Neural Plasticity of Language Systems

Evidence from fMRI experiments with adult language learners

Doctoral Thesis by

Kshipra Gurunandan

Supervised by

Dr. Pedro M. Paz-Alonso & **Dr. Manuel Carreiras**

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Universidad del País Vasco
Euskal Herriko Unibertsitatea

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> *I wandered everywhere, through cities and countries wide,*
> *And everywhere I went, the world was on my side.*
>
> *- Roman Payne*

In this academic journey that has taken me to so many cities and countries, I have had the support of a great many wonderful people.

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LIST OF ACRONYMS

ACC: Anterior Cingulate Cortex

ANT: Attention Network Task

BAC: Basque Autonomous Community

BIA: Bilingual Interactive Activation

BOLD: Blood Oxygen Level Dependent

BSC: Beta Series Correlation

CSF: CerebroSpinal Fluid

dlPFC: dorsolateral PreFrontal Cortex

DRC: Dual Route Cascade

DVF: Divided Visual Field

FDR: False Discovery Rate

fMRI: functional Magnetic Resonance Imaging

GLM: General Linear Model

GM: Grey Matter

HRF: Haemodynamic Response Function

IC: Inhibition Control

IFG: Inferior Frontal Gyrus

IPL: Inferior Parietal Lobule

LH: Left Hemisphere

LI: Laterality Index

LRM: Levelt-Roelofs-Meyer

MCC: Multiple Comparison Correction

MRI: Magnetic Resonance Imaging

MUC: Memory, Unification, Control

PET: Positron Emission Tomography

PPI: PsychoPhysiological Interaction

RHM: Revised Hierarchical Model

SPM: Statistical Parametric Mapping

STG: Superior Temporal Gyrus

REA: Right Ear Advantage

RH: Right Hemisphere

ROI: Region of Interest

VF: Verbal Fluency

vOTC: ventral Occipito-Temporal Cortex

WLG: Wernicke-Lichtheim-Geschwind

WM: White Matter

LIST OF ABBREVIATIONS

- **L1**: first language (i.e. native language)
- **L2**: second language
- **Ln**: new or non-native language (includes both second and third languages)

ABSTRACT

Functional specialisation and plasticity are fundamental organising principles of the brain. Language is a uniquely human phenomenon that requires a delicate balance between neural specialisation and plasticity, and language learning offers the perfect window to study these principles in the human brain. Though the human brain exhibits a remarkable ability to support a variety of languages that may be acquired at different points in the life span, the capacity for neural reorganisation decreases with age. Further, language is a complex construct involving linguistic as well as visual, auditory, and motor processes. The current doctoral thesis asked two main questions: (1) Do large-scale functional changes accompany language learning in adulthood? and (2) Are these neural changes similar across different language systems such as reading, speech comprehension, and verbal production? We investigated these questions in three fMRI experiments with adult language learners. In Experiments I and II, we examined comprehension and production in 30-to-60-year-old intermediate and advanced language learners and comprehensively characterised functional learning-related changes in each modality. In Experiment III, we compared and contrasted hemispheric lateralisation of reading, speech comprehension, and verbal production, and extended the analyses to a second longitudinal study with a contrasting participant sample. We found evidence for significant functional plasticity well into adulthood, and showed that different language systems exhibited different patterns of hemispheric specialisation and plasticity. The results have theoretical and practical implications for our understanding of fundamental principles of neural organisation of language, language learning in healthy populations, and language testing and recovery in patients. ■

RESUMEN EN CASTELLANO

Es una idea popular que los niños tienen un talento especial para los idiomas que es inaccesible para la mayoría de los adultos. Este concepto está asociado con la hipótesis del período crítico (Lenneberg, 1967). En línea con esta hipótesis se plantea que la capacidad de aprendizaje de idiomas disminuye en un momento en que otras capacidades cognitivas aún están en aumento o mejora. Este hecho ha generado acalorados debates en varios frentes en el campo de la psicolingüística y, entre otras cosas, se ha señalado que las diferentes habilidades lingüísticas, como la fonología, el vocabulario, la sintaxis, etc., están asociadas con mejoras diferenciales en el aprendizaje de lenguas en distintas edades. Sin embargo, hay pocas dudas de que, empíricamente, los adultos tienden a ser peores estudiantes de idiomas y que la mayoría de ellos no progresa a los más altos niveles de competencia lingüística o comunicativa en nuevos idiomas. En particular, incluso los estudiantes adultos de idiomas que exhiben un nivel razonable de comprensión a menudo no pueden hablar con un nivel similar de competencia. Sin embargo, un pequeño porcentaje de adultos domina nuevos idiomas: un ejemplo particularmente famoso de esto es el autor polaco-británico Joseph Conrad, quien comenzó a aprender inglés a los 20 años y pasó a ser ampliamente considerado como uno de los mejores novelistas que escribieron en inglés. Se ha argumentado que los malos resultados del aprendizaje de idiomas en adultos se explican, al menos en parte, por factores socioculturales, y que la capacidad de aprendizaje de idiomas disminuye con la edad al mismo ritmo que otras habilidades cognitivas (Bialystok y Hakuta, 1994, 1999). Se cree que esto se debe a la disminución general de la plasticidad neural con el aumento de la edad.

El aprendizaje de idiomas es una tarea exigente a cualquier edad, pero se cree que aprender un nuevo idioma es particularmente difícil después de la primera infancia debido a la disminución de la plasticidad neural. Los estudios de neuroimagen han encontrado diferencias funcionales y estructurales entre adultos monolingües y bilingües que aprendieron un segundo idioma en la infancia, y se ha demostrado que en parte dichas diferencias cerebrales están moduladas por la edad de adquisición y competencia en el segundo idioma. Por ejemplo, la densidad de la corteza parietal inferior izquierda parece ser mayor en bilingües que en monolingües, y esta densidad cortical parece aumentar con el dominio del segundo idioma, pero disminuye al aumentar la edad de adquisición de la segunda lengua (Mechelli y cols., 2004). Al margen de la hipótesis del "período crítico", generalmente se acepta que existe una asociación negativa entre la edad a la que los alumnos están expuestos a un idioma y su competencia final en dicha lengua (Newport y cols., 2001). Se puede afirmar que hay un fino balance entre la edad de adquisición y la competencia en la segunda lengua: los cambios neurales son menores con la edad, pero mayores con el aumento de la habilidad o competencia, lo cual podría explicar la dificultad del aprendizaje de idiomas en los estudiantes adultos. Sin embargo, la mayoría de los estudios de bilingües se llevan a cabo con adultos que adquirieron su segundo idioma en la infancia, y se han realizado muy pocos estudios ecológicamente válidos sobre el aprendizaje de idiomas de población adulto. Sólo unos pocos estudios han examinado los cambios cerebrales en los estudiantes de intercambio de adultos jóvenes en los primeros 3-5 meses de clases intensivas de idiomas y han encontrado cambios en la función y estructura de la red del lenguaje en relación con su estado monolingüe anterior (por ejemplo, Mårtensson y cols., 2012; Schlegel y cols., 2012; Barbeau y cols., 2016).

Un fenómeno menos estudiado aún que el declive de la plasticidad del lenguaje con la edad es la brecha entre la comprensión y la producción. En 1963, Fraser y sus colegas notaron que la comprensión del habla era sintácticamente más avanzada que la producción verbal en niños de 3 años. Demostraron que la capacidad de los niños tanto para comprender el habla como para imitar de memoria era mayor que su capacidad para una producción verbal significativa correcta. Esto también se observó en diferentes dominios, desde la fonología y la sintaxis hasta la semántica y la pragmática (Hendriks y Koster, 2010). Si se tratara simplemente de una cuestión de desarrollo, cabría esperar que esta brecha entre la comprensión del habla y la producción verbal se eliminara con la edad, pero de hecho se observó que persistía a lo largo de la vida (Gershkoff-Stowe y Hahn, 2013; Hendriks, 2014). En los bilingües, se observó que los niños en guarderias tenían un vocabulario receptivo significativamente menor que el vocabulario expresivo, particularmente en su segundo idioma (Gibson y cols., 2012), y la brecha entre la comprensión y la producción es particularmente prominente en los estudiantes tardíos dónde se observa que generalmente son capaces de entender mucho más de lo que son capaces de producir (por ejemplo, Walsh y Diller, 1981). Aunque empíricamente bien establecida, la evidencia a favor o en contra de diferentes explicaciones es escasa, y la cuestión aún no se ha abordado de manera específica en el campo neurocientífico.

La presente tesis doctoral aborda dos preguntas principales: (1) ¿Los cambios neurales a gran escala acompañan al aprendizaje de idiomas en la edad adulta? y (2) ¿Son estos cambios neurales similares en diferentes sistemas de lenguaje como lectura, comprensión del habla y producción verbal? Investigamos estas preguntas en tres experimentos de resonancia magnética funcional en adultos que estan aprendiendo nuevas lenguas. Con el fin de examinar si una mayor competencia en el aprendizaje de lenguas en adultos puede reemplazar los efectos negativos de la disminución de la plasticidad relacionada con la edad, realizamos un estudio transversal con estudiantes de 30 a 60 años que eran hablantes nativos de Español (L1) y aprendían Euskera (L2) en niveles intermedios y avanzados. En el Experimento I, realizamos análisis exhaustivos de los cambios dependientes del aprendizaje en la lectura y la comprensión del habla. Usamos tres enfoques analíticos: (i) convergencia funcional de lectura y comprensión del habla, (ii) similitud funcional de L1 y L2, y (iii) conectividad funcional entre regiones del lenguaje clásico y regiones de control del lenguaje. En el Experimento II, investigamos los cambios dependientes del aprendizaje en la producción verbal, examinando: (i) el curso temporal de la activación funcional, (ii) la lateralización de la activación y (iii) el acoplamiento funcional entre el lenguaje y las regiones de control del lenguaje. En el Experimento III, comparamos la lectura, la comprensión del habla y la producción verbal. Este experimento constaba de dos partes: (A) datos de los Experimentos I y II, y (B) un estudio longitudinal con jóvenes de origen español-vasco de 17 años que estaban aprendiendo Inglés en un programa extraescolar. En los Experimentos IIIA y IIIB, examinamos la lateralización de la lectura, la comprensión del habla y la producción verbal en lenguas nativas (L1) y no nativas (Ln), y cómo esto cambió con el aumento de la competencia en la Ln. Para examinar tanto la replicabilidad como la generalizabilidad de los hallazgos, los Experimentos IIIA y IIIB se contrastaron en varios factores como la experiencia lingüística temprana de los participantes (monolingüe versus bilingüe) y la lengua que se está aprendiendo actualmente, y los pares L1-Ln en los dos experimentos tuvieron diferencias grados de superposición en familias lingüísticas, fonología y ortografía. Nuestras hipótesis fueron que (i) la lateralización de la comprensión del habla sería más variable entre los individuos, pero la producción verbal estaría lateralizada en hemisferio izquierdo, y (ii) al aumentar la competencia en la Ln, la comprensión del habla podría mostrar cambios en el dominio hemisférico, mientras que la producción permanecería lateralizada en hemisferio izquierdo.

En el Experimento I sobre plasticidad funcional de la comprensión, encontramos que: (i) la convergencia de la lectura-comprensión del habla no se vio afectada significativamente por la competencia en la segunda lengua, (ii) la similitud entre las lenguas nativas y las nuevas lenguas disminuyó con un mayor dominio de la segunda lengua, y (iii) la conectividad funcional entre las regiones cerebrales de procesamiento del lenguaje y de control aumentó con la competencia y la exposición a la segunda lengua. En el Experimento II sobre la plasticidad funcional de la producción verbal, encontramos: (i) cambios significativos relacionados con el aprendizaje en los correlatos funcionales de la fluidez verbal, (ii) ausencia de cambios significativos en lateralización con el aprendizaje de la segunda lengua, pero incremento significativo en el reclutamiento de las regiones del hemisferio derecho a medida que se incrementa la dificultad de la tarea de producción verbal y (iii) aumento en la conectividad funcional entre las regiones de procesamiento de lenguaje y de control con el aumentó de la competencia y exposición a la segunda lengua. En el Experimento III, encontramos un patrón de resultados muy consistente en los experimentos IIIA y IIIB, que muestra que (1) tanto en las lenguas nativas como en las no nativas, mientras que la producción del lenguaje permanece lateralizada en el hemisferio izquierdo, la lateralización para la comprensión del lenguaje fue muy variable entre los individuos; y (2) con el aumento de la competencia en las lenguas no nativas, la lectura y la comprensión del habla mostraron cambios sustanciales en el dominio hemisférico, con lenguas tendiendo a lateralizarse a hemisferios opuestos, mientras que la producción verbal mostró cambios insignificantes y permaneció lateralizada a la izquierda. La plasticidad para la lectura fue mayor que para la comprensión del habla, que a su vez fue mayor que para la de la producción verbal.

En conclusión, en estos tres experimentos de resonancia magnética funcional con estudiantes adultos de idiomas encontramos evidencia de una plasticidad funcional significativa hasta bien entrada la edad adulta, y mostramos que los diferentes sistemas de lenguaje (lectura, comprensión del habla, producción verbal) muestran diferentes patrones de especialización y plasticidad hemisférica. Estos resultados mostraron patrones robustos y convergentes de lateralización y plasticidad dependientes del sistema del lenguaje y se obtuvieron con experimentos que presentaron diseños transversales y longitudinales, muestras distintas de estudiantes de idiomas del mundo real, pruebas de diferentes sistemas lingüísticos y un enfoque analítico multimodal. Nuestros hallazgos sugieren que la lateralización del lenguaje para la lectura y la comprensión del habla es plástica hasta la edad adulta, mientras que la producción muestra una fuerte especialización y lateralización en hemisferio izquierdo. También la conectividad funcional entre las regiones cerebrales del lenguaje y las control aumentaba en todas las modalidades al aumentar la competencia y la exposición al segundo idioma. ■

INTRODUCTION

CHAPTER 1

BACKGROUND AND MOTIVATION

Chapter 1 outlines the questions addressed by this doctoral thesis and details the background for the experiments and experimental designs. The final section contains a walk through of the thesis structure.

It is a popular idea that children have a special talent for languages that is inaccessible to most adults. This concept is associated with the critical period hypothesis (Lenneberg, 1967). Central to this hypothesis is the idea that language learning ability declines at a time when other cognitive abilities are still on the rise. This has been fiercely debated on a number of fronts in the field of psycholinguistics, and among other things, it was pointed out that different language skills such as phonology, vocabulary, syntax, etc. are associated with differing rates of learning success at different ages. There is little doubt, however, that, empirically, adults tend to be sub-optimal language learners and that the majority do not progress to high levels of linguistic or communicative competence in new languages. In particular, even adult language learners who exhibit a reasonable level of comprehension are often unable to speak at a similar level of proficiency. However, a small percentage of adults do master new languages: a particularly famous example of this being Polish-British author Joseph Conrad, who started learning English in his 20s and went on to be widely regarded as one of the greatest novelists who wrote in English. It has been argued that poor language learning outcomes in adults are at least partly explained by sociocultural factors, and that language learning ability declines with age at the same rate as other cognitive abilities (Bialystok and Hakuta, 1994, 1999). This is thought to be due to overall decline in neural plasticity with increasing age.

The current doctoral thesis addresses two main questions: (1) Do large-scale neural changes accompany language learning in adulthood? and (2) Are these neural changes similar across different language systems such as reading, speech comprehension, and verbal production? We investigated these questions in three fMRI experiments with adult language learners.

1.1 NEURAL PLASTICITY OF LANGUAGE SYSTEMS

Learning and memory are central questions in neuroscience. The brain's ability to learn and remember are thought to occur through growth and reorganisation of neural networks in the brain, i.e. neural plasticity. We can make the distinction between two types of plasticity: (i) developmental plasticity or maturational changes in typical development over the lifespan, and (ii) learning-dependent plasticity or brain changes affected by skill-learning. These two types of plasticity necessarily interact with each other: neural plasticity decreases over the lifespan, and it becomes proportionally harder to learn new skills and affect neural change (Figure 1.1). One of the best illustrations of this interaction is in language learning.

NEURAL PLASTICITY IN ADULT LANGUAGE LEARNING

Language learning is a demanding task at any age, but learning a new language is thought to be particularly difficult after early childhood due to decreasing neural

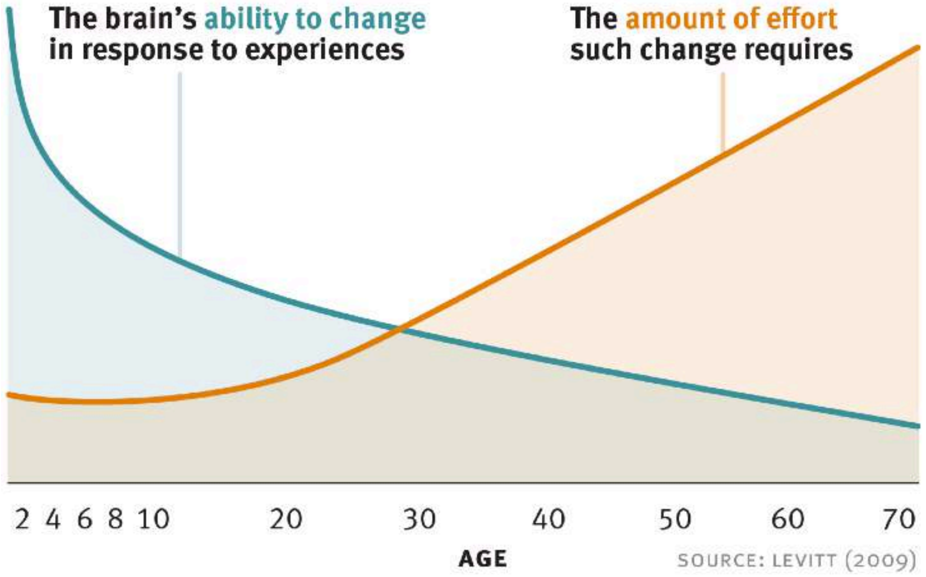

Figure 1.1 Neural plasticity through the lifespan.
Figure adapted from https://developingchild.harvard.edu/science/key-concepts/brain-architecture/

plasticity. Neuroimaging studies have found functional and structural differences between monolingual and bilinguals adults who learnt a second language in childhood, and differences were shown to be modulated by the age of acquisition of the second language and proficiency in the second language. For example, it was found that cortical density of the left inferior parietal cortex was higher in bilinguals than in monolinguals, and that this density increased with second-language proficiency but decreased with increasing age of acquisition (Mechelli et al., 2004). The exact definition of "critical period" notwithstanding, it is generally accepted that there is a negative association between the age at which learners are exposed to a language and their ultimate proficiency (Newport et al., 2001). The tug-of-war between age of acquisition and proficiency, such that neural changes are smaller with increasing age, but greater with increasing skill or proficiency, could explain the difficulty of language learning in adult learners. However, most studies of bilinguals involve adults who acquired their second language in childhood, and very few ecologically-valid studies of adult language learning have been conducted. A handful of studies have examined neural changes in young adult exchange students in the first 3-5 months of intensive language classes, and found changes in function and structure of the language network relative to their earlier monolingual state (e.g. Mårtensson et al., 2012; Schlegel et al., 2012; Barbeau et al., 2016).

In order to test whether further increasing proficiency in adult language learning can supersede the negative effects of age-related decline in plasticity, we conducted a cross-sectional study with 30-to-60-year-old adult language learners who were at intermediate and advanced levels of proficiency in their new language. In Experiment I, we conducted comprehensive analyses of learning-dependent changes in reading and speech comprehension, and in Experiment II, we investigated learning-dependent changes in language production.

NEURAL PLASTICITY OF COMPREHENSION AND PRODUCTION

A much less studied phenomenon than age-related decline in language plasticity is the comprehension-production gap. In 1963, Fraser and colleagues noted that comprehension was syntactically more advanced than production in 3-year-old children. They showed that children's ability for both understanding as well as rote imitation was greater than their ability for correct meaningful production. This was also observed in different domains from phonology and syntax to semantics and pragmatics (Hendriks and Koster, 2010). If it were simply a question of development, one would expect this comprehension-production gap to close with age, but it was in fact observed to persist across the lifespan (Gershkoff-Stowe and Hahn, 2013; Hendriks, 2014). In bilinguals, it was observed that kindergarteners had significantly higher receptive vocabulary than expressive vocabulary, particularly in their second language (Gibson et al., 2012, 2014), and the comprehension-production gap is particularly prominent in late language learners who are typically able to understand much more than they are able to produce (e.g. Walsh and Diller, 1981). Though empirically well-established, evidence for or against different explanations is sparse, and the question is yet to be addressed in the neuroscientific field.

In Experiment III, we compared neural changes between reading, speech comprehension, and verbal production in the cross-sectional study. In order to test the generalisability of our results, we then extended the same analyses to a second longitudinal study on a participant sample with a contrasting linguistic background.

The following section describes the sociolinguistic background and factors involved in participant sample selection for the cross-sectional and longitudinal studies.

1.2 MULTILINGUALISM IN THE BASQUE COUNTRY

Due to its sociolinguistic history, the Basque Country today has a unique linguistic environment. Recognising the wealth of opportunities to study various linguistic phenomena, the Basque Center on Cognition, Brain and Language in Donostia-San Sebastián, Spain, was established in 2008, with the aim to investigate the cognitive and neural mechanisms underlying language processing, with a special emphasis on bilingualism and multilingualism.

1.2.1 SOCIOLINGUISTIC HISTORY AND DEMOGRAPHICS

The Basque Country or Basque Autonomous Community (BAC) is an autonomous community in northern Spain (Figure 1.2A). The Basque language *Euskara* is spoken in the Basque Country greater region comprised seven historic provinces (Figure 1.2B). It has been recognised as an official language along with Spanish in the BAC since 1979, and in parts of Navarre since 1982, but not in the other provinces.

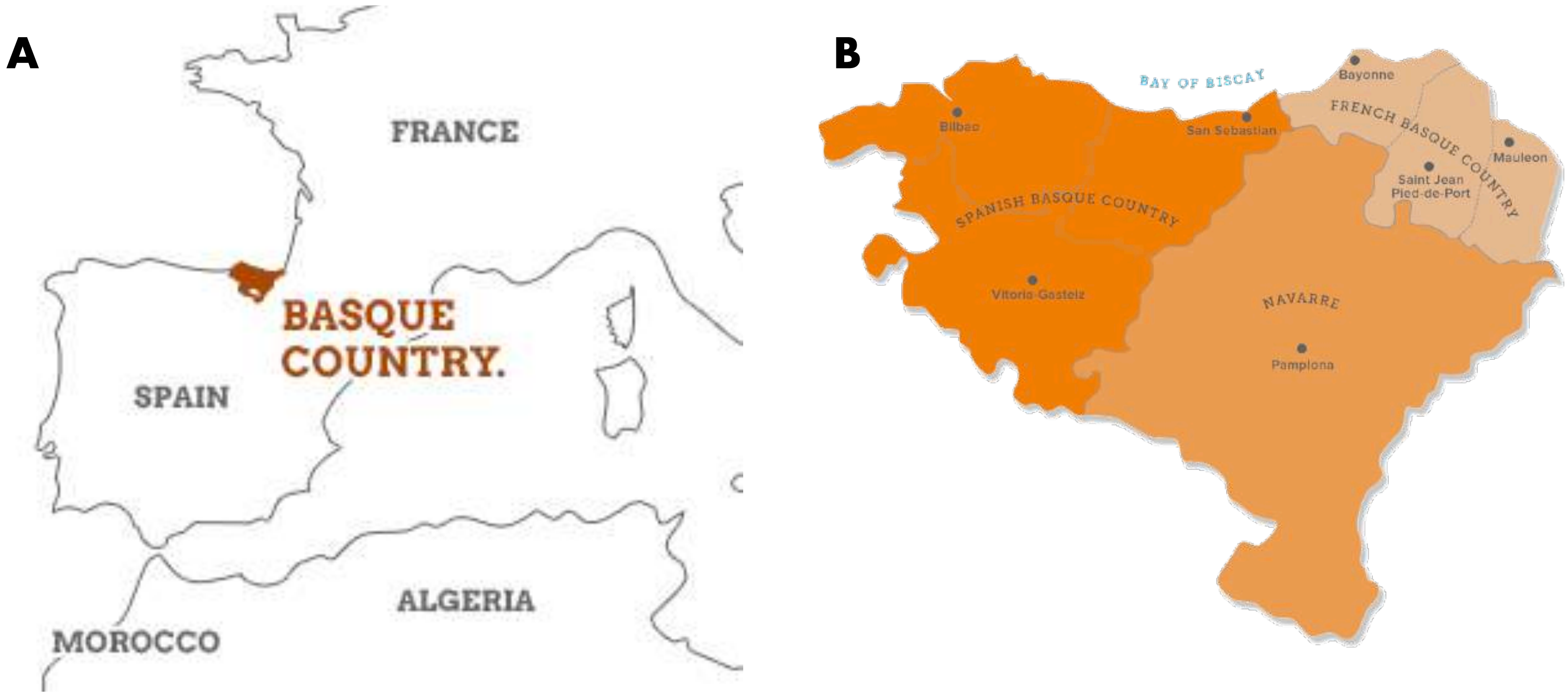

Figure 1.2 The Basque Country. (A) Basque Autonomous Community, Spain (B) The Basque Country (greater region), a collection of regions inhabited by Basque people.

Basque is thought to be one of the oldest languages in Western Europe, preceding Indo-European languages. It is a language isolate, and does not belong to any known language families. In the 19th and 20th centuries, its co-existence with Spanish and French was fraught due to the “one nation, one language” dogma in both countries. The efforts to marginalise Basque were successful in France, where it is considered “severely endangered” by the UNESCO today. It was a different story in Spain. In the mid-twentieth century, under the military dictatorship of Franco [1936-1975], Basque was banned in Spain, and it was forbidden to read, write or speak in any language but Spanish — even Basque names were illegal — leaving a generation of Basque people who could not speak their traditional language. Basque survived only in rural areas and clandestine schools, but with the rise of Basque nationalism in response to the dictatorship, the language took on enormous symbolic value. Concerted efforts have been made since then to revive the language, and it is considered one of the best examples of linguistic recovery in the world. Language centres were set up for adults to learn and perfect Basque, and since the 1960s, the *euskaldunberri* or person who learned Basque as an adult is a common sight. Today there are around 40,000 adults learning or advancing their Basque in public and private centres.

The Basque Country thus has a unique population of adult language learners. The adult Basque language learners are native to the region but grew up with a different native language that belongs to a separate language family. They had little childhood exposure to Basque due to sociopolitical circumstances, but are now living in bilingual environments (Figure 1.3), with access to native bilinguals and numerous cultural events centred around the language. Many of these adult learners go on to achieve a high level of linguistic and communicative competence.

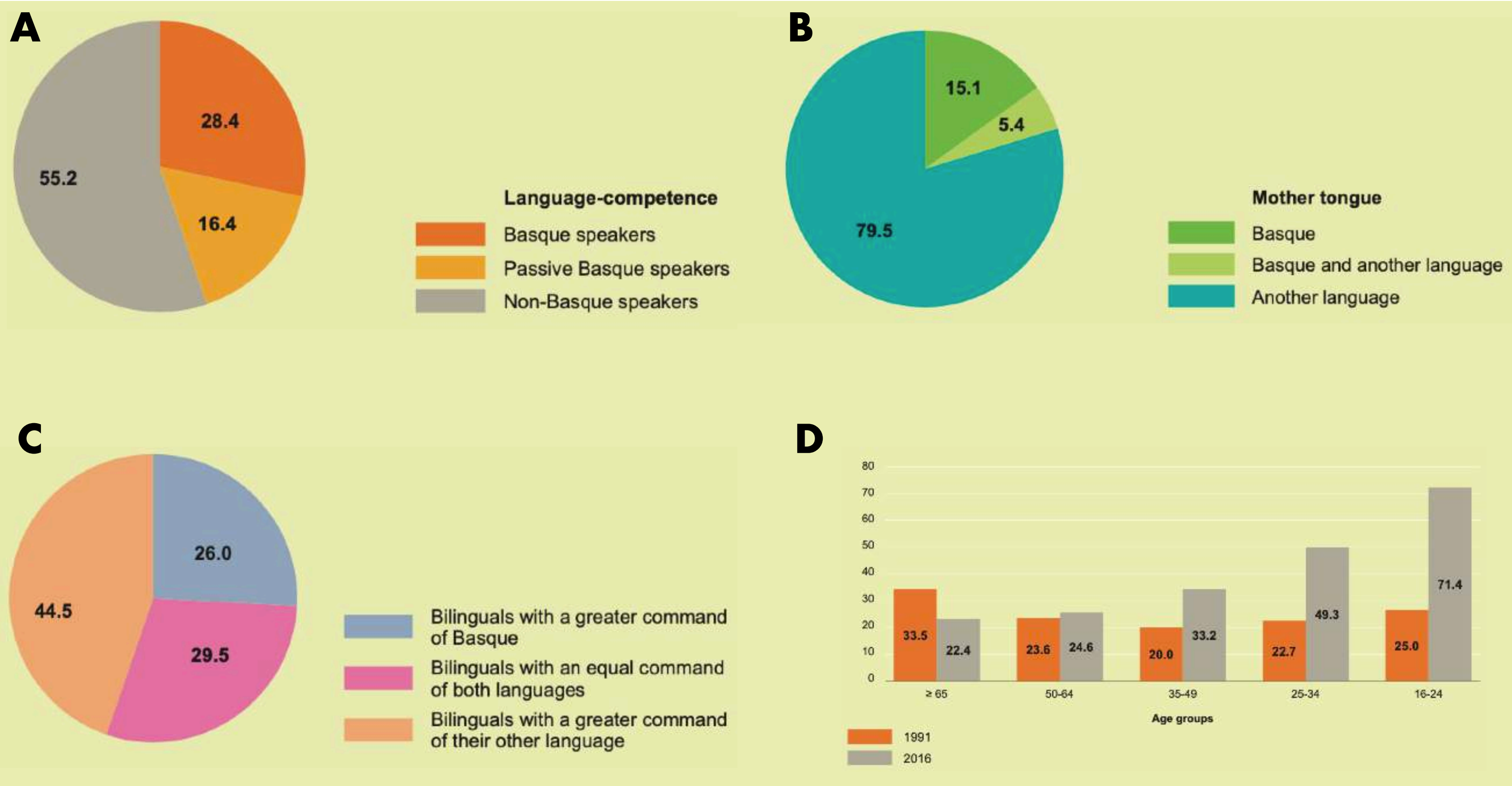

Figure 1.3 Population demographics of people aged 16+ years in the Basque Country (Sixth Sociolinguistic Survey, 2016). (A) Language background, (B) Native language, i.e. language acquired from parents or guardians by the age of 3, (C) Linguistic competency of the bilingual population, (D) Changing demographics from 1991 to 2016: percentage of Basque speakers by age group.

