lead to increases of the space occupied by axons in a given voxel and increases in FA (Stikov et al., 2011). These developmental effects of myelination and axon density on diffusion measurements have been confirmed in animal models and also in humans (Beaulieu et al., 2005; Pierpaoli et al., 2001).

Empirical evidence suggests that the development of cognitive abilities, such as reading is correlated with increases in FA values within tracts that connect relevant reading regions, such as the left arcuate fasciculus (Nagy et al., 2004; Yeatman et al., 2012). Thus, reading development is the result of white-matter microstructural changes, measured by FA, in tracts within the reading network (Yeatman et al., 2012; Figure 10). Indeed, empirical evidence observed that FA values in the left temporo-parietal lobe correlated with reading performance in both poor and normal readers (Klingberg et al., 2000), which suggests that axons in this area are important for efficient connectivity between temporo-parietal and frontal regions and thus may be important for reading. Studies such as this, demonstrate the usefulness of FA measures to investigate structural brain changes associated with specific cognitive functions. This explains why DTI has gaining increased popularity among clinicians and researchers, providing a tool for studying WM architecture in living humans.

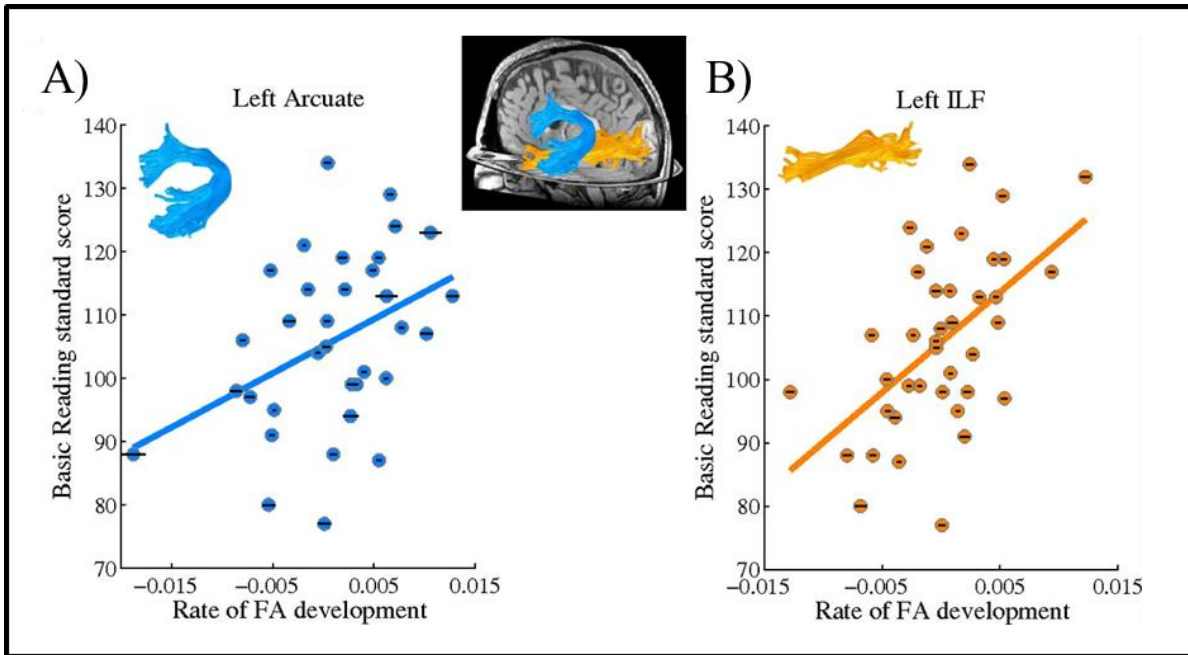


Figure 12. Rate of FA development in two tracts within the reading network A) left arcuate and B) left inferior longitudinal fasciculus (ILF), which correlates with reading skills (Yeatman et al, 2012).

Chapter 5. Functional dynamics of bilingual reading as a function of the language orthography

5.1 Overview

Evidence from the few available neuroimaging studies investigating bilingual reading has showed differences in regional activation profiles based on the L2 age-of-acquisition (AoA; (Perani et al., 2003; Wartenburger et al., 2003) language proficiency (Meschyan & Hernandez, 2006), and language orthography (Das et al., 2011; Jamal et al., 2012). Regarding language orthography, several studies have suggested that orthographic depth may modulate the engagement of regions along the dorsal and ventral reading networks. Reading in transparent orthographies with a strong letter-to-sound correspondence (e.g., Spanish, Italian, Basque) is thought to rely more on phonological processes supported by dorsal regions, while reading in opaque orthographies (e.g., English) would rely more on lexico-semantic processes supported by the ventral pathway (Das et al., 2011; Meschyan & Hernandez, 2006; Paulesu et al., 2000).

In the present study, we sought to investigate the involvement of regions along the dorsal and ventral networks in bilingual reading as a function of the native versus non-native language used to read (i.e., L1, L2) and L2 orthographic depth (i.e., opaque, transparent). To this end, we controlled for AoA and language proficiency, selecting two groups of late sequential reading bilinguals composed of native Spanish-speakers who either have an opaque (English; Spanish-English group) or a transparent (Basque; Spanish-Basque group) L2. Both groups acquired L1

reading first and then L2 reading after 6 years of age and have similar high proficiency levels in their L1 and L2. An additional main motivation of the present study was to examine to what extent the involvement of the dorsal and ventral networks in bilingual reading and the recruitment of the left vOT depends on the demands posed by the reading task. Most reading studies conducted with monolingual and bilingual populations have used either low-level (i.e., passive reading) or high-level (i.e., reading for meaning) reading tasks and, to date, no studies have examined within the same bilingual sample the influence of reading demands. Placing perceptual or semantic task demands on reading processes can modulate the neural computations carried out by dorsal and ventral reading networks, and especially of the left vOT within the ventral stream.

The left vOT plays a crucial role in reading and has been proposed as a critical site for orthographic processing during visual word recognition. However, its functional role is still the subjected to important debates. Some theoretical accounts highlight its involvement in bottom-up prelexical computation processes of visual word forms (Dehaene & Cohen, 2011), while others emphasize its implication in integrating visuospatial features abstracted from sensory inputs with higher-level associations, *via* bottom-up and top-down connections (Price & Devlin, 2011). Interestingly, studies supporting a prelexical computational role of the vOT have mainly used low-level reading tasks (e.g., passive silent reading; (Cohen et al., 2002; Dehaene et al., 2010; Pegado et al., 2011) whereas most of the studies favoring an interactive account of the vOT have used high-level reading tasks (e.g., lexical decision; Seghier & Price, 2013; Twomey et al., 2011; Woollams et al., 2011).

Thus, the present fMRI study is aimed at investigating the involvement of the main regions along dorsal and ventral reading networks and the functional dynamics among these in

late bilinguals as a function of the native versus non-native language (L1, L2), L2 orthographic depth (transparent, opaque), and the demands of the reading task (perceptual, semantic). To do so, in line with previous neuroimaging studies, the reading tasks included words (i.e., orthographically legal pronounceable letter strings that have both semantic and phonological representations), pseudowords (i.e., orthographically legal pronounceable letter strings that have corresponding word-like phonological, but not semantic representations) and consonant strings (i.e., illegal non-pronounceable letter strings, lacking both semantic and phonological word-like associations (e.g., Price et al., 1996). This stimuli manipulation allows examination of reading processes that typically rely on phonological computations carried out by regions along the dorsal stream, and on mapping orthographic-lexical stimuli onto semantic representations supported by regions along the ventral stream (Mechelli et al., 2003; Sandak et al., 2004; Schlaggar & McCandliss, 2007).

Based on previous evidence, we expect that I) reading in L2, the later acquired language, will show stronger engagement of regions along the dorsal and ventral streams relative to reading in L1 (e.g., Wartenburger et al. 2003); II) regarding orthographic depth, whereas the group with a transparent L2 will exhibit greater reliance on regions along the dorsal (phonologically-tuned) pathway, the group with an opaque L2 will show stronger recruitment of ventral (lexico-semantic-tuned) regions (e.g., Das et al., 2011); III) with respect to task demands, we will specifically test if the left vOT will be similarly recruited across the semantic and perceptual reading tasks, which would support the prelexical computational hypothesis (e.g., Dehaene and Cohen 2011), or if task demands will modulate the engagement of left vOT, which would support the interactive account hypothesis (e.g., Price and Devlin 2011); IV) stimuli will modulate the engagement of reading networks, with dorsal regions subserving phonological

processing more strongly recruited for pseudowords (which are assumed to lack semantic information and rely on phonological representations) relative to words (e.g., Mechelli et al., 2003).

Additionally, we also expect that V) functional connectivity analyses will reveal different dynamics among dorsal and ventral regions during word reading in the same direction as the regional hypotheses mentioned above, with the exception that we expect to observe tighter functional coupling among regions for reading in L1 relative to reading in L2 due to a larger prior history of coactivations for reading in L1 in late bilinguals (Hebb, 1949).

5.2 Materials and Methods

Participants

The final study sample consisted of 37 right-handed late bilinguals with Spanish as their L1 (mean age 29.10 ± 6.54 ; 22 females). All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. The sample was divided into two groups of participants who either have an L2 with an opaque orthography (English; $n = 19$) or a transparent orthography (Basque; $n = 18$). All subjects acquired the L2 after age 6 and were highly proficient in their L1 and L2, with minimal exposure to other languages (see Table 1).

Language proficiency was assessed using objective and subjective measures. An adaptation of the Boston Naming Test (Kaplan et al., 1983) in Basque, English and Spanish, controlling for cognates across these three languages, was used as an objective measure of vocabulary. Participants performed this picture-naming test, including 77 to-be-named drawings, in their respective two languages. They also filled in a language background questionnaire where

they self-rated their proficiency levels in L1 and L2 and also rated the percentage of daily exposure to L1 and L2. Importantly, there were no differences between the groups in terms of age, AoA of the L2, L1 and L2 proficiency measures, or in their overall daily exposure to L1 and L2 (all $ps > .05$). At the within-group level, while both objective and subjective measures indicated high proficiency in L1 and L2, proficiency and daily exposure were significantly higher in the L1 than in the L2 and age of acquisition was of course later in the L2 than in the L1 ($ps > .001$). Data from 1 additional participant were excluded from analysis due to excessive head motion during imaging (i.e., > 2 mm across the entire scan session). Prior to taking part in the experiment, all participants gave written informed consent in compliance with the ethical regulations established by the BCBL Ethics Committee and the guidelines of the Helsinki Declaration. Participants received monetary compensation for their participation.

Table 1. Participants' demographics and linguistic characteristics by group. Standard deviations in parentheses.

	Spanish-Basque (n=18)	Spanish-English (n=19)	<i>p</i> values
Age (years)	31.0(7.8)	27.3(4.5)	$p = .10$
Gender (% female)	66.6	52.6	$p = .38$
Age of acquisition (years)			
L1	0	0	
L2	11.2 (7.1)	8.0 (2.1)	$p = .09$
Proficiency (correctly-named pictures)*			
L1	76.3 (1.3)	76.7 (0.7)	$p = .41$
L2	63.7 (10.0)	68.2 (7.6)	$p = .15$
Proficiency (self-rated)†			
L1	9.5 (0.7)	9.6 (0.6)	$p = .80$
L2	8.0 (0.9)	8.2 (0.8)	$p = .42$
Average daily exposure (%)§			
L1	68.1 (14.2)	72.2 (11.8)	$p = .36$
L2	22.5 (16.1)	26.6 (10.8)	$p = .38$

*Out of 77 pictures; § Average percentage across reading, writing, hearing, and speaking. *p* values corresponds to the t-test between groups, except for gender where a non-parameter chi-square test was used

Materials and Experimental Procedure

Participants carried out perceptual (low level) and semantic (high level) Go/No-Go tasks. In both tasks, subjects were visually presented with different character strings: words (e.g., curtain), pseudowords (e.g., cinguda), and consonant strings (e.g., fstgklg). Stimuli were visually presented in the center of the screen. During the perceptual task, participants were asked to press a button any time they saw a colored letter within a string (e.g., brother). In the semantic task, they were required to press a button when they were presented with the name of an animal (e.g., turtle).

The number of L1 (Spanish) stimuli presented within each task included 40 high-frequency words, 40 low-frequency words, 40 pseudowords, 40 consonant strings and 13% go trials. In the L2 (English or Basque), participants were presented with a similar number of stimuli and go trials per task as in the L1. Cognate words across languages were excluded to eliminate ambiguity. All words, between and within languages, were matched on frequency, number of orthographic neighbors and length (i.e., 5-8 characters). All pseudowords were created as a function of the selected words using Wuddy (Keuleers & Brysbaert, 2010).

The study was administered in two separated sessions based on the language of the materials: L1 or L2. The order of these L1 or L2 sessions was counterbalanced across participants. However, to prevent participants generalizing the reading strategy used in the semantic task to the perceptual task within each of the language sessions, the perceptual task was always administered first, followed by the semantic task.

fMRI Data Acquisition

Whole-brain fMRI data acquisition was conducted on a 3-T Siemens TRIO whole-body MRI scanner (Siemens Medical Solutions, Erlangen, Germany) at the Basque Center on Cognition, Brain and Language (BCBL), using a 32-channel whole-head coil. Snugly fitting headphones (MR Confon, Magdeburg, Germany) were used to dampen background scanner noise and to enable communication with experimenters while in the scanner. Participants viewed stimuli back-projected onto a screen with a mirror mounted on the head coil. To limit head movement, the area between participants' heads and the coil was padded with foam and participants were asked to remain as still as possible.