Recent generations in the Basque Country have a very different linguistic background (Figure 1.3). Growing up in an era of Basque linguistic pride, younger populations tend to be early bilinguals (Figure 1.3D). The Spanish-Basque model of instruction is common in schools, with 59% of parents, many of whom do not speak Basque, choosing partial instruction in Basque for their children.

1.2.2 EXPERIMENT DESIGN

The samples for the cross-sectional and longitudinal experiments in the current thesis were drawn from the above-mentioned two populations in the Basque Country. Real-life language learning is a complex and varied process and thus sample selection was a critical part of the experiment design. Participants filled out detailed questionnaires of language experience, and were carefully chosen to control for language backgrounds as much as possible.

The cross-sectional study was conducted with native Spanish speakers who were learning Basque as adults (ages 30 to 60), and had two groups of participants: intermediate level Basque learners, and advanced Basque learners. Due to the bilingual environment, participants' exposure to Basque was largely proportional to their proficiency, with advanced learners as a group reporting higher daily exposure to Basque than the intermediate learners.

The longitudinal study was conducted with younger Spanish-Basque sequential bilinguals (age 17) who had learnt Spanish at home and Basque at school, and were learning English as a foreign language at school in an after-school language training programme. English has culturally low common usage outside of classrooms and certain work environments, resulting in low exposure outside of these contexts. Popular English media such as tv series, movies, etc. are regularly dubbed into Spanish, further lowering opportunities for exposure. Thus, despite increasing English proficiency, participants in the longitudinal study reported uniformly low levels of exposure to English both before and after their language training programme.

1.2.3 HOW DO THE LANGUAGES COMPARE?

Let's look at an example sentence, and compare across languages (Figure 1.4):

Spanish: *El precio no influye en la calidad de el agua que se consume.*

Basque: *Prezioak edanten dan uraren kalitatean ez du eraginik.*

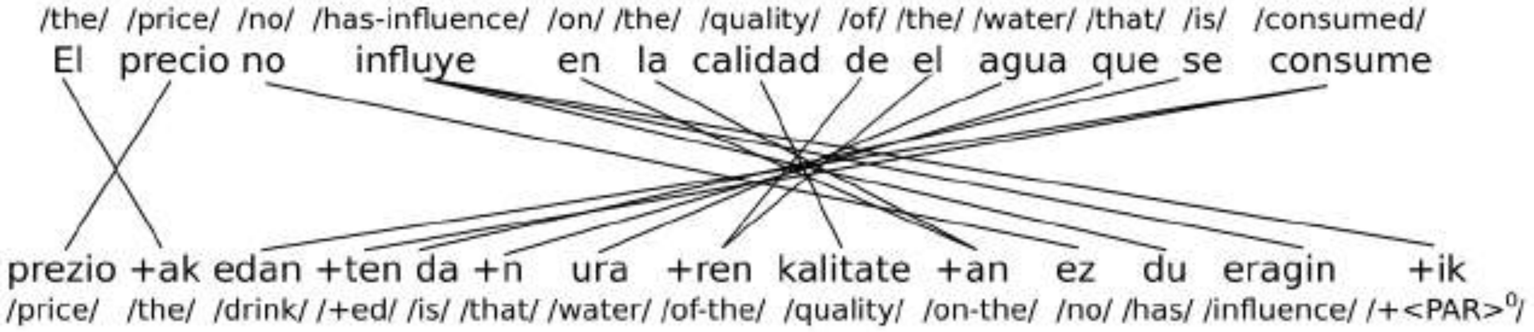

Figure 1.4 Comparison of Spanish, Basque, and English. Figure from Alegria et al. (2013)

In the cross-sectional study, native speakers of Spanish were learning Basque. Spanish is an Indo-European language, while Basque is a language isolate, and thus the only commonalities are Spanish loan words in Basque. The syntax differs substantially, for example, Spanish has a Subject-Verb-Object order, while Basque has a Subject-Object-Verb order, and Spanish is a grammatically gendered language, while Basque is not (Figure 1.4). Phonologically and orthographically, however, they are extremely similar. Both languages have highly overlapping phonology or sounds, and both use the same Latin alphabet and are transparent languages with similar letter-sound mapping, i.e. there is high correspondence and consistency between the way the words are written and pronounced. Thus, while the two languages could not be more different in some ways, they are visually and auditorily very similar (Figure 1.5).

In the longitudinal study, native Spanish-Basque sequential bilinguals were learning English. Both Spanish and English are Indo-European languages, with overlapping Latin roots. There is also some overlap in syntax, e.g. similar word order, but while Spanish is grammatically gendered, English is not. The two languages are phonologically and orthographically quite distinct. There are several phonemes that are unique to each language, and unlike the transparent Spanish, English has an opaque orthography, with very low consistency between the way words are written and pronounced. Thus, the two languages have some overlap in each aspect, but are not very similar in any of them (Figure 1.5).

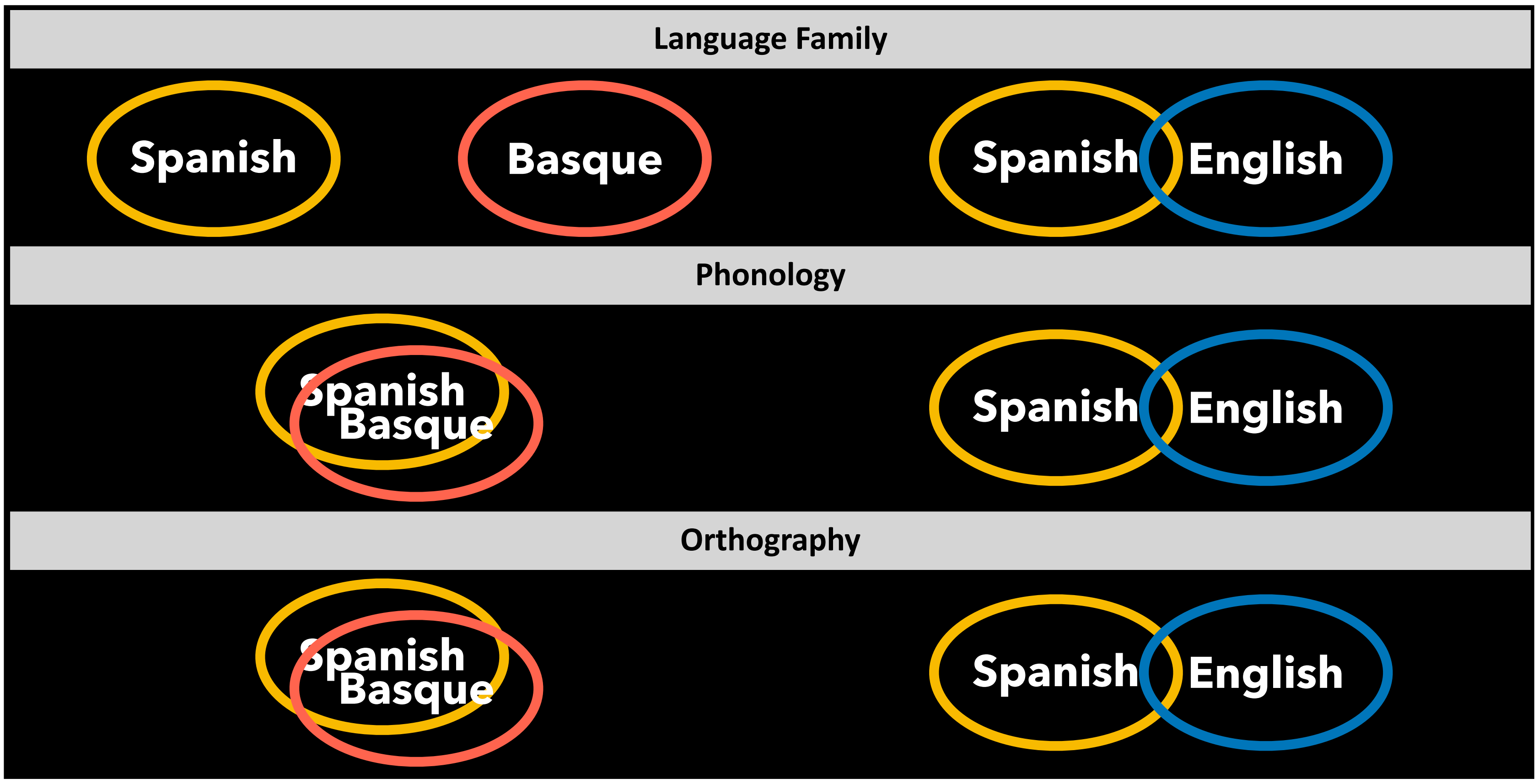

Figure 1.5 Linguistic overlap between languages

1.3 THESIS STRUCTURE

This doctoral thesis examined neural plasticity of language systems in a series of fMRI experiments with adult language learners. Chapters 2 and 3 provide literature reviews of the cognitive neuroscience of language and neural plasticity of language, respectively. **Chapter 4** provides an overview of the research technique, i.e. functional magnetic resonance imaging. **Chapters 5, 6, and 7** present experiments I, II and III, and are organised in the form of journal articles with introduction, methods, results, and discussion specific to the questions at hand. Chapter 5 focuses on language comprehension, Chapter 6 focuses on language production, and Chapter 7 compares and contrasts comprehension and production. The findings presented in Chapter 5 have been published in *NeuroImage* (Gurunandan et al., 2019), Chapter 6 is in preparation to be submitted to a peer-reviewed journal, and the findings in Chapter 7 have been published in *The Journal of Neuroscience* (Gurunandan et al., 2020). Finally, **Chapter 8** provides a general discussion of the overall findings. ■

We cannot clearly be aware of what we possess till we have the means of knowing what others possessed before us. We cannot really and honestly rejoice in the advantages of our own time if we know not how to appreciate the advantages of former periods.

- Johann Wolfgang von Goethe

THEORETICAL CHAPTERS

- BACKGROUND -

- LITERATURE REVIEW -

- METHODS -

CHAPTER 2

COGNITIVE NEUROSCIENCE OF LANGUAGE

Chapter 2 provides an overview of the cognitive neuroscience of language, tracing its roots from the fields of linguistics and neuropsychology, and describes key cognitive and neuroanatomical models of language.

Cognitive neuroscience of language lies at the intersection of linguistics, psychology and neuroscience research. Different aspects of language have historically been of interest to scientists from a wide variety of fields ranging from anthropology and sociology, to psychology, philosophy, physiology, and physics (Pronko, 1946). The study of language thus has an incredibly rich and heterogenous history, with several schools of thought whose influence has waxed and waned over the years.

In the 1860s, the groundbreaking work of physicians Paul Broca and Carl Wernicke laid the foundations of modern neuropsychology and cognitive neuroscience. Their individual discoveries provided the first empirical evidence for connections between specific brain regions and language processing. This established the idea that language could be studied by examining the brain, and thus the field of aphasiology — the study of linguistic deficits or aphasias occurring as the result of brain damage — was born. Around the same time, psycholinguistics as a field began to be developed as the "psychology of language" and the term psycholinguistics was coined by psychologist Jacob Kantor in 1936 (Levelt, 2013). Psycholinguistics was briefly rooted in behaviourism — the idea that all behaviours are learned through interaction with the environment through conditioning — till it was upended by Chomsky's work in generative grammar and the information processing approach to cognition pioneered by cognitive psychologists like George Miller and computer scientists such as Newell and Simon in the 1950s (Tanenhaus, 1989). At the same time, neurolinguistics also developed as a field, rooted in the field of aphasiology (Peng, 1985). It used models from psycholinguistics and theoretical linguistics to inform the study of the physiological mechanisms by which the brain processes language, using aphasiology and electrophysiology. In the 1990s, the advent of functional neuroimaging led to the next leap forward in the field, allowing, for the first time, *in vivo* brain imaging and the ability to see various brain regions process language in real-time.

2.1 COGNITIVE MODELS

Three topics form the core of language research: language acquisition and learning, language comprehension, and language production. Cognitive models of language typically divide the language system into two integrated but distinct sub-systems: language comprehension and language production.

Nineteenth century cognitive neuroscientists first popularised modular models of language processing, and the box-and-arrow diagram notation for defining such models, e.g. Lichtheim (1885) (Figure 2.1). At the beginning of the twentieth century, this localisationist perspective was strongly criticised and subsequently discarded — only for it to resurge in popularity in the 1960s.

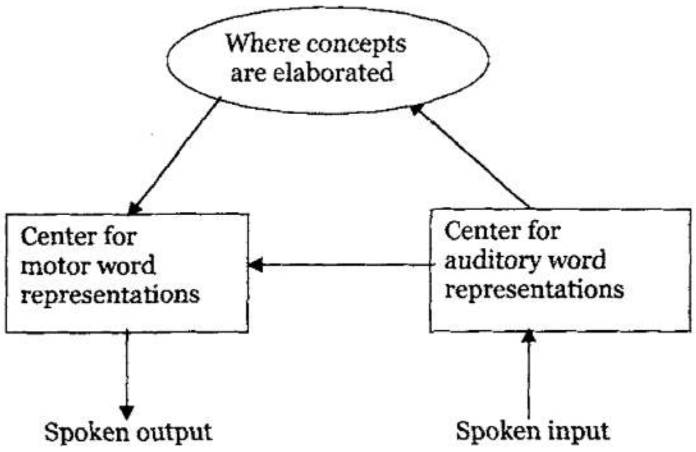

Figure 2.1 Early model of spoken language processing (figure from Coltheart et al., 2001)

Computational approaches became popular in the 1950s and have since remained the dominant approach. Basic language processes are typically described in the framework of three types of knowledge: (i) semantics: conceptual knowledge, (ii) phonology: the sound structure of words, and (iii) orthography: letter combinations in written words. Comprehension involves mapping of orthography or phonology onto

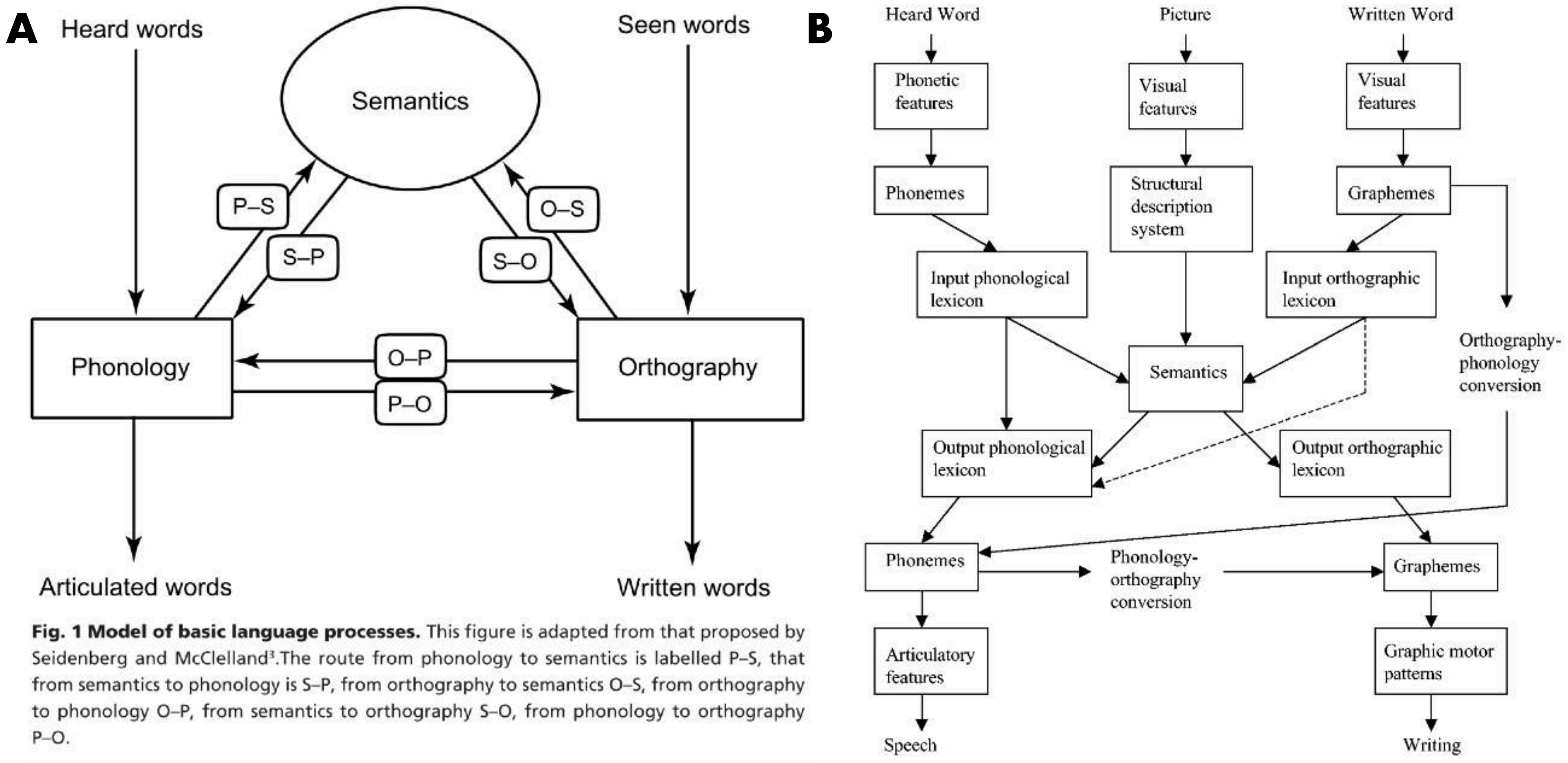

Fig. 1 Model of basic language processes. This figure is adapted from that proposed by Seidenberg and McClelland[3].The route from phonology to semantics is labelled P–S, that from semantics to phonology is S–P, from orthography to semantics O–S, from orthography to phonology O–P, from semantics to orthography S–O, from phonology to orthography P–O.

Figure 2.2 (A) Basic model of lexical processing (Price, 1998), and (B) Elaborated model of lexical processing (Martin, 2003) semantics, while production involves generation of phonology or orthography (Figure 2.2 A). This framework (Figure 2.2B) forms the basis of various widely used standard models of comprehension and production, e.g. DRC (Dual Route Cascade) model for reading by Coltheart and colleagues (2001) and the LRM (Levelt, Roelofs, and Meyer, 1999) model of lexical production.

The dual-route theory of reading aloud was first described in the early 1970s (Forster and Chambers, 1973; Marshall and Newcombe, 1973). It postulated two cognitive routes: a lexical route in which known words are visually recognised and the pronunciation retrieved from the mental lexicon, and a non-lexical route in which words (and non-words) are read by mapping graphemes to phonemes (Figure 2.3 A). This was later formulated into the computational DRC model by Coltheart and colleagues (2001) (Figure 2.3 B).

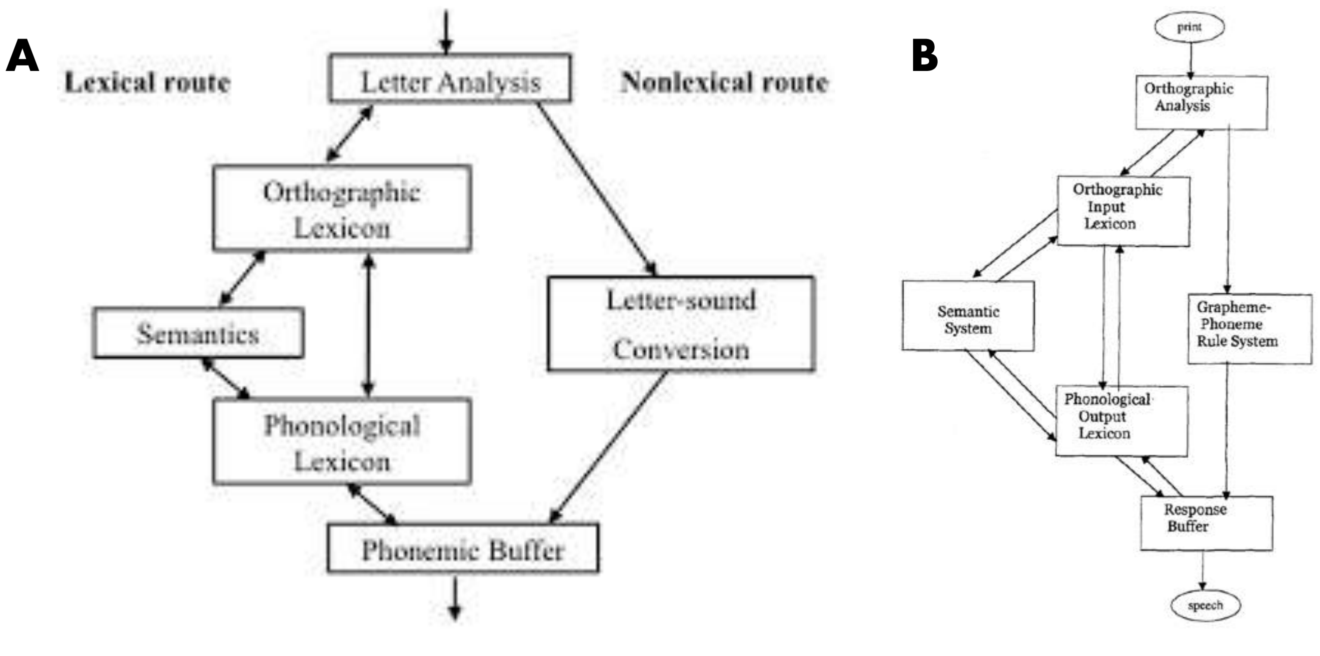

Figure 2.3 Dual route model of reading aloud

Language production models originally included three main components: conceptualisation, formulation and articulation (Figure 2.4 A, dotted box). The first two steps were further elaborated in the LRM model (1999), and consisted of four processing stages: conceptual preparation, lexical selection, morphophonological encoding and syllabification, and phonetic encoding (Figure 2.4 B). Around the 1970s, language production models began to include language control systems for editing, monitoring, and feedback, conceptualising the existence of two interacting systems: a linguistic system and a conceptual system (Berg, 1986). Levelt (1989) formally included monitoring and the speech comprehension system in his production model, postulating monitoring of one's own speech (both internal and overt) as well as that of other speakers (Figure 2.4 A).

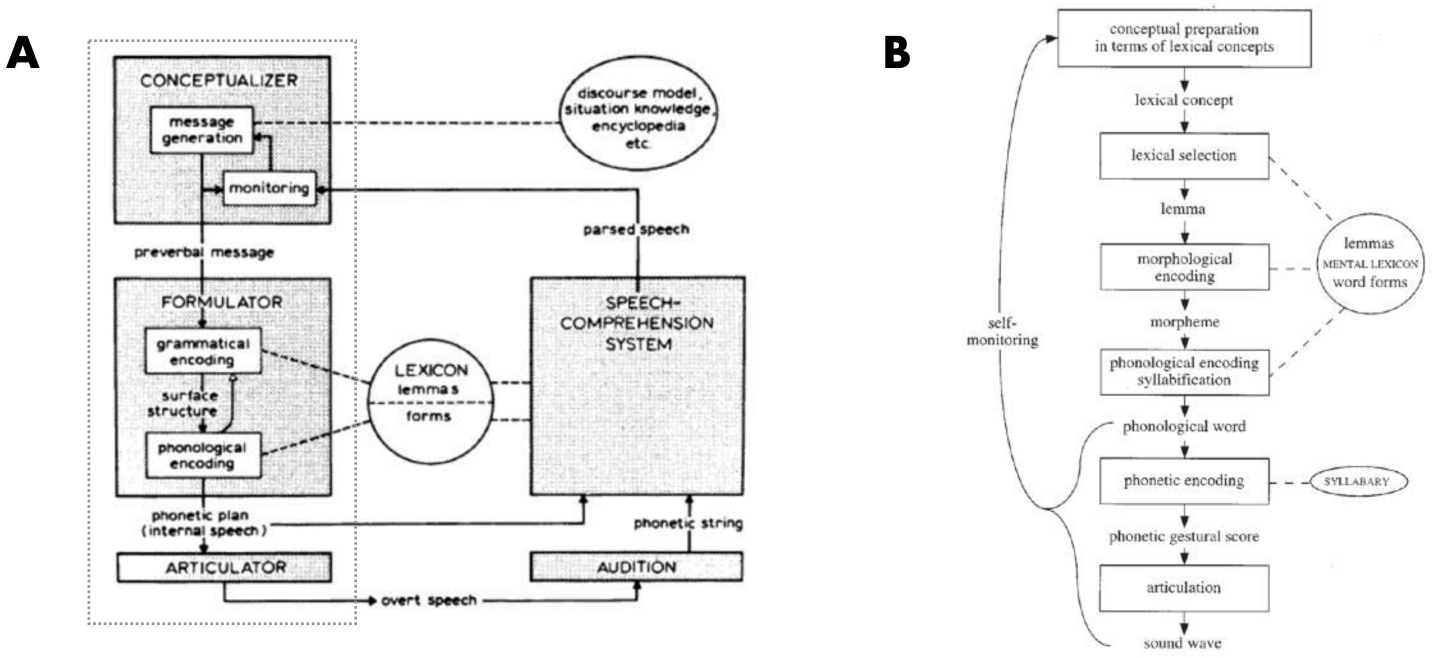

Figure 2.4 Models of language production. (A) Levelt (1989), and (B) LRM

Research interest in bilingualism spiked in the 1990s. Early bilingualism research was based on monolingual theories, until bilingualism researchers criticised and discredited the idea that bilingualism is simply an extension of monolingualism. They emphasised that bilinguals were not the sum of two monolinguals with two separate and isolable language competencies (Grosjean, 1989). Unlike in monolinguals, conceptual representations in bilinguals are linked to different lexical representations (Kroll and Stewart, 1994), and one of the important questions was whether language access was selective or non-selective. For example, does the English word “cat” also activate the Spanish word “gato” in an English-Spanish bilingual, or does the context constrain activation only to English? The language-selective access hypothesis proposed that the languages in bilinguals have independent lexicons that are accessed selectively depending on language set information (Kolers, 1963) while the non-selective access hypothesis proposed that bilinguals possess a single integrated lexicon in which lexical representations from both languages are simultaneously activated during the processing of word input (Caramazza and Brones, 1979; Beauvillain and Grainger, 1987). There is now a general consensus that bilingual word recognition is subserved by a language-non-selective access system that is sensitive to task demands and context (French and Jacquet, 2004; Dijkstra and Kroll, 2005).

Numerous studies investigated the organisation of the bilingual language system and how processing in one language is influenced by the other. This led to the formulation and development of several psycholinguistic models of bilingual language representation and processing that remain influential today, such as the Inhibition-Control (IC) model, the Revised Hierarchical model (RHM), the Bilingual Interactive Activation (BIA) model, etc.

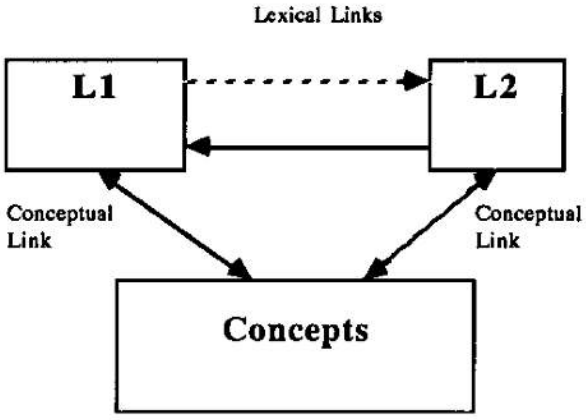

Figure 2.5 Revised Hierarchical Model (Kroll and Stewart, 1994)

The RHM (Kroll and Stewart, 1994) is an influential model whose predictions continue to remain relevant in the literature today (e.g. Perani and Abutalebi, 2005;

Grainger et al., 2010). However, due to its framework of separate lexicons for each language, it is now considered obsolete in its original form (Kroll et al., 2010). The RHM (Figure 2.5) proposed a common semantic conceptual store with separate lexicons for each language. In less proficient bilinguals, it was postulated that in the second language, concepts would be accessed through the first language via translation, but that with greater proficiency, it would be possible to access concepts directly through the second language. Thus, bilinguals at different levels of proficiency would utilise these two routes to differing degrees.