In each session, functional images were acquired in four separated runs using a gradient-echo echo-planar pulse sequence with the following acquisition parameters: TR= 2000 ms, TE= 25 ms, 35 contiguous 3-mm axial slices, 0-mm inter-slice gap, flip angle = 90°, Field of view = 218 mm, 64 x 64 matrix. Prior to each scan, four volumes were discarded to allow T1-Equilibration effects. High-resolution T1-weighted anatomical images were also collected. Within each functional run, the order of the study conditions (i.e., words, pseudowords, consonant strings, go trials) and the inter-trial intervals of variable duration corresponding to the MR frames that served as baseline or null events (i.e., fixation cross presented in the center of the screen, 30% of the total collected functional volumes) were determined with an algorithm designed to maximize the efficiency of the recovery of the blood oxygen level-dependent (BOLD) response (Optseq II; Dale 1999).

fMRI Data Analysis

Standard SPM8 (Wellcome Department of Cognitive Neurology, London) preprocessing routines and analysis methods were employed. Images were corrected for differences in timing of slice acquisition and were realigned to the first volume by means of rigid-body motion transformation. High-resolution anatomical T1 images and functional volumes were then co-registered and spatially normalized to T1 and echo-planar imaging templates, respectively, to enable anatomical localization of the activations. Templates were based on the MNI305 stereotaxic space (Cocosco et al., 1997) an approximation of Talairach space (Talairach & Tournoux, 1988). The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. During normalization, the volumes were sampled to 3-mm cubic voxels. Functional volumes were spatially smoothed with an 8-mm full width at half-maximum (FWHM) isotropic Gaussian kernel.

Statistical analyses were performed on individual participant data using the general linear model (GLM). fMRI time series data were modeled by a series of impulses convolved with a canonical hemodynamic response function (HRF). The motion parameters for translation (i.e., x, y, z) and rotation (i.e., yaw, pitch, roll) were included as covariates of noninterest in the GLM. Each trial was modeled as an event, time-locked to the onset of the presentation of each character string. The resulting functions were used as covariates in a GLM, along with a basic set of cosine functions that high-pass filtered the data, and a covariate for session effects. The least-squares parameter estimates of the height of the best-fitting canonical HRF for each study condition were used in pairwise contrasts. Contrast images from each subject were submitted to group analyses. At the group level, whole-brain contrasts between conditions were computed by performing one-sample t tests on these images, treating participants as a random effect. Brain coordinates

throughout the text, as well as in tables and figures, are reported in MNI atlas space (Cocosco et al. 1997).

Region-of-interest (ROI) analyses were performed with the MARSBAR toolbox for use with SPM8 (Brett et al., 2002). Based on previous neuroimaging evidence, we functionally selected five left-lateralized regions, including pars triangularis (BA 45; center of mass = -48 27 14; volume = 9776 mm³), pars orbitalis (BA 47; center of mass = -40 30 -7; volume = 2160 mm³), pars opercularis (BA 44; center of mass = -49 11 18; volume = 6184 mm³), STG (BA 22; center of mass = -51 -44 7; volume = 783 mm³) and inferior parietal cortex (IPC) (BA 40; center of mass = -30 -54 46; volume = 1984 mm³). All these regions consisted of active voxels identified from the whole-brain contrast All > Null across all participants, $q < .001$ false discovery rate (FDR) corrected.

Given recent evidence emphasizing the strong inter-subject variability in the location of the left vOT region involved in reading (Glezer et al., 2009, 2013; Vogel et al., 2012), in the present study we identified the left vOT following three different criteria: 1) literature ROI (litROI) or ROI identified based on a prior meta-analysis of reading studies (Jobard et al. 2003), building a 5-mm radius ROI sphere centered at -44 -58 -15 MNI coordinates; 2) based on the group activation (gROIs), performing a whole-brain analysis across all participants for the contrast Words > Null ($q < .01$ FDR; masked with Words > Consonant Strings, $p < .05$ uncorrected) and identifying a) the highest T value within the fusiform gyrus (FG) and b) the highest T value within the FG closest to Cohen's VWFA definition ($x = -43$, $y = -54$, $z = -12$; Cohen et al. 2002) to build 5-mm radius sphere ROIs centered at those values and 3) based on individual ROIs (iROIs), following the same approach described for the gROIs but identifying each of the local maximas to build the 5-mm radius sphere ROIs for each criteria at the

individual level and extracting the parameter estimates for each region at the single-subject level. The thresholding for these ROIs were Words > Null ($q < .05$ FDR; masked with Words > Consonant Strings, $p < .01$ uncorrected).

Thus, for the gROIs and iROIs approaches, masking the Word > Null contrast with Words > Consonant Strings allowed us to seek for activations in the left vOT that were related to identifying series of familiar strings. Moreover, for the gROIs and iROIs approaches, we also sought to examine whether the manner in which the local maxima within the left vOT is selected can determine the pattern of observed results: a) highest T value within the FG; and, b) highest T value within the FG closest to Cohen's VWFA definition.

We assessed functional connectivity via the beta correlation method (Rissman et al., 2004), implemented in SPM8 with custom Matlab scripts. The canonical HRF in SPM was fit to each occurrence of each condition and the resulting parameter estimates (i.e., beta values) were sorted according to the study conditions to produce a condition-specific beta series for each voxel. Two different functional connectivity analyses were performed: 1) pairwise connectivity between regions of interest within the ventral and dorsal reading networks; and 2) whole-brain functional connectivity with a left vOT seed region.

First, for the pairwise analysis we calculated beta-series correlation values for each pair of ROIs, participant and condition. Since the correlation coefficient is inherently restricted to range from -1 to +1, an arc-hyperbolic tangent transform (Fisher, 1921) was applied to these beta-series correlation values to make its null hypothesis sampling distribution approach that of the normal distribution. Then, seeking to test for dorsal versus ventral differences in functional connectivity strength as a function of our experimental design, these Fisher's Z normally

distributed values were submitted to a mixed-model analysis of variance (ANOVA) including Group (Spanish-English vs. Spanish-Basque) as a between-subjects factor and Network (ventral vs. dorsal), Language (L1 vs. L2), Task (perceptual vs. semantic) and Stimuli (words, pseudowords and consonant strings) as within-subjects factors. The selected ROIs for these functional connectivity analyses included the previously-described left-lateralized regions identified at the group level (i.e., pars orbitalis, triangularis, opercularis, STG, IPC) and the individually identified left vOT iROIs based on the highest T value within the FG. To ensure that differences between dorsal and ventral networks dynamics were not determined by differences in the cluster size of the functionally defined ROIs, we used 5-mm radius spheres centered at the highest local maximas for all the ROIs.

Second, for the whole-brain functional connectivity analysis, the beta series associated with the left vOT litROI seed were correlated with voxels across the brain to produce beta correlation images. Contrasts between beta correlation images were also subjected to an arc-hyperbolic tangent transform to allow for statistical inference based on the correlation magnitudes. Group-level and two-sample t-test were performed on the resulting subject contrast images to produce group correlation contrast maps.

5.3 Results

Behavioral and fMRI Results

Participants responded to the go trials during the fMRI task with an overall percentage of 90.18%, indicating that they paid attention to the task. Both groups responded to the same go trials across conditions. We performed two separate one-way ANOVAs with Group (Spanish-Basque bilinguals, Spanish-English bilinguals) as the between-subjects factor, with accuracy and

the average RTs on the in-scanner go trials as the dependent measures. These analyses did not reveal any effect of the factor Group either for accuracy, ($F(1, 34) = .74, p = .40, \eta_p^2 = .03$), or for the reaction time ($F(1, 34) = 1.13, p = .30, \eta_p^2 = .04$) measures.

To identify brain regions associated with reading processes across all participants and factors in the experimental fMRI design, we computed a whole-brain contrast for All trials > Null (see Figure 12A). Consistent with prior neuroimaging evidence (e.g., Lau, Phillips, & Poeppel, 2008), this contrast revealed the involvement of a predominantly left-lateralized set of regions including pars triangularis (BA 45), pars orbitalis (BA 47), pars opercularis (BA 44), STG (BA 22), IPC (BA 40), and vOT (BA 37).

ROI Analyses

We conducted ROI analyses to characterize the activation profile of regions of a priori interest for the main experimental conditions: Group (Spanish-English vs. Spanish-Basque), Language (L1 vs. L2), Task (perceptual vs. semantic), and Stimuli, (words, pseudowords and consonant strings). To avoid potential biases in the patterns of activation observed in these ROI analyses, these regions were selected from the general whole-brain All > Null contrast across all subjects, $q < .001$ FDR corrected, which yielded activations in most of the left-lateralized key regions involved in reading processes: IFG, posterior STG, inferior parietal cortex and vOT (see Figure 12B). Also, given the importance for the present study of the differential involvement of left IFG subregions in reading processes and evidence indicating that pars opercularis is part of the dorsal reading network and that pars orbitalis and triangularis are part of the ventral reading network, we sought to separately examine the pattern of activation within these IFG regions. Thus, we extracted fMRI parameter estimates from these ROIs and conducted hypotheses-driven

analyses based on 2 (Group: Spanish-Basque, Spanish-English) X 2 (Language: L1, L2) X 2 (Task: perceptual, semantic) x 3 (Stimuli: words, pseudowords, consonant strings) mixed-model ANOVAs, with the last three factors varied within-subjects. Here, we just describe the ROI results for the higher order interactions specifically related to the main study hypotheses. Table 2 summarizes all the significant main and interactive effects that emerged in these analyses.

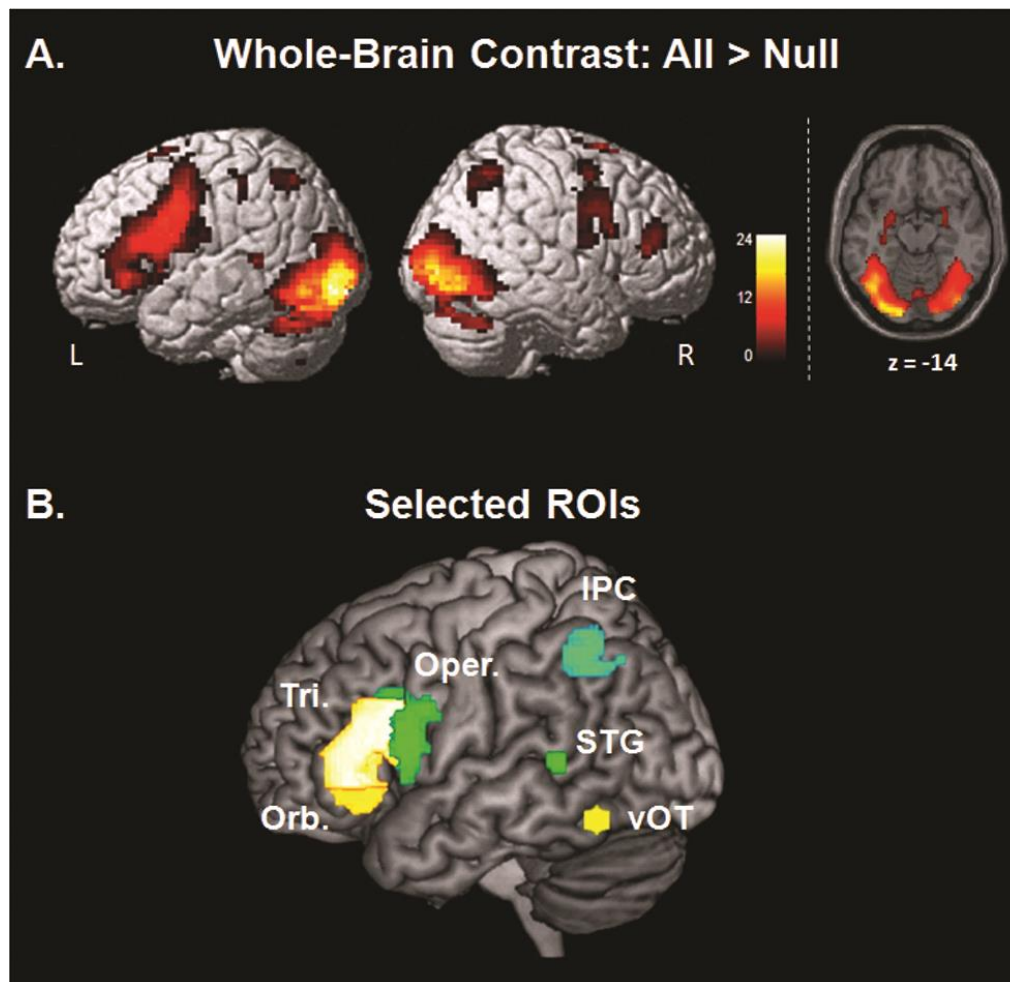


Figure 13. Brain renderings showing (A) activations for the All > Null whole-brain contrast across all subjects at a statistical threshold of $q < .001$ FDR-corrected and z-axis slice section for vOT cortex, and (B) location of the selected left-hemisphere ROIs within the ventral reading network (yellow shades), including pars triangularis, pars orbitalis and vOT, and within the dorsal reading network (green shades), including *pars opercularis*, STG y IPC for the dorsal reading network. Tri. = *pars triangularis*; Orb. = *pars orbitalis*; vOT = ventral occipitotemporal cortex; Oper. = *pars opercularis*; STG = superior temporal gyrus; IPC = inferior parietal cortex.

Table 2. Summary of the statistically significant effects observed in the ROI analyses of regions along the dorsal and ventral reading streams.

Region-of-interest (ROIs)	Coordinates (center of mass)			Main effects and interactions	<i>p</i> values
	x	y	z		
Dorsal-stream regions					
Left <i>pars opercularis</i> (BA 44)	-49	11	18	Group Language Stimuli Group X Stimuli Language X Stimuli Task X Stimuli	<i>p</i> < .05 <i>p</i> < .05 <i>p</i> < .001 <i>p</i> < .01 <i>p</i> < .001 <i>p</i> < .001 <i>p</i> < .01
Left superior temporal gyrus (STG; BA 22)	-51	-44	7	Group Language Stimuli Group X Stimuli Language X Stimuli	<i>p</i> < .01 <i>p</i> < .05 <i>p</i> < .001 <i>p</i> < .01 <i>p</i> < .01 <i>p</i> < .01
Left inferior parietal cortex (IPC; BA 40)	-30	-54	46	Language Group X Stimuli	<i>p</i> < .001 <i>p</i> < .05
Ventral-stream regions					
Left <i>pars triangularis</i> (BA 45)	-48	27	14	Stimuli Language X Stimuli Task X Stimuli	<i>p</i> < .001 <i>p</i> < .05 <i>p</i> < .05 <i>p</i> < .05
Left <i>pars orbitalis</i> (BA 47)	-40	30	-7	Language Stimuli Language X Stimuli	<i>p</i> < .05 <i>p</i> < .001 <i>p</i> < .01 <i>p</i> < .01
Left ventral occipitotemporal cortex (vOT; BA 37)*	-44	-58	-15	Language Stimuli Language X Stimuli Task X Stimuli	<i>p</i> < .01 <i>p</i> < .001 <i>p</i> < .01 <i>p</i> < .01 <i>p</i> < .01

* Left vOT was localized using different approaches (i.e., litROI / groupROI/ iROI). Here the reported coordinates correspond to the litROI. Results were similar across the approaches used to define this region

Dorsal Regions

Left pars opercularis. The ANOVA for this region revealed Group X Stimuli, ($F(2, 66) = 5.25, p < .01, \eta_p^2 = .14$) and Language X Stimuli ($F(2, 66) = 11.30, p < .001, \eta_p^2 = .25$) statistically significant interactions (see Figure 13). Post-hoc analyses showed that the *Group X Stimuli* interaction was due to a stronger engagement of this region for pseudowords by the group with transparent L1 and L2 (i.e., Spanish-Basque) relative to the group with transparent L1 and opaque L2 (i.e., Spanish-English) ($p < .05$), in line with hypothesis II. With respect to the *Language X Stimuli* interaction, simple-effect analyses also revealed greater activation for L2 words than L1 words ($p < .001$), confirming hypothesis I. Also, consistent with our prediction (hypothesis IV), this region was more strongly engaged for pseudowords than words in L1 reading ($p < .001$).