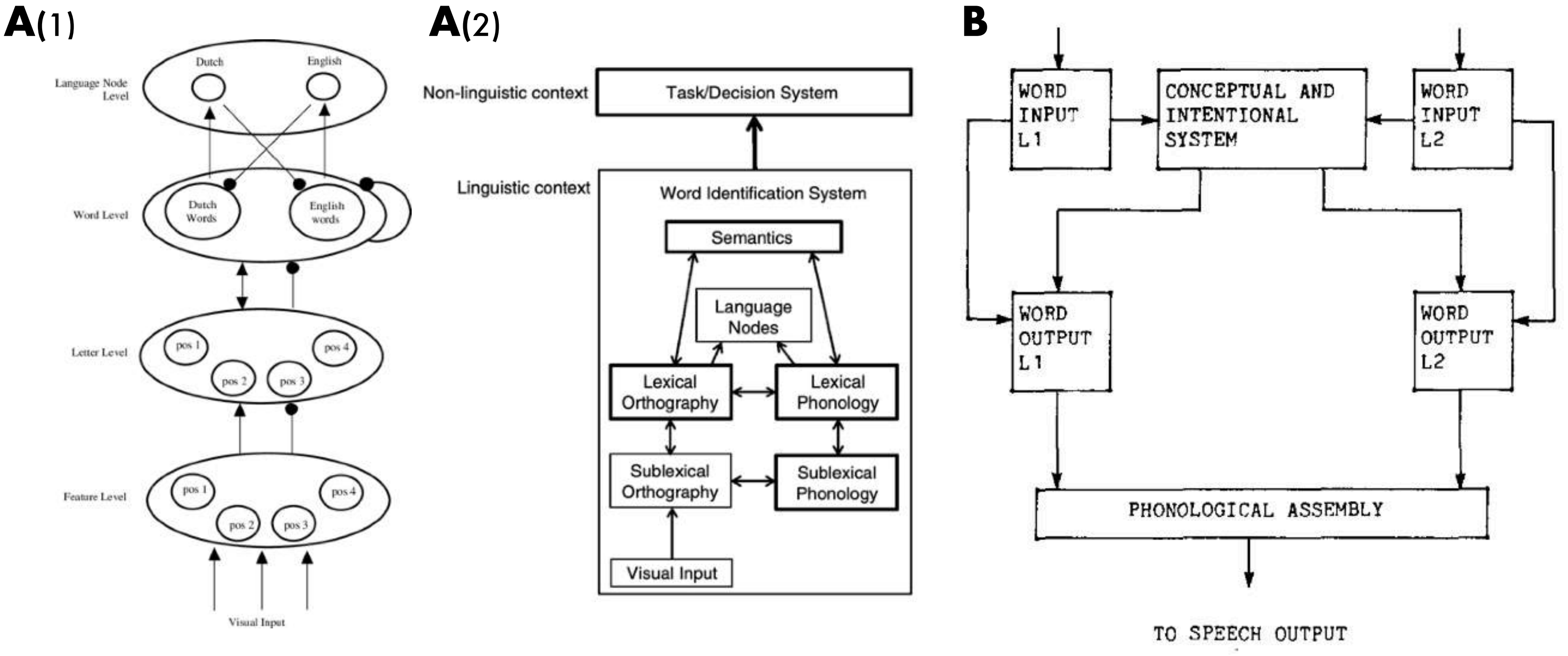

Figure 2.6 Bilingual models of language processes. (A) BIA and BIA+ models of word recognition, and (B) IC model of word production

The BIA (Figure 2.6 A1) is a language non-selective model of bilingual visual word recognition (Dijkstra and van Heuven, 1998). There are four levels of nodes: features, letters, words and language tags. During reading of a word, feature nodes activate the relevant letters, letter nodes activate words in the relevant language, and words from both languages interact depending on language proficiency and context. Due to the interaction between languages in the model, activation of features and letters in one language spreads to both words in the target language as well as words in the other language. A top–down inhibitory control mechanism using language nodes controls the cross–language activation. The BIA+ model (Dijkstra and van Heuven, 2002) (Figure 2.6 A2) was proposed as an extension to the BIA model, and explicitly incorporated semantic and phonological representations, as well as a non–linguistic control system. Neither the BIA nor the BIA+ models, however, account for changes in proficiency, and thus Grainger and colleagues (2010) formulated a developmental variant, the BIA–d model, that incorporated the predictions of the RHM. The IC model (Figure 2.6 B) is a bilingual language production model inspired by the RHM and Levelt's model, and is complementary to the BIA/BIA+ model of bilingual comprehension (Green, 1986). It was the first bilingual model to explicitly include inhibition as the mechanism that supports bilingual processing, and continues to remain the dominant model of bilingual language production.

Overall, however, all of these models were based on behavioural data. With the advent of neuroimaging, new evidence for or against these models built up, and the models continue to be evaluated and updated (van Heuven and Dijkstra, 2010).

2.2 NEUROANATOMICAL MODELS

2.2.1 CLASSICAL LANGUAGE MODEL

The seminal work of Broca, Wernicke, Lichtheim, etc. in the late 1800s led to the first neuroanatomical models of language processes in the brain. These models were synthesised and popularised almost a century later in the form of what is often called the Wernicke-Lichtheim-Geschwind (WLG) or simply the classical model (Figure 2.7), consisting of Broca’s Area, Wernicke’s Area, and the arcuate fasciculus.

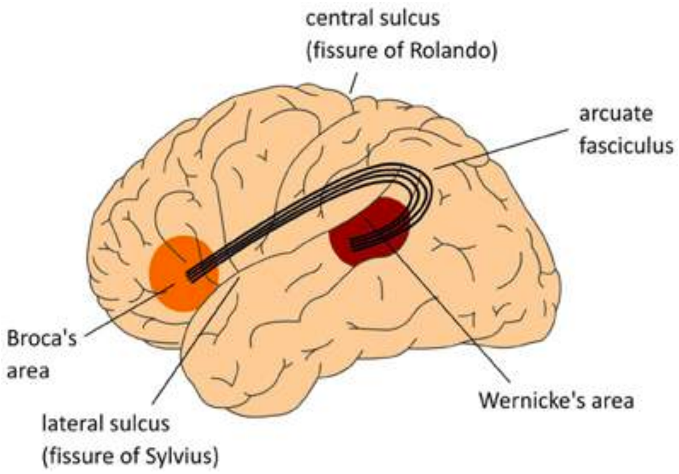

Figure 2.7 Classical language model

The foundations of the classical model were laid in the 1860s with the work of French physician Paul Broca. His seminal discovery came about when he was consulted about a 51-year-old patient Leborgne with various neurological problems and no language production ability. When Leborgne's brain was autopsied after his death (Figure 2.8 A), Broca found a test-case for his idea about localisation of language in the brain and presented his findings at various conferences (Broca, 1861a, 1861b). Over the next four years, he documented twelve cases and noticed that many of them involved left-hemisphere lesions. Marc Dax had postulated a similar theory at a conference in 1836, but his originally unpublished work did not include autopsy results, and he died before his work was later published by his son Gustave Dax (Dax, 1865; Finger, 2000). In 1865, Broca's carefully documented work established the connection between speech and the left inferior frontal gyrus (Broca, 1865). This area came to be called Broca's area, and it was considered to be the seat of language production.

Ten years after Broca's discoveries, German neurologist Carl Wernicke described two patients whose comprehension was severely compromised, even though they were able to articulate fluently (Wernicke, 1874). Their autopsies revealed lesions in the superior temporal gyrus (STG), and this led him to conclude that it was essential for language comprehension. Wernicke then proposed the rudiments of the first neuroanatomical language model (Figure 2.8 B). In 1885, German physician Ludwig Lichtheim described a detailed connectionist model of language processing that was both neuroanatomical and functional and made predictions about the consequences of damage to different brain regions (Lichtheim, 1885). Besides Broca's and Wernicke's areas, he further included various "concept fields" such as visual, auditory and motor word-representations, with nerve fibre tracts inter-connecting all of these, as well as the respective sensory structures required for input and output (Figure 2.8 C).

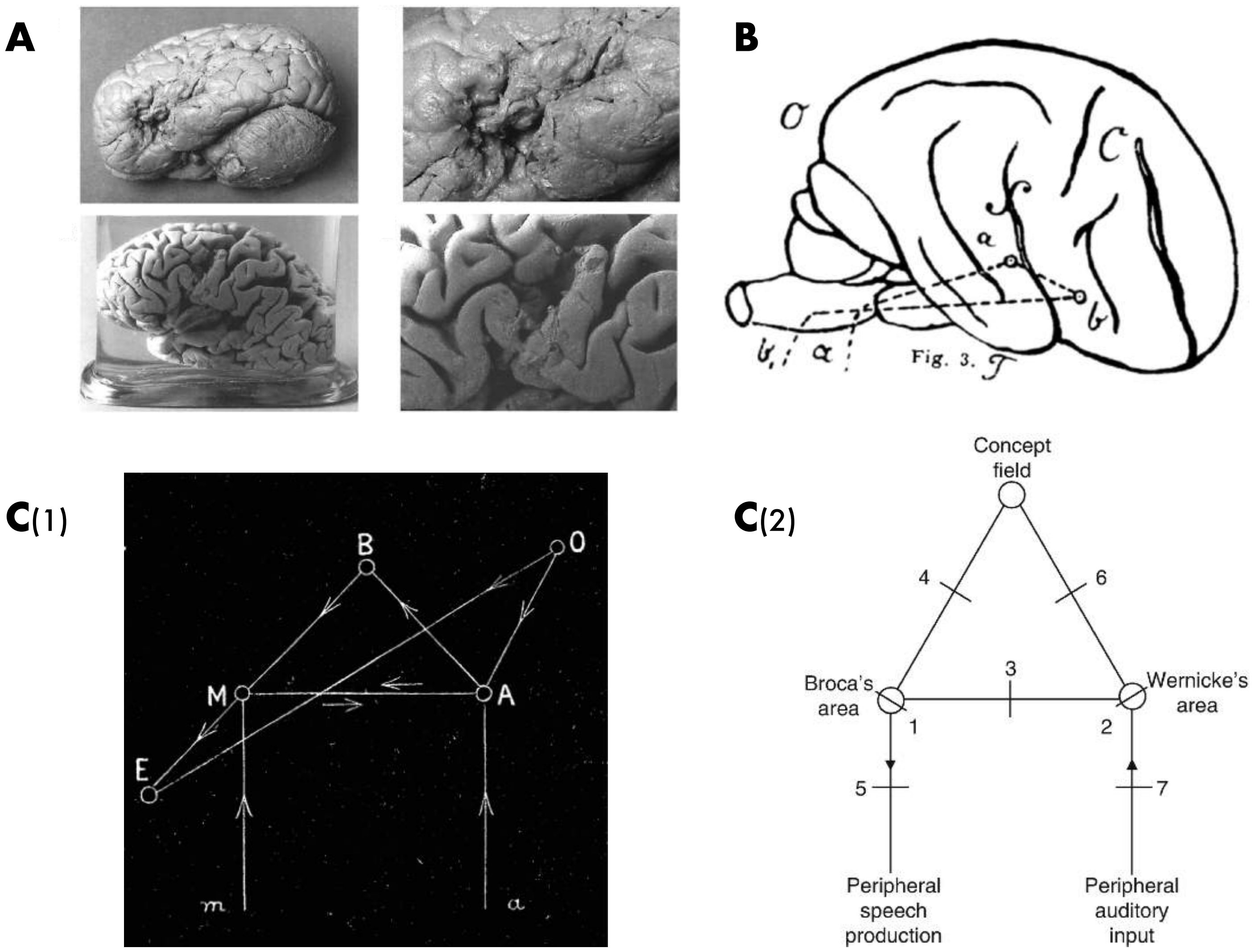

Figure 2.8 Building the classical language model. (A) Autopsied brains of Broca's patients (figure from Dronkers et al., 2007), (B) Wernicke's model of language processing (Wernicke, 1874), (C) Lichtheim's connectionist model: (1) an original figure from Lichtheim, 1885 and (2) a modern description by Hux (2011).

In the first half of the twentieth century, however, this modular localisationist view of language processing fell sharply out of favour. Pierre Marie, who was Broca's intern early in his career, published a series of paper questioning the role of Broca's area (e.g. Marie, 1906a, 1906b). He was joined by other neurologists such as Brain, Freud, Goldstein, Head, etc. in espousing the anti-localisationist "holistic" view that brain functions did not localise to specific regions but arose from complex interactions between different regions. This movement also coincided with the rise of behaviourism, which emphasised external, observable behaviour and dismissed the study of the "unobservable" mental states and architecture (Watson, 1913). Thus over the next several decades, cognitive and neuroanatomical models disappeared from cognitive neuroscience.

The cognitive revolution of the 1950s put an end to behaviourism, and American neurologist Norman Geschwind resurrected a simplified version of the classical language model with resounding success in a series of publications in the 1970s (Figure 2.9). In this version, Broca's area is considered the seat of language production, Wernicke's area is responsible for language comprehension, and the arcuate fasciculus facilitates communication between the two. Today, this iconic WLG model featuring the left hemisphere of the brain (figure 2.7) is considered the classical model and the blueprint for modern understanding of the neuroanatomical correlates of language.

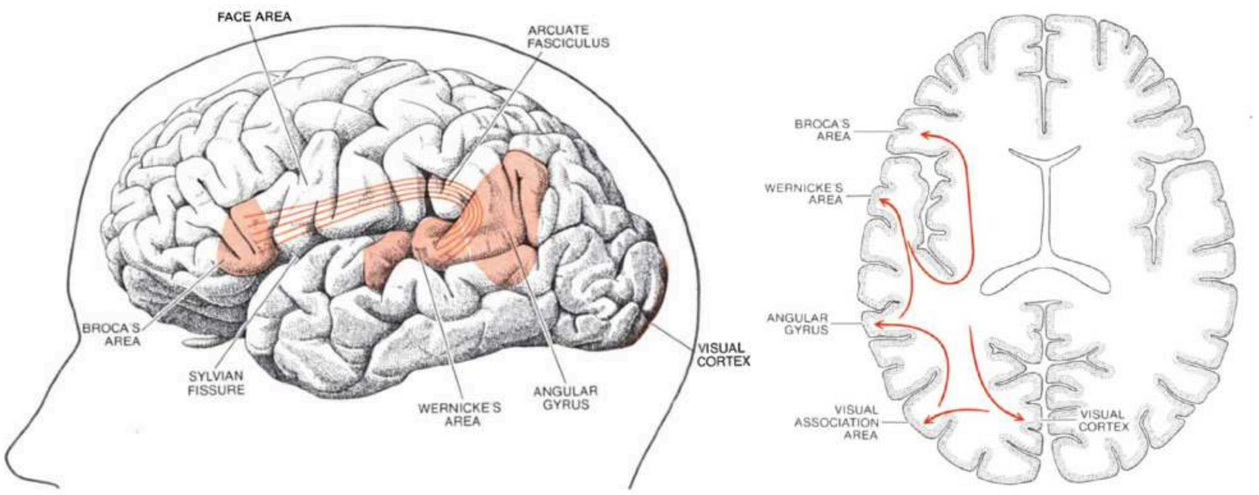

Figure 2.9 Wernicke-Lichtheim-Geschwind model (Geschwind, 1972)

2.2.2 UPDATED LANGUAGE MODELS

Till the invention and widespread use of functional neuroimaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), neuroanatomical language models depended on relatively coarse indicators from neuropsychological studies and deficit-lesion mapping, electrophysiological data, and the Wada test and behavioural dichotic listening tests for language lateralisation. Functional neuroimaging, however, made it possible to study the living brain while it processed language, and thus ushered in the next era of understanding of the neural correlates of language. Since the original conception of the classical model, the framework of language processing has advanced significantly in two ways: (i) at the conceptual level, language comprehension and production have been elaborated into various overlapping sub-processes (as previously described in section 2.1), and (ii) at the neuroanatomical level, the contributions of additional brain regions have been discovered due to functional neuroimaging. Neuroanatomical language models now combine modelling and neuroimaging data in addition to neuropsychological and electrophysiological data, and are thus increasingly sophisticated.

The classical language model has a turbulent scientific history, and we have now come full circle in once again considering Geschwind's model excessively localisationist (Price, 1998, 2000, 2010, 2012; Hagoort, 2005, 2013; Poeppel et al., 2012; Tremblay and Dick, 2016; Duffau, 2018). Though this model is correct in that the perisylvian area is still considered to be specialised for language, our understanding of what it means to be "specialised for language" has changed substantially. We now know that the functional roles of these regions are significantly more complicated than simply "production" or "comprehension", and that these regions are also involved in other cognitive functions, for example, Broca's area has been shown to also be involved in processing music (Maess et al., 2001; Koelsch et al., 2004; Fadiga et al., 2009).

Consequently, language regions are now referred to by their anatomical names, and the nomenclature of Broca's and Wernicke's areas has been largely abandoned in the literature, since it is, for one, misleading to think of them as exclusive centres of production or comprehension, and second, there is little consensus on which anatomical regions comprise Broca's and Wernicke's areas (Figure 2.10), as demonstrated in an extensive review and survey by Tremblay and Dick (2016).

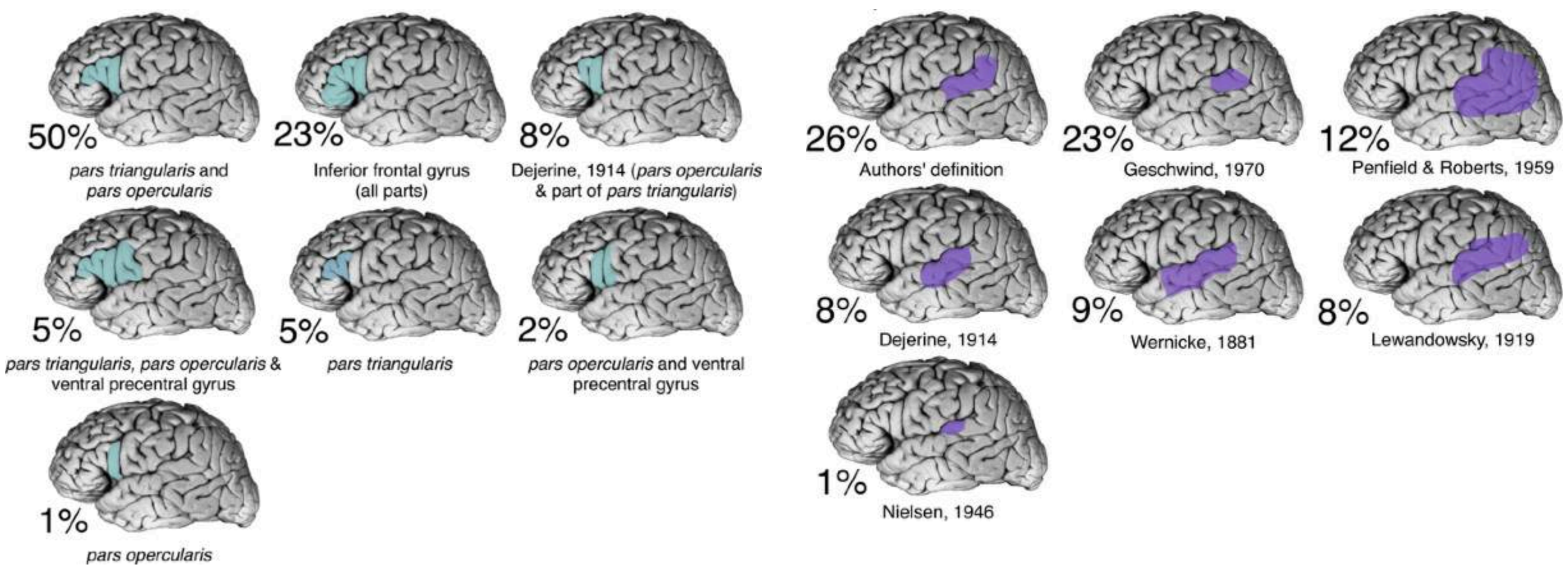

Figure 2.10 Percentage of respondents (n=159) endorsing each anatomical definition of Broca's Area (left panel) and Wernicke's Area (right panel). Figure adapted from Tremblay and Dick (2016).

The two earliest successors of the classical model were Price's model (2000) and the Memory, Unification, Control (MUC) model (Hagoort, 2005, 2013). In the largest departure from the classical language model and the psycholinguistic tradition of studying language comprehension and production separately, these models proposed shared circuitry for comprehension and production, each model subdividing language processes along different lines. Price (2000) combined neuropsychological and neuroimaging data with tripartite (semantics, phonology, orthography) cognitive models of lexical processing (Figure 2.11 A). The MUC model also subdivided language processing into three, albeit very different, components: memory, unification, and control. Out of these, only the memory component was linguistic, referring to the linguistic knowledge encoded and consolidated in the temporal cortex and the angular gyrus. Unification referred to combining elements from memory in novel ways, at the phonological, semantic and syntactic levels in the ventrolateral frontal regions. Finally, the control component specified the social communicative aspect of language such as social interaction and joint action in the dorsolateral prefrontal cortex, anterior cingulate cortex, and parietal regions. For example, executive control for choosing the appropriate language or register in different social contexts and for handling the joint action aspects of conversation, etc. In addition, the MUC specified anatomical connections between these regions beyond the arcuate fasciculus (figure 2.11 B).

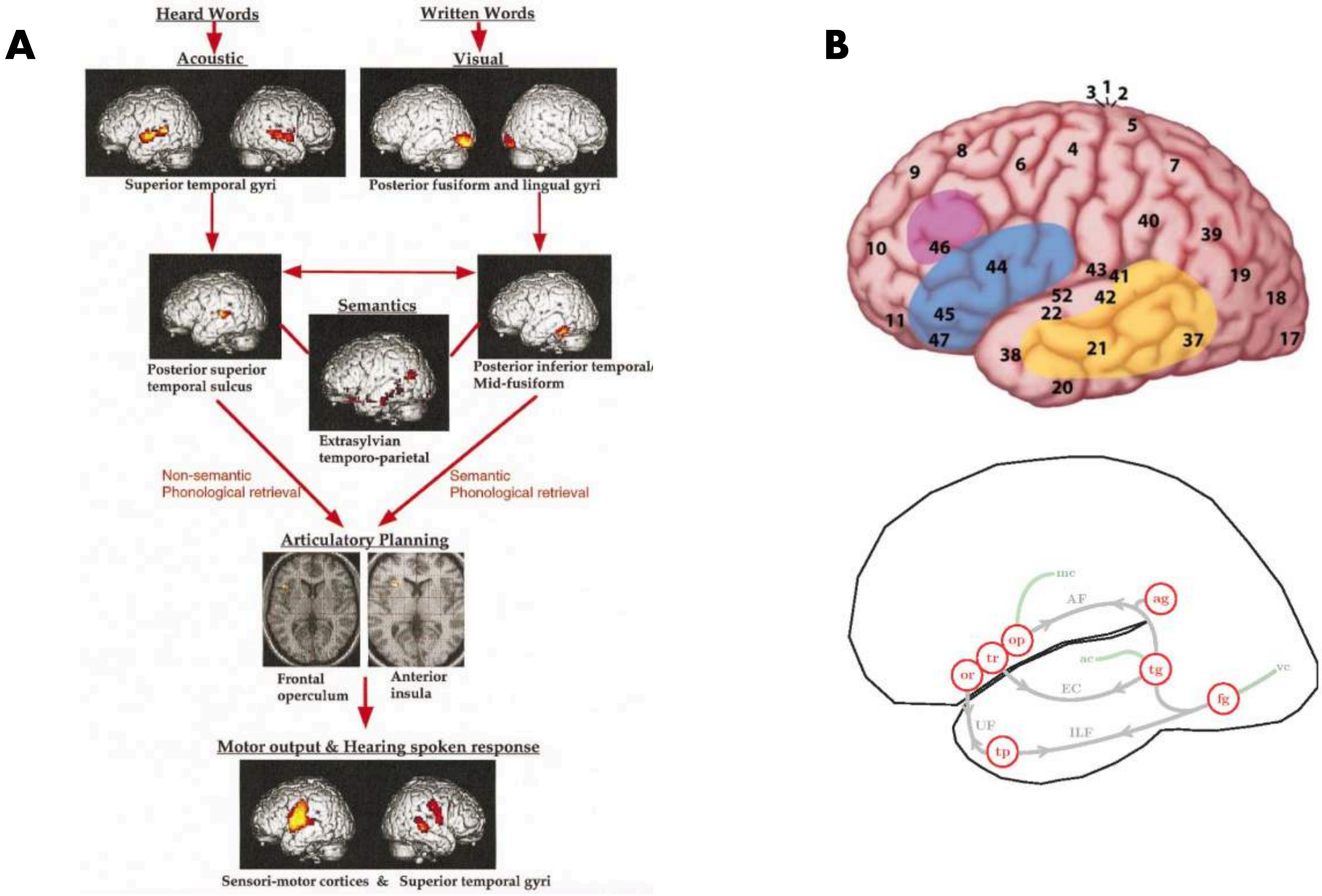

Figure 2.11 Modern neuroanatomical language models. (A) Price (2000), (B) MUC model (Hagoort, 2005, 2013)

Thus, in broad strokes, there was a general consensus that a fronto-temporo-parietal network of regions was specialised for language (and was supported by various non-linguistic regions), but the functional roles of the different regions continues to be studied. One of the big questions in neuroimaging studies was how similar the neural correlates of language are across different modalities and languages. It was found that comprehension and production shared a common language network (Heim et al. 2003; Mar, 2004; Menenti et al., 2011; Segaert et al., 2012), and that this network of regions was similar across various languages (Honey et al., 2012; Rueckl et al., 2015). However, the functional division of labour between regions depends on the specific task at hand, and over the following years, several models were developed in various research sub-fields specific to each of the main language systems: reading, auditory comprehension, and verbal production[1].

2.2.3 COMPREHENSION MODELS

A number of influential semantic memory models have proposed a widely distributed network of conceptual knowledge or semantics in the brain (e.g. Patterson et al., 2007; Lau et al., 2008; Binder and Desai, 2011). Interestingly, the dual pathway, a key feature from Wernicke's original model (1874) (Figure 2.8 B) that was lost in the Geschwind version came to be resurrected in modern language comprehension models. In the 1980s, data from the visual systems of macaques indicated that the visual regions were organised into dorsal and ventral streams (Ungerleider and Mishkin, 1982). This idea also found favour in the language comprehension field, and dual pathway models are now the standard in reading and speech comprehension.

READING

In 2000, Pugh and colleagues proposed a dual stream model of reading, postulating that fluent word identification in reading is related to a dorsal fronto-temporo-parietal network and a ventral fronto-occipito-temporal network (Figure

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[1] Research on writing (e.g. Planton et al., 2017) is relatively sparse and not as prominent in the language literature.

2.12). They proposed that normally developing readers would begin by recruiting a non-lexical dorsal network as they learnt to integrate orthographic features with phonological and lexical-semantic features, and that with increasing skill, readers would develop a lexical ventral network that would subserve fluent word recognition. This hypothesis was corroborated by various subsequent studies on dorsal and ventral contributions to reading (Schlaggar and McCandliss, 2007; Cohen et al., 2008, 2009; Zhou et al., 2016).

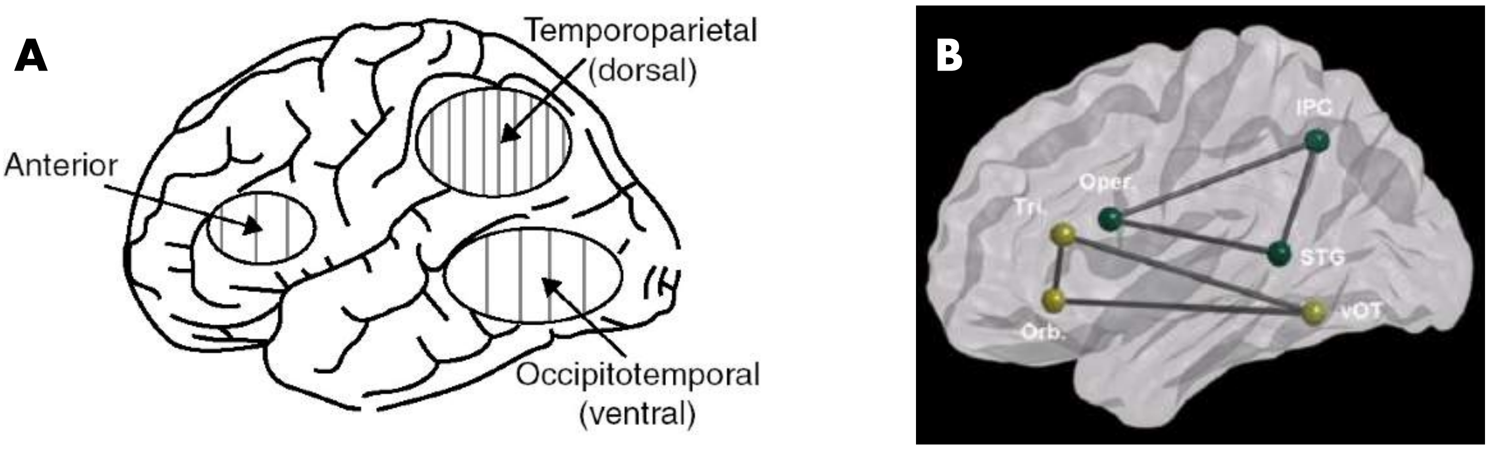

Figure 2.12 Dorsal and ventral pathways in reading. (A) Pugh et al.'s initial model (2000), figure adapted from Sandak et al. (2012). (B) A current model with individual regions, figure adapted from Oliver et al. (2017).

SPEECH COMPREHENSION

The main models of auditory comprehension were developed by Hickok and Poeppel (2000, 2004, 2007) and by Friederici (2002, 2011).

Hickok and Poeppel conceptualised speech comprehension as comprising of two systems: a conceptual system and a motor–articulatory system. They proposed a dual stream model with a dorsal stream involved in mapping sound onto articulatory-based representations, and a ventral stream involved in mapping sound onto meaning. They postulated that the bilateral posterior superior temporal lobes were the locus of sound-based representations, with both streams beginning here. The dorsal stream was hypothesised to project to the posterior Sylvian fissure at the parietal–temporal boundary and then the frontal regions, while the ventral stream was hypothesised to project to the bilateral posterior middle temporal gyrus and then to widely distributed conceptual representations (Figure 2.13 A). In 2008, Saur and colleagues combined fMRI and diffusion tensor imaging and showed that the dorsal pathway connected the superior temporal lobe and premotor cortices in the frontal lobe via the arcuate and superior longitudinal fascicle, and that the ventral pathway connected the middle temporal lobe and the ventrolateral prefrontal cortex via the extreme capsule.