Left STG. Results for this region revealed statistically significant Group X Stimuli ($F(2, 64) = 6.72, p < .01, \eta_p^2 = .17$) and Language X Stimuli ($F(2, 64) = 4.87, p < .01, \eta_p^2 = .13$) interactions (see Figure 13). Post-hoc comparisons for the *Group X Stimuli* interaction revealed that the group with transparent L1 and L2 (i.e., Spanish-Basque) showed a stronger activation for words and pseudowords than the Spanish-English group, where L1 is transparent and L2 is opaque ($p < .05$). Simple-effect analyses for the *Language X Stimuli* interaction showed greater activation for L2 words than L1 words, and no other significant difference between L1 and L2 for the other Stimuli conditions ($ps > .05$). Additionally, within the L1, pseudowords elicited higher activation than words ($p < .001$). These results are consistent with hypotheses I and II, and qualified our prediction of stronger engagement of this region for pseudowords relative to words, which was observed only for L1 reading (hypothesis IV).

Left IPC. The ANOVA for this region revealed a statistically significant *Group X Stimuli* interaction ($F(2, 58) = 3.60, p < .05, \eta_p^2 = .11$; Figure 13). Simple-effects analyses showed that, consistent with hypothesis II, this interaction was due to a stronger recruitment of this region for words and pseudowords than for consonant strings only in the group of Spanish-Basque bilinguals ($p < .05$).

Ventral Regions

Left pars triangularis. ROI results for this region revealed a statistically significant *Language X Stimuli* ($F(2, 56) = 6.26; p < .05, \eta_p^2 = .18$) interaction. Simple-effect analyses revealed that this interaction was due to stronger activation for L2 words than L1 words ($p < .001$; Figure 13), in line with hypothesis I. In contrast, no differences between L1 and L2 were found for the other Stimuli conditions ($ps \geq .05$). Moreover, left *pars triangularis* was more strongly engaged for words than pseudowords in the L2 ($p < .01$). These differences were not observed in the L1 ($p = .20$).

Left pars orbitalis. The ANOVA for left *pars orbitalis* also showed a *Language X Stimuli* statistically significant interaction ($F(2, 46) = 5.76; p < .01, \eta_p^2 = .20$; see Figure 13). Simple-effect analyses revealed that this interaction was due to a stronger recruitment of this region for words in the L2 relative to words in the L1 ($p < .001$), confirming our hypothesis I. No other stimuli conditions showed differential engagement for L2 vs. L1. Also, L2 words showed greater activation than L2 pseudowords ($p < .01$). In contrast, the L1 pseudowords elicited greater activation than L1 words ($p < .01$).

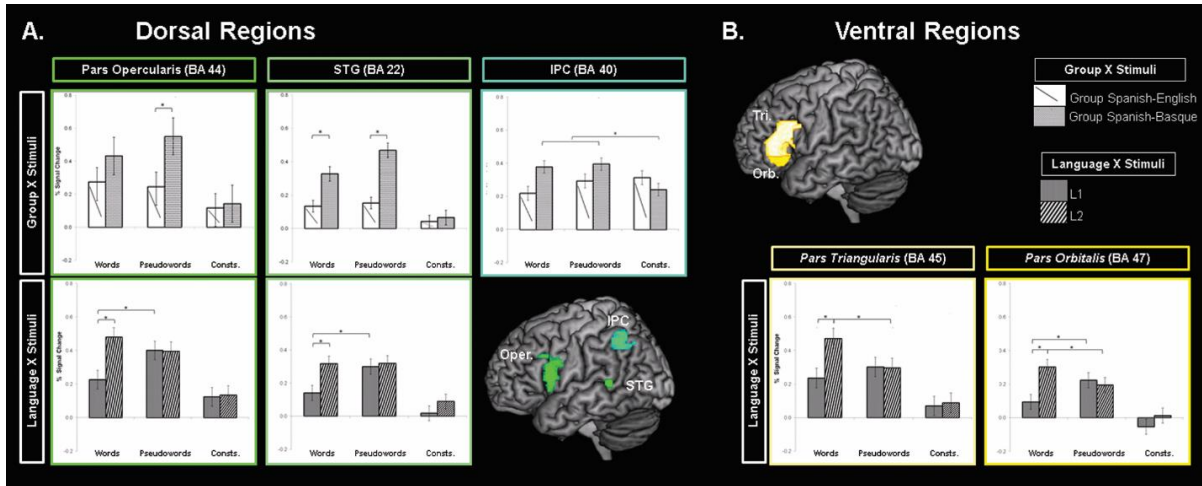


Figure 14. ROI analyses for left-lateralized regions within the dorsal and ventral reading network. A) Dorsal regions showed Group X Stimuli and Language X Stimuli interactions in *pars opercularis* (-49 11 18; BA 44) and STG (-51 -44 7; BA 22), and Group X Stimuli interaction in IPC (-30 -54 46; BA 40). B) Ventral regions within the left IFG, including *pars triangularis* (-48 27 14; BA 45) *pars orbitalis* (-40 30 -7; BA 47), showed Language X Stimuli interactions. Bar graphs show averaged parameter estimates (% signal change) for these interactions as a function of Group/Language and Stimuli. Asterisks within bar graphs indicate comparisons that showed statistically significant differences in % signal change ($p < .05$). Consts. = consonant strings; Oper. = *pars opercularis*; STG = superior temporal gyrus; IPC = inferior parietal cortex; Tri. = *pars triangularis*; Orb. = *pars orbitalis*.

Left vOT. Due to recent evidence emphasizing the strong inter-subject variability in the location of the left vOT (Glezer et al. 2009, 2013), here we used three different criteria to identify this region: 1) *litROI*; 2) *gROIs*, identifying the a) highest T value within the FG and the b) highest T value within the FG closest to Cohen’s VWFA definition (Cohen et al. 2002); and, 3) *iROIs*, following the same approach described for the *gROIs* but identifying each of the local maximas to build the ROIs at the individual level and extracting the parameter estimates for each region at the single subject level (see *Methods* section for further details).

The ANOVA carried out for the *litROI* revealed statistically significant Language X Stimuli ($F(2, 62) = 6.29, p < .01, \eta_p^2 = .17$) and Task X Stimuli ($F(2, 62) = 5.50, p < .01, \eta_p^2 =$

.15) interactions (Figure 15). Post-hoc analyses for the *Language X Stimuli* interaction revealed that this region was more strongly engaged for words and consonant strings in L2 than in L1 ($ps < .05$), in line with hypothesis I. This Language effect was not observed for pseudowords. Additionally, L1 pseudowords recruited this region more strongly than L1 words ($p < .01$); an effect that was not present in L2 ($p = .30$).

Regarding the *Task X Stimuli* interaction, this left vOT *litROI* showed the Task effect¹, or stronger activation for words in the semantic-task than in the perceptual-task ($p < .001$), in line with hypothesis III. This effect was not observed for pseudowords and consonant strings ($p = .20$). Moreover, words also showed higher activation than consonant strings only in the semantic-task ($p < .001$), an effect that was not observed in the perceptual task ($p = .60$).

Four separate ANOVAs for the *gROIs* and *iROIs* identified based on the highest T value within the FG and on the highest T value within the FG closest to Cohen's VWFA definition were also conducted. In line to what we observed in the *litROI* analysis, in all these ANOVAs interactions involving Language X Stimuli ($F(2, 60) \geq 4.10$, $ps < .05$, $\eta_p^2 \geq .10$) and Task X Stimuli ($F(2,60) \geq 6.50$, $ps < .05$, $\eta_p^2 \geq .17$) emerged.

To test for potential differences between these two ROI definitions and the selection of their local maximas, we carried out two separated 2 (ROI approach: *gROIs* vs. *iROIs*) X 2 (Local maxima selection: highest T value vs. highest T value closest to Cohen's VWFA) repeated measures ANOVAs, one for the language effect (i.e., activation for L2 words minus activation for L1 words) and one for the task effect (i.e., activation for words in the semantic task minus

¹ This Task effect for word reading also emerged in left pars opercularis and triangularis ROIs (see Table 2). As indicated at the beginning of the ROI Analyses section, here we just describe the higher order interactions related to our main hypotheses and, therefore, results related to task demands are restricted to analysis involving the left vOT.

activation for words in the perceptual task). These analyses revealed no statistically significant main effects or interactions for the ROI approach and Local maxima selection factors for the language effect ($F(1, 28) \leq 4.22, ps \geq .05, \eta_p^2 \leq .13$), or for the task effect analyses ($F(1, 28) \leq 1.35, ps \geq .26, \eta_p^2 \leq .05$). Figure 15 shows ROI activations for *gROIs* and *iROIs* where local maximas were selected based on the highest T value within the FG, at the group or at the individual level, respectively. Thus, regional activation of the left vOT was modulated by language and task effects. These results were consistently confirmed across the different criteria used to identify this region, in line with hypotheses I and III.

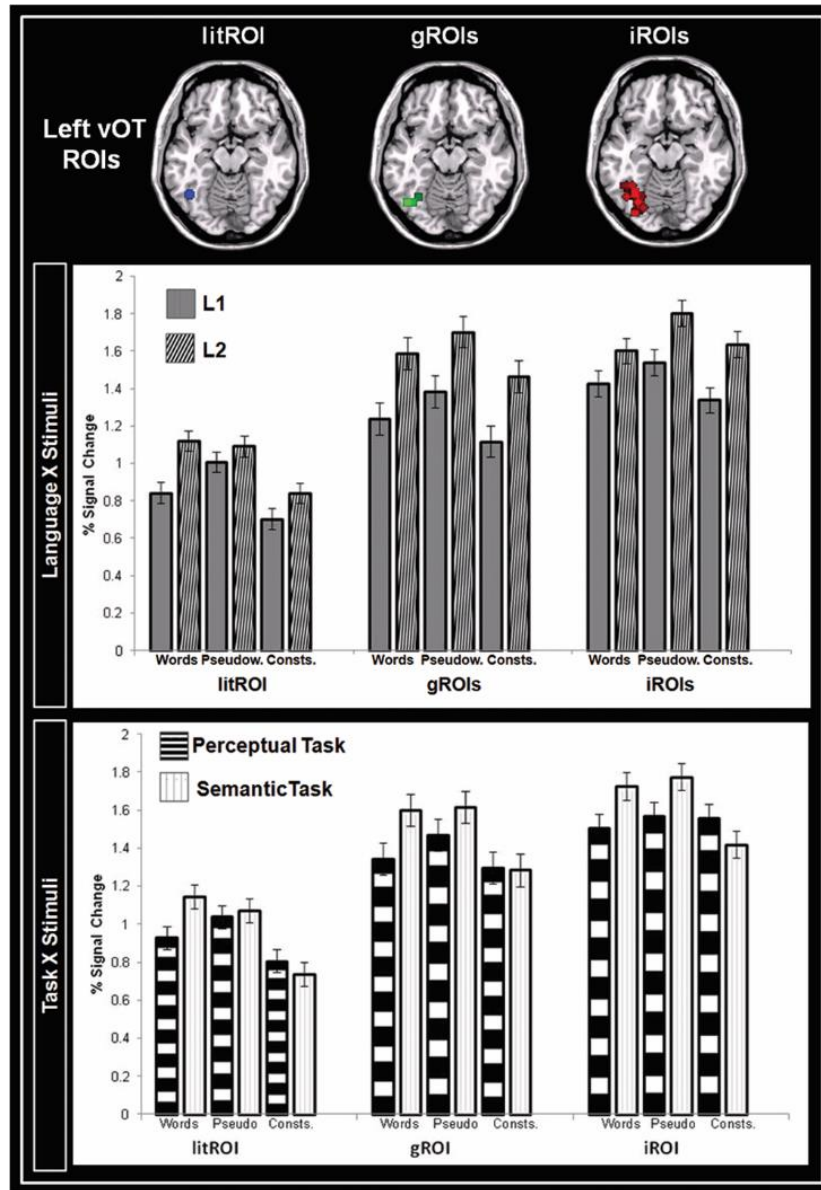


Figure 15. Left vOT ROI analyses based on three different approaches: Literature-based ROI (litROI), group-based ROIs (gROIs), and individually defined ROIs (iROIs). Bar graphs show averaged parameter estimates (% signal change) for these three left vOT ROI definitions as a function of Language/Task and Stimuli. For gROIs and iROIs the bar graphs show results for ROIs where local maximas were selected based on the highest T value within the FG, at the group or at the individual level, respectively. Pseudow. = pseudowords; Consts. = consonant strings.

Functional Connectivity among Dorsal and Ventral Reading Networks

Here, we sought to investigate differences in temporal coupling between nodes within the main dorsal and ventral reading networks as a function of Group (Spanish-English vs. Spanish-Basque), Language (L1 vs. L2), Task (perceptual vs. semantic), and Stimuli, (words, pseudowords and consonant strings). To do so, we used the beta-series correlation method (Rissman et al., 2004), building 5-mm-radius spheres centered at the highest local maxima within the previously described left-lateralized ROIs (see Methods section for further details).

Fisher *z*-score transformed beta-series correlation values between all nodes within the ventral (pars triangularis, pars orbitalis, vOT) and dorsal (pars opercularis, STG, IPC) reading networks (Figure 16A) for each condition in our experimental design were averaged and submitted to mixed-model ANOVAs including Group (Spanish-English vs. Spanish-Basque) as a between-subjects factor and Network (ventral vs. dorsal), Language (L1 vs. L2), and Task (perceptual vs. semantic) as within-subject factors. Based on prior evidence supporting a differential involvement of these reading networks as a function of stimuli type, we carried out three separate ANOVAs for words, pseudowords and consonant strings². The ANOVA for word stimuli revealed statistically significant Network X Language ($F(1, 35) = 4.19, p < .05, \eta_p^2 = .11$), and Network X Task ($F(1, 35) = 8.88, p < .01, \eta_p^2 = .20$) interactions. In contrast, these interactions did not emerge for the pseudowords ($F(1, 35) \leq 1.01, ps \geq .30, \eta_p^2 \leq .03$) and consonant strings ($F(1, 34) \leq 1.30, ps \geq .26, \eta_p^2 \leq .04$) analyses.

² We also conducted the full ANOVA including Stimuli as a within-subject factor. This analysis revealed Type Network X Language X Stimuli ($F(2, 68) = 4.42, p < .05, \eta_p^2 = .12$), and Network X Task X Stimuli ($F(2, 68) = 7.07, p < .01, \eta_p^2 = .17$) as the highest order interactions. These results also support carrying out separated ANOVAs for each stimuli type.

Post-hoc analyses for the Network X Language interaction for word stimuli revealed a statistically significant decrease in the strength of functional coupling in the dorsal network for reading words in L2 relative to L1 ($p < .001$; see Figure 16A.1). This effect was not observed in the ventral network, which showed similar connectivity strength for word reading in the L1 and L2 ($p = .10$). The Network X Task interaction for word stimuli was due to a statistically significant increase in the coupling strength between nodes within the ventral network for the semantic task relative to the perceptual task ($p < .01$; Figure 16A.2). This Task effect was not observed in the dorsal network ($p = .75$). Thus, whereas functional connectivity between regions within the dorsal network was modulated by Language, showing tighter coupling for reading words in L1 than in L2, functional connectivity between regions within the ventral network was modulated by Task demands, with stronger coupling observed for the semantic than for the perceptual task.

These results confirmed and qualified our prediction (hypothesis V), showing a stronger functional coupling for L1 relative to L2 only in the dorsal network and tighter connectivity among regions along the ventral for semantic versus perceptual word reading.

Whole-brain functional connectivity with left vOT

Given that the implementation of additional phonological and semantic processes supporting reading in transparent and opaque orthographies (e.g., Paulesu et al. 2000) depends upon initial stages of visual word recognition thought to be carried out by left vOT (Twomey et al. 2011), here we sought to use whole-brain functional connectivity methods to identify brain regions that were recruited in concert with left vOT during word reading as a function of L2 orthographic depth. To do so, the beta series associated with the left vOT litROI were correlated

with voxels across the brain to produce beta correlation images. Group-level t-tests were performed on the resulting subject contrast images to produce group correlation contrast maps for reading words relative to baseline, separately for the group of bilinguals with a transparent L2 (i.e., Spanish-Basque) and for the group with an opaque L2 (i.e., Spanish-English) at a statistical threshold of $q < .0001$ FDR-corrected.

The analysis for the group with a transparent L2 revealed coactivations extending anteriorly from left vOT to lateral temporal cortex (57 voxels in superior temporal gyrus, BA 22; 26 voxels in middle temporal gyrus, BA 21), as well as coactivated clusters in left parietal cortex (76 voxels in IPC, BA 40; 30 voxels in supramarginal gyrus, BA 40), IFG (37 voxels in *pars opercularis*, BA 44) and middle frontal gyrus (10 voxels, BA 9/46; see Figure 16B.1). In contrast, the analysis for the group with an opaque L2 revealed extended coactivations anteriorly from the left vOT to posterior lateral temporal cortex (37 voxels in middle temporal gyrus, BA 21; 35 voxels in inferior temporal gyrus, BA 22), as well as coactivated clusters in left IFG (81 voxels in *pars triangularis*, BA 45) and middle frontal gyrus (23 voxels, BA 9/46). Thus, as expected, whereas regions along the dorsal reading network showed tight coupling with left vOT for the group with a transparent L2, regions along the ventral reading network were strongly coactivated with left vOT for the group with an opaque L2. Importantly, this pattern of coupling dynamics with left vOT as a function of L2 orthographic depth also holds for the contrast involving reading L2 words versus resting baseline (at a slightly lower statistical threshold of $q < .005$ FDR-corrected due to the lower number of observations in this analysis) but this was not the case for the contrast involving reading L1 words versus baseline. These results strongly support our predictions (hypothesis V, in line with hypothesis II), showing a clearly segregated profile of

coactivations during L2 word reading along the dorsal pathway for the group with a transparent L2 and along the ventral pathway for the group with an opaque L2.

Finally, we conducted a two-sample t-test comparison for the whole-brain functional connectivity with left vOT for reading words relative to baseline, which confirmed significant between-group differences ($q < .05$ FDR-corrected) in the coupling strength of the left vOT with regions along the dorsal stream for the comparison Spanish-Basque > Spanish-English and along the ventral reading pathway for the comparison Spanish-English > Spanish-Basque (Figure 16B.2).

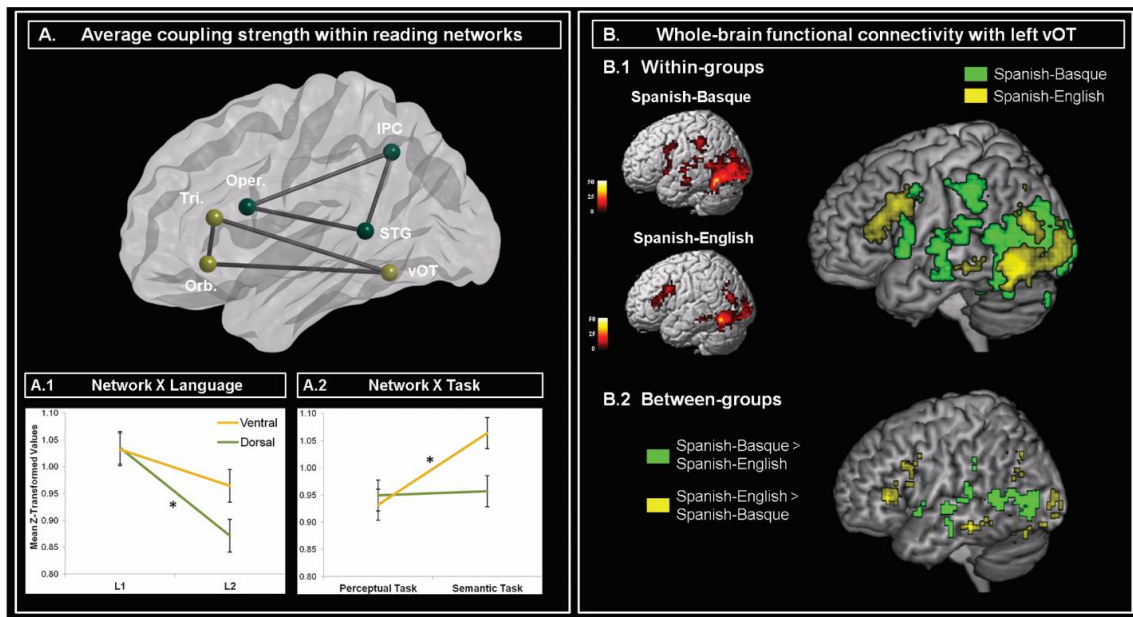


Figure 16. Functional connectivity analyses for ventral and dorsal reading networks. (A) A schematic sagittal view of the regions within dorsal (green) and ventral (yellow) reading networks and the pairwise connections among them that were submitted to functional connectivity analyses. All nodes correspond to 5-mm radius spheres centered at the highest local maxima for left-lateralized regions identified at the group level (i.e., *pars orbitalis*, *triangularis*, *opercularis*, STG, IPC) and at the individual level (iROIs) for the left vOT, based on the highest T value within the FG. Line graphs show average coupling strength (i.e., mean z-transformed values of the beta-series correlation) for processing word stimuli for the (A.1) Network X Language and (A.2) Network X Task interactions. Asterisks indicate comparisons that showed statistically significant differences in average strength of functional connectivity ($ps < .05$). (B) Left-hemisphere brain renderings showing whole-brain functional connectivity maps with left vOT for the contrast Words > Null (B.1) separately for the Spanish-Basque (in green) and Spanish-English (in yellow) groups at a FDR-corrected statistical threshold of $q < .0001$ (top panel) and (B.2) between-group Spanish-Basque > Spanish-English (in green) and Spanish-English > Spanish-Basque (in yellow) comparisons at a FDR-corrected statistical threshold of $q < .05$ (bottom panel). Tri. = *pars triangularis*; Orb. = *pars orbitalis*; vOT = ventral occipitotemporal cortex; Oper. = *pars opercularis*; STG = superior temporal gyrus; IPC = inferior parietal cortex.

5.4 Discussion

The present study was aimed at investigating bilingual reading and the contributions of the native versus non-native language (L1, L2), L2 orthographic depth (transparent, opaque), task demands (perceptual, semantic) and stimuli type (words, pseudowords, consonant strings) to the regional activation and functional connectivity of areas within dorsal and ventral reading networks. To this end, we tested two groups of late bilinguals matched in terms of their L1 and L2 proficiency levels, daily exposure to their respective L1 and L2, age of acquisition of their L2 and minimal exposure to other languages, and differentiated in terms of the orthographic depth of their L2 (transparent vs opaque).

Our findings support the dual-stream hypothesis in bilingual reading (Pugh et al, 2001). In line with our main hypotheses, we found evidence from both regional and functional connectivity analyses indicating 1) effects of the native versus non-native language (L1, L2) with stronger recruitment of regions for word reading in L2 relative to L1, as well as tighter coactivation among regions within the dorsal reading network for word reading in L1 versus L2; 2) L2 orthographic depth was associated with differential engagement of areas along the dorsal pathway, being more strongly engaged for participants in the Spanish-Basque group than for participants in the Spanish-English group, as well as tighter functional connectivity during L2 word reading between the left vOT and the dorsal regions for the group with a transparent L2 and between the left vOT and ventral regions for the group with an opaque L2; 3) semantic reading demands relative to perceptual reading demands elicited stronger recruitment of the left vOT across the several methodological approaches used to identify this region, as well as stronger coupling between regions within the ventral reading network; and, 4) stronger activation for pseudowords relative to words in left *pars opercularis* and left STG dorsal regions,

exhibiting a phonological pattern of activation during L1 reading. These main findings are discussed below in four sections related to the main hypotheses and factors manipulated in the present study: Language used to read, L2 orthographic depth, Task demands and Stimuli type (hypothesis V focused on functional connectivity is discussed throughout the four sections in relation to findings from this analysis associated with these factors.

Language Effects (L2 > L1) across Ventral and Dorsal Regions and Strengthened Coupling within the Dorsal Stream for L1 Reading

L1 and L2 word reading modulated regions across both ventral and dorsal streams. As predicted by hypothesis I, all IFG regions, STG, and vOT showed greater regional activation for reading words in L2 than in L1. This effect is thought to be determined by the higher effort required to read in L2 in late bilinguals (Wartenburger et al., 2003; Yetkin et al., 1996) and is consistent with the linguistic profile of our participants, whose L2 proficiency level is high but still lower than their L1 proficiency level. Regarding language effects of reading in the native versus non-native language in left vOT, previous reading studies with monolingual samples suggested that activation in this region can be tuned by language experience (Song et al., 2010; Xue et al., 2006; 2010). Our results suggest that this seems also to be the case in late bilinguals who showed stronger left vOT engagement for reading words in the L2 relative to the L1 across all the ROI approaches used to identify this region.

Our functional connectivity results support and qualify inferences from the regional activation data regarding language effects, in line with hypotheses V. Functional coactivation between regions within dorsal and ventral networks was similar for L1 word reading, but it decreased significantly for L2 relative to L1 in the dorsal stream and numerically in the ventral

route. Stronger coactivation for L1 relative to L2 reading can be explained based on the prior history of coactivation among these brain regions, in line with a Hebbian-like learning rule (Harmelech et al., 2013; Hebb, 1949). This can be especially plausible for a cognitive function we train on a daily basis such as reading and for comparisons involving L1 versus L2 in late bilinguals. Nevertheless, our data showed that this difference in the coactivation among regions for reading words in L2 relative to L1 was only statistically significant in the dorsal stream.

Prior research suggests that L2 is acquired through the same neural pathways responsible for L1 acquisition (Perani & Abutalebi, 2005). According to Pugh et al.'s (2001) brain model of reading, when new words are read they are initially assigned to the dorsal pathway for a correct integration of semantic, orthographical, lexical and phonological processes. Then, once they are learnt, words are mainly read to the ventral pathway for rapid word identification, which is the main process involved in reading. Thus, the use of the available neural scaffolding from the L1 may contribute to make reading in L2 less dependent on the specific computations carried out between all the nodes within the dorsal network.

L2 Orthographic Depth modulates Regional Activation and Functional Connectivity along the Dorsal and Ventral Reading Networks

Consistent with hypothesis II, all regions along the dorsal pathway showed greater activation for the group with a transparent L2 relative to the group with an opaque L2. Neuroimaging studies on reading have previously suggested that the activation in the dorsal areas here examined is strongly related to phonological processing (Buchsbaum & D'Esposito, 2008; Graves et al., 2008). Specifically, the IPC has been previously linked to the phonological loop (Paulesu et al., 1993). In fact, in prior studies using bilingual samples, second-language

phonetic contrast has also shown parietal cortex engagement (Callan et al., 2003; Das et al., 2011). With respect to the STG, Meschyan and Hernández (2006) found that this region was more strongly engaged for reading in a transparent (Spanish) than in an opaque orthography (English). However, this finding included both the effects of language transparency and native versus non-native language, since Meschyan and Hernández's (2006) study only included one group of participants with a transparent L1 and an opaque L2. In the present study, we varied the orthographic depth of the L2 between groups, while controlling for proficiency and language (L1, L2) exposure. Our results of stronger engagement of dorsal regions for the group with both transparent languages (i.e., Spanish-Basque) reflect the sensitivity of regions within this network to sublexical orthography-to-phonology conversions, probably due to the more consistent grapheme-to-phoneme mapping of orthographically transparent languages (Paulesu et al. 2000; Rueckl et al., 2015).