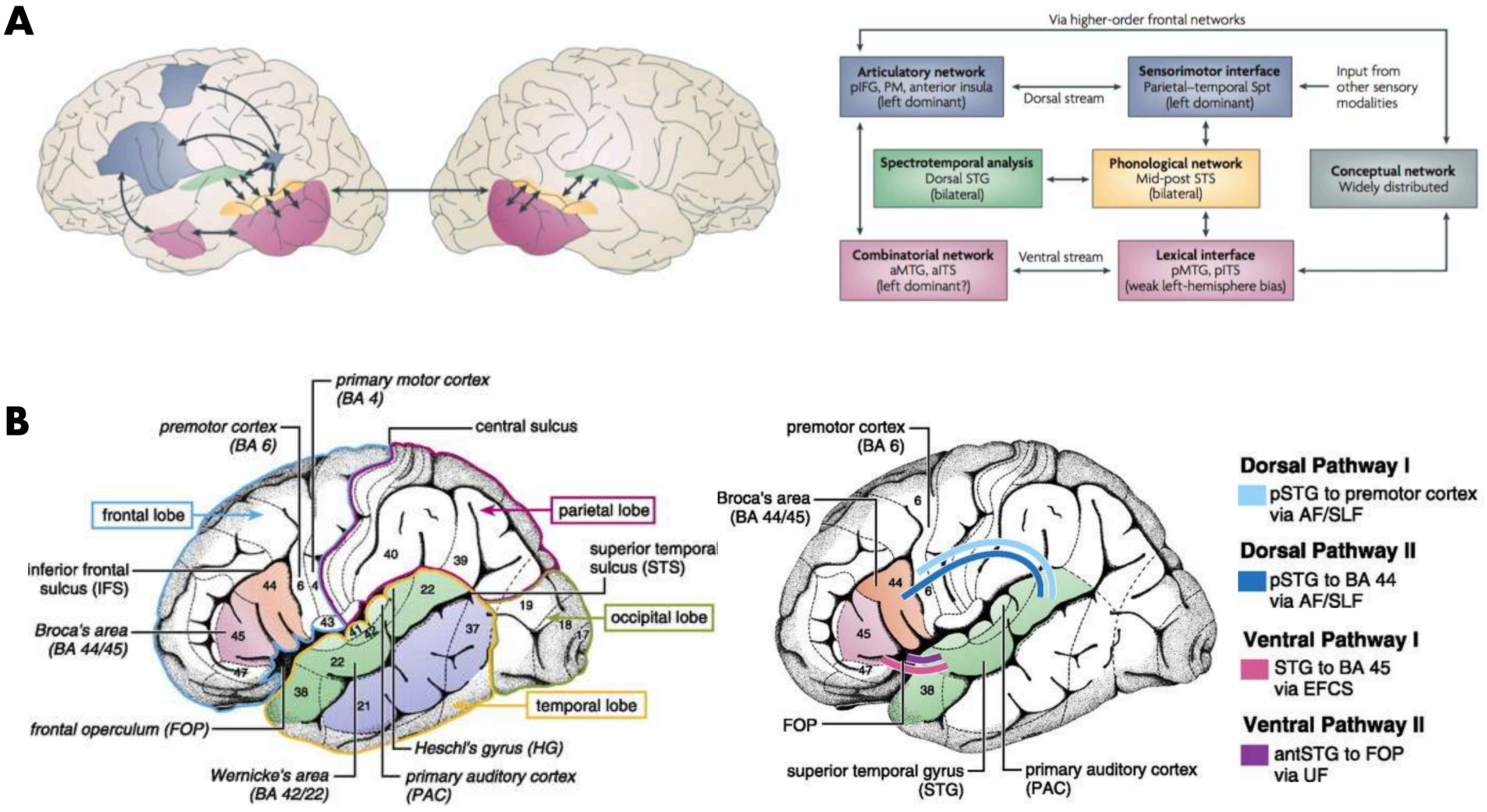

Figure 2.13 Models of speech comprehension. (A) Hickok and Poeppel (2007), (B) Friederici (2011)

Friederici (2002) described the first model of auditory sentence comprehension, specifying a bilateral fronto-temporal network that underlay semantic, syntactic and prosodic processing. Syntactic, and to a lesser extent, semantic processing were shown to be left-lateralised, while prosodic information was shown to be processed primarily in the right hemisphere (Friederici, 2002, 2011). In 2011, the model incorporated the dual stream hypothesis and tractography findings, and additionally proposed that short-range and long-range structural connections might form two dorsal and ventral pathways each between language-relevant regions in the frontal and temporal cortices, suggesting that they may have different directionality (Figure 2.13 B).

2.2.4 PRODUCTION MODELS

Indefrey and Levelt extended Levelt's cognitive models of language production to neuroanatomical models (Figure 2.14) with three meta-analyses of neuroimaging studies of word production (Indefrey and Levelt, 2000, 2004; Indefrey, 2011). The cognitive models of language production were well supported by the neuroimaging data and they found that, as they had expected, the neural correlates of production largely overlapped with comprehension.

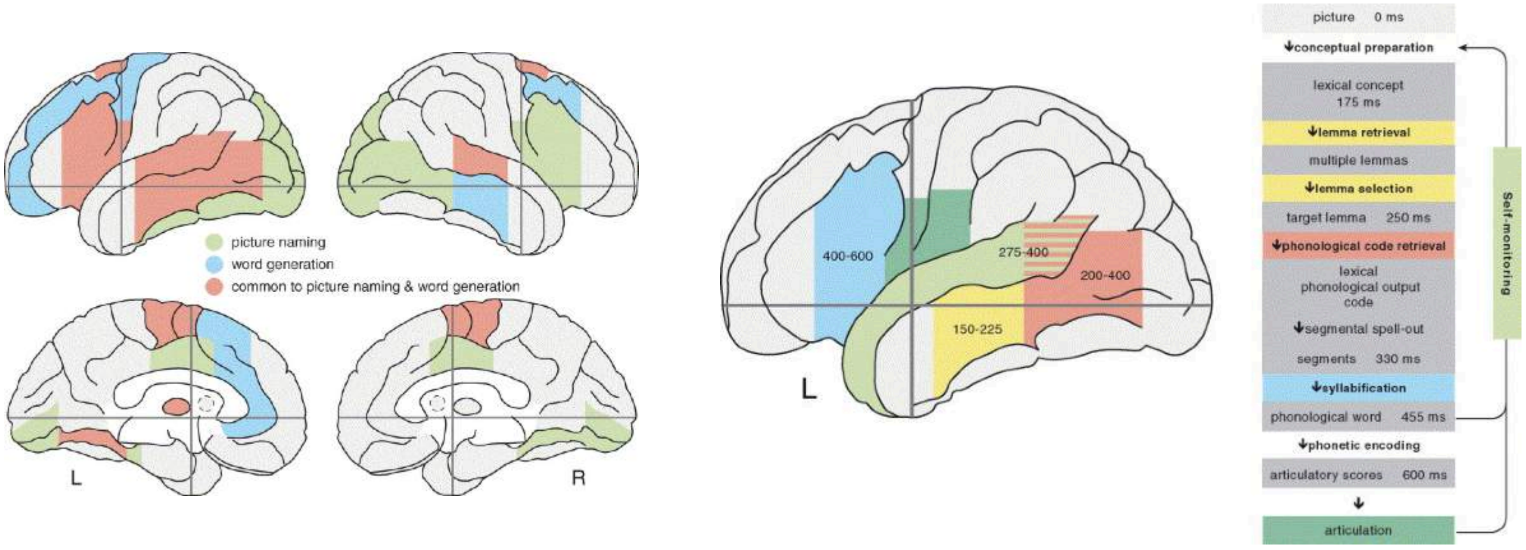

Figure 2.14 Language production model (Indefrey and Levelt, 2004). It was extended to include the inferior parietal cortex, though its role is not yet clear (Indefrey, 2011)

Other lines of research focusing on lexical retrieval further specified the roles of the left inferior prefrontal cortex in language control during verbal production, suggesting dissociable roles for the *pars orbitalis* and *pars triangularis*, with the former supporting controlled access to semantic representations, and the latter supporting domain-general selection processes (e.g. Wagner et al., 2001; Badre and Wagner, 2007).

2.2.5 BILINGUAL MODELS

Studies of bilingualism found that the neural correlates of language were highly overlapping in monolinguals and bilinguals, and that the similarity in activation between languages in bilinguals was variable as a function of age of acquisition and proficiency in the second language (Perani and Abutalebi, 2005) (Figure 2.15). This experience-dependent neural plasticity of language networks is explored in detail in the following chapter.

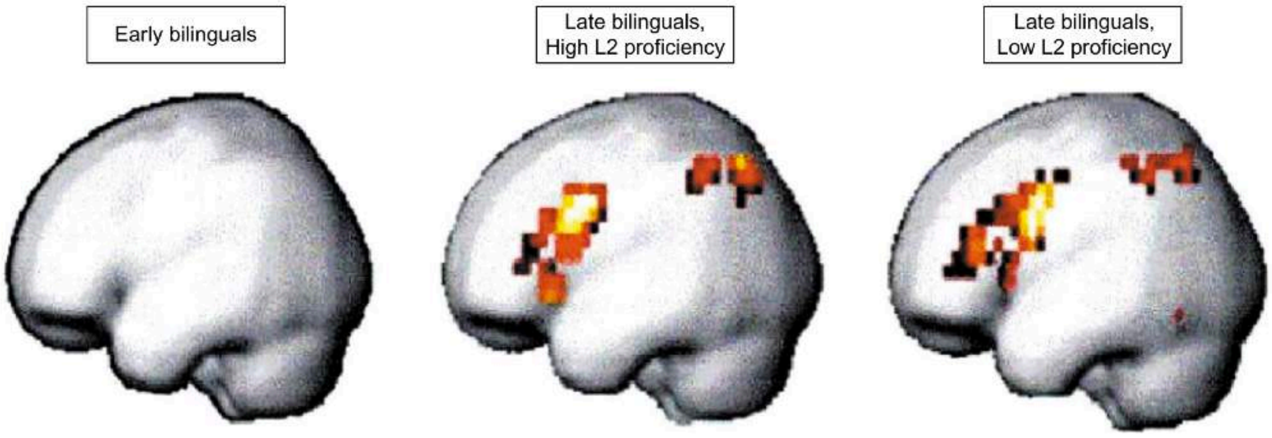

Figure 2.15 L1-L2 similarity in bilinguals as a function of age of acquisition and proficiency in the second language (Perani and Abutalebi, 2005).

One particularly salient feature of bilingualism is the higher demand on the executive control system to choose and switch between languages as required. Abutalebi and Green (2007) extended Green's IC model (Green, 1986), proposing a neuroanatomical model of bilingual language production with multiple levels of cognitive control (Figure 2.16). They proposed that language production in bilinguals is a dynamic process involving cortical and subcortical structures that make use of inhibition to resolve lexical competition and to select the intended language.

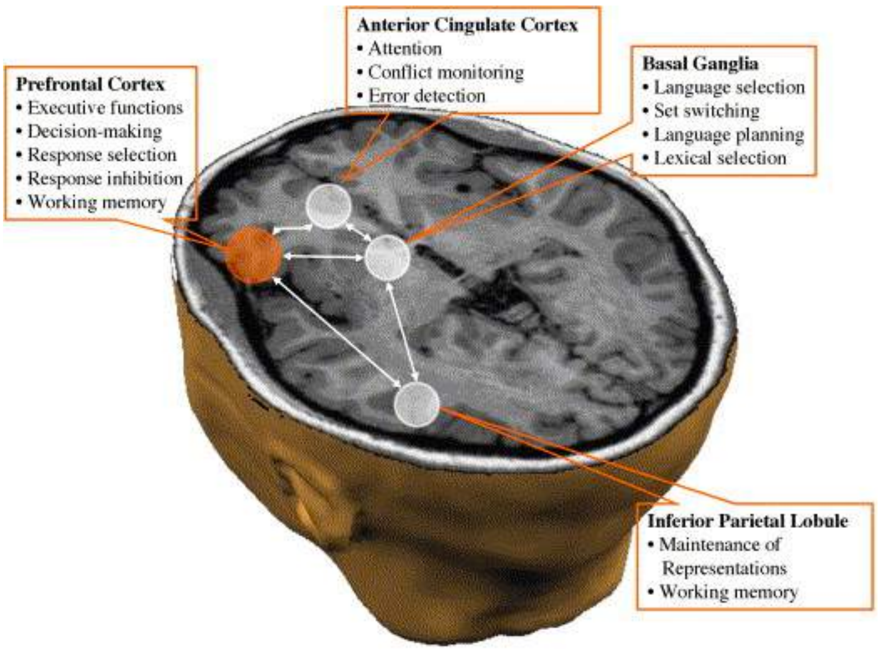

Figure 2.16 Bilingual cognitive control model
(Abutalebi and Green, 2007)

Overall, we can see that the neuroanatomical correlates of language are largely overlapping in the various models, and that there are several points of agreement between them on the larger functional picture. However, the finer details of the roles of each region, how they interact with each other, and indeed the theoretical framework itself, continue to be fiercely debated. The modern classical viewpoint grounds neurobiological function in a linguistic framework that was developed largely from studies using single words and short sentences. Reflecting the overall trend in cognitive neuroscience, there has been a steady push to move towards more complex naturalistic language paradigms to better reflect real-life language use (Blanco-Elorrieta and Pylkkänen, 2018; Hagoort, 2019; Nastase et al., 2020), and, more radically, to move away entirely from the framework of linguistics to understand and explain the neurobiology of language (Hasson et al., 2018; Hasson et al., 2020).

There also remain a few areas of neurobiology that are yet to be explored in greater depth, primarily the contribution of the subcortical areas to language. High resolution functional imaging of deeper brain structures is a work in progress, and more from expediency than any reflection on their importance, subcortical regions are under-studied. Future work is likely to shed greater light on their role and expand the current neuroanatomical models of language to further include subcortical, and possibly cerebellar, structures.

2.3 LANGUAGE LATERALISATION

Hemispheric asymmetry is the idea that the two hemispheres of the brain differ in anatomy and function, and that cognitive functions lateralise differently in the brain, the most famous example being language. The 19th century discovery of language lateralisation created a monumental shift in understanding of the brain, and led to an explosion of interest in hemispheric asymmetry that continues unabated in the present day.

Though the relationship between brain and cognition did not gain widespread acceptance till the 19th century — almost 200 years after it was formally proposed by Thomas Willis in his *Cerebri Anatomie* — the *effects* of hemispheric lateralisation have been noted since at least 1676, when Johann Schmidt described a patient with aphasia and right-side paralysis (Benton and Joynt, 1960; Finger, 2001). Amongst Broca's findings in the 1860s was the observation that the lesions in patients with expressive aphasia were in the left hemisphere. He famously announced his conclusion at a conference with the declaration, "Nous parlons avec l'hémisphère gauche" ("We speak with the left hemisphere"). Until this point, the prevailing view was that the brain hemispheres, like other paired organs in the body, were symmetrical in form and interchangeable in function (named Bichat's law of symmetry after influential French anatomist Marie Francois Xavier Bichat [1771-1802]). Broca's finding thus created a fundamental shift in the field. In 1874, English neurologist John Hughlings-Jackson proposed that just as the left hemisphere is specialised for speech, the right hemisphere is specialised for visuospatial functions (Harris, 1999).

For the next century, lateralisation was considered unique to humans (though evidence to the contrary began to accumulate in the 1970s onwards (for a review of cross-species brain asymmetry studies, see Ocklenburg and Gunturkun, 2012)):

> **The phenomenon of cerebral dominance — that is, the predominant importance of one side of the brain for a class of learned behaviour — occurs, as far as we know, in no mammal other than man. The dominance of the left side of the brain for speech is the most striking example of this phenomenon. Contrary to generally accepted views, there is a striking anatomical asymmetry between the temporal speech region on the left side and the corresponding region of the right hemisphere. (Geschwind, 1970, p. 944)**

In the latter half of the 20th century, three methods were developed that became extremely popular in language lateralisation research: the Wada test (Wada, 1949), divided visual field (DVF) paradigm (Mishkin and Forgays, 1952), and the dichotic listening paradigm (Broadbent, 1956).

In the early 1960s, Doreen Kimura published her groundbreaking studies on hemispheric differences using dichotic listening tasks. Adapting the paradigm developed by Donald Broadbent to study attention and attention switching, Kimura demonstrated that when different digits are presented simultaneously to the two ears, the total number of digits correctly reported from both ears was higher for the right ear than the left ear in various groups of patients and healthy subjects (Kimura, 1961, 1963). This was called the right ear advantage (REA), and it was further demonstrated in perception of melodies and in visual perception (Kimura, 1964, 1966).

A few years earlier, Roger Sperry had begun his split-brain research in animals that would eventually lead to his 1981 Nobel prize (along with David Hubel and

Torsten Wiesel). In a series of experiments with human patients who had undergone corpus callosotomy, i.e. surgical separation of the brain hemispheres, his student Gazzaniga and colleagues showed that the two hemispheres were largely independent in verbal and visuospatial functioning (Gazzaniga et al., 1962; Hamilton and Gazzaniga, 1964; Gazzaniga and Sperry, 1967). They administered several tests, including DVF tests, providing insights into interactions between the two hemispheres during various cognitive processes.

The intracarotid amobarbital procedure, commonly referred to as the Wada test, was devised by Juhn Wada to assess language dominance in psychiatric patients in order to target the opposite hemisphere for electroconvulsive therapy (Wada, 1949). Intracarotid injections of amobarbital were used to anaesthetise either brain hemisphere and language tests could be administered to assess language dominance. A series of highly cited large-scale patient studies of language lateralisation were carried out using this procedure, that further established the importance of the left hemisphere in language (Wada and Rasmussen, 1960; Branch et al., 1964; Milner et al., 1964; Milner, 1975; Rasmussen and Milner, 1975, 1977). This test is still widely used today, mostly for epilepsy patients, to gauge the impact of surgery on language and memory function.

These initial studies were massively influential in establishing left hemisphere dominance for language. However, throughout the years, various scientists have pushed back against the mainstream narrative that the right hemisphere does not participate in language, pointing out concerns about the interpretations of the data from each of these lines of investigation. For example, Jerre Levy and Eran Zaidel contested Gazzaniga's claims that the right hemisphere has no language and that its cognition is limited (Levy, 1983; Zaidel, 1983). Zaidel further pointed out that split-brain studies showed that the right hemisphere displayed greater comprehension than production ability (Zaidel, 1976, 1977, 1978; Gainotti et al., 1983). Jäncke and colleagues (1992) pointed out that different dichotic tests reveal different results and had low inter-test correlations, and Hugdahl took the view that dichotic listening is not related to a single mechanism, and that in addition to language asymmetry, it is a measure of temporal lobe function, attention, and stimulus processing speed (Hugdahl, 1995). Similar concerns were expressed about DVF tests, and methodological recommendations were suggested to mitigate them (Sergent and Hellige, 1986). Snyder and colleagues (1990) performed an extensive international survey of epilepsy surgery centres, which revealed heterogenous methods of performing the Wada test and a lack of consensus regarding the theoretical assumptions of the procedure that led to large reported differences in the prevalence of mixed speech dominance in their patient populations. Benbadis and colleagues (1998) pointed out that different investigators used different language tasks during the Wada test, and came to the conclusion that the popularly used speech arrest measure was not a valid measure of language dominance. Loring and colleagues (2012) carried out a detailed review of the large-scale Wada test studies of the 1970s, pointing out methodological irregularities (which are inherent to patient studies) that potentially inflated the incidence of left-lateralisation. Finally, a small but steady stream of reviews of the right hemisphere's role in language continued to be published over the years, and many scientists remained unconvinced that the right hemisphere was unnecessary for language (e.g. Moscovitch, 1976; Day, 1977; Searleman, 1977; Lambert, 1982a, 1982b; Bishop, 1988; Bryan, 1988; Code, 1997; Beeman and Chiarello, 1998; Jung-Beeman, 2005).

By the 1980s, interest in bilingualism added a new layer of complexity to the question. A number of studies provided some evidence for effects of age of acquisition and proficiency in the second language on language lateralisation (e.g. Genesee et al., 1978; Sussman et al., 1982). This experience-dependent plasticity of language lateralisation is reviewed in detail in the following chapter. Though the finding of differential lateralisation in bilinguals was disputed by some (e.g. Soares and Grosjean, 1981), it is of note that the prevailing view of left hemisphere dominance had changed substantially by this time:

> **However, this is not to say that one hemisphere can mediate a certain function, while the other cannot. Instead, it can be said that certain stimulus-response relations can be processed faster or more accurately by one hemisphere than by the other in the performance of a certain task. For example, the right hemisphere, although specialized for the processing of visuospatial information, can also perform a variety of linguistic functions, although not as efficiently or to the same degree as the left hemisphere. (Soares and Grosjean, 1981, p. 599)**

In the 1990s, functional and structural neuroimaging methods became available, and the new findings followed the same pattern as with previous methods: (1) A number of studies found left hemisphere lateralisation of language, along with right hemisphere involvement (Binder et al., 1997; Frost et al., 1999; Pujol et al., 1999); (2) The amount of right hemisphere involvement — and mainstream acceptance of it — varied with the sub-field and the language tasks used. For example, using lexico-semantic tasks, Vikingstad and colleagues (2000) reported left hemisphere dominance at the group level, but found that lateralisation varied at the individual level continuously from left to bilateral. Bilateral activation was most commonly noted in speech comprehension (e.g. Belin et al., 1998). For example, the speech perception model by Hickok and Poeppel (2000) detailed differential lateralisation of various hypothesised language sub-processes (Figure 2.17); (3) There were reviews questioning conflicting findings about the extent of the left-lateralisation and calling for methodological reforms (Bradshaw et al., 2017a, 2017b).

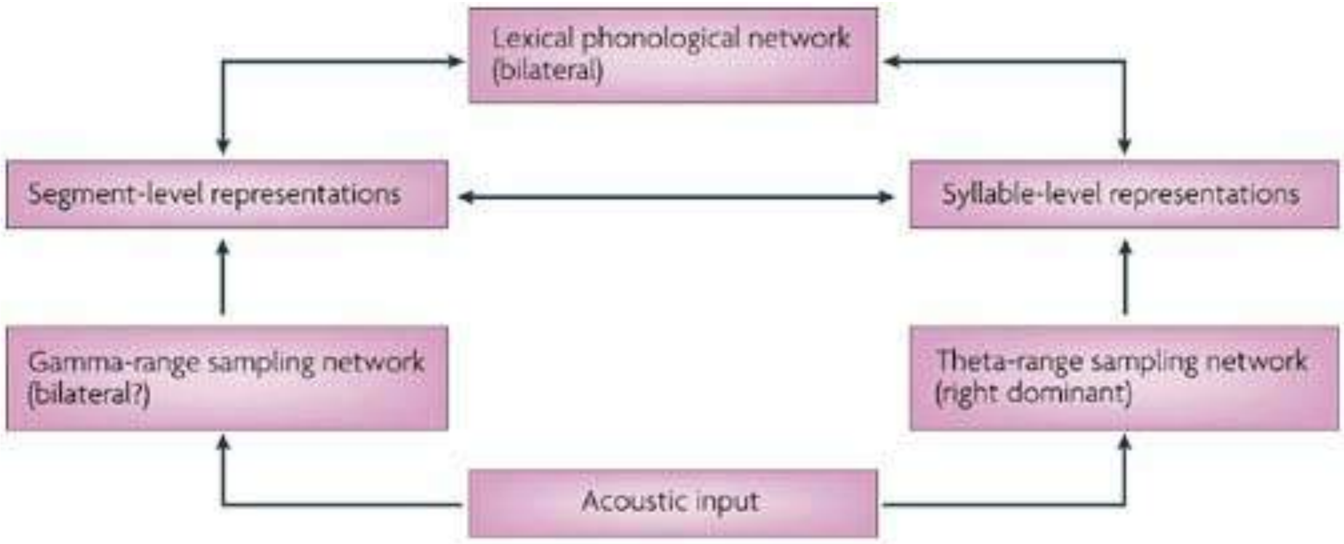

Figure 2.17 A speech comprehension model with hypothesised lateralisation of various sub-processes (Hickok and Poeppel, 2000)

At the same time, functional magnetic resonance imaging also opened the door to testing a wide variety of normal populations from infants (Dehaene-Lambertz et al., 2002, 2010; Perani et al., 2011) to older adults (Cabeza, 2002), and new theoretical and methodological refinements were now possible. For one, it was possible to compare the lateralisation of different brain regions, and it was generally found that the frontal regions were more lateralised than the temporal regions (e.g. Friederici et al., 2000; Opitz et al., 2002; Spreer et al., 2002). Second, lateralisation was seen to be modulated by development, with adults exhibiting greater overall left lateralisation than children (Szaflarski, 2006; Weiss-Croft and Baldeweg, 2015; Skeide and Friederici, 2016; Enge et al., 2020), and also with older adults exhibiting decreasing lateralisation (Cabeza, 2002; Wingfield and Grossman, 2006; Tyler et al., 2010; Yeung et al., 2016).

Finally, it is worth mentioning the historically hypothesised connection between language lateralisation and handedness (Broca, 1865; Eling, 1984; Knecht et al., 2000). Language studies have typically been carefully controlled for handedness, and studies have found that the incidence of left-lateralisation is around 90% in right-handers as compared to around 75% in left-handers and ambidextrals (Szaflarski et al., 2002; Tzourio-Mazoyer et al., 2016). Recent studies have found multiple partially-independent mechanisms that affect language lateralisation, such as head size, manual preference strength, and familial sinistrality, i.e. having left-handers among one's close relatives (Josse et al., 2006; Tzourio-Mazoyer et al., 2010a, 2010b), and reviews show that language lateralisation is modulated by demographic, anatomical, developmental, genetic, clinical, and psycholinguistic factors (Hervé et al., 2013; Tzourio-Mazoyer et al., 2016; Villar–Rodríguez et al., 2020).

Overall, we see that hemispheric lateralisation is a central feature of language function, and the idea continues to hold that language is a left-lateralised function, though our understanding of what that means has evolved over the decades. The field has moved from considering the right hemisphere completely uninvolved in language to the current idea that at least some aspects of language necessarily involve the right hemisphere and that this is modulated by language experience. Various theories on language lateralisation have been proposed over the years, such as its connection to handedness and genetics, sex differences, connection to developmental disorders, etc., but the theories are still evolving, and are currently leaning towards finding clues in the specific processing demands of different aspects of language (Lidzba et al., 2011; Badillo et al., 2017; Woodhead et al., 2019). Thus, language lateralisation remains an active area of research, and studies utilising a variety of approaches continue to disentangle the various factors involved and further our understanding of how the two brain hemispheres contribute to various language processes. ■

CHAPTER 3

NEURAL PLASTICITY OF LANGUAGE

Chapter 3 provides the background for this thesis, describing the evolution of ideas about brain plasticity and highlighting relevant studies of language plasticity in typical development and learning.

Neural plasticity is the ability of the brain to adapt and change. The term can refer to a variety of different processes at different levels of brain architecture and different temporal scales.

3.1 NEUROBIOLOGY OF PLASTICITY

Since the end of the 19th century, neural plasticity has been conceptualised as the mechanism of behavioural change, but it would remain a mostly theoretical idea for almost another century. The term “plasticity” was first loosely used by William James (1890) when he postulated that the plasticity of neural pathways underlay the formation of behavioural habits. Around the same time, Santiago Ramón y Cajal, closely followed by Eugenio Tanzi and Ernesto Lugaro, hypothesised synaptic changes as the mechanism of learning. This idea was neglected during the next half-century of behaviourism as the Pavlov-Lashley debates on physiological versus psychological explanations for classical conditioning held centre stage (Lashley and Wade, 1946). In

1949, Donald Hebb resurrected the idea of synaptic plasticity in his influential theory that came to be known as *Hebbian plasticity*, proposing the famous principle that “cells that fire together, wire together”[2]. Twenty years later, the first empirical evidence that this was indeed the mechanism underlying learning and memory was finally provided by Eric Kandel and colleagues (Castellucci et al., 1970) in a series of experiments that won Kandel the Nobel Prize in 2000.

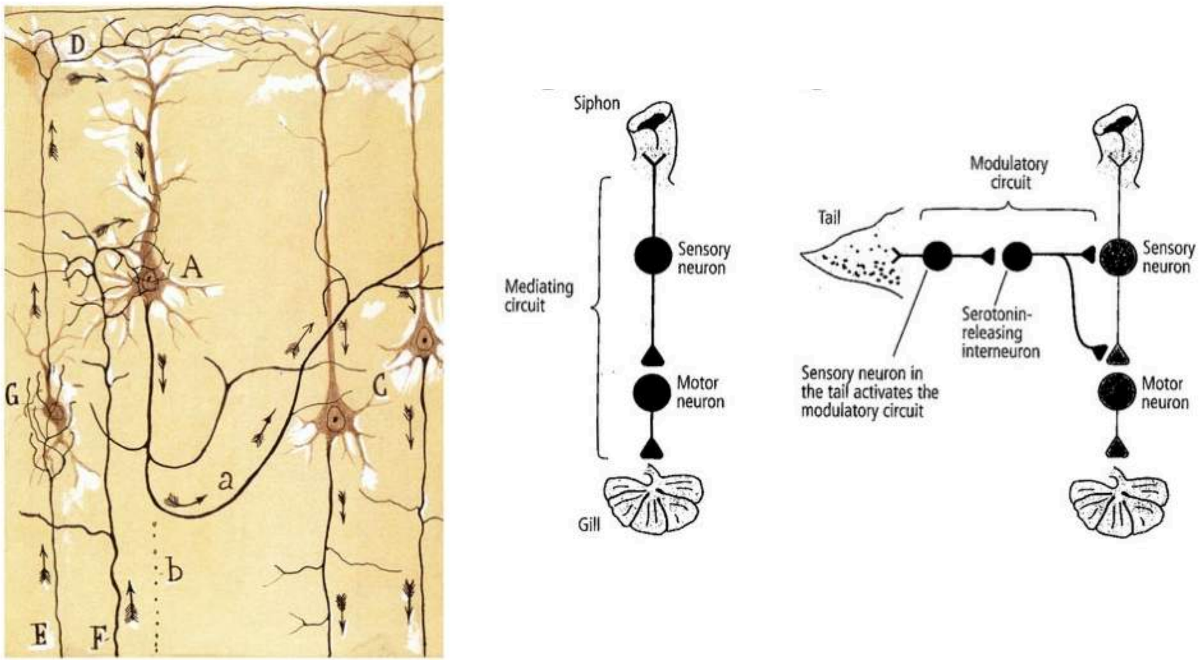

Figure 3.1 Neural plasticity at the level of synapses: from conception (left) to evidence (right). Figures adapted from Ramón (1913) and Kandel (2007).