Nevertheless, it is important to note that results of the present study did not fully support our hypothesis II in regard to stronger engagement of regions along the ventral network for the group with an opaque L2 compared to the group with a transparent L2. Having a group with mixed (transparent and opaque) orthographies might reduce the sensitivity of the design to capture this regional modulation in the engagement of areas along the ventral network. Prior studies testing monolinguals with either an opaque or a transparent L1 suggest that this may indeed be the case (e.g., Paulesu et al., 2000).

Given previous evidence suggesting that orthographic depth has an impact on the semantic and phonological computations needed for successful reading (e.g., Das et al., 2011) and that the left vOT is a critical hub for visual word recognition (e.g., Twomey et al. 2011), we considered that the left vOT may be a critical region to observe differential functional dynamics

with ventral and dorsal reading networks. Thus, in line with hypothesis V and different from the connectivity analysis circumscribed to the functional coupling within each of the reading networks, whole-brain connectivity analysis using the left vOT as a seed was carried out to examine the profile of functional coactivation based on L2 orthographic depth. This analysis revealed a strikingly segregated profile in the coupling of left vOT with regions along the ventral network in the group with an opaque L2 and with regions along the dorsal network for the group with a transparent L2. Importantly, these results were observed during word reading, with further analysis indicating that this pattern of coactivation with left vOT holds for word reading in L2, but not for word reading in L1.

These findings are consistent with evidence suggesting that transparent orthographies with strong letter-to-sound mapping rely more on dorsal regions and that opaque orthographies rely more on lexico-semantic processes carried out by regions along the ventral pathway (Das et al. 2011; Paulesu 2000). Moreover, the present evidence highlights the importance of examining not only functional connectivity among the main nodes within the reading networks, but also the interactions among regions between both networks and in particular with the left vOT.

Semantic Reading Demands Elicit Stronger left vOT Engagement and Functional Connectivity among Regions within the Ventral Stream.

Within the ventral stream, special attention was paid in the present study to the left vOT. It has been suggested that this region is involved in processing prelexical representations of visual word forms (Dehaene & Cohen, 2011). However, other views have challenged this interpretation, based on evidence indicating that left vOT also participates in top-down predictions mediated by feedback connections interacting with bottom-up sensory inputs

(Carreiras et al., 2014b; Price & Devlin, 2011). To further unravel to what extent this region is sensitive to task-related modulations in bilinguals, in line with our hypothesis III, we manipulated reading demands in our fMRI experimental design. To our knowledge, this is the first study to examine in bilinguals whether the activation profile of the vOT differs as a function of perceptual versus semantic reading tasks, using a within-subject manipulation. Moreover, based on recent evidence (Glezer et al. 2009; 2013), here we sought to examine the regional activation of the vOT attending to different criteria to identify it: coordinates from a prior meta-analysis and activation at the group and individual subject levels. It has been suggested that there is a strong inter-subject variability in the location of this region, probably due to its rapid re-adaptation to support a phylogenetically new skill (Bouhali et al., 2014; Dehaene & Cohen, 2011) which may have determined the mixed results and interpretations put forward in previous studies in regard to the putative role of this region in reading (Glezer et al. 2013).

Importantly, across the different approaches used in the present study to identify the left vOT (i.e., litROI, gROIs and iROIs), our results consistently revealed that task effects modulated its pattern of regional activation. Since experimental stimuli were carefully matched across both tasks, this effect cannot be due to purely prelexical computation processes. Modulation of vOT activation by reading demands suggests that this region integrates bottom-up with higher order information in line with the interactive account (Devlin et al., 2006; Price & Devlin, 2011). Moreover, the consistency of the effects observed in left vOT across the different localization strategies used here strongly support that these findings are not a mere topographic artifact.

Finally, in line with hypothesis V and previous evidence highlighting the role of the ventral reading stream in semantic processing, we observed tighter coupling among nodes within the ventral network for word reading under semantic versus perceptual demands. A remaining

open question is to what extent using a reading task that further taxes phonological computations, such as a rhyming reading task (Booth et al., 2006; Cao et al., 2013) would yield stronger coupling among nodes within the dorsal network relative to a semantic reading task. Future neuroimaging research on bilingual reading should further characterize the impact of reading demands on the dynamics of ventral and dorsal reading pathways.

Stronger Engagement of Pseudowords versus Words in Dorsal Regions for L1 Reading

The language used to read (L1, L2) interacted with stimuli types, revealing relevant results of comparisons involving words and pseudowords in regions along the dorsal network. *Pars opercularis* and STG were more strongly recruited for pseudowords than words in L1 reading, while this effect was not present in L2 reading. The *pars opercularis* and STG are known for their involvement in phonological decoding (Simos et al., 2002; Zatorre et al., 1992). As pseudowords have no stored semantic representations, they may activate phonological processes more strongly because the phonological associations are less readily retrieved (Price et al. 1996). Thus, greater engagement of these regions for pseudowords likely reflects phonological decoding or examining the correspondence between graphemes and phonemes to compute word and pseudoword pronunciation.

Additionally, stronger engagement for pseudowords than words during L1 reading was observed in *pars orbitalis*. Extensive evidence has linked *pars orbitalis* with increasing demands on semantic retrieval in the context of conflict (Badre & Wagner, 2007; Nosarti et al., 2010; Ye & Zhou, 2009). Pseudowords may also strongly recruit related semantic representations because of a more prolonged search for the missing meaning (Mechelli et al. 2003). The fact that this effect in the *pars opercularis*, STG and *pars orbitalis* was only present in L1 reading may be due

to further attempts to phonologically decode and retrieve representations in the native language. Although there is prior evidence showing higher activation for pseudowords than words in these regions (Burton et al., 2005; Hagoort et al., 1999), this is the first study showing that this effect is present in L1 but not in L2 reading. These results partially confirmed, and qualified, our hypothesis IV.

These findings have implications for second language reading teaching and acquisition in line with studies that have stressed the importance of taking into account languages' specificities, such as orthographic depth (Ziegler et al., 2010) in educational reading practices (Share, 2008). In transparent languages, most letters equal one sound and, therefore, it is easier to stress letter-sound conversion rules when teaching transparent L1 and L2 languages. Conversely, this strategy might not be the most optimal for learning to read in opaque languages, where the same letter can be associated with more than one sound, especially when individuals with a transparent L1 are taught to read in an opaque L2. Our findings also have implications for current theories and debates within the field of the neurobiology of language, pave the road for further examinations of functional interactions among dorsal and ventral reading networks in samples with different language profiles, and provide novel insights about how the bilingual brain reads; a matter of growing theoretical and applied interest, especially given that bilingualism is increasingly common in today's world.

Chapter 6: Functional and structural differences in bilingual reading as a function of the age-of-acquisition

6.1 Overview

What functional and structural brain changes occur due to learning a L2 earlier or later in development? Some perspectives suggest that early childhood is the best timing for L2 acquisition because at this developmental stage the brain is more flexible and plastic (Lenneberg, 1967). Others propose that children are somehow harmed by early bilingual exposure and therefore establish the native language first is preferable (Crawford et al., 1999). Based on this later account, in some educational settings, children start acquiring a L2 in high school years, after the native language is consolidated. Further research is needed to better understand the effects of L2 AoA and its neural correlates.

Children, compared to adults, tend to show less consolidated and more bilateral brain activation during L1 processing (Gaillard et al., 2003). How consolidated the L1 can influence the acquisition of the L2. Specifically, it has been argued that in early bilinguals similar regions of the brain serve both L1 and L2 processes. In contrast, among late bilinguals the L1 and L2 seem to be more distributed (Kim et al., 1997; Wartenburger et al., 2003). Nevertheless, other factors can have a crucial impact on L1 and L2 overlap, such as language proficiency and exposure of the L2 and language orthography. For instance, increases in the proficiency and exposure to the L2 are associated with a higher L1 and L2 networks overlap during reading

(Abutalebi, 2008; Perani et al., 2003). Regarding language orthography, neuroimaging studies have showed that in bilinguals, transparent languages (i.e., Spanish) seem to rely more on dorsal-phonological regions due the strong letter-to-sound correspondence. In contrast, opaque languages (i.e., English) are thought to rely on ventral-semantic regions due to the higher complexity on the letter-to-sound mapping (Jamal et al., 2000). Altogether, these studies suggest that the L2 AoA may have important effects on the functional organization of the language system, and that these effects can be also modulated by other linguistic factors (i.e., exposition, proficiency, orthography) that it will be critical to either control or manipulate.

Previous studies have revealed the crucial role of left-perysylvian regions in reading, including the vOT, inferior and superior parietal cortex, IFG regions (*pars opercularis*, *pars triangularis* and *pars orbitalis*) and the STG (Jobard et al., 2003; Sandak et al., 2004). Neuroimaging studies revealed the implication of these regions in reading-related tasks involving orthographic and phonological processing (Schlaggar & McCandliss, 2007). Within these regions, the left IFG has pointed out as a key component of reading (Price, 2012). Empirical evidence has showed the engagement of this region in word reading (Mechelli et al., 2005), lexical and semantic retrieval (Binder et al., 2009) and mapping orthography to semantics (Jobard et al., 2003). Additionally, studies on bilingualism have revealed the involvement of right IFG (Abutalebi et al., 2008; Park et al., 2012), consistent with evidence underscoring the role of right hemisphere regions in language processing (van Ettinger-Veenstra et al., 2010; Vigneau et al., 2011). Specifically, later acquisition and exposure to a L2 was associated with structural gray matter and cortical thickness differences in bilateral IFG (Klein et al., 2014; Stein et al., 2012). Moreover, stronger functional connectivity at rest has been found between left and right IFG for early compared to late bilinguals (Berken et al., 2016).

Therefore, acquiring a second language in different developmental stages might result in differences in the reading neural circuitry. However, are those brain differences between early and late bilinguals due to L1 or to L2 processing? Some authors support the view that L2 processing mostly depends on the previous L1 scaffolding (Hernandez, 2013). Thus, acquiring a L2 early in life occurs while neural networks are still under development. In contrast, acquiring a L2 late in life takes place after these networks are already established. Considering that functional activation is related to the underlying brain structure, it is likely that combining evidence from functional and structural connectivity might help us to better understand the possible reasons of these changes between early and late bilinguals.

In the present study, we will use a multimodal MRI approach to investigate the functional and structural changes in bilinguals as a function of L2 AoA. To do so, we compare Spanish-Basque early (i.e., L2 acquired before age 3) and late bilinguals (L2 learned after age 6) using functional and structural measures, while controlling for the above mentioned linguistic factors: proficiency level, both groups were high-proficient in both languages; language exposure, groups were equated in terms of their L1 and L2 exposure; and language orthography, both languages (Spanish, Basque) are transparent. We will specifically look for group differences and examine if they are due to L1 or L2 processing. Based on previous evidence, we hypothesized that the engagement of bilateral IFG will be modulated by L2 AoA (Berken et al., 2016). Additionally, we will explore group differences in functional connectivity based on the language used to read. Furthermore, we will examine structural differences in regions that will exhibit functional group differences. In this vein, since functional differences among these groups of participants will be associated to their L1 and L2 processing from early childhood, we predict to also find structural changes in these regions and their connections. This multimodal MRI approach focused on group

differences might bring new insights about the nature of bilingual language processing and the impact of L2 AoA on the functional and structural organization pattern of the brain of bilingual readers.

6.2 Materials and Methods

Participants

The final study sample consisted of 36 right-handed bilinguals with Spanish as their L1. The sample was divided into two groups of participants who either acquired their L2 before age 3 (Early bilinguals group; $n = 18$) or after the age 6 (Late bilinguals group; $n = 18$). All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. All subjects were highly proficient in their L1 and L2, while having minimal exposure to other languages. Language proficiency was assessed by means of objective and subjective measures. An adaptation of the Boston Naming Test (Kaplan et al., 1983) in Basque, English and Spanish, controlling for cognates across these three languages, was used as an objective measure of vocabulary. Participants performed this picture-naming test, including 77 to-be-named drawings. They also filled in a language background questionnaire where they self-rated their proficiency levels in L1 and L2 and also rated the percentage of daily exposure to L1 and L2. Importantly, there were no differences between groups in age, in their L1 and L2 proficiency measures, and in their overall daily exposure to L1 and L2 (all $ps > .05$; see Table 3). At the within-group level, while both objective and subjective measures indicated high proficiency in L1 and L2, proficiency and daily exposure were significantly higher in the L1 than in the L2. Data from 1 additional participant were excluded from analysis due to excessive head motion during imaging (i.e., >3 mm across the entire scan session). Prior to taking part in the

experiment, all participants gave written informed consent in compliance with the ethical regulations established by the BCBL Ethics Committee and the guidelines of the Helsinki Declaration. Participants received monetary compensation for their participation.

Table 3. Linguistic profile of both languages (L1 and L2) for early and late bilinguals.

	Early bilinguals (n=18)	Late bilinguals (n= 18)	<i>p values</i> †
Age (years)	26.8(5.6)	31.0(7.7)	<i>p</i> = .08
Gender (% female)	44.4	66.6	<i>p</i> = .18
AoA (years)			
L1	0	0	
L2	1.9(1.4)	11.2 (7.0)	<i>p</i> = .00003
Correctly named pictures*			
L1	76.1(1.5)	76.3 (1.3)	<i>p</i> = .70
L2	65.6(6.7)	63.7 (10.0)	<i>p</i> = .50
Average daily exposure (%)§			
L1	66.3 (12.0)	68.1 (14.2)	<i>p</i> = .70
L2	25.5(10.3)	22.5 (16.1)	<i>p</i> = .50
Self-perception			
L1	9.3(0.9)	9.5 (0.7)	<i>p</i> = .42
L2	8.2(1.00)	8.0 (0.9)	<i>p</i> = .71

* Out of 77 pictures; ¶1-to-5 scale; § Average percentage across reading, writing, hearing, and speaking; † *p*values of t-test comparing early and late bilinguals.

Materials and Experimental Procedure

At the scanner, participants were administered with perceptual (low-level) and semantic (high-level) Go/No-Go tasks. In both tasks, subjects were visually presented with different character strings: words (e.g., curtain), pseudowords (e.g., cinguda), and consonant strings (e.g., fstgklg). Stimuli were visually presented in the center of the screen. During the perceptual task, participants were asked to press a button any time they saw a colored letter within a string (e.g.,

brother). Instead, in the semantic task, they were required to press a button when they were presented with the word of an animal (e.g., turtle).

Regarding the stimuli, in L1 (i.e., Spanish) the amount of the stimuli presented within each task included 40 high-frequency words, 40 low-frequency words, 40 pseudowords, 40 consonant strings and 13% go trials. In the L2, English or Basque, participants were presented with a similar amount of stimuli and go trials per task than in the L1. Cognate words across languages were excluded to eliminate ambiguity. All words, between and within languages, were matched on frequency, number of orthographic neighbors and length (i.e., 5-8 characters). All pseudowords were created as a function of the selected words using Wuddy (Keuleers and Brysbaert, 2010).

The study was administered in two separated sessions based on materials language, L1 or L2. The order of these L1 or L2 sessions was counterbalanced across participants. However, to prevent that participants can generalize the reading strategy used in the semantic task to the perceptual task within each of the language sessions, they were always administered first with the perceptual task, followed by the semantic task.

fMRI Data Acquisition

Whole-brain fMRI data acquisition was conducted on a 3-T Siemens TRIO whole-body MRI scanner (Siemens Medical Solutions, Erlangen, Germany) at the BCBL, using a 32-channel whole-head coil. Snugly fitting headphones (MR Confon, Magdeburg, Germany) were used to dampen background scanner noise and to enable communication with experimenters while in the scanner. Participants viewed stimuli back-projected onto a screen with a mirror mounted on the

head coil. To limit head movement, the area between participants' heads and the coil was padded with foam, and participants were asked to remain as still as possible.

In each session, functional images were acquired in four separated runs using a gradient-echo echo-planar pulse sequence with the following acquisition parameters: TR= 2000 ms, TE= 25 ms, 35 contiguous 3-mm axial slices, 0-mm inter-slice gap, flip angle = 90°, Field of view = 218 mm, 64 x 64 matrix. Prior to each scan, four volumes were discarded to allow T1-Equilibration effects. The order of the study conditions (i.e., words, pseudowords, consonant strings, go trials) and the inter-trial intervals (jitter fixation, 30% of total trials) within each functional run were determined with an algorithm designed to maximize the efficiency of the recovery of the blood oxygen level- dependent response (Optseq II; Dale, 1999).

Structural Data Acquisition

Structural images were also acquired on a 3-T Siemens TRIO whole-body MRI scanner (Siemens Medical Solutions, Erlangen, Germany) at the BCBL. DW-MRI images were recorded using a single-shot spin echo-planar imaging (EPI) sequence, along 64 gradient directions at b-value=1500 s/mm² and 1 unweighted (b = 0) image. Acquisition parameters were: echo time (TE) = 99ms, repetition time (TR) = 9300 ms, FOV = 1840 x 1840 mm², matrix size 1024 × 1024, 58 contiguous slices and an isotropic voxel resolution = 1.79 mm³. The total scan time for the DW-MRI protocol was approximately 10 min. A high-resolution T1-weighted scan was also acquired, with the following acquisition parameters: matrix size 256 × 256; 160 contiguous axial slices; voxel resolution 1 mm³ isotropic; TE/TR/TI= 2.97 ms/2300 ms/1100 ms, respectively; and flip angle = 9°.

fMRI Data Analysis

Standard SPM8 (Wellcome Department of Cognitive Neurology, London) preprocessing routines and analysis methods were employed. Images were corrected for differences in timing of slice acquisition and were realigned to the first volume by means of rigid-body motion transformation. Then, high-resolution anatomical T1 images and functional volumes were coregistered and spatially normalized to T1 and echo-planar imaging templates, respectively, to enable anatomical localization of the activations. Templates were based on the MNI305 stereotaxic space an approximation of Talairach space. The normalization algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. During normalization, the volumes were sampled to 3-mm cubic voxels. Functional volumes were spatially smoothed with an 8-mm FWHM isotropic Gaussian kernel.

Statistical analyses were performed on individual participants' data using the GLM. fMRI time series data were modeled by a series of impulses convolved with a canonical HRF. The motion parameters for translation (i.e., x, y, z) and rotation (i.e., yaw, pitch, roll) were included as covariates of noninterest in the GLM. Each trial was modeled as an event, time-locked to the onset of the presentation of each character string. The resulting functions were used as covariates in a GLM, along with a basic set of cosine functions that high-pass filtered the data, and a covariate for session effects. The least-squares parameter estimates of the height of the best-fitting canonical HRF for each study condition were used in pairwise contrasts. Contrast images from each subject were submitted to group analyses. At the group level, whole-brain contrasts between conditions were computed by performing one-sample t tests on these images, treating participants as a random effect. Brain coordinates throughout the text, as well as in tables and figures, are reported in MNI atlas space (Cocosco et al., 1997).

ROI analyses were performed with the MARSBAR toolbox for use with SPM8. ROIs were selected from the general whole-brain All > Null across all subjects, $q < .05$ FDR corrected, which yielded activations in most of the left-lateralized key regions involved in reading processes: pars triangularis (BA 45; center of mass = -45 27 13; volume = 13352 mm³), pars orbitalis (BA 47; center of mass = -41 28 -7; volume = 3280 mm³), pars opercularis (BA44; center of mass = -48 11 18; volume = 6224 mm³), inferior parietal (center of mass = -30 -52 47; volume = 2752 mm³), superior parietal (center of mass = -25 -59 50; volume = 3336 mm³), middle temporal gyrus (center of mass = -52 -44 3; volume = 4896 mm³), superior temporal gyrus (center of mass = -53 -36 9; volume = 512 mm³), and their right homologous; right pars triangularis (center of mass = 49 26 18; volume = 5960 mm³), right pars opercularis (center of mass = 49 13 28; volume = 3192 mm³), right pars orbitalis (center of mass = 37 26 -10; volume = 1488 mm³), right inferior parietal (center of mass = 32 -51 50; volume = 1192 mm³), right superior parietal (center of mass = 29 -58 54; volume = 1496 mm³), right middle temporal gyrus (center of mass = 47 -66 2; volume = 1608 mm³), right superior temporal gyrus (center of mass = 47 -27 0; volume = 352 mm³).

Cortical Thickness Analysis

Regional cortical thickness for left and right pars triangularis was estimated using FreeSurfer version 4.05. The cortical surface was reconstructed to measure thickness at each surface location, or vertex, using a semi-automated approach (Fisch et al., 1999, 2001). Briefly, processing involves intensity normalization, registration to Talairach space, skull stripping, segmentation of white matter, tessellation of the WM boundary, smoothing of the tessellated surface and automatic topology correction. Thickness measurements were obtained by reconstructing representations of the GM-WM boundary (Dale et al., 1999) and the pial surface

and then calculating the distance between those surfaces at each point across the cortical mantle. This process was done for each subject. After that, cortical thickness between- and within-group comparisons were performed for the functionally identified left and right pars triangularis ROIs.

DTI Structural Connectivity Analysis

The two functional left and right pars triangularis were used to perform fiber tracking between them. The fiber tractography and fractional anisotropy (FA) values were obtained using DSI-Studio (available at <http://dsi-studio.labsolver.org>). The fiber-tracking algorithm implemented in DSI Studio is a generalized deterministic tracking algorithm that uses quantitative anisotropy as the termination index (Yeh et al., 2013). The RK4 tracking method was used to perform tractography with the following parameters: the anisotropy threshold was 0.08, the angular threshold was 60 degrees, the step size was 0.25 mm and length constraint was set between 0 and 150mm. A total of 500 fibers were calculated. Fiber tracts are defined via tractography on a publicly available DSI template. The DSI template is the CMU-30 atlas, which is an averaged map of reconstructed fiber orientations from a 257-direction diffusion spectrum imaging (DSI) sequence from 30 neurologically healthy volunteers. Individual subject DTI fiber tract profiles of FA are extracted automatically using the atlas mapping information. These fiber tract profiles are then analyzed using the statistics toolbox called Functional Analysis of Diffusion Tensor Tract Statistics (FADTTS) (Zhu et al., 2011). FADTTS delineate the association between diffusion properties along major white matter fiber bundles with a set of covariates of interest. Specifically, it performs several statistics tests including a multi-variate coefficient model. These tests produce local tests statistics and the local values are corrected for multiple comparisons with FDR. Hypothesis testing can be done to identify the specific voxels

within the fibers where the two groups differ from each other. To do so, approximately a total of 450 voxels were identified within each fiber (from a total of 500 fibers).

Functional Connectivity Analysis

We assessed functional connectivity via the beta correlation method (Rissman et al., 2004), implemented in SPM8 with custom Matlab scripts. The canonical HRF in SPM was fit to each occurrence of each condition and the resulting parameter estimates (i.e., beta values) were sorted according to the study conditions to produce a condition-specific beta series for each voxel. To examine pairwise functional connectivity between left and right *pars triangularis*, we calculated beta-series correlation values between these regions for, participant and condition. Since the correlation coefficient is inherently restricted to range from -1 to +1, an arc-hyperbolic tangent transform (Fisher 1921) was applied to these beta-series correlation values to make its null hypothesis sampling distribution approach that of the normal distribution. Then, these Fisher's Z normally distributed values were submitted to a mixed-model analysis of variance (ANOVA) including Group (Early vs. Late) as a between-subjects factor and Language (L1 vs. L2), Task (perceptual vs. semantic) and Stimuli (words, pseudowords and consonant strings) as within-subjects factors. To ensure that differences between left and right *pars triangularis* in the group dynamics were not determined by differences in the cluster size of the functionally defined ROIs, we used 5-mm radius spheres centered at the highest local maximas for all the ROIs.

6.3 Results

Behavioral and fMRI Results

Percentages of correct responses to go trials and standard deviation between parenthesis, for the early bilinguals group were: L1 Perceptual-task 99% ($SD = 4.7$), L1 Semantic-task 95% ($SD = 5.4$), L2 Perceptual-task 100% (0) and L2 Semantic-task 82% ($SD = 9.4$). Late bilingual's group percentages were: L1 Perceptual-task 93% ($SD = 23.6$), L1 Semantic-task 91% ($SD = 23.8$), L2 Perceptual-task 99.5% ($SD = 1.5$) and L2 Semantic-task 72% ($SD = 23.6$). No significant differences between correct responses were found between groups indicating that both groups performed equally and paid attention to the task ($ps \geq .40$). To identify brain regions associated with reading processes across all participants and factors in the experimental fMRI design, we computed a whole-brain contrast for All trials > Null (see Figure 17). Consistent with prior neuroimaging evidence (e.g., Lau et al. 2008), this contrast revealed the involvement of a predominantly left-lateralized reading set of regions and their right homologous regions (see Methods sections)

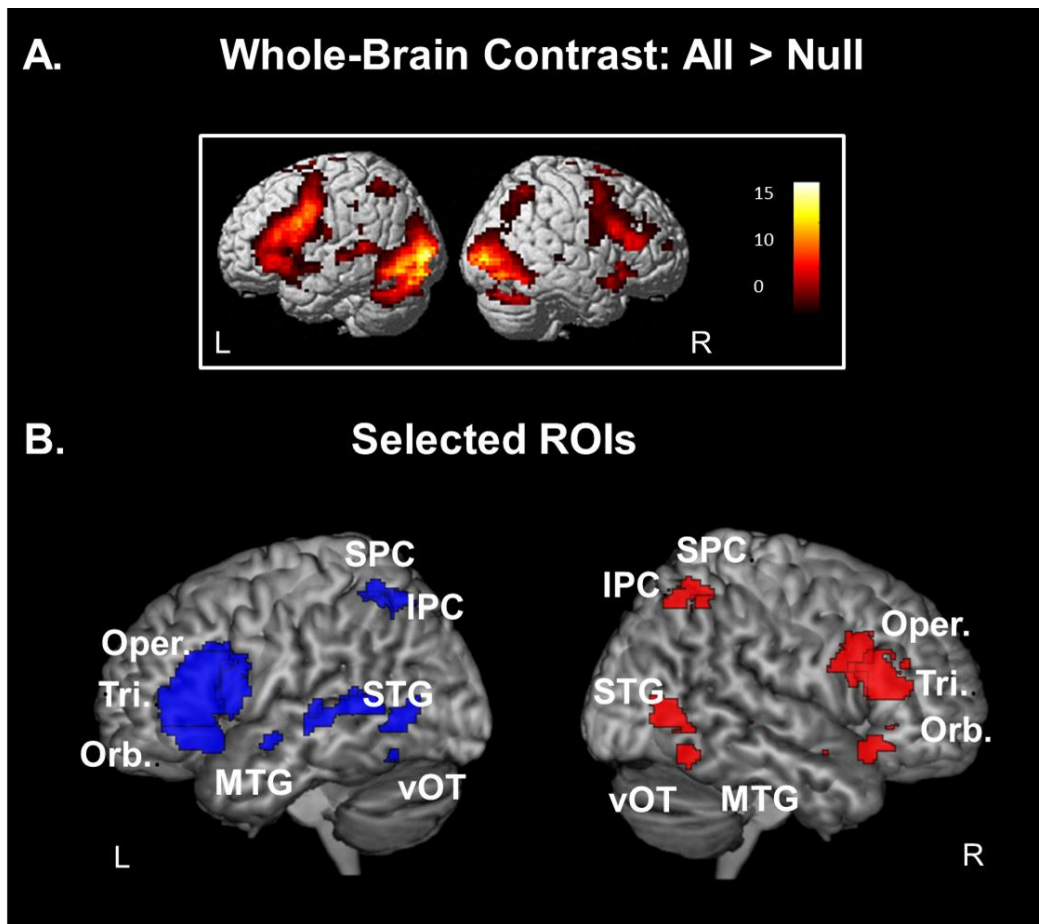


Figure 17. Brain renderings showing (A) activations for the All > Null whole-brain contrast across all subjects at a statistical threshold of $q < .05$, FDR-corrected, and (B) selected left-hemisphere (blue) and right-hemisphere (red) ROIs. vOT = ventral occipitotemporal cortex; IPC = inferior parietal cortex; SPC = superior parietal cortex; Oper. = *pars opercularis*; Tri. = *pars triangularis*; Orb. = *pars orbitalis*; MTG = middle temporal gyrus; STG = superior temporal gyrus;

ROI Analyses

We conducted ROI analyses to characterize the activation profile of regions of a priori interest for the main experimental conditions: Group (Early vs. Late bilinguals), Language (L1 vs. L2), Task (semantic vs. perceptual), and Stimuli, (words, pseudowords and consonant strings). As indicated, to avoid potential biases in the patterns of activation observed in these ROI analyses, these regions were selected from the general whole-brain All> Null across all

subjects, $q < .05$ FDR corrected, which yielded activations in most of the left-lateralized key regions involved in reading processes and their right homologous (see Methods section). Thus, we extracted fMRI parameter estimates from these ROIs and conducted hypothesis-driven analyses based on $2 \times 2 \times 2 \times 3$ mixed-model ANOVAs, followed by simple-effect analyses for the higher order interactions showing a group effect. In this series of ANOVAs the only regions that revealed group effects were left and right pars triangularis.