In the 1930s, Konrad Lorenz popularised the concept of developmental critical periods with his influential discovery of imprinting in geese (Lorenz, 1935) that earned him a Nobel Prize in 1973. This effect was also reported in several studies with birds, insects, fish, and some mammals (Hess, 1959). Hubel and Wiesel performed a series of experiments that would win them a Nobel Prize in 1981, and demonstrated that kittens deprived of vision in the first months of life displayed abnormal development of visual pathways in the brain and behavioural blindness, while an adult cat blinded for a similar amount of time exhibited no such changes (Wiesel and Hubel, 1963). They thus concluded that brain plasticity is limited to the early years of life. This was also

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[2] This aphorism was coined by Carla Schatz (1992) for a popular science article and not actually by Hebb himself.

demonstrated in other sensory modalities, and the idea of critical periods became hugely influential and carried over to many other fields of science — especially language research.

Soon after, however, this idea that the brain is plastic *only* during the critical periods was challenged by the work of Marian Diamond and Michael Merzenich, who demonstrated structural and functional learning-dependent changes in trained adult animals. Their work was initially met with great scepticism that eventually gave way to great excitement as replication studies proved the results to be robust. In a series of experiments, Diamond and colleagues established that rats in an enriched environment (e.g. in a cage with toys and social interaction with other rats) showed greater cortical thickness and weight than rats in impoverished conditions (Figure 3.2 A) (Diamond et al., 1964). Merzenich and colleagues showed that somatosensory maps in the monkey brain could be modified depending on how much the corresponding body part was used, for example, amputation of fingers or surgical fusion of two fingers changed their somatotopy (Figure 3.2 B) (Clark et al., 1988). Though such neural changes were not as large as changes affected during the critical period, it laid to rest once and for all the idea that the brain is fixed in adulthood.

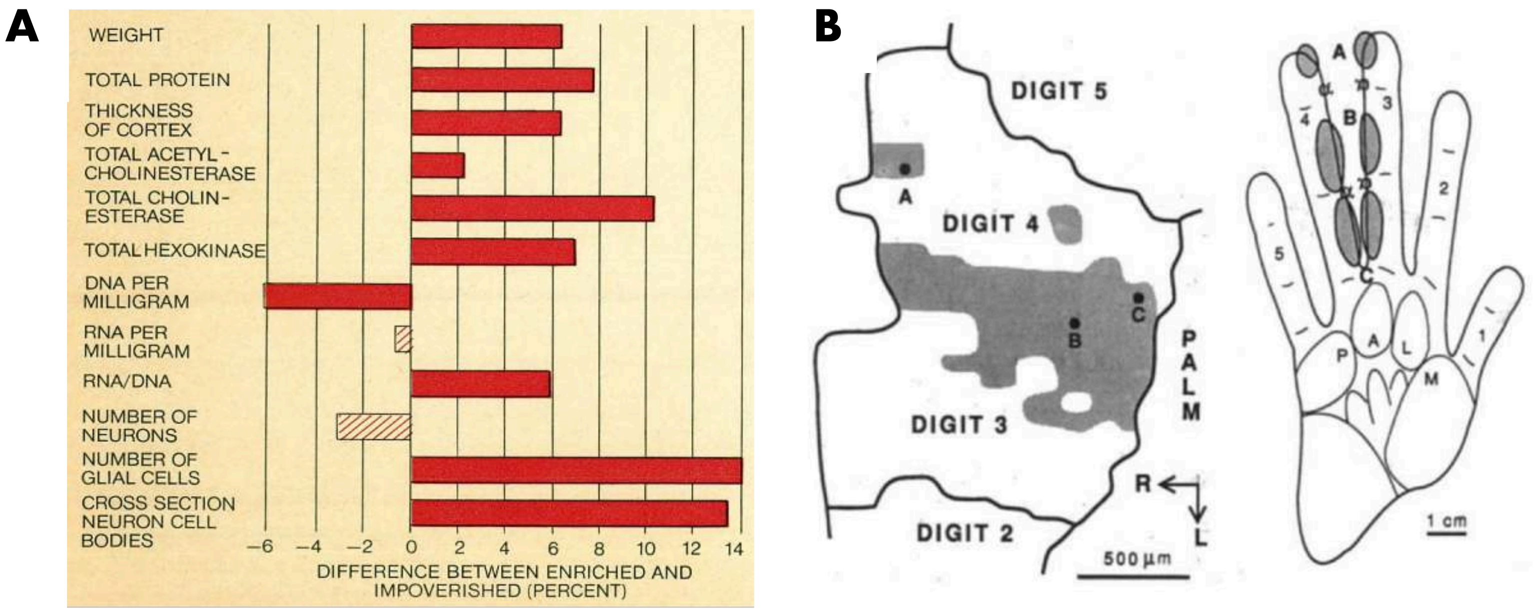

Figure 3.2 Learning-dependent structural and functional changes in adult animals. (A) Increased cortical weight and other chemical changes in the rat occipital cortex (Bennett et al., 1964), (B) Changing somatotopy in monkeys with two fingers sutured together (Clark et al., 1988)

This opened the floodgates to enormous fields of research in brain training and rehabilitation in humans that continues today. Functional neuroimaging (fMRI) had just been invented around this time, and a number of neuroimaging studies found that training in human adults in various domains also results in a range of structural and functional changes, e.g. functional changes associated with mirror-reading training (Poldrack et al., 1997), bilingualism (Kim et al., 1997), learning to read (Dehaene et al., 2010), and structural changes associated with extensive navigation experience (Maguire et al., 2000), bilingualism (Mechelli et al., 2004), juggling training (Draganski et al., 2004), learning to read (Carreiras et al., 2009), reasoning training (Mackey et al., 2012), etc.

The following sections present the relevant background for this thesis, focusing on studies of typical development, bilingualism and language learning. The sections are organised according to two types of plasticity: (i) developmental plasticity or maturational changes in typical development over the lifespan - studies focus primarily on children or differences between children and adults, and (ii) experience-dependent plasticity or brain changes affected by second language learning - studies focus on adults with different language experiences. These two types of plasticity are closely related (Figure 3.1).

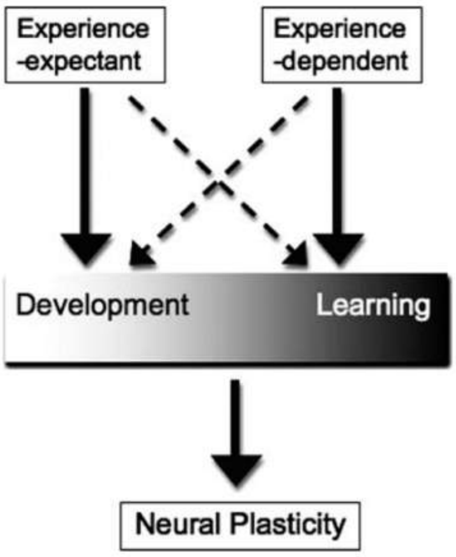

Figure 3.1 Two types of plasticity (Galván, 2010).

3.2 DEVELOPMENTAL PLASTICITY

Developmental studies investigate the course of cognitive and neural development over the lifespan, examining the age of onset of various cognitive skills and concomitant neural changes. Such studies typically examine children at different developmental stages or compare children and adults. Here we focus on typical development.

3.2.1 CRITICAL PERIOD HYPOTHESES

The concept of critical periods was extremely influential in language research long after the field of animal research that gave rise to the original concept had moved on to the idea of lifelong plasticity. Since there is no single definition of "language", the debates raged on for the better part of three decades as various researchers operationalised language proficiency in terms of accent, grammar, vocabulary, etc., and argued for or against the idea of a critical period for language acquisition and learning.

The critical period hypothesis for language was first formulated by Penfield and Roberts (1959) and later popularised by Lenneberg (1967). They surmised that organisational neural plasticity was only possible in the early years of life and that after the end of this critical period, the neural substrate for language learning is largely unavailable. Early formulations of this hypothesis were primarily applied to first language acquisition and based on case studies of feral or abused children who were deprived of language in the early years of their lives (Curtiss, 1977, 1989). There is no doubt that early language deprivation is detrimental to development, but it is nearly impossible to dissociate language from socio-emotional factors, and thus later formulations extended the critical period hypothesis to second language acquisition, where the bulk of the debate has centred.

Lenneberg himself had considered second language learning possible till much later in life:

> **A person can learn to communicate in a foreign language at the age of forty. This does not trouble our basic hypothesis on age limitations because we may assume that the cerebral organization for language learning as such has taken place during childhood, and since natural languages tend to resemble one another in many fundamental aspects, the matrix for language skills is present. (Lenneberg, 1967, p. 176)**

However, other scientists argued that maturational processes fundamentally alter language learning ability, advancing various theories. For example, Pinker (1994) proposed the "Use it, then lose it" theory, arguing that "Language-acquisition circuitry is not needed once it has been used," and Newport (1991) proposed the "Less is more" hypothesis, arguing that cognitive immaturity was an asset to language learning:

> **Perhaps the child succeeds better at language learning precisely because she begins with the ability to extract only limited pieces of the speech stream, with a gradual increase over maturation and learning in the amount of material to be analysed; in contrast, the more capable adult extracts more of the input but is then faced with a more difficult problem of analyzing everything all at once. (Newport, 1991, p.126)**

Debates in the 1990s centred around the definition of critical periods and whether the decline in language learning ability was sharp enough to be considered a critical period, or whether the decline was gradual enough to be accounted for by overall age-related cognitive decline. A number of studies showed it to be the latter (e.g. Bialystok and Hakuta, 1994; Flege, 1995), and thus the critical period hypothesis was further relaxed.

It is now generally accepted that, regardless of the exact definition of "critical period", there is a negative association between the age at which learners are exposed to a language and their ultimate proficiency in the “formal” aspects of language such as phonology and grammar, while semantic and lexical processing were considered to have the ability to be “formed or re-formed by experience at virtually any time in life” (Newport et al., 2001). Recently, the question of a critical period for syntax processing has also been challenged by a substantial body of electrophysiological research that suggests that native-like processing of syntax is in fact possible at higher levels of proficiency, regardless of the age of acquisition of the second language (Steinhauer et al., 2009). Thus the increasingly high temporal and spatial resolution of various neuroimaging methods continues to shed light on adult neural plasticity. Overall, though plasticity indeed declines over the lifespan, research consistently points to much more learning-dependent plasticity of second language acquisition than is popularly surmised.

3.2.2 LANGUAGE NETWORK DEVELOPMENT

Language is a uniquely human ability subserved by a network of frontal, temporal and parietal brain regions connected by fibre tracts. With the advent of non-invasive functional neuroimaging methods such as fMRI, it became possible to trace development of this network over the lifespan. Studies of infants showed that fledgling language networks were present at birth, and developmental studies comparing children and adults show that adult-like networks appear to be in place by around 7 years of age.

One of the earliest fMRI studies of non-sedated infants was conducted by Dehaene-Lambertz and colleagues (2002). They scanned 20 3-month-old infants as they listened to excerpts of a children’s book, and showed that the precursors of the language network are already active in infants, well before the onset of speech production. A few years later, Perani and colleagues (2011) scanned 15 2-day-old infants while they listened to a fairy-tale and showed that a fledgling language network was already in place at birth (Figure 3.4).

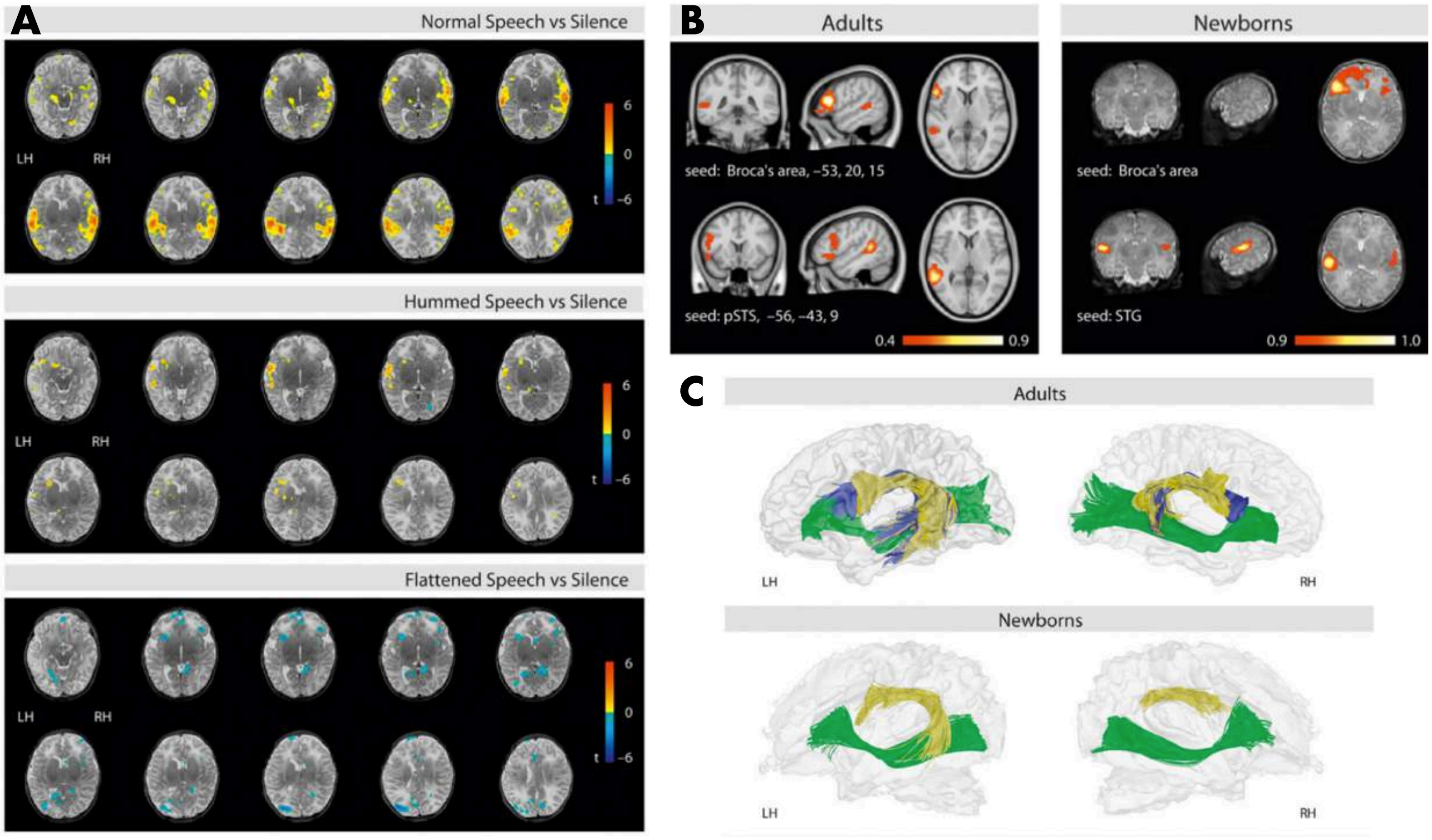

Figure 3.4 Language network at birth (Perani et al., 2011). (A) Functional activation in 2-day-old infants, (B) Functional connectivity of language regions, (C) Structural connectivity between language regions.

Children typically learn to read around ages 3-6, and learning to read fundamentally alters the brain. In studies comparing adults with different levels of literacy, i.e. literate, late-literate, and illiterate adults, it was found that the left ventral occipito-temporal cortex was especially responsive to visual words and that literacy enhanced phonological activation to speech in the planum temporale as well as top-down activation of orthography (Dehaene et al., 2010; Hervais-Adelman et al., 2019). Structural changes were also found in the splenium of the corpus callosum and in bilateral angular, dorsal occipital, middle temporal, left supramarginal and superior temporal gyri (Carreiras et al., 2009). Other large-scale functional changes were also found in children. For example, Preston and colleagues (2016) conducted a longitudinal study with 68 children between the ages of 6 and 10, and found that greater print-speech convergence in beginning readers predicted higher reading achievement two years later, beyond the effects of brain activity for either modality alone. Chyl and colleagues (2017) scanned 111 children who had either not yet learnt to read or were emergent readers, and found that print-speech convergence was observed only in readers, and that there was a positive correlation between reading skill and convergence in the left superior temporal region. In a study of bi-literate children, Cherodath and Singh (2015) examined 34 children learning to read simultaneously in languages such as Hindi and English that have different writing systems, and found that they recruited the same reading network for both languages, but the activation patterns were modulated by orthographic depth or consistency of the writing system.

A number of studies defined the developmental differences between children and adults, demonstrating that language activation was more frontal/parietal in adults, while children showed greater activation of regions associated with lower-level processing. For example, Schlaggar and colleagues (2002) scanned 19 7-to-10-year-old children and 21 adults as they performed single-word generation, and found that children exhibited greater activation in extrastriate regions, while adult exhibited greater activation of frontal regions. Brown and colleagues (2005) extended this to 95 7-to-32-year-old participants, and showed age-related decrease in activity across a number of “earlier processing regions” such as bilateral extrastriate cortex, and increases in “newly recruited, later-stage processing regions”, such as left frontal and parietal regions. Turkeltaub and colleagues (2003) scanned 41 6-to-22-year-old participants as they performed a covert reading task, and showed that children showed greater reliance on superior temporal regions than adults, and that higher frontal activity was associated with greater reading skill.

Gaillard and colleagues investigated language lateralisation in a number of experiments with 16 right-handed children 5 to 8 years old, and came to the conclusion that left hemispheric activation for language is set by age 8 (Ahmad et al., 2003; Gaillard et al., 2003a, 2003b). They scanned the children as they read stories (Figure 3.5 A), listened to stories with a reverse speech control condition (Figure 3.5 B), and performed covert word generation (Figure 3.5 C). In the covert word generation task, the children's data was compared with data from 29 adults, and no significant difference was found between the children and adults in location and lateralisation of activation, though adults exhibited greater extent of activation, which was not associated with performance (Gaillard et al., 2003b).

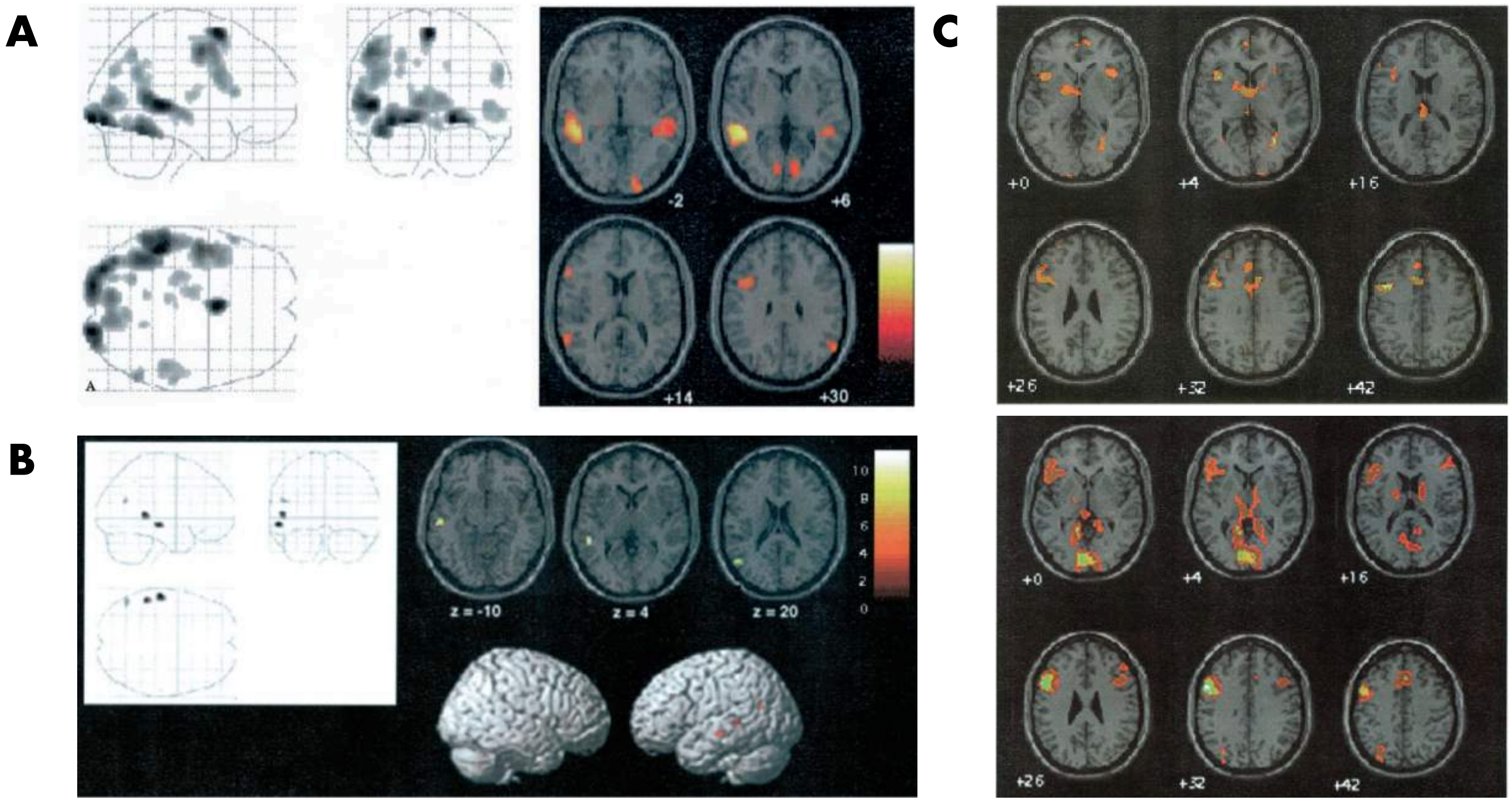

Figure 3.5 Group functional activation maps of 5-8-year-old children during (A) story reading (Gaillard et al., 2003a), (B) story listening (Ahmad et al., 2003), (C) covert word generation in children (above) and adults (below) (Gaillard et al., 2003b).

Increasingly sophisticated studies continue to refine these initial findings. Szaflarski and colleagues (2006) investigated language lateralisation in 170 right-handed participants ranging from 5 to 67 years old. They scanned participants as they performed a covert verb generation task and showed a non-linear relationship between age and lateralisation, with increasing lateralisation from 5 to 20 years, a plateau from 20 to 25 years, and a slow decrease from 25 to 70 years (Figure 3.6 A). Lidzba and colleagues (2011) compared 36 participants ages 6 to 24 years in speech comprehension and verbal production tasks, and found a more bilateral pattern of activation in comprehension than in production. With increasing age, there was more focal activation in both tasks, but a significant increase in lateralisation was observed only in production (Figure 3.6 B). Olulade and colleagues (2020) examined activation in 53 4-to-29-year-old participants as they listened to sentences. Significant activation was found in both hemispheres, with increasing left lateralisation with age. Importantly, they found a large amount of individual variability that was not captured in group-level analyses.

Overall, the language network displays substantial learning-dependent plasticity over the course of development, with changes in patterns of activation with increasing age and proficiency, such as a shift in reliance from lower-level to higher-level regions, and changes in focus and lateralisation of language networks.

3.2.3 COMPREHENSION-PRODUCTION ASYMMETRY

The comprehension-production asymmetry or gap refers to the idea that language users have greater ability for comprehension than for production. In 1963, Fraser and colleagues noted that comprehension was syntactically more advanced than production in 3-year-old children. They showed that children's ability for both understanding as well as rote imitation was greater than their ability for correct meaningful production.

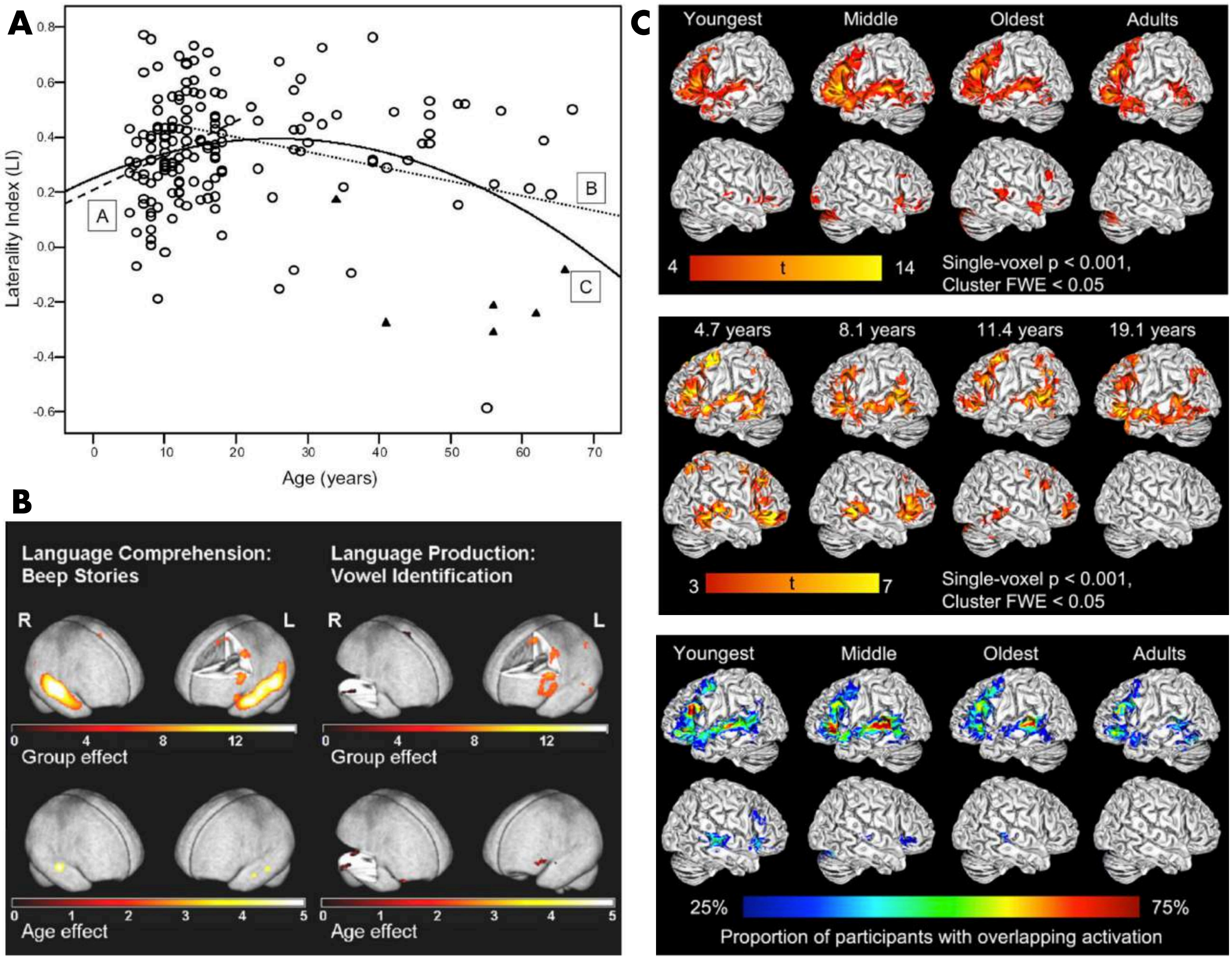

Figure 3.6 Functional lateralisation of language. (A) Lateralisation through the lifespan (Szaflarski et al., 2006), (B) Comprehension vs production in children and adults (Lidzba et al., 2011), (C) Individual variability of lateralisation by age: group maps (top panel), example individual maps (middle), and proportion of participants displaying typical group-level activation (bottom panel) (Olulade et al., 2020).

This was also reported in different domains from phonology and syntax to semantics and pragmatics (Hendriks and Koster, 2010), and it was found to persist across the lifespan (Hendriks, 2014).

For example, monolingual adults were shown to exhibit extremely rapid adaptation to accented speech: Clarke and Garrett (2004) showed that native English speakers exposed to Spanish- and Chinese-accented speech initially exhibited slower processing of accented than native speech, but the deficit diminished within a minute of exposure. Maye and colleagues (2008) exposed participants to a narrated story segment in which they had shifted a subset of vowels, and showed that participants exhibited significant context-specific vowel adaptation (i.e. only for the shifted vowels) that was easily generalised to words that they had not heard in the segment. On the other hand, Markham (1999) found that imitation of even native language accents is difficult for adults. In word-learning, Gershkoff-Stowe and Hahn (2013), found that a similar gap between comprehension and production of the same set of novel words in 2-year-old children and in 20-year-old adults.

In bilinguals, Gibson and colleagues (2012) showed that Spanish-English kindergarteners (n=124) had significantly higher receptive vocabulary than expressive vocabulary, particularly in their second language. In a follow-up study with 800 subjects (Gibson et al., 2014), they found that language exposure did not affect the comprehension-production gap in either language. Keller and colleagues (2015) studied 406 3-to-4-year-old bilingual children with 46 different first languages, and reported a significant comprehension-production gap, though they found some positive effect of language exposure. Finally, late language learners exhibit the most well-known and pronounced receptive-expressive gap, as they are typically able to understand much more than they are able to produce (e.g. Walsh and Diller, 1981).

Huttenlocher (1974) and Bates (1993) proposed that even shallow and incomplete storage of an existing word form might be sufficient for semantic access, while lexical production requires greater phonological elaboration and motor articulation control. This is likely to have a range of effects on the neural correlates of language processing, and though the comprehension-production difference has received little attention in neuroscience, it is a particularly relevant distinction to make in studies of plasticity and rehabilitation.

3.3 EXPERIENCE-DEPENDENT PLASTICITY

Children display a host of maturational changes, and language experiences such as bilingualism or multilingualism affect developmental trajectories: for example, bilingual children have smaller vocabularies in both languages compared to monolingual children. However, this effect is attenuated in adulthood (Bialystok et al., 2012), and thus experience-dependent plasticity and the cumulative effects of bilingualism can be studied in adults with different language backgrounds, allowing us to avoid the confounds of maturational development. Adult language learners can further provide unique evidence for neural plasticity of language in the developed brain. The following sections highlight key findings from MRI studies of bilinguals and language learners.