Left pars triangularis. The ANOVA for this region revealed the main effects of Language ($F(1, 28) = 9.89, p < .01, \eta_p^2 = .26$), Stimuli ($F(2, 56) = 37.64, p < .001, \eta_p^2 = .57$), and three different interactions: Language X Stimuli ($F(2, 56) = 4.87, p < .01, \eta_p^2 = .15$), Task X Stimuli interaction ($F(2, 56) = 9.92, p < .001, \eta_p^2 = .26$) and Language X Task X Stimuli X Group interaction ($F(2, 56) = 3.66, p < .05, \eta_p^2 = .11$; see Figure 18A).

Post-hoc analyses revealed that the Language X Task X Stimuli X Group interaction was due to a stronger engagement of this region for words in the semantic-task than in the perceptual-task across languages for both groups ($p < .05$), except for the L1 in early bilinguals. No task differences for L1 were found in this group ($p = .30$). Additionally, L2 words showed greater activation than L1 words across tasks in the late bilinguals group ($p < .05$). In contrast, in early bilinguals, this effect was only present in the semantic-task ($p < .05$).

Right pars Triangularis. The ANOVA for right pars triangularis revealed the main effects of Language ($F(1, 25) = 5.60, p < .05, \eta_p^2 = .18$), Stimuli ($F(2, 50) = 4.33, p < .05, \eta_p^2 = .15$) and Group ($F(1, 25) = 6.91, p < .05, \eta_p^2 = .22$). The main effect of group showed greater activation for late relative to early bilinguals ($p < .05$; Figure 18B)

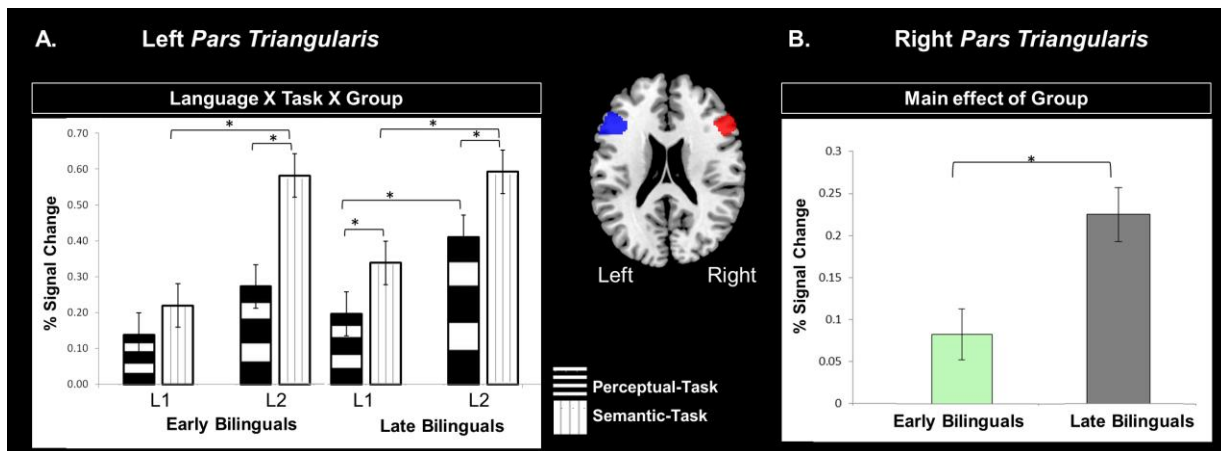


Figure 18. ROI analyses for left and right *pars triangularis*, the only regions that showed a group effect. A) Language X Task X Group interaction during word reading in left *pars triangularis* (-49 11 18; BA 44). B) Main effect of Group in right *pars triangularis*. Bar graphs show averaged parameter estimates (% signal change). Asterisks indicate comparisons that showed statistically significant differences in % signal change ($p < .05$).

Cortical Thickness Analysis of left and right IFG

We examine differences in cortical thickness for the specific areas showing between-groups regional effects in the ROI analyses: left and right *pars triangularis*. Results revealed that left *pars triangularis* was significantly thicker in early relative to late bilinguals ($p < .05$; Figure 19). In contrast, no significant between group differences were found in right *triangularis*. We next investigated the within group cortical thickness differences for left relative to right *pars triangularis*. In early bilinguals, left *pars triangularis* showed thicker cortex compared to right *pars triangularis* ($p < .05$). No significant cortical thickness differences were found between left and right *pars triangularis* in the late bilinguals group ($p = .17$).

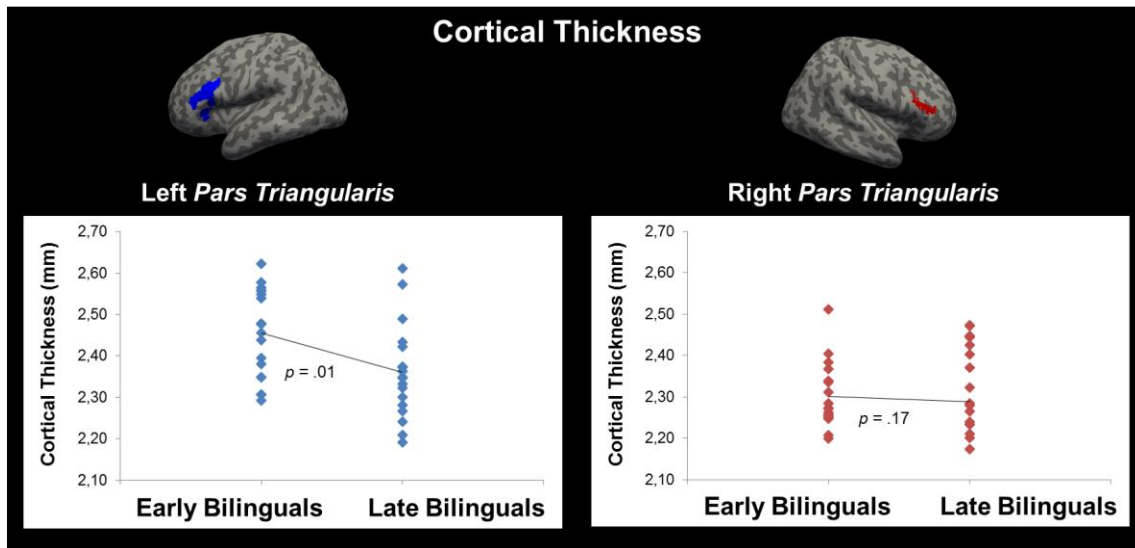


Figure 19. Cortical Thickness differences between early and late bilinguals in left and right *pars triangularis* regions. Line graphs show cortical thickness in mm. Only left *pars triangularis* revealed between group differences ($p = .01$).

DTI Structural Connectivity

We identify the tract connecting left and right *pars triangularis* (see Methods section for further details). These two regions were previously selected from our functional data. The FADTTS statistical toolbox allows identifying in which specific voxels along this tract the general fractional anisotropy (gFA) values differ between groups: early versus late bilinguals. Our results revealed higher gFA values for early relative to late bilinguals ($p < .05$), in 152 consecutive voxels within the tract that connects left and right *pars triangularis*. Specifically, these voxels are localized in the right hemisphere part of the tract (Figure 20A).

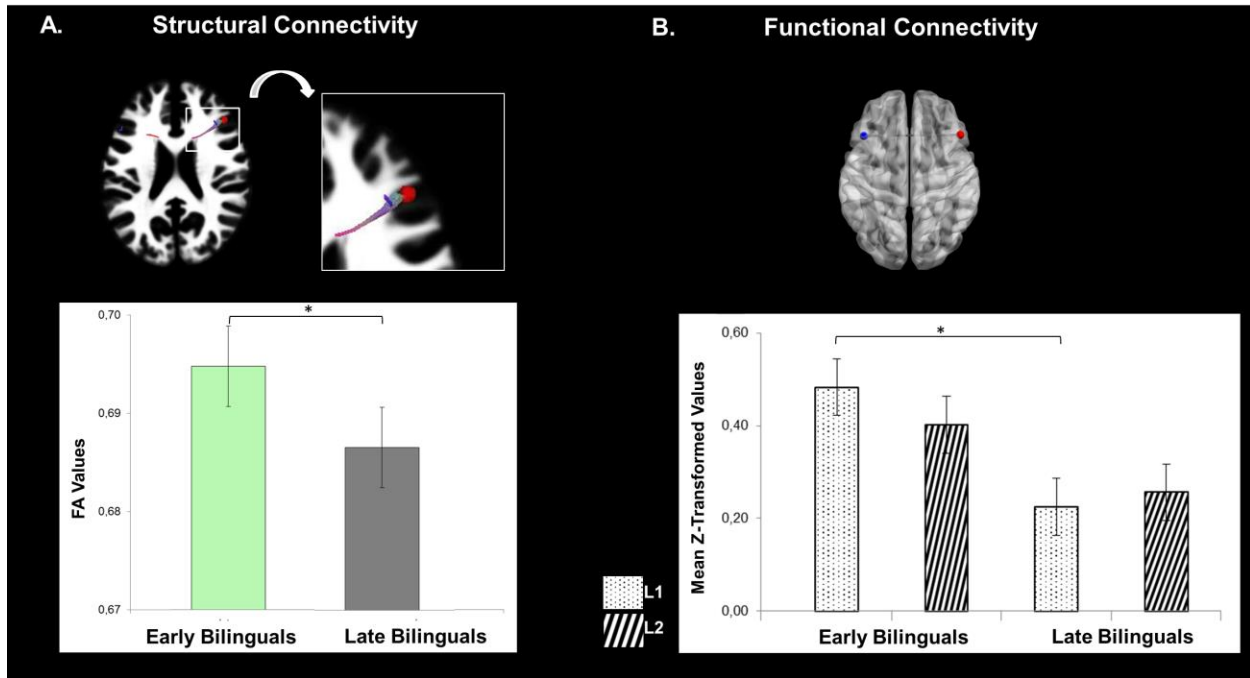


Figure 20. Connectivity analyses between left and right *pars triangularis* regions. A) Structural connectivity analysis. The axial slice shows voxels within the WM tract connecting both left and right *pars triangularis* that revealed statistically significant FA differences for early versus late bilinguals. Bar graph shows FA values in voxels the WM tract that showed significant between-group differences. B) Functional connectivity analyses. A schematic sagittal view of left and right *pars triangularis* and the pairwise connection among them that was submitted to functional connectivity analyses. Both nodes correspond to 5-mm radius spheres centered at the highest local maxima within these ROIs. Bar graph shows average coupling strength (i.e., mean z-transformed values of the beta-series correlation) for processing word stimuli for the Task x Language x Group interaction. Asterisks indicate comparisons that showed statistically significant differences in functional connectivity ($p < .05$)

Functional Connectivity

Here, we sought to examine changes in functional coupling during the task between ROIs that showed differential between-groups regional engagement as a function of Group (Spanish-English vs. Spanish-Basque), Language (L1 vs. L2), Task (semantic vs. perceptual), and Stimuli (words, pseudowords and consonant strings). To do so, we used the beta-series correlation method (Rissman, Gazzaley, & D'Esposito, 2004), building 5-mm-radius spheres centered at the

highest local maxima within left and right *pars triangularis* (see Methods section for further details).

Fisher z-score transformed beta-series correlation values between left and right *pars triangularis* for each condition in our experimental design were averaged, and submitted to mixed-model ANOVAs including Group (Early vs. Late) as a between-subject factors, Language (L1 vs. L2), and Task (semantic vs. perceptual) as within-subject factors. Based on prior evidence supporting a differential involvement of these reading networks as a function of stimuli type, we carried out three separate ANOVAs for words, pseudowords and consonant strings. The ANOVA for word stimuli revealed a statistically significant Group X Language interaction ($F(1, 34) = 3.83, p < .05, \eta_p^2 = .10$). In contrast, this effect or other interactions did not emerge significantly in the ANOVAs for pseudowords or consonant string ($ps \geq .05$). Post-hoc analyses for the Group X Language interaction for word stimuli revealed that early bilinguals exhibited stronger functional connectivity between left and right *pars triangularis* during L1 reading relative to early bilingual ($p < .05$). No group differences were observed for L2 reading ($p > .10$; see Figure 20B)

6.4 Discussion

The present study was aimed at investigating functional and structural brain differences as a function of L2 in bilingual reading. To this end, we tested two groups of high-proficient Spanish-Basque bilinguals living in the same bilingual context, that were matched in their L1 and L2 proficiency levels and daily exposure to their respective L1 and L2, had minimal exposure to other languages, and that only differ in their L2 AoA (early versus late bilinguals). Our study shows that L2 AoA modulates brain function and structure. The earlier the second

language is acquired, the stronger engagement of bilateral *pars triangularis*, greater the thickness of left *pars triangularis* and the more structural and functional connectivity between bilateral *pars triangularis*. Importantly, the observed between-group functional effects were associated with L1 reading processing.

The ROI analysis of left perisylvian regions and their right homologous revealed group differences only in the left and right *pars triangularis*. Although traditionally reading function has been mostly attributed to the left hemisphere (Price, 2012), the role of the right hemisphere in word processing and in determining sentence meaning has also been pointed out (Benson & Zaidel, 1985; Caplan et al., 1996; van Ettinger-Veenstra et al., 2010; Vigneau et al., 2011; Vingerhoets et al., 2013). Specifically, left and right *pars triangularis* activity is associated with performance in language and reading related tasks, such as, picture naming and word and sentence reading (Meinzer et al., 2009; Menenti et al., 2009; Wierenga et al., 2008).