3.3.1 EVIDENCE FROM BILINGUALS

A plethora of studies have shown that monolingual and bilingual adults exhibit functional, structural, connectivity, and lateralisation differences. Two primary factors are considered to affect experience-dependent neural plasticity: the age of acquisition of the second language and proficiency in the second language. Besides these, other factors such as language exposure, similarity between known and new languages, motivation, method of learning, etc. have also been seen to have some influence. Bilinguals are classified as “early” or “late” bilinguals depending on the age at which they acquired their second language, and “simultaneous” or “sequential” bilinguals depending on whether both languages were acquired from birth or one was acquired or learned later. The primary remnant of the critical period hypothesis debates is that the cut-off for early vs late bilinguals is typically considered to be between 3 and 6 years of age.

One of the first questions investigated with functional neuroimaging was the spatial overlap between first and second languages. Multiple studies showed that overlap between first and second languages was a function of age of acquisition and the proficiency, with later age and lower proficiency being associated with more variability in representation of the second language (Perani and Abutalebi, 2005; Liu and Cao, 2016). For example, Kim and colleagues (1997) scanned early and late bilinguals as they performed covert sentence-generation tasks in each of their languages, and found that early bilinguals showed no difference between activation in native and second languages, while activation for the two languages in late bilinguals was spatially distinct in the frontal lobe. Perani and colleagues (1998) compared two groups of highly proficient early and late bilinguals while they listened to stories in each languages and showed that with a sufficiently high level of proficiency in the second languages, age of acquisition had no significant effect on functional representation of the second language. This was also found to be the case in various studies of different language pairs (e.g. Chee et al., 1999; Liu and Cao, 2016; Xu et al., 2017).

In addition to language representation, language control is a prominent question in bilingualism. The dorsolateral prefrontal cortex is considered to the primary hub of language control, along with the anterior cingulate cortex, basal ganglia, and inferior parietal lobule (Abutalebi and Green, 2007). Hernandez and colleagues (2000, 2001) scanned early bilinguals and found greater activation in the dorsolateral prefrontal cortex during trials that required language switching compared to trials that did not. Abutalebi and colleagues (2008) additionally found greater activation of the anterior cingulate cortex and the left caudate when bilinguals switched between languages compared to task-switching in the same language. Several other studies also implicated the caudate and putamen in language switching (Crinion et al., 2006; Friederici, 2006; Hervais-Adelman et al., 2015a, 2015b). More recently, studies have begun to explore functional connectivity, showing the effect of bilingualism in intrinsic functional networks. For example, Berken and colleagues (2016) found stronger functional connectivity in simultaneous bilinguals compared to late bilinguals between the left and right inferior frontal gyri, and between the inferior frontal gyrus and language control regions such as dorsolateral prefrontal cortex, inferior parietal lobule, and cerebellum. Structural and structural connectivity differences have also been observed in various language regions (Mechelli et al., 2004; Klein et al., 2014) as well as the tracts connecting them (Luk et al., 2011; García-Pentón et al., 2014; Pliatsikas et al., 2015).

Lateralisation has been of particular interest in bilinguals since before the advent of neuroimaging (Paradis, 1990). Though the behavioural studies had various methodological issues (Obler et al., 1982), meta-analyses of behavioural studies in healthy bilinguals found that lateralisation was strongly influenced by age of acquisition, and to a lesser extent, by proficiency (Hull and Vaid, 2006, 2007). Early bilinguals who had acquired both languages by age 6 exhibited bilateral hemispheric involvement for both languages, while late bilinguals exhibited left lateralisation for both languages, with greater left lateralisation in less-proficient bilinguals. Few functional MRI studies have explored bilingual lateralisation specifically, but structural connectivity studies showed that early bilinguals display more bilateral organization of the arcuate fasciculus compared to monolinguals and late bilinguals (Mohades et al., 2015; Hämäläinen et al., 2017).

3.3.2 EVIDENCE FROM ADULT LANGUAGE LEARNERS

Language learning even as a young adult has been shown to affect functional and structural changes in the language network. Here we focus on MRI studies of ecologically-valid language learning in adults.

Stein and colleagues (2009, 2012) examined functional and structural changes in 10 17-year-old English-speaking exchange students in Switzerland roughly one month and six months into learning German. Participants were scanned as they read words and indicated with a button press whether or not they knew the meaning of the word. It was found that participants showed greater bilateral frontal activation in session-1 than in session-2. Proficiency-related grey matter density increases were found in the left inferior frontal gyrus and left temporal pole. Mårtensson and colleagues (2012) studied structural changes in 14 18-year-old Swedish interpreter conscripts studying either Arabic, Dari, or Russian as part of their military training, and 17 matched controls. They were scanned before and after the first three months of training, revealing increases in hippocampal volume and in cortical thickness of the left middle frontal gyrus, inferior frontal gyrus, and superior temporal gyrus in the language learners.

Barbeau and colleagues (2016) examined functional changes in 14 24-year-old English-speakers enrolled in a 12-week intensive French immersion language-training program in Montreal. Participants were scanned while they read aloud short sentences, and it was found that they exhibited higher activation in session-2 in the left inferior parietal lobule that correlated with faster reading speed. It was further found that reading speed increase was predicted by pre-training intrinsic functional connectivity between the visual word form area and the left middle temporal gyrus, while improved lexical retrieval was predicted by connectivity between the anterior insula and posterior superior temporal gyrus and dorsal anterior cingulate cortex (Chai et al., 2016).

Schlegel and colleagues (2012) examined structural connectivity in 11 20-year-old English-speaking students enrolled in an intensive Chinese university course and 16 matched controls. They were scanned once a month for the duration of the nine-month course, and exhibited significant increases in fractional anisotropy of the language related tracts in the left and right hemisphere, and significant decrease in the frontal lobe tracts crossing the genu of the corpus callosum. Xiang and colleagues (2015) examined structural connectivity changes in 37 19-year-old German students in the Netherlands before and after an intensive 6-week course in Dutch. They found that lateralisation of the arcuate fasciculus showed a non-linear correlation with proficiency — they were negatively correlated before training and positively correlated after training.

Overall, studies of young adult language learners found functional activation changes in the bilateral frontal and left parietal regions during reading tasks, cortical thickness increases in the left frontal, temporal, and parietal regions as well as the right hippocampus, and structural connectivity changes indicative of changes in lateralisation, providing evidence for neural plasticity throughout the language network at least until early adulthood. ■

CHAPTER 4

MAGNETIC RESONANCE IMAGING

Chapter 4 provides a non-technical overview of the research technique used in the current thesis — functional magnetic resonance imaging (fMRI) — from data acquisition to data analysis. Standard technical descriptions and the specifics of the analyses employed in each experiment are further included in the methods section of each empirical chapter.

Magnetic Resonance Imaging (MRI) is a non-invasive imaging technology that produces detailed anatomical and functional images. In the life sciences, it is widely used in medical imaging for disease detection and diagnosis, as well as in basic research in cognitive neuroscience.

4.1 DATA ACQUISITION

The quest to examine the living human brain has long occupied scientists, and only in recent times have the tools finally become available. MRI first gained widespread medical use in the 1980s to produce structural images of organs, but it was the emergence of fMRI in the 1990s that profoundly changed the field of cognitive neuroscience. Unlike previous methods, MRI is both non-invasive and does not involve radiation, making it suitable for routine use in basic research. MRI provides two main types of data: three-dimensional structural images and four-dimensional functional images.

4.1.1 PHYSICS AND PHYSIOLOGY

To obtain MR images, participants are placed inside the MRI scanner and requested to remain very still during the imaging process in order to not blur the images. Magnets align the protons in the brain and then a radio frequency pulse is used to stimulate the protons to spin out of alignment with the magnetic field. The time it takes for the protons to realign with the magnetic field and the amount of energy released affect the brightness of the image, thus differentiating between different types of tissues (for technical details of MRI physics, see Huettel et al., 2004).

The tissues of the brain can be classified into three major classes: grey matter (GM), white matter (WM) and cerebrospinal fluid (CSF). GM consists primarily of neuronal cell bodies and is found at the surface of the brain. GM regions are the main areas of nerve connections and processing. WM is made of mostly neuronal axons that connect the GM regions to each other and to the rest of the body. In the WM, bundles of axons form tracts that connect different cortical regions within the same hemisphere, between hemispheres or between cortical and subcortical structures. The brain is surrounded by CSF, which is produced and circulates within the ventricular system of the brain.

MRI scanners are specified by the field strength of the magnet defined in teslas (T), and most medical and research scanners are typically 1.5T or 3T scanners, though they can go up all the way to 10T for highly specialised research. MRI sequences are specific settings of the magnets and radio frequency pulses, and can be used to produce different types of images that highlight different tissue types (Figure 3.1). Structural images typically have a spatial resolution of 1 mm^3. When viewed as two-dimensional images, MR images are specified by the plane or direction of the image: axial (from above), sagittal (from the side) and coronal (from the front).

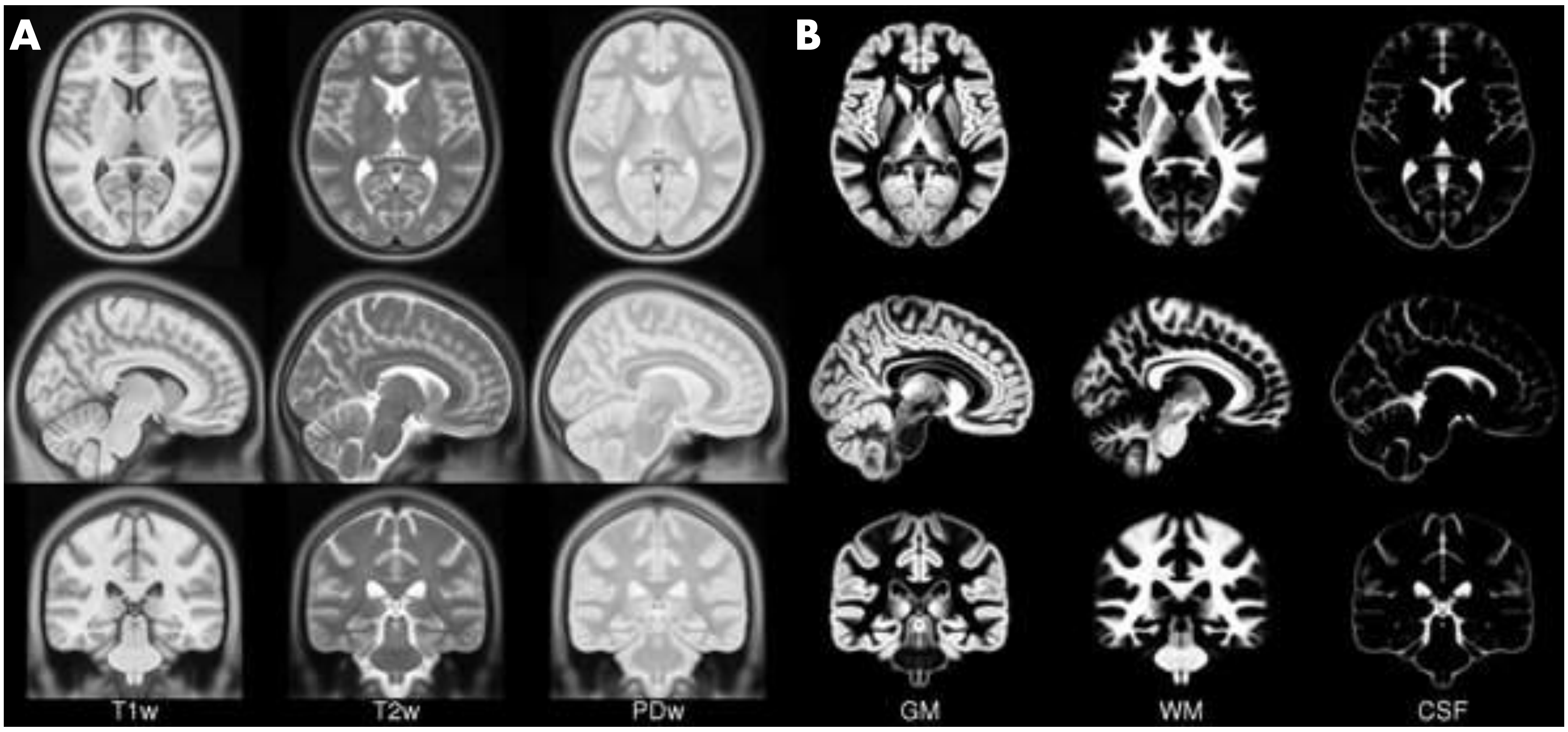

Figure 3.1 (A) Different types of MRI structural images, and (B) Three types of brain tissue: grey matter, white matter, and cerebrospinal fluid. Each row presents images in either the axial, sagittal or coronal view respectively.

Figure adapted from https://www.bic.mni.mcgill.ca/ServicesAtlases/ICBM152NLin2009

4.1.2 THE F IN FMRI: BOLD HAEMODYNAMIC RESPONSE

fMRI is a technique for measuring brain activity by detecting changes in blood oxygenation. fMRI relies on neurovascular coupling, i.e. the fact that local increases and decreases in brain activity are accompanied by changes in blood flow. Increased neural activity in brain regions is accompanied by a local increase in glucose and oxygen-rich blood, called the haemodynamic response, and a decrease from the resting baseline in other brain areas. Critically, the increase in blood flow exceeds the increase in the oxygen consumption, and the consequent increase in oxygenation level can be measured by MRI since oxygenated and deoxygenated haemoglobin have different magnetic properties (Ogawa et al., 1990). This measure is called the blood oxygenation level dependent or BOLD fMRI signal, and it constitutes the primary dependent measure in fMRI analyses. The BOLD response generated by neural activity is called the haemodynamic response function (Figure 3.2). It begins approximately 2 seconds after the onset of neural activity and peaks 5–8 seconds after the neural activity has peaked (Aguirre et al., 1998).

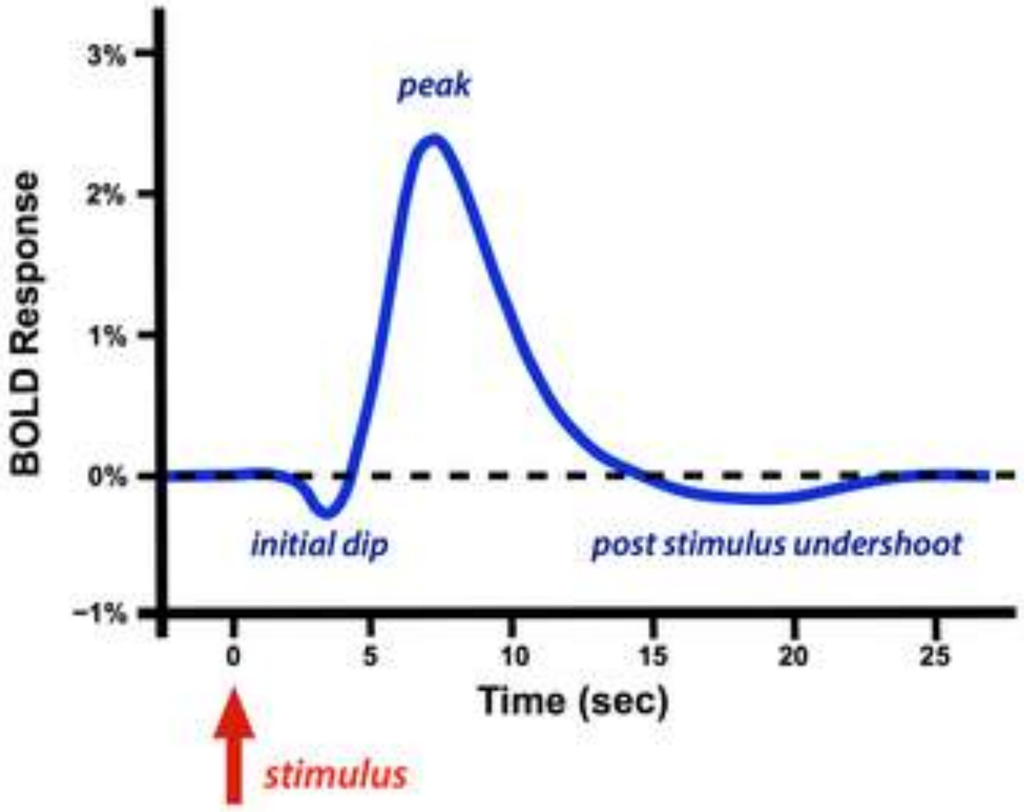

Figure 3.2 BOLD haemodynamic response.
Figure adapted from http://mriquestions.com/does-boldbrain-activity.html

fMRI scans are collected by rapidly acquiring multiple two-dimensional brain slices and stacking them to create three-dimensional volumes. Each volume takes around 0.5 to 4 seconds to acquire depending on the fMRI acquisition parameters (for technical details of MRI sequences, see Huettel et al., 2004). A series of volumes are collected in the course of scanning and provide four-dimensional fMRI images, which can then be analysed in different ways to make inferences about brain activation. The spatial resolution of functional images is typically lower than that of structural images, i.e. in the range of 1-3 mm^3.

There are two types of fMRI experiments, task fMRI and resting state fMRI. In task fMRI experiments, the goal is to map patterns of neuronal activation in the brain while participants perform specific tasks inside the MRI scanner. Using the relative change in BOLD signal from the baseline during task performance, it is possible to infer that certain areas of the brain are activated during specific tasks. Task-related fMRI signal changes are usually less than 5% from the baseline, and the other 95% constitutes the "resting state" (Fox and Raichle, 2007). In resting state fMRI, there is no task, and the focus is on synchronous activations between brain regions while participants are "at rest" and not performing any directed cognitive tasks. This has led to the discovery of consistent, large-scale brain networks and provide insights into large-scale circuit organisation (Figure 3.3).

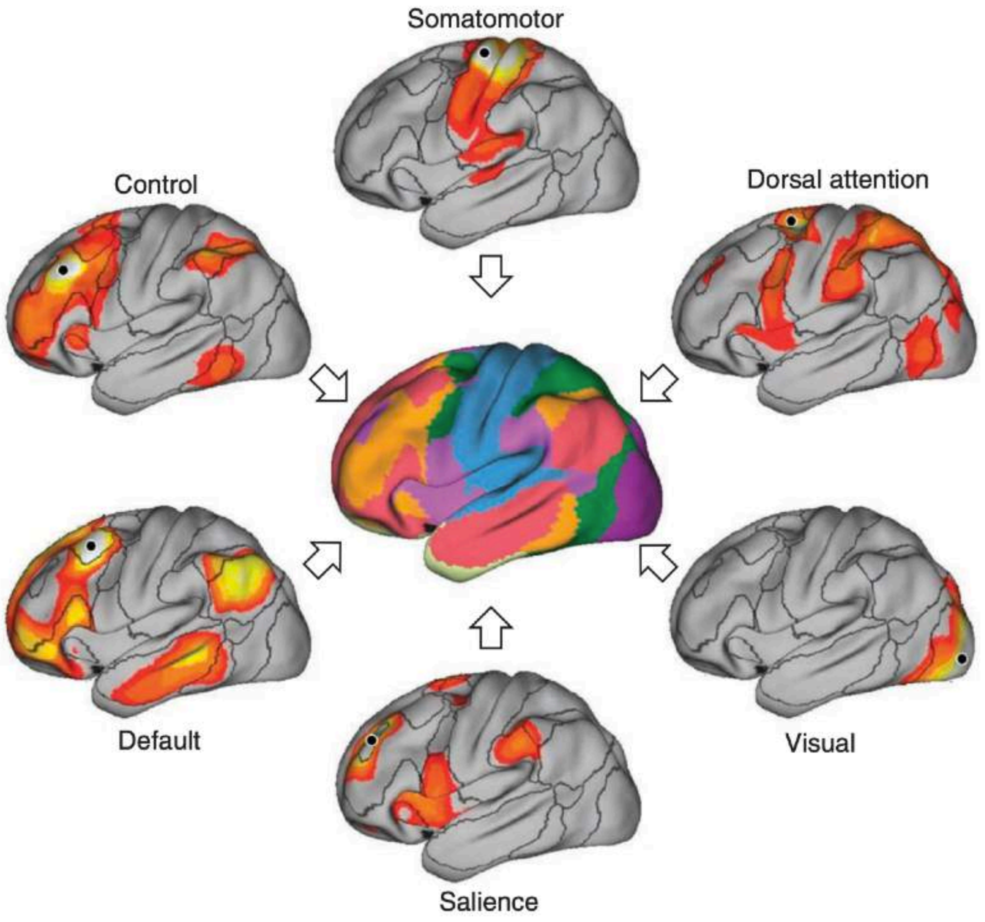

Figure 3.3 Large-scale resting state cerebral networks (Buckner et al., 2013)

4.1.3 FMRI TASK DESIGN: BLOCKS AND EVENTS

Depending on the way stimuli are presented, there are three main types of task design: block, event-related, and mixed designs (Figure 3.4).

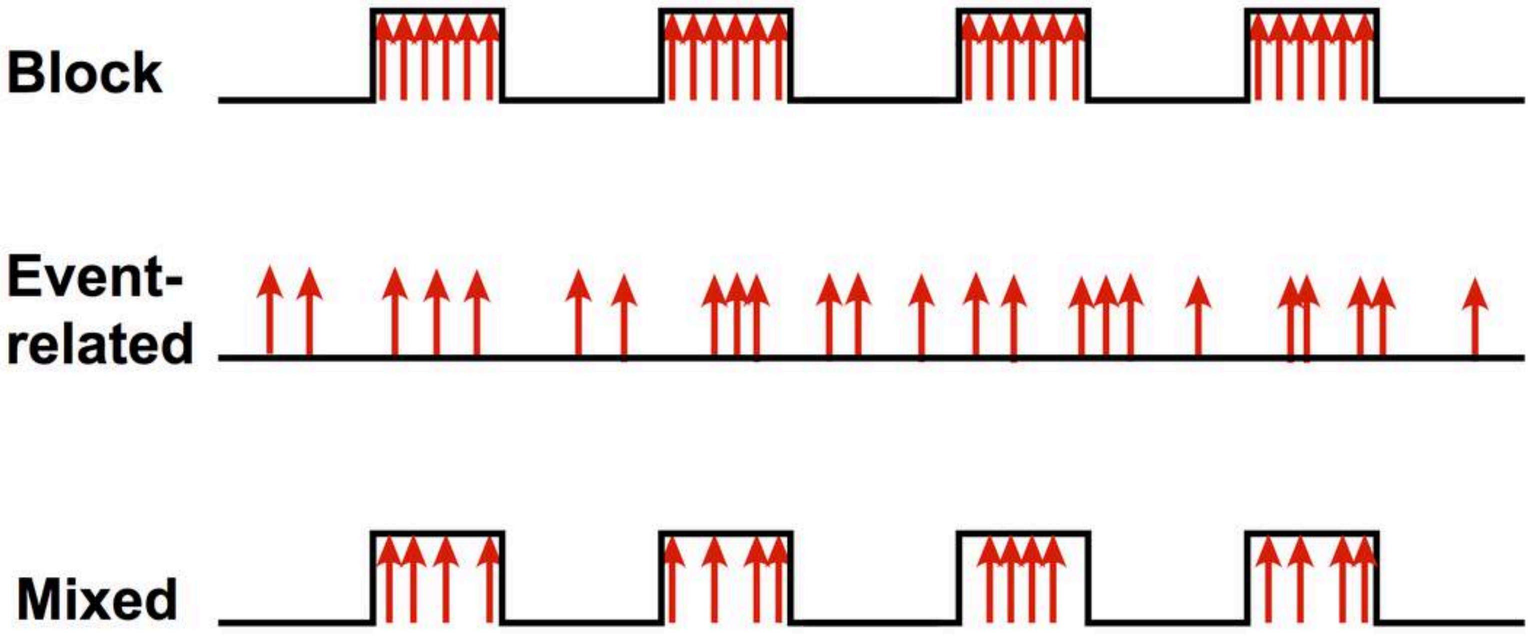

Figure 3.4 fMRI task designs. Figure adapted from http://mriquestions.com/fmri-paradigm-design.html

Block designs are the oldest functional imaging paradigms, widely used for Positron Emission Tomography (PET) studies prior the invention of fMRI. In a block design, the different experimental conditions are separated into extended time intervals, or blocks of around 15-50 seconds. Activation blocks are usually followed by rest blocks of equal time, and activation blocks for different experimental conditions usually alternate in time. Subtraction of different task conditions can be used to reveal focal areas of cortical activation. Compared to other fMRI paradigms, block designs possess the highest signal-to-noise and statistical power (Friston et al., 1999), but on the flip side, cannot distinguish between trial types within a block, such as correct versus incorrect responses.

Event-related designs were developed to provide greater flexibility to design sophisticated experiments. In event-related designs, the stimulus consists of short discrete events whose timing can be randomised (Buckner, 1998). Thus, events can be randomised and different types of events can be mixed, allowing detection of transient variations in haemodynamic response, as well as analysis of individual responses to trials such as correct vs incorrect responses. However, analysis of the data is significantly more complex and dependent on accurate modelling of the HRF, and event-related designs possess lower signal-to-noise and statistical power, requiring longer imaging times and more trials per subject.

Finally, mixed designs have features of both blocked and event-related designs. Task blocks contain semi-randomised events, interspersed with periods of rest. Mixed paradigms are thus able to capitalise on the favourable signal-to-noise characteristics of block designs and the flexibility of event-related designs, and allow for simultaneous modelling of both transient, trial-related activity and sustained, task-related BOLD activity (Petersen and Dubis, 2011). This is, however, the most difficult type of design to optimise, and poorly designed experiments can lead to loss of power as well as misattribution of signals, adversely affecting results and conclusions.

Further details about these and other fMRI experiment designs can be found in Huettel et al. (2004).

4.2 DATA ANALYSIS

MRI is a complex imaging method, and the acquired data requires extensive processing. Various software packages such as SPM, FSL, AFNI, BrainVoyager, etc., are available to perform a wide variety of analyses. fMRI analyses involve three major steps: data preprocessing, statistical modelling, and inference (Figure 3.5).

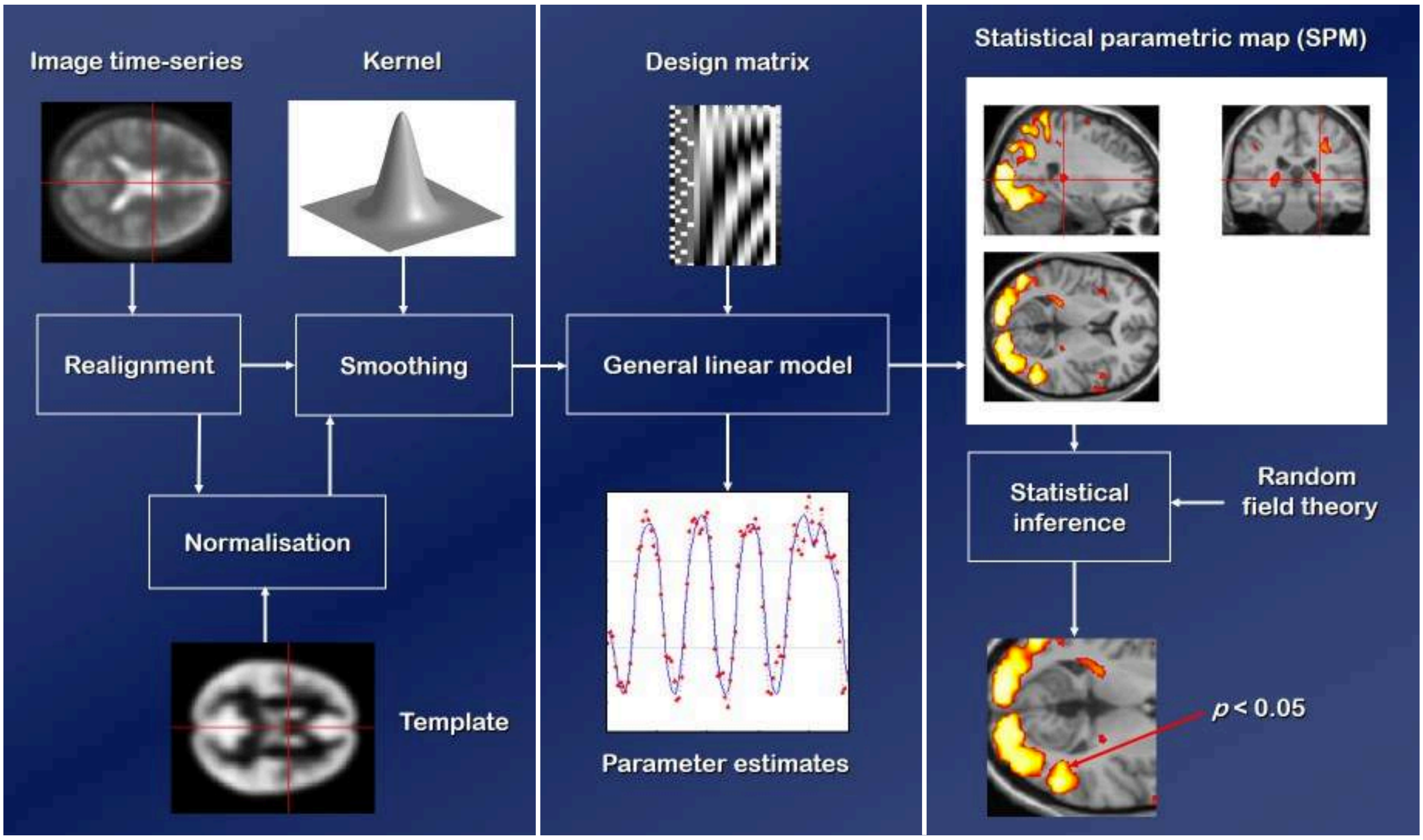

Figure 3.5 fMRI preprocessing and analysis pipeline.
Figure adapted from https://www.fil.ion.ucl.ac.uk/spm/

4.2.1 DATA PREPROCESSING

Preprocessing consists of three main steps: realignment, normalisation, and smoothing. The following section describes these core preprocessing steps, but several variations and additions are typically used in order to tailor the preprocessing to the data and subsequent fMRI analyses. In recent times, due to the ever-increasing complexity of preprocessing pipelines, special preprocessing software such as *fMRIPrep* (Esteban et al., 2019) has been developed to incorporate best practices from a number of state-of-the-art software packages.

In the first step, fMRI images undergo temporal and spatial interpolation. Since the two-dimensional slices in each brain volume cannot be acquired instantaneously, there is thus an accumulation of offset delays between the first slice and all remaining slices. This is corrected by temporal interpolation or slice-timing correction. Participants move in the fMRI scanner, which means that brain volumes are not perfectly aligned and require spatial realignment using rigid body correction to mitigate the effects of head motion. In addition to these steps, it is possible and desirable to use more sophisticated motion-correction algorithms to further reduce motion artefacts.

In the second step, functional and structural images are coregistered, and optionally, normalised, to each other. This step provides higher spatial resolution by aligning each participant's high resolution structural image to their functional images. Since participants' brains have different shapes and sizes, brain images can be normalised. This is done by non-linearly warping structural images into a standard stereotaxic space, and the warping parameters are then applied to the functional images. Thus, each participant's data is now available in a standard space, which allows group comparisons and spatial comparisons across studies and scanners. The first stereotaxic space for MRI was the Talairach atlas (Talairach and Tournoux, 1988), which was electronically derived from axial sectional images of the postmortem brain of a 60 year-old woman. The most common stereotaxic space is now the MNI (Montreal Neurological Institute) template, which is based on the average of MRI scans of several healthy young adults (e.g. MNI152 template is based on the average of 152 individuals).

In the final preprocessing step, fMRI images undergo spatial smoothing, i.e. BOLD signal data points are averaged with their neighbours. This is done by convolving the fMRI signal with a Gaussian function of a specific width, typically between 4 and 8 mm. This has benefits such as increased signal-to-noise ratio, improved validity of statistical tests by making the error distribution more normal. However, this also reduces the spatial resolution of the data, and excessive smoothing can shift or merge activity peaks, leading to mis-localisation.

4.2.2 STATISTICAL MODELLING AND INFERENCE

After preprocessing, the fMRI images are ready for statistical analysis. Among the most widely used methods to model the fMRI data and test whether brain activity is related to the paradigm is the general linear model (GLM; Friston et al., 1994). The GLM is a way of modelling an observed signal in terms of one or more explanatory variables, also known as regressors.

First, subject-level data is modelled, called first-level analysis. This involves modelling the BOLD time series data as a linear function of regressors of interest, nuisance regressors, and the error term (Figure 3.6). Regressors of interest consist of the experimental conditions, nuisance regressors include known confounds such as head motion or signal drift, and everything else falls into the error term. A least

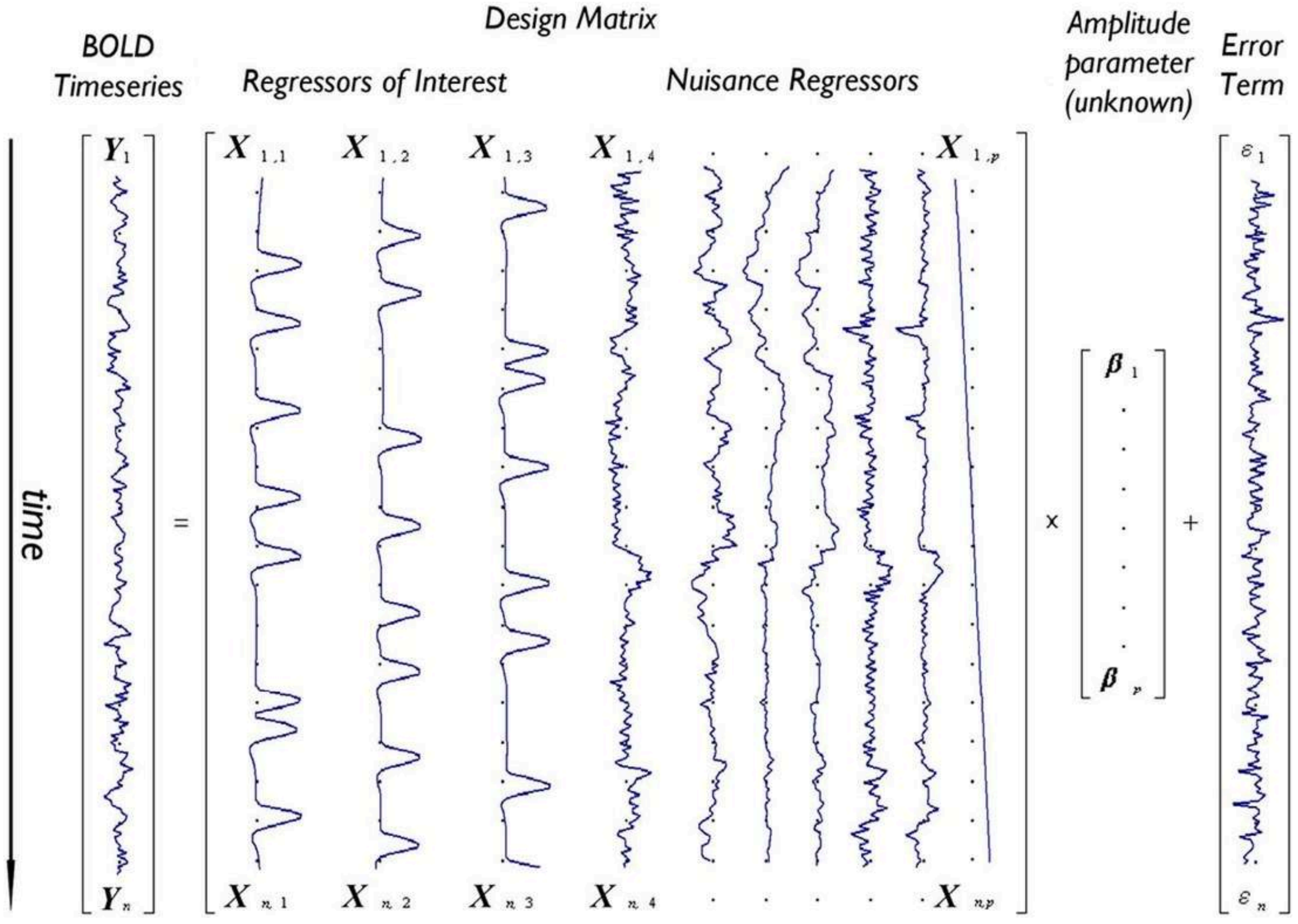

Figure 3.6 First level fMRI analysis GLM.
Figure adapted from http://mriquestions.com/general-linear-model.html

squares optimisation procedure calculates values for the weighting factors (β1, β2, etc.) corresponding to each design variable, resulting in statistical parametric maps.

Second-level or group-level analysis is used to model the data and make inferences at the group-level. Each subject's first-level parameter estimates (betas or contrast of betas) are carried forward to the second-level analysis where they serve as the dependent variables in a one-sample t-test assessing the consistency of effects within or between groups based on the between-subject variability in the first-level estimates.

The procedure described above is a mass-univariate method, where first and second-level analyses are typically carried out at the voxel-level (i.e. the minimum spatial resolution unit of the fMRI images) with the underlying assumption that each voxel in independent of the other. In voxel-by-voxel testing, over 100,000 tests are performed, which leads to a massive number of false positives. It is thus necessary to correct for multiple comparisons. The two most popular procedures for multiple comparison correction (MCC) are Family Wise Error rate (FWE) and False Discovery Rate (FDR).

Functional segregation and functional integration are thought to be important organising principles of the brain, and thus fMRI analyses have two typical objectives: (1) to localise brain activity associated with a given cognitive task or its experimental conditions and to determine the brain regions involved in the underlying cognitive processes, and (2) to examine the interactions between spatially distant brain regions using functional connectivity.

Brain activation analyses can be performed at the whole brain level (i.e. voxel-wise) or may be focused on specific regions of interest (ROI). ROIs can be used to constrain analyses and reduce the severity of MCC, and can be chosen in one of two ways (Friston et al., 2006; Poldrack, 2007). One, ROIs can be defined by focusing on regions that respond significantly to all events relative to their inter-event baseline or by using a functional localiser or by using the results of previous studies or meta-analyses of the task or cognitive domain. Second, in the presence of pre-existing anatomical hypotheses, *a priori* ROIs may be defined anatomically based on the hypotheses being tested.

The term functional connectivity was first defined by Friston (1994) as temporal correlations between spatially remote brain regions. Two approaches are primarily used to study task modulated connectivity, namely generalised psychophysiological interaction (gPPI) and beta series correlation (BSC). Functional connectivity can be measured between a ROI and every other voxel in the brain, or between pairs of ROIs.

gPPI is a method to explain responses in one cortical area in terms of an interaction between the influence of another area and some experimental parameters (Friston et al., 1997; McLaren et al., 2012). Traditionally, the PPI term is defined using a pre-defined ROI, and voxel-wise analysis is performed to identify regions in the whole brain that showed task modulated connectivity with the seed ROI. The PPI method can also be applied to every pair of regions in the brain in order to map whole-brain task modulated connectivity, i.e. task connectome (Di and Biswal, 2019).

BSC was originally proposed for slow event-related designs in order to model functional connectivity between brain regions during distinct stages of a cognitive task (Rissman et al., 2004). The premise of this method is that if two areas of the brain are functionally interacting with each other during a particular stage of a cognitive task, then the amount of activity that the two areas exhibit during that stage should be correlated across trials. It is implemented by using separate covariates to model the activity evoked during each stage of each individual trial in the context of the

GLM. The resulting parameter estimates (beta values) are sorted according to the stage from which they were derived to form a set of stage-specific beta series. Regions whose beta series are correlated during a given stage can be inferred to be functionally interacting during that stage. ■

The test of all knowledge is experiment.
Experiment is the sole judge of scientific truth.

- Richard Feynman

EMPIRICAL CHAPTERS

- EXPERIMENT I -

- EXPERIMENT II -

- EXPERIMENT III -

CHAPTER 5

LANGUAGE COMPREHENSION

This chapter presents Experiment I, focusing on reading and speech comprehension in adult second language learners. We performed three different analyses in order to comprehensively characterise the functional neural changes concomitant with language learning in adulthood. The following work has been published in NeuroImage (Gurunandan et al., 2019).

5.1 INTRODUCTION

Learning a new language in adulthood is becoming increasingly common and is typically a complex and effortful process. Adult language learners thus offer an excellent window into a range of learning-dependent neural changes occurring in an ecological context. Language learning in adults has often been studied by using artificial languages or discrimination tasks focusing on specific skills such as word learning (López-Barroso et al., 2013; Plante et al., 2015; Li et al., 2018), foreign speech sound discrimination (Golestani et al., 2002, 2007; Golestani and Zatorre, 2004; Golestani and Pallier, 2007), and learning of pitch patterns (Wang et al., 2003; Wong et al., 2007). These experimental approaches have provided valuable insights into the neural changes concomitant with these aspects of L2 learning, but the multi-dimensionality of language also means that investigating the full neural impact of real-world language learning requires ecologically valid experiments.

Classical studies have found that the age of acquisition and proficiency in the second language (L2) modulate functional and structural neural differences in bilingual adults (e.g. Kim et al., 1997; Mechelli et al., 2004). The influence of these two factors has been well studied in adults who acquired their L2 as children (e.g. Perani et al., 1998, 2003, 2005; Chee et al., 2001; Wartenburger et al., 2003; Liu and Cao, 2016), but fewer studies have examined adults who are actively learning a new language. Learning-dependent neuroplasticity has been seen in adults within the first 3–5 months of learning a new language (Stein et al., 2009, 2012; Mårtensson et al., 2012; Schlegel et al., 2012; Xiang et al., 2015; Chai et al., 2016; Barbeau et al., 2016), but less attention has been paid to what happens next. After the initial effort of L2 learning, do language networks continue to change in adults progressing from the intermediate to the advanced stages of L2 learning?

To examine learning-dependent plasticity in adults past the initial stage of L2 learning, we studied two groups of adults enrolled in the same language school: one group from intermediate level classes and the other from advanced level classes. The study sample was controlled for both extra-linguistic and linguistic factors — all participants were native to the region and were learning a local language that differs substantially from their native language in morphology and syntax, but has largely overlapping phonology and orthography. We used a semantic judgement task with single words presented visually and auditorily to map the reading and speech comprehension networks in the participants' native language (L1) and in the language being learnt (L2). To comprehensively map changes in the neural representations of L1 and L2, we examined three things: (i) functional convergence of reading and speech comprehension, (ii) functional similarity of L1 and L2, and (iii) functional connectivity between classical language regions and language control regions.

First, we examined the role of language proficiency in the functional convergence of print- and speech-comprehension. It has been shown that print-speech convergence varies with reading skill in monolingual children and adults — above and beyond general activation for printed and spoken stimuli — since skilled reading involves integration of print-processing with pre-existing spoken language networks (Shankweiler et al., 2008; Frost et al., 2009; Preston et al., 2016). Not limited to specific languages, this convergence between reading and speech comprehension networks has been found in adult native speakers of highly contrasting languages with different writing systems, levels of orthographic depth, and morphological properties, and is thus considered a universal signature of proficient reading (Rueckl et al., 2015). A study with late bilingual-biliterates (bilinguals whose languages use different writing systems, e.g. English and Chinese) extended these results to L2, finding differences in the pattern of print-speech convergence between L1 and L2 that were indicative of the greater effort and lower automaticity of L2 reading in a new writing system (Brice et al., 2019). However, monolinguals and many bilingual-biliterates learn to speak before they learn to read, which is not the case for late bilinguals whose L2 uses the same writing system as their L1. Hence, the effect of overall L2 proficiency on convergence of reading and spoken language networks when reading is already proficient remains an important open question for the reliability of print-speech convergence in L2. In the current experiment, all participants were proficient readers in their L1, and their L2 uses the same writing system and has phonology and a transparent orthography largely overlapping with the L1, thus allowing us to specifically examine the effect of language proficiency on print-speech convergence, independent of reading skill. We expected to find substantial print-speech convergence reflecting proficient reading in both L1 and L2, and hypothesised that any effects specifically due to increased L2 proficiency would emerge as differential patterns of convergence in the intermediate and advanced groups.

Second, we examined the effect of L2 proficiency on the similarity of L1 and L2 activation patterns. While L1 and L2 have been found to utilise common semantic "hubs" in proficient bilinguals (Chee et al., 1999; Perani and Abutalebi, 2005; Buchweitz et al., 2012; Correia et al., 2014), psycholinguistic studies make the case for L1-mediated access to L2 in the early stages of L2 learning, with L1-dependence decreasing in the later stages (Kroll and Stewart, 1994; Kroll et al., 2010). This could suggest higher similarity between L1 and L2 activation in the intermediate L2-learners due to L1-dependence of L2, and greater separation in the advanced learners as the L2 became less dependent on L1. Previous studies of bilinguals have found substantial proficiency-dependent variability in L2 activation, particularly in lateralisation (Dehaene et al., 1997; Abutalebi et al., 2001; Hull and Vaid, 2007). To take this variability into account and to examine the idea that similarity of L1 and L2 vary as a function ofL2 proficiency, we used laterality indices to compare L1 and L2 activation in the language network areas presented in prominent neuroanatomical models of language (e.g. Lau et al., 2008; Hagoort, 2013). By restricting the analysis to classical language regions, we aimed to avoid conflating activation in regions associated with language control (addressed separately in the subsequent analysis). Further, we analysed the contributions of the dorsal and ventral pathways to laterality changes in the reading and speech comprehension networks. The dorsal and ventral streams are known to subserve phonological processing and lexico-semantic mapping, respectively (Jobard et al., 2003; Hickok and Poeppel, 2004; Schlaggar and McCandliss, 2007; Friederici, 2012; Oliver et al., 2016), and may thus be differentially modulated in the course of language learning.

Finally, we examined the role of L2 proficiency and exposure in functional coupling of the language regions and language control regions. One of the recurring themes in bilingual language processing is the recruitment of areas not typically included in the classical language networks, such as the dorsolateral prefrontal cortex (dlPFC) and anterior cingulate cortex (ACC), which are thought to be involved in control processes associated with language (e.g. Chee et al., 2001; Abutalebi et al., 2007; Marian et al., 2007; Hernandez, 2009). This effect, at least in the lexico-semantic domain, appears to be independent of the age of L2 acquisition and to rely primarily on L2 proficiency and exposure (see Abutalebi et al., 2001; Indefrey, 2006 for reviews). Supporting the role of L2 exposure, a verbal production study found more extensive activation in left and right prefrontal areas associated with lower L2 exposure in early, highly proficient bilinguals (Perani et al., 2003). If more diffuse activation of control areas is associated with lower L2 proficiency and exposure, this might imply that with increasing proficiency and exposure, functional connectivity between control areas and classical language regions in L2 learners becomes stronger. To examine functional interactions between the dlPFC and ACC and the classical language areas during L2 processing, we conducted functional connectivity analyses. We expected to observe stronger functional coupling in advanced L2-learners who had more experience in the L2 than the intermediate group.

5.2 METHODS

5.2.1 PARTICIPANTS

The final study sample consisted of 29 right-handed native Spanish speakers (mean age = 43.7 ± 9.7 years; 15 female) studying Basque in the same language school. Data from five other participants was excluded due to excessive head motion during imaging. Participants were native to the Basque Country, Spain, and had grown up primarily exposed to Spanish (L1) at home and in school. They were now living in Spanish-Basque bilingual environments, and enrolled in Basque (L2) classes at either the A23 level (intermediate group, n = 14) or C1 level (advanced group, n =15), and had uniformly high performance in class. Language proficiency was further assessed using objective and subjective measures. Participants performed a picture-naming task in their two languages — an adaptation of the Boston Naming Test (Kaplan et al., 1983) controlled for cognates across L1 and L2 — and completed a language background questionnaire in which they rated their proficiency and percentage of daily exposure outside the classroom to each language (Table 5.1).

The two groups were matched on age, gender, IQ and Spanish proficiency (Table 5.1). Participants had limited knowledge of English or other languages, with little day-to-day exposure to them, and there was no difference between groups in this regard (p = 0.83). All participants had normal or corrected-to-normal vision, and no history of neurological or psychiatric disorders. In compliance with the ethical regulations established by the BCBL Ethics Committee and the guidelines of the Helsinki Declaration, all participants gave written informed consent prior to taking part in the experiment, and received monetary compensation for their participation.

Table 5.1: Participant demographics and linguistic scores by group

	Intermediate L2 group	**Advanced L2 group**	***p*-value**
Age	42.86 (10.10)	44.53 (10.51)	0.66
Gender	7 female, 7 male	8 female, 7 male	0.86
IQ	117 (13.78)	122 (9.43)	0.12
L1 proficiency	99.35 (1.88)	99.64 (0.77)	0.61
L2 proficiency	52.6 (14.66)	87.96 (10.58)	0.00
L1 exposure	85.23 (16.96)	71.31 (24.43)	0.11
L2 exposure	8.54 (8.32)	23.46 (22.93)	0.04

Values correspond to the mean with standard deviation in parentheses.
p-values correspond to the t-test between groups (chi-square test for gender).

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[3] Common European Framework of Reference for Languages (CEFR)

5.2.2 TASK DESIGN

Inside the MRI scanner, participants performed an animacy judgement task. Participants were presented with either written or spoken words in their L1 and L2, and had to indicate whether the stimuli was living or non-living via button presses, using their dominant (right) hand. To avoid language-switching effects, the languages were separated and their order was counterbalanced across participants. We used an event-related fMRI design, with three runs for each language. Each run had 48 stimuli with inter-mixed reading and listening trials. Printed stimuli subtended visual angles of 4°-6° and were all displayed for 1000 ms, while auditory stimuli had a mean duration of 565 ms (sd=86 ms). Stimuli were high frequency, concrete, imageable nouns with an even split between living and non-living items. The baseline condition consisted of a fixation cross presented in the centre of the screen.

5.2.3 MRI DATA COLLECTION

Whole-brain MRI data was acquired using a 3-T Siemens Magnetom Trio whole-body MRI scanner and a 32-channel head coil at the Basque Center on Cognition, Brain and Language (BCBL). Padded headphones were used to dampen background scanner noise and enable clear transmission of the auditory stimuli. Participants viewed the print stimuli on a screen via a mirror mounted on the head coil. To limit head movement, the head coil was padded with foam and participants were asked to remain as still as possible.

Functional MRI was acquired in the course of six separate runs using a gradient-echo echo-planar pulse sequence with the following parameters: TR 2000 ms, TE 30 ms, 32 axial slices with a 3.4 x 3.4 x 4 mm voxel resolution, 10% inter-slice gap, flip angle (FA) = 80°, field of view (FoV) = 220 x 220 mm, 64 x 64 matrix. 186 volumes were collected for each of the six functional runs. Prior to each scan, four volumes were discarded to allow for T1-equilibration effects. To improve estimation of the resting baseline in functional analyses, functional runs contained three silent fixation periods of 20 s each. Within each functional run, the order of the trials (reading and listening conditions) and the inter-trial intervals of variable duration (4-20 s) corresponding to the baseline MR frames (30% of total collected functional volumes) were determined by an algorithm designed to maximise the efficiency of the recovery of the blood oxygen level dependent response (optseq2, Dale, 1999). Structural T1-weighted images were acquired with a MPRAGE sequence with TR = 2530 ms, TE = 2.97 ms, inversion time = 1100 ms, FA = 7°, FoV = 256 x 256 mm, 176 slices and voxel size = 1 mm^3.

5.2.4 MRI DATA ANALYSES

Standard SPM8 (Penny et al., 2011) preprocessing routines and analysis methods were employed. Images were first corrected for differences in timing of slice acquisition and then realigned to the first volume using rigid-body registration. Each subject's functional volumes were spatially smoothed with a 4-mm full-width half-maximum (FWHM) Gaussian kernel. Next, motion parameters obtained from realignment were used to inform a volume repair procedure (ArtRepair, Mazaika et al., 2009) that identified bad volumes on the basis of scan-to-scan movement (>1 mm) and signal fluctuations in global intensity (>1.3%), and corrected bad volumes via interpolation between the nearest non-repaired scans. Data from five subjects requiring more than 20% of their volumes to be repaired were discarded. The number of corrected volumes was similar between groups (p=0.19). After volume repair, high-resolution anatomical T1 images and functional volumes were co-registered and spatially normalised to T1 and echo-planar imaging templates, respectively, to enable anatomical localisation of the activations. Templates were based on the MNI305 stereotaxic space (Cocosco et al., 1997), an approximation of Talairach space (Talairach and Tournoux, 1988). The normalisation algorithm used a 12-parameter affine transformation together with a nonlinear transformation involving cosine basis functions. During normalisation, the volumes were sampled to 3-mm cubic voxels. The resulting volumes were then spatially smoothed with a 7-mm FWHM Gaussian kernel. Finally, time series were temporally filtered to eliminate contamination from slow frequency drift (high-pass filter with cut-off period of 128 s).

Statistical analyses were performed on individual subject data using the general linear model (GLM). fMRI time series data were modelled by a series of impulses convolved with a canonical haemodynamic response function. Six motion parameters for translation (x, y, z) and rotation (yaw, pitch, roll) were included as covariates of non-interest in the GLM. Each trial was modelled as an event, time-locked to the onset of the presentation of each stimulus. Error responses were modelled separately. The remaining functions were used as covariates in the 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 the images, treating subjects as a random effect. Brain coordinates throughout the text, as well as in tables and figures, are reported in MNI atlas space.

PRINT-SPEECH CONVERGENCE

We first obtained each subject's whole-brain contrasts Print_correct>Rest and Speech_correct>Rest in each language condition, with a voxel-wise corrected false discovery rate (FDR) threshold set at $q<0.05$, and used these contrasts to compute voxel-to-voxel Pearson correlations (WFU Biological Parametric Mapping Toolbox, Casanova et al., 2007) across subjects within each proficiency group. We used two methods to test for differences between the intermediate and the advanced groups in each language: (i) we performed minimum conjunction in each subject to retain only voxels that were significantly active in both the reading and speech conditions, and carried out statistical non-parametric mapping (SnPM13 toolbox, Nichols and Holmes, 2001) on the resulting images to identify voxels that differed significantly between groups or languages, and (ii) calculated a correlation coefficient (Pearson's r) between voxels in print and speech conditions for each subject and used a 2x2 ANOVA to test for group differences in either language.

L1-L2 SIMILARITY

To test similarity of L1 and L2 activation in the language network regions, we correlated the laterality indices of activation in each language. Laterality is calculated by dividing the difference between activation in each hemisphere by the sum, resulting in an index between –1 (fully right-lateralised activation) and +1 (fully left-lateralised activation). In line with the latest recommendations (Bradshaw et al., 2017), we used a threshold-independent method to calculate the index (LI-Toolbox, Wilke and Lidzba 2007). We chose six bilateral anatomical regions of interest (ROI) from standard neuroanatomical language models (e.g. Hagoort 2013): inferior frontal gyrus (IFG) pars orbitalis, IFG pars triangularis, IFG pars opercularis, inferior parietal lobule (IPL), superior temporal gyrus (STG), and ventral occipito-temporal cortex (vOTC), and masked each subject's whole-brain contrasts for the reading and speech conditions with the selected anatomical regions from the AAL atlas (Tzourio-Mazoyer et al., 2002). We acquired laterality indices for three networks: (i) the language network consisting of all six ROIs, (ii) the dorsal phonological network consisting of the IPL, STG and IFG pars opercularis, and (iii) the ventral lexical network consisting of the IFG pars orbitalis, IFG pars triangularis, and vOTC. We then calculated correlation between indices (using Pearson's *r*) to test the similarity between L1 and L2 language networks within each group, as well as (i) a two-sample t-test to test between-group differences in L1-L2 laterality, and (ii) Cohen's *d* to test for group differences in each language.

FUNCTIONAL CONNECTIVITY

We assessed functional connectivity using the beta-series correlation method (Rissman et al. 2004) implemented in SPM8 with custom MATLAB scripts. The canonical HRF in SPM was fitted to each occurrence of each condition and the resulting parameter estimates (beta values) were sorted according to the study conditions to produce a condition-specific beta series for each voxel. Pairwise connectivity was calculated between selected ROIs in the bilateral language networks and control regions for each participant and condition. Since the correlation coefficient ranges from –1 to +1, an arc-hyperbolic tangent transform (Fisher, 1922) was applied to these beta-series correlation values to make its null hypothesis sampling distribution approach that of the normal distribution. To test for group differences in functional connectivity strength as a function of our experimental design, the normally distributed Fisher's Z values were submitted to group comparisons within each of the conditions of interest: L1 reading, L1 speech, L2 reading, and L2 speech. The regions selected for these functional connectivity analyses included the previously described bilateral language network regions (IFG *pars orbitalis, triangularis, opercularis,* STG, IPL, and vOTC) and two bilateral cognitive control regions: dorsolateral prefrontal cortex (dlPFC) and anterior cingulate cortex (ACC). Functionally defined ROIs were identified from the whole-brain contrast All_Correct_Trials>Rest with a voxel-wise FDR-corrected threshold q<0.05 and 4-mm radius spheres were centred at the highest local maxima within each ROI to ensure that differences in the functional connectivity between regions were not affected by the size of the ROIs. This gave us five spheres for cognitive control: two in the left dlPFC and one in the right, and one each in the left and right ACC.

5.3 RESULTS

5.3.1 IN-SCANNER BEHAVIOURAL PERFORMANCE

Mixed-model ANOVAs were separately conducted on the behavioural measures of the fMRI task, i.e. accuracy (percentage of correct responses) and reaction times, with Group (intermediate, advanced) as a between-subjects factor and with Language (L1, L2) and Modality (print, speech) as within-subjects factors. The first ANOVA for accuracy revealed a Group x Language interaction in the accuracy of participants' responses during the fMRI task (F(1,23)=20.65, p=0.0001). Post-hoc simple-effect analyses showed that the intermediate and advanced L2-learners exhibited no difference in accuracy in their L1 (t(18.33)=−1.44, p=0.17), but a significant difference in L2 (t(21.94)=5.02, p=0.00005), with the intermediate group showing

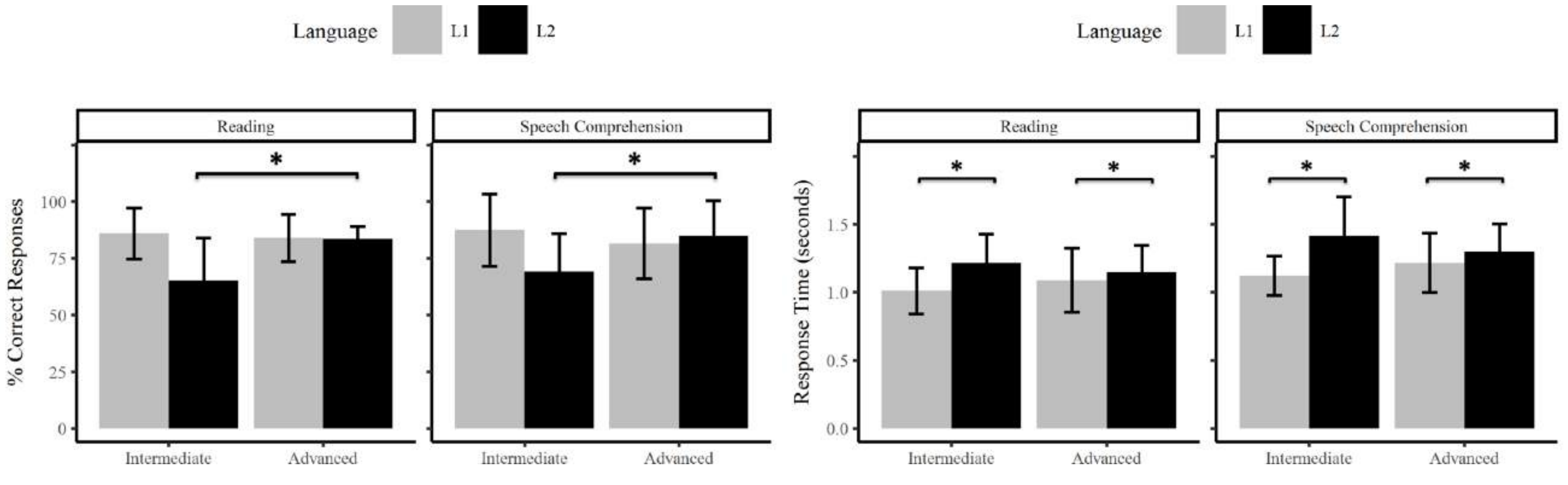


Figure 5.1 Behavioural results of the semantic judgement task inside the scanner revealed (A) Group x Language interaction in accuracy of responses, and (B) main effect of Language in reaction times of participants. Error bars represent standard deviation and asterisks statistically significant differences at $p < 0.05$.

significantly lower L2 accuracy than the advanced group (Figure 5.1). This effect was observed in both modalities, reading and speech. The ANOVA for participants' reaction times found only a main effect of Language (Figure 5.1), with both groups significantly slower in their L2 compared to their L1 (F(1,23)=44.5, p=0.0000008).