Given that function reflects structure (Martenson et al., 2012; Stein et al., 2014) it is significant that we consider functional and structural anatomical substrates of these two regions involved in bilingual reading. Our results revealed that early bilinguals exhibited thicker cortex in the left *pars triangularis* compared to the late bilinguals group. Differences in cortical thickness associated with L2 AoA seem to suggest that acquiring a L2 in different age stages induces distinct structural changes, which may be related to the typical sculpting of the brain during development. More specifically, previous studies showing that during infancy and early childhood there is an initial overproduction of neurons and synaptic connections followed by the process of synaptic pruning that continues well into adolescence (Fuster, 2002; Shaw et al., 2008). The process of synaptic pruning refers to the reduction in the size or number of neuron cell bodies or their synaptic processes, which increases the efficiency of neural transmission,

leading to cortical thinning (Paolicelli et al., 2011; Tamnes et al., 2010). Therefore, greater left *pars triangularis* thickness may be related to less reliance on this region in early, but not in late bilinguals. Our results support previous studies suggesting differences in cortical thickness due to the acquisition of new skills, such as second languages (Klein et al., 2004; Martensson et al., 2012) and complex motor skills such as juggling (Draganski et al., 2004).

Nevertheless, language processing requires coordinated interactions among distributed brain regions. To further unravel interactions between left and right *pars triangularis*, structural and functional connectivity analysis were carried out. Our structural connectivity results revealed higher FA values in the tract that connects left and right *pars triangularis* for early relative to late bilinguals. Higher values in FA have been associated with increase variations in axon count, density of axonal packing and myelination. Myelination occurs more actively during development but it has been also observed in the adult brain (e.g., Ishibashi et al., 2006). Myelination increases the space occupied by axons in a voxel, leading to greater FA values (Stikov et al., 2001). Development of cognitive abilities, such as reading, is correlated with increases in FA values within tracts that connect relevant reading regions (Yeatman et al., 2012). Our data seems to suggest that acquiring an L2 as a new skill during early childhood may lead to increase myelination between the tract that connects left and right *pars triangularis*. This result is consistent with previous structural studies suggesting inter-hemispheric distributed reading networks in bilinguals (Berken et al., 2016; Schlegel et al., 2012).

A matter of debate is if the here observed changes are associated with L1 or L2 processing. Our functional connectivity results revealed greater coactivation between left and right *pars triangularis* in early relative to late bilinguals for L1 word reading. This result goes in line with our structural connectivity results, and suggests that differences between early and late

bilingual seems to be present during L1 processing. A possible explanation is that in the case of monolinguals and late bilinguals during the initial stages of reading development in the native language there is greater bilateral activation followed by left-hemisphere dominance after language consolidation processes over development (Shaywitz et al., 2003; Turkeltaub et al., 2003). Indeed, previous studies showed increased activation in left-lateralized language related regions in monolinguals adults compared to children (Gaillard et al., 2003; Turkeltaub et al., 2003). However, it might be that when learning two languages in early stages, as in the case of early bilinguals, bilateral language processing, rather than left dominant, lead to more efficient mechanism especially for the native language (Feng et al., 2015). This is consistent with empirical evidence suggesting greater bilateral pattern in early relative to late bilinguals (Birdsong & Molis, 2001; Hull & Vaid, 2006, 2007; Long, 1990). In contrast, in late bilinguals, L1 processing may follow the ordinary bilateral to left-dominant reading development. Then, late bilinguals become more like monolinguals with respect to their first language, leading to less bilateral processing in their L1 (Hull & Vaid, 2007).

Furthermore, no differences were found between groups for L2 functional connectivity, which seems to suggest that L2 processes are more similar between early and late bilinguals for reading in the L2. This can be explained by the fact that for early bilinguals the L2 is not the primary language and, therefore, it might rely in a larger extent of the left consolidated language regions. Similarly, in the case of late bilinguals, the L2 will be acquired when language regions are already consolidated in the left hemisphere and, therefore, the L2 will use the same networks than L1.

In sum, our multimodal MRI results provide evidence that L2 AoA influences brain function and structure associated with reading processes beyond the classical left-lateralized

language regions, as well as new insights into the neural plasticity of language learning. Additionally, our data support the view that L2 AoA, irrespective of the high proficiency level of our participants, determines reading neural patterns. The knowledge about how language is organized in the bilingual brain and the modulations associated with AoA shed further light regarding how learning influences neuroplasticity and provide information of how reading is distributed in the bilingual brain. Furthermore, these results can pave the road for future neuroimaging and neuropsychological research examining how lesions in critical brain language regions in bilingual patients may impair either the L1 or the L2, or both acquired languages.

Chapter 7: General Discussion

Bilingualism is a world fact. In many countries bilingualism is often the norm, while in countries predominantly monolinguals (i.e., United States) the amount of bilingual population has steadily grown over the last two decades. One of the reasons of this increase in the number of bilinguals seems to be globalization, which stimulates the flow of people (e.g., tourism, immigration) and international information transfer. Thus, it is not surprising that the interest in studying the neural correlates underlying bilingualism is also growing. Further research on this field holds much promise to inform teaching methods and interventions dealing with language and reading impairments. Nevertheless, the bilingual brain cannot be viewed as the sum of two monolingual language systems, but as a unique and complex neural system. As previously reviewed, there are several language-related variables that may be responsible for differences in the neural correlates of bilingual reading, such as the language orthography, L2 AoA, language proficiency and exposure, and these aspects have been often confounded in previous neuroimaging research.

In the present doctoral thesis, special care was taken to control for language proficiency and exposure in the bilingual samples here examined. More specifically, all participants were high proficient in both L1 and L2, exposed to the same extent to L1 and L2 in their daily lives and have minimal exposure to third languages. Controlling for these covariates allowed us to disentangle the specific neural effects of the two main factors here examined on bilingual reading in two separate experiments: Experiment 1 was aimed at investigating the neural correlates of bilingual reading as a function of the language orthography (transparent versus opaque), whereas

Experiment 2 sought to examine the functional and structural correlates associated with L2 AoA comparing early versus late bilinguals. Additionally, both experiments examined the impact of these factors in the neural reading networks engaged as a function of the language used to read (L1 versus L2), reading demands (semantic versus perceptual) and stimuli type (word, pseudoword and consonant strings). The findings of the present doctoral thesis bring new relevant insights to the Neurobiology of Reading field and carry implications pertaining to teaching and intervention procedures for reading in bilinguals. In this chapter, an overview of the main questions answered in this work and their implications are discussed.

Are the Brain Reading Networks Influenced by Language Orthography in Bilinguals?

Although different studies have stressed the importance of taking into account specificities of the languages when studying reading (Ziegler et al., 2010), the neural correlates associated with language orthography in bilingual reading have been rarely investigated. Experiment 1 examined the influence of language orthography on the neural reading networks by comparing two samples of late bilinguals, which differ in their L2 language orthography: Spanish-Basque versus Spanish-English bilinguals. Regional activation showed that transparent orthographies with high grapheme-to-phoneme mapping consistency (i.e., Spanish/Basque) strongly relied on regions along the dorsal reading network. In contrast, reading in opaque languages (i.e., English) relied on ventral regions due to the need of greater semantic representations. Furthermore, functional connectivity patterns replicated the findings of the regional activation results. L2 orthographic depth was associated with a strikingly segregated profile of left vOT coactivation with dorsal regions for the group with a transparent L2, and with ventral regions for the group with an opaque L2. This indicates that the left vOT is critical to further evince differential functional coactivations involved in phonological and semantic

computations required for successful L2 word reading as a function of language orthography. This study offers a novel contribution regarding the important role of language orthography and how it involves a reallocation of resources within distinct processing pathways. Additionally, it supports evidence detailing the role of language orthography in teaching strategies (Share, 2008). Therefore, the response to one of the questions that motivated Experiment 1 is affirmative; language orthography modulated the engagement of the dorsal and ventral networks in bilingual reading and this is a factor that should be taken into account in future reading studies.

Is Reading in L1 and L2 Supported by the Same Neural Networks and Functional Dynamics in Late Bilinguals?

A classic question in language research is whether or not reading in a L2 that was learned later in life can be processed through the same neural dynamics underlying L1 acquisition and processing. Experiment 1 offered a unique window to assess directly the neural representations of L1 and L2 reading in late bilinguals. Our results suggest that L1 and L2 seem to rely on the same ventral and dorsal reading networks, but stronger regional recruitment was found for reading in L2 relative to reading in L1. This may be due to the higher effort required during reading in the language that was acquired later in life (i.e., L2). Furthermore, while functional coactivation patterns within ventral and dorsal networks were similar for L1, they decreased numerically for L2 in both reading networks and significantly in the dorsal pathway. According to Pugh's et al., (2001) brain model of reading, acquiring a language relies on both dorsal and ventral regions; however, once words are learned mainly ventral regions are used to read them. The stronger coactivation for both networks during L1 reading might be related to Hebbian-like learning rule (Hebb 1949), which is explained on the prior history of coactivations among these regions during reading acquisition. In contrast, L2 reading may use the available L1 neural

scaffolding, leading to a decrease in the coactivation in the reading networks, which is consistent with the fact that L2 learning in late bilinguals takes place once the reading networks have been already established. This evidence goes in line with previous research (Hernandez et al., 2005; Hernandez & Li, 2007).

In conclusion, L1 and L2 processing are supported by the same neural networks. However, both, regional activation and functional connectivity among reading networks differ upon the language used to read.

Do Task and Stimuli Modulate the Recruitment of Ventral and Dorsal Reading Regions?

The results from Experiment 1 provide us with useful information to address this question. First, regional activation revealed that ventral regions were more strongly engaged during semantic demands. In contrast, dorsal regions showed greater modulation during phonological processing. This dissociation is found through word and pseudoword reading, which requires distinct semantic and phonological processing respectively. This division between semantic and phonological demands was also observed in the anterior versus the posterior IFG regions supporting previous findings (Price, 2012). Second, functional connectivity reveal tighter coupling among ventral regions for semantic-task demands. This result is consistent with the pattern of regional activation observed in ventral regions previously described. Overall, coupling strength among ventral regions appeared to be more relevant for semantic-related processes (i.e., word processing, semantic reading task), since tighter coupling among these regions was found for the semantic relative to the perceptual task. Third, the left vOT revealed sensitivity to task-related manipulations, showing greater engagement during the semantic than during the perceptual reading task. The three different localization strategies used

to define this region confirmed that this finding is not a mere a topographic artifact. This is the first neuroimaging study showing that the activation of the left vOT during bilingual reading is modulated upon the task demands. This is an important finding that contributes to better understanding of the role of the left vOT, which is crucial given that this region is considered as the gateway from vision to language. Our results suggest that left vOT participates in the integration of incoming visual information with semantics, which bring new insights about the extensive debate within the language literature about the specific role of this region (Dehaene & Cohen, 2011; Price & Devlin, 2011).

Hence, task and stimuli demands were associated with distinct semantic and phonological processing, which modulate the engagement of different regions within the reading networks. Specifically, semantic demands highly relied on ventral regions, and phonological processing on dorsal regions.

Does AoA of the Second Language Modulate Functional and Structural Reading Networks?

Classically, among researchers, the effects of L2 AoA have been largely debated, with the so-called “critical period hypothesis” being a constant source of controversy (Lenneberg, 1967; Elman et al., 1997; Perani et al., 2001). Experiment 2 examined the influence of L2 AoA in the neural reading network comparing two samples of high proficient early and late Spanish-Basque bilinguals. Our results revealed group regional activation differences only in left and right *pars triangularis*, key regions within the reading network. Further analysis showed that the earlier the L2 was acquired, the greater the cortical thickness in left *pars triangularis*. Also, early bilinguals showed higher structural and functional connectivity between left and right *pars triangularis*, with group effects in functional connectivity being only significant for L1 reading.

These findings indicate that at the functional and structural level, language representation differs between early and late bilinguals, even when exposure, proficiency and language orthography are carefully controlled for. This evidence corroborates previous findings from results that also observed reliable patterns of functional and structural inter-hemispheric networks in early relative to late bilinguals (Berklen et al., 2016; Hull & Vaid, 2007; Klein et al., 2014). This result may be due to biological development differences happening in the brain when the second language is learned. In early bilinguals, second language learning occurs when language is bilateralized, which is a typical reading signature during development. In contrast, in late bilinguals, second language learning occurs when the first language is already left lateralized (Turkeltaub et al., 2003; Shaywitz et al., 2003). Therefore, our results indicate that the process of learning a second language in different developmental stages adapts to the preexisting architecture of the reading networks.

Implications

The findings from this doctoral dissertation suggest that the human reading neural system is modulated by linguistic properties (i.e., language orthography) and environmental experiences (i.e., L2 AoA). This aspect has implications for current theories and debates within the field of neurobiology of language, pave the road for further examinations of the functional and structural reading networks in samples with different language profiles, and provide novel insights about reading mechanism in the bilingual brain. Furthermore, the present doctoral work constitutes an initial step towards advancing our knowledge in bilingual reading and it has the potential to provide important inputs for future translational research on the fields of education, language teaching and rehabilitation fields. The findings from this work point out the need of further research investigating the role of linguistic factors such as language orthography, in a variety of

educational contexts. For example, choosing a reading instruction approach is a major concern among educational practitioners across the globe (Erdener & Burnham, 2013; Seidenberg, 2013). Briefly, in the whole-language reading approach children are asked to identify a word based on a picture, and little guidance is given to the children regarding the complex rules of sound-to-letter correspondence (Reutzel, 2015). In contrast, in the phonics reading approach, children learn the rules about the way words are written and spelled. In this latter approach, children are explicitly taught the specific spelling-sound relations (Erdener & Burnham, 2013). Empirical evidence emphasizes that the choice of the proper method for learning to read might be based on the age of a child's first bilingual exposure, as it corresponds to different periods in development (Kovelman et al., 2015). However, our findings reveal the importance of taking into account the language orthography of the target reading language. Probably, in transparent languages (i.e., Spanish/Basque), which showed higher engagement of phonological regions, the whole-language reading instruction may be more beneficial due to the strong consistency between graphemes and phonemes. Conversely, this strategy might not be the most optimal for learning to read in opaque languages (i.e., English), where the same letter can be associated with more than one sound. Advancing our scientific knowledge about how reading networks are organized in bilinguals will also help us finding answers to some misconceptions associated with bilingualism, such as the belief that infants exposed simultaneously to two languages suffer incomplete language acquisition (Crawford et al., 1999). This is fundamental given the controversial nature of the subject, which has been widely discussed in immigration or education (Wiese & Garcia, 2001).

It is my hope that the empirical evidence showed in the present doctoral dissertation will provide useful information to scientists, parents, educators, therapists, and educational

policymakers alike, especially when planning optimal educational environments, both for bilingual and for monolingual children and adults.

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