5.3.2 PRINT-SPEECH CONVERGENCE

Print-speech convergence in each language was calculated from the subjects' whole-brain contrasts Print_correct>Rest and Speech_correct>Rest using voxel-to-voxel Pearson correlation. The bilateral striate and extrastriate regions were significantly active only for the reading conditions, while posterior parts of the superior temporal gyrus (STG), including primary auditory cortex, were active only for the listening conditions. In L1 (Figure 5.2), convergence of printed and spoken language processing (r>0.31, p<0.05) was found in bilateral areas associated with both phonological and semantic processing such as the IFG, middle temporal gyrus (MTG) and STG, and IPL. In L2 (Figure 5.2), the pattern of convergence encompassed similar areas, but with slightly more extensive visual cortex activation for the reading condition, and greater convergence in the dlPFC in comparison to L1, which showed greater convergence in parietal regions. Neither the statistical non-parametric mapping

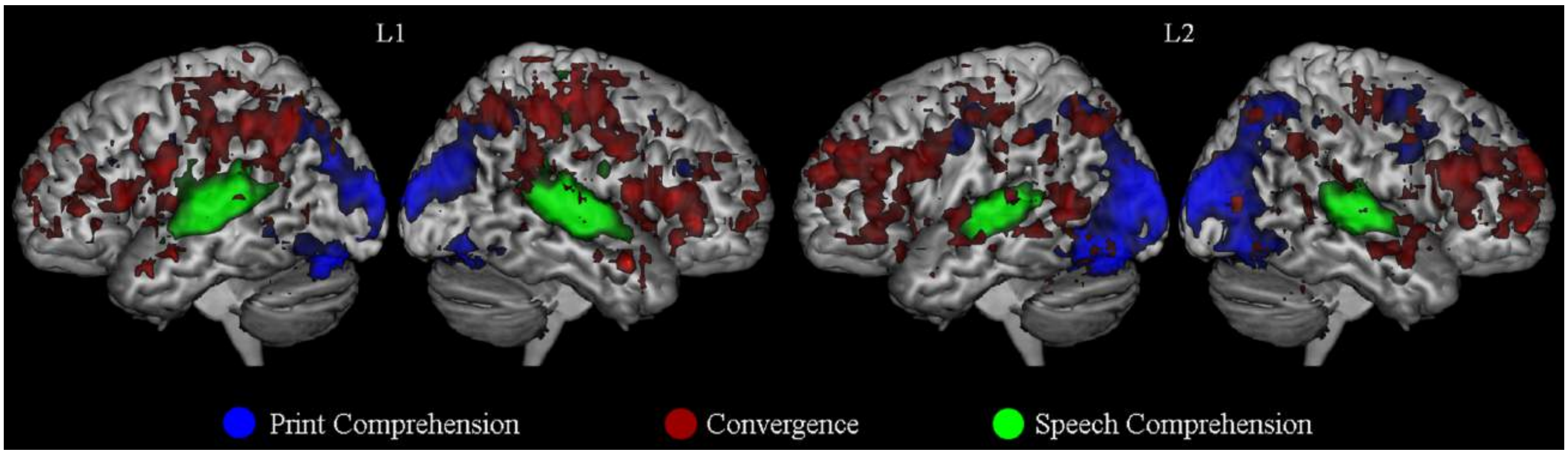


Figure 5.2 Print-speech convergence in L1 and L2, all subjects (n = 29); FDR-corrected q < 0.05; Pearson's r> 0.31, p < 0.05.

nor the ANOVA revealed significant differences at $p<0.05$ threshold (FDR-corrected for SnPM) between the two groups in either language.

5.3.3 L1-L2 SIMILARITY

To investigate whether the intermediate and advanced groups displayed similar activation patterns in L1 and L2, we correlated the laterality indices for L1 and L2 activation in the language network regions within each group (Figure 5.3). Laterality indices of activation in L1 and L2 in each modality were calculated for each subject, giving us values between -1 (completely right-lateralised activation) and $+1$ (completely left-lateralised activation). In the intermediate group, we found a positive correlation between L1 and L2 laterality in reading ($r=0.54$, $p=0.029$) and speech comprehension ($r=0.72$, $p=0.001$). In contrast, the advanced group exhibited a negative correlation in reading ($r=-0.46$, $p=0.048$) and a non-significant correlation in speech comprehension ($r=0.43$, $p=0.951$). A two-sample t-test of L1-L2 similarity

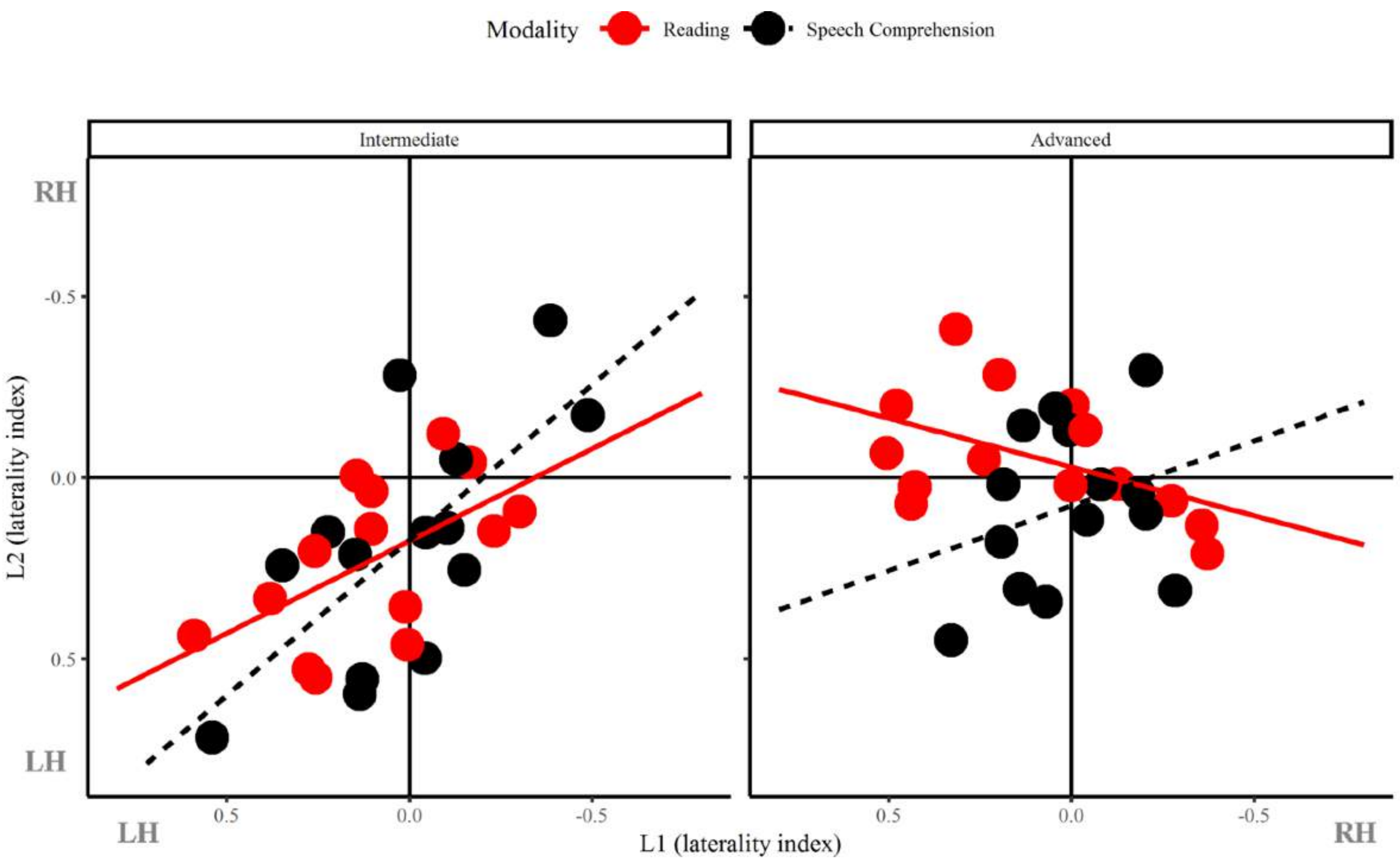


Figure 5.3 L1-L2 correlation of laterality indices. LH indicates greater activation in the left hemisphere; RH indicates greater activation in the right hemisphere.

confirmed a statistically significant difference between the groups in the language network in reading (t(19.51)=2.25, p=0.018) but not in speech comprehension (t(25.98)=1.79, p=0.15).

To further verify that the difference in activation patterns between groups came from differences in L2 and not differences in L1, we calculated the effect sizes (Cohen's d) of the indices. We found negligible differences in L1 lateralisation between the intermediate and advanced L2-learner groups, and large and medium effects in L2 lateralisation (Table 5.2), with the advanced group showing more bilateral activation in L2 than the intermediate group. In L2 reading, the dorsal and ventral networks both showed large effects of L2 proficiency, but in L2 speech comprehension, only the ventral network exhibited a medium effect of L2 proficiency.

Table 5.2: Effect sizes (Cohen's d) of between-group differences in laterality

Stimuli	**Network**	**Between-group difference in L1**		**Between-group difference in L2**	
Print	**Language**	**negligible**	**0.07**	**large**	**1.41**
	dorsal	negligible	0.02	large	1.10
	ventral	negligible	0.06	large	0.98
Speech	**Language**	**negligible**	**0.03**	**small**	**0.38**
	dorsal	negligible	0.04	small	0.27
	ventral	small	0.27	medium	0.68

5.3.4 FUNCTIONAL CONNECTIVITY

To examine functional interactions between the language network and language-control regions, we performed pairwise connectivity analyses using the beta-series correlation method. In L2 reading, we found significantly ($q<0.05$, FDR-corrected) stronger left dlPFC – left STG, and left dlPFC – right IFG pars opercularis connectivity in the advanced L2-learner group, compared to the intermediate L2-learner group

(Figure 5.4). No group differences in coupling strength between regions were observed in L2 speech comprehension.

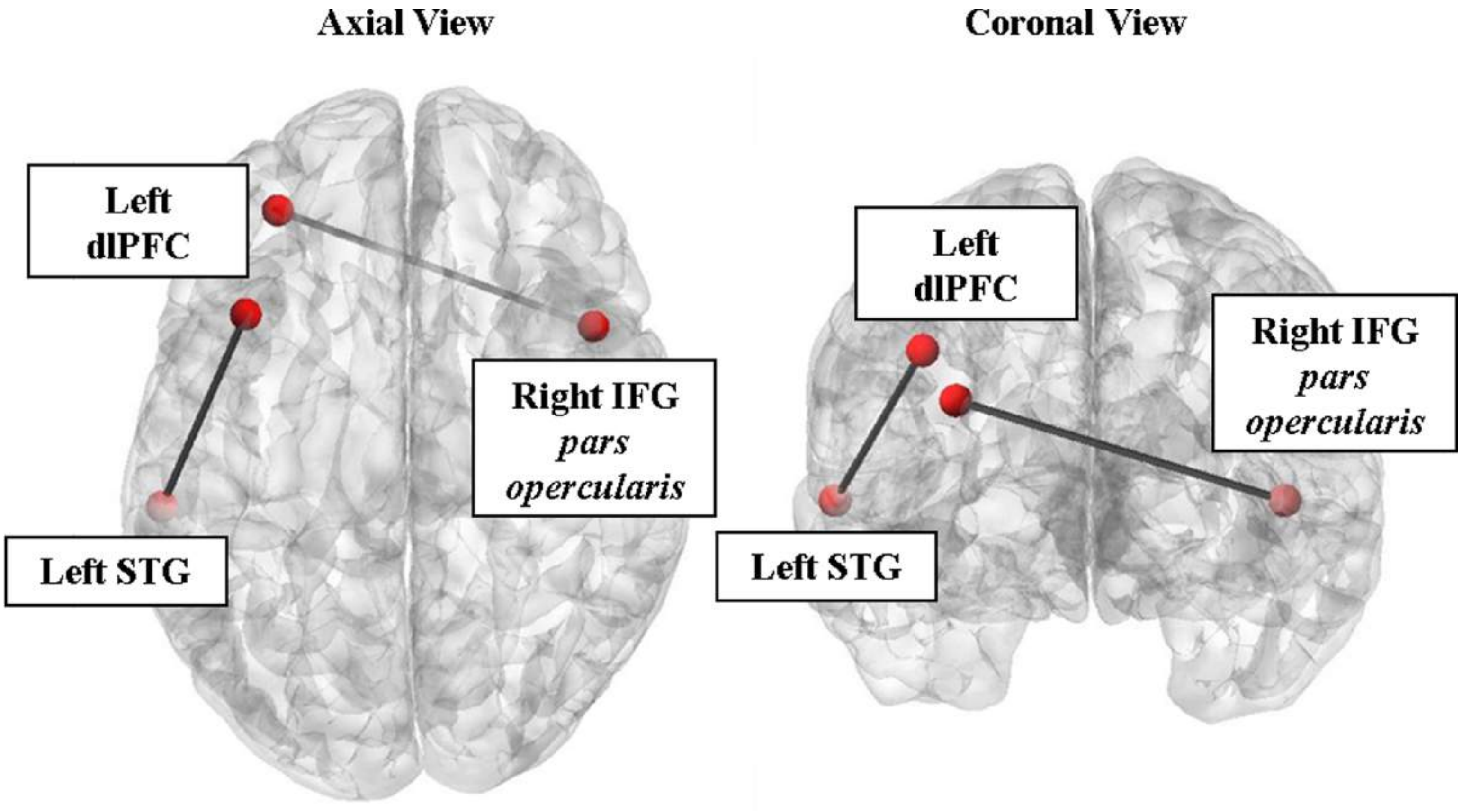


Figure 5.4 Advanced > Intermediate functional connectivity in L2 reading ($q < 0.05$, FDR-corrected) dlPFC = dorsolateral Prefrontal Cortex, IFG = Inferior Frontal Gyrus, STG = Superior Temporal Gyrus.

5.4 DISCUSSION

In the current experiment, we examined functional differences between adult intermediate and advanced language learners. While structural and functional changes have previously been observed in young adults learning completely new languages, functional correlates of neural changes in higher proficiency adult language learners had yet to be investigated. To ensure sufficient proficiency differences, we used a cross-sectional design and studied two groups of adult language learners from intermediate and advanced level classes at the same language school. All participants were studying a local language with very different morphology and syntax, but similar phonology and the same writing system and a transparent orthography as in their native language, thus controlling for extra-linguistic factors such as immigration or foreignness, as well as the more sensory (visual and phonological) differences between languages. To ensure semantic access inside the scanner, we used a semantic judgement task with single words to separately map activation for each language. Our analytical approach included three measures: print-speech convergence, L1-L2 similarity, and functional connectivity with language control regions. We found that (i) print-speech convergence was not affected by L2 proficiency, (ii) L1-L2 similarity was significantly higher in intermediate than in advanced L2 learners, and (iii) functional coupling of language and language control areas was higher in the advanced relative to the intermediate group during reading comprehension. Collectively, our results point to significant functional differences between adult language learners in the intermediate and the advanced stages of learning, indicating that increasing L2 proficiency engenders plasticity well into adulthood.

In both L1 and L2, we found significant convergence of reading and speech comprehension in classical language areas. In L1, the convergence was consistent with previous findings in native speakers of different languages (Rueckl et al., 2015), indicating that print-speech convergence in L1 was not affected by L2 acquisition. In L2, we saw a convergence pattern very similar to L1, with more extensive activation of sensory areas and slightly more extensive convergence in frontal and less in parietal regions. However, two separate statistical analyses using different convergence measures found no significant differences in print-speech convergence between the intermediate and advanced L2-learner groups in either language (or between languages in either group), indicating that print-speech convergence in L2 is unaffected by overall L2 proficiency level in skilled readers.

The similarity of L1 and L2 activation in classical language areas was significantly higher in the intermediate L2-learners compared to the advanced group. To test the hypothesis that L1-L2 similarity varies as a function of L2 proficiency, decreasing with increased L2 proficiency, we calculated within-group correlations between L1 and L2 laterality indices, and found high correlations in the intermediate group, which were not present in the advanced group. Finally, in L2 reading, we found large between-group differences in both dorsal and ventral pathways, while in L2 speech comprehension, there was a medium effect of proficiency in the ventral pathway and none in the dorsal.

In our final analysis, we examined the recruitment of extra-linguistic areas such as the dlPFC and ACC in L2 comprehension. Pairwise functional connectivity analyses between language network and language control regions revealed no differences between the groups in L1 or in L2 speech comprehension, but showed differential functional coupling of the dlPFC with language regions during L2 reading. We found that advanced L2-learners exhibited significantly stronger coupling than did the intermediate L2-learners, indicating that coordination between the left dlPFC and language-related regions was significantly higher in L2 reading.

While neural changes in young adults have consistently been associated with learning a completely new skill (see May, 2011 for a review), lack of practice has been seen to reduce or even reverse some of these changes when the skill is not maintained, particularly in older adults (Boyke et al., 2008). The effects of ongoing practice of skills acquired in adulthood have received relatively little attention, and in the current experiment, we investigated neural changes concomitant with ongoing improvement of a complex skill such as language learning. By comparing intermediate and advanced adult language learners, we found that: print-speech convergence was unaffected by L2-proficiency differences, lower similarity between L1 and L2 activation was associated with higher L2 proficiency, and stronger functional connectivity with dlPFC during reading was seen with greater L2 proficiency and exposure, indicating that language learners well into adulthood display functional plasticity of language comprehension networks. ■

CHAPTER 6

LANGUAGE PRODUCTION

This chapter presents Experiment II, focusing on verbal fluency in adult second language learners. Paralleling the structure of the previous chapter, here we present the findings from three analyses of learning-dependent changes in verbal production.

6.1 INTRODUCTION

Retrieving words for language production is typically a fast and accurate process. We generate 120-150 words per minute in fluent conversation (Maclay and Osgood, 1959) and err little more than once or twice in 1000 words (Cutler, 1982). When we consider the fact that our words are selected from a mental lexicon of fifty to a hundred thousand words (Miller, 1991), phonologically encoded and then verbally articulated, the enormity of this task — and how good we are at it — becomes apparent.

Bilingual language production requires not only language knowledge, but also language control. Language control allows bilinguals to selectively communicate in a target language while minimising interferences from the non-target language (Abutalebi et al. 2008). Knowledge and control both change with increasing second language proficiency: more proficient bilinguals have larger second language vocabulary as well as more refined language control. On the other hand, the words in the mental lexicon of more proficient bilinguals are effectively at a lower level of functional frequency, which can negatively affect language production (Costa, 2005; Michael and

Golan, 2005). These multidimensional changes indicate that second language acquisition substantially affects the cognitive processes underlying language production and is likely associated with complex changes in its neural correlates.

Verbal fluency is a key component of language production. In a typical verbal fluency task, participants/patients are presented with a series of semantic categories such as “animals” or phonemic categories such as “words beginning with the letter A”, and asked to produce as many examples of each category as possible within a given time period, typically 60 s. This simple task has long been used in psycholinguistic research to study language production, and in clinical settings to evaluate brain function in healthy ageing (Baciu et al., 2016) as well as a variety of disorders including Alzheimer's disease, attention deficit hyperactivity disorder, autism spectrum disorders, depression, Huntington’s disease, schizophrenia, and traumatic brain injury (Miller, 1984; Birn et al., 2010). Verbal fluency tasks have been employed since at least the late 1930s (Thurstone, 1938), when they were used to test “primary mental abilities”. And yet, despite their incredibly long and widespread use, it is as yet unclear what exactly verbal fluency tasks measure. In part, this is due to the versatility of the task, and the possibility of adapting task demands to study a wide variety of questions. There are robust group differences between clinical and healthy populations in verbal fluency task performance, but after years of extensive examination of the correlation between different metrics of verbal fluency task performance and cognitive batteries, the evidence is mixed. Overall, however, there is a general consensus that verbal fluency, especially semantic category fluency, has components of both language and executive function (Shao et al. 2014; Whiteside et al., 2015; Aita et al., 2018), though the question of whether these components are differential and dissociable remains open.

In the current experiment, we examine the idea that the hybrid nature of the verbal fluency task has a temporal component, i.e. different cognitive and neural processes come into play at different stages of the task. Crowe (1998) studied the drop-off in the number of exemplars produced as the verbal fluency task progressed, and suggested that there is a store of high-frequency words which is more readily accessible, called the ‘’topicon’’ (Smith and Claxton, 1972), and that once this is exhausted, the search is extended to a more extensive lexicon. In 2010, Luo and colleagues examined differences between monolinguals and low/high vocabulary bilinguals in verbal fluency performance and found complex interactions in the starting point and slopes of the time-course. Finally, in the context of time-varying contributions of the medial temporal lobe to semantic retrieval for categories that might be aided by episodic memory instances, Sheldon and Moscovitch (2012) suggested that early responses are based on well-rehearsed prototypical knowledge while later responses rely more on open-ended strategies. Here we propose that the beginning of the verbal fluency task is more dependent on lexical retrieval of frequent words from the “topicon”, and as the task progresses, more strategic executive processes come into play. Since second language acquisition affects the lexicon and executive language control, we expect the concomitant behavioural and neural changes to magnify the differential contribution of the language and executive processes.

The goal of the current experiment was two-fold: (i) to comprehensively investigate the effect of second language acquisition on the neural substrates of language production, and (ii) to examine the neural dynamics of verbal fluency and dissociate the contributions of language knowledge (i.e. vocabulary) and executive control. To this end, we recruited two groups of adults enrolled in a language school: one group from intermediate level classes and the other from advanced level classes. The study sample was controlled for both linguistic and extra-linguistic factors — all participants were native to the region and were learning a local language that differs substantially from their native language in morphology and syntax, but has largely overlapping phonology and orthography. This ensured that motor learning of phonology and articulation were unlikely to be implicated (Berken et al., 2015). Inside the MRI scanner, participants performed verbal fluency tasks in their native language (L1) and in the language being learnt (L2). The task was carefully designed to allow investigation of its time course: it was an overt, paced, semantic verbal fluency task. Overt responses allowed us to examine the behavioural performance, and several studies have demonstrated that covert or silent speech, though popular in fMRI paradigms, does not activate the same networks as overt speech (Barch et al., 1999; Huang et al. 2001; Gracco et al., 2005; Shuster and Lemieux, 2005; Sörös et al, 2006; Christoffels et al. 2007). Heim and colleagues (2006) found that careful head fixation minimised motion artefacts, and participants were instructed to respond overtly with “pass” if they had no response in order to control articulatory motion and activation throughout the task. Paced responses allowed control over timing of responses, and the number of exemplars produced during paced and free recall tasks inside the scanner have been found to be similar (Basho et al., 2007). Finally, we used semantic categories since this is most directly relevant to natural language production (Levelt et al., 1999). All analyses were performed by partitioning the task into two parts, A and B, where part A comprised the first half of the task, and part B comprised the second half of the task.

To test our hypotheses, we first examined behavioural performance on the in-scanner verbal fluency task. We acquired measures of L1 and L2 vocabulary and executive control using picture-naming tasks (de Bruin et al., 2017) and the attention network task (ANT) (Fan et al., 2002) respectively. If early word generation is associated with linguistic knowledge and later word generation with executive control, then performance in the first half of the task should be predicted by language proficiency, and performance in the second half by executive control. Next, to comprehensively map the neural dynamics of verbal fluency and the effects of language learning, three analytical approaches were used: (i) time course of functional activation, (ii) lateralisation of activation, and (iii) functional coupling between language and language control regions.

First, we examined the time course of activation during the task. Previous studies of verbal fluency have found involvement of the frontal and temporal regions (e.g. Birn et al., 2010). These were static measures, and we hypothesised that executive control regions would be more active as the task becomes progressively harder with each new response. Due to the L2 vocabulary differences between the two groups, we expected to see group differences in the second half of the L2 verbal fluency task. Second, we examined the lateralisation of activation during the verbal fluency task. Verbal fluency tasks have been previously used to localise language functioning in the brain (e.g. Gaillard et al., 2003). Here, we hypothesised that as responses get more effortful in the later part of the task, right hemisphere participation in the task would increase, and thus left-lateralisation would decrease. Finally, we examined the role of L2 proficiency and exposure in functional coupling of the language regions and language control regions. One of the recurring themes in bilingual language processing is the recruitment of areas not typically included in the classical language networks, such as the dorsolateral prefrontal cortex (dlPFC) and anterior cingulate cortex (ACC), which are thought to be involved in control processes associated with language (e.g. Chee et al., 2001; Abutalebi et al., 2007; Marian et al., 2007; Hernandez, 2009). This effect, at least in the lexico-semantic domain, appears to be independent of the age of L2 acquisition and to rely primarily on L2 proficiency and exposure (see Abutalebi et al., 2001; Indefrey, 2006 for reviews). Supporting the role of L2 exposure in verbal fluency, more extensive activation was found in left and right prefrontal areas associated with lower L2 exposure in early, highly proficient bilinguals (Perani et al., 2003). If more diffuse activation of control areas is associated with lower L2 proficiency and exposure, this might imply that with increasing proficiency and exposure, functional connectivity between control areas and classical language regions in L2 learners becomes stronger. To examine functional interactions between the dlPFC and ACC and the classical language areas during L2 processing, we conducted functional connectivity analyses. We expected to observe stronger functional coupling in advanced L2-learners who had more experience in the L2 than the intermediate group.

6.2 METHODS

6.2.1 PARTICIPANTS

The final study sample consisted of 31 right-handed native Spanish speakers (mean age = 45.19 ± 10.64 years; 17 female) studying Basque in the same language school. Data from three other participants was excluded due to either technical issues or excessive head motion during imaging. Participants were native to the Basque Country, Spain, and had grown up primarily exposed to Spanish (L1) at home and in school. They were now living in Spanish-Basque bilingual environments, and were enrolled in Basque (L2) classes at either the A2 level (intermediate group, n = 17) or C1 level (advanced group, n = 14), and had uniformly high performance in class. Language proficiency and exposure were further assessed: participants performed a picture-naming task in their two languages — an adaptation of the Boston Naming Test (Kaplan et al., 1983) controlled for cognates across L1 and L2 — and completed a language background questionnaire in which they indicated the percentage of their daily exposure outside the classroom to each language (Table 6.1).

The two groups were matched on age, gender, IQ and Spanish proficiency (Table 6.1). Participants had limited knowledge of English or other languages and had little day-to-day exposure to them; and there was no difference between groups in this regard (p = 0.91). All participants had normal or corrected-to-normal vision, and no history of neurological or psychiatric disorders. In compliance with the ethical regulations established by the BCBL Ethics Committee and the guidelines of the Helsinki Declaration, all participants gave written informed consent prior to taking part in the experiment, and received monetary compensation for their participation.

Table 6.1: Participant demographics and linguistic scores by group

	Intermediate group	**Advanced group**	***p*-value**
Age	44.47 (11.14)	46.07 (10.34)	0.68
Gender	8 female, 9 male	9 female, 5 male	0.55
IQ	113.38 (13.78)	120.31 (10.08)	0.16
L1 proficiency	99.38 (1.66)	99.71 (0.83)	0.53
L2 proficiency	51 (15.36)	88.62 (9.95)	0.00
L1 exposure	85.87 (15.79)	70.54 (23.95)	0.06
L2 exposure	8.4 (7.77)	24.23 (22.61)	0.03

Values correspond to the mean with standard deviation in parentheses.
p-values correspond to the t-test between groups (chi-square test for gender).

6.2.2 TASK DESIGN

The participants performed a paced semantic verbal fluency task in their two languages. The task had a block design with two runs per language, each run containing eight semantic categories and eight control blocks. To avoid language-switching, the languages were separated and the order of languages was counterbalanced across participants. In each run, participants fixated on a white cross in the middle of a black screen, and semantic category cues (e.g. fruits, animals, clothes) were presented on the screen. Each cue was displayed consecutively eight times over the course of 30 seconds, and participants were instructed to respond overtly to each cue with an exemplar (e.g. fruits: apple, pear, banana). Each cue required a novel response, or failing this, an overt response saying “pass”. In the control condition, participants repeated the word presented on the screen, i.e. “rest”. Fluency was scored as the percentage of valid answers averaged across the sixteen categories. Repetitions, inflections of the same word and erroneous responses were removed, and responses were scored only for correctness and not accent or pronunciation.

6.2.3 MRI DATA COLLECTION

Whole-brain MRI data was acquired using a 3-T Siemens Magnetom Trio whole-body MRI scanner and a 32-channel head coil at the Basque Center on Cognition, Brain and Language (BCBL). Padded headphones were used to dampen background scanner noise and enable clear transmission of the auditory stimuli. Participants viewed the print stimuli on a screen via a mirror mounted on the head coil. To limit head movement, the head coil was padded with foam and participants were asked to remain as still as possible.

Functional MRI was acquired in the course of four separate runs using a gradient-echo echo-planar pulse sequence with the following parameters: TR 3000 ms, TE 25 ms, 43 axial slices with a 3.0 x 3.0 x 3.0 mm voxel resolution, 10% inter-slice gap, flip angle (FA) = 90°, field of view (FoV) = 192 mm, 64 x 64 matrix. 240 volumes were collected for each of the functional runs. Prior to each scan, four volumes were discarded to allow for T1-equilibration effects. Structural T1-weighted images were acquired with a MPRAGE sequence with TR = 2530 ms, TE = 2.97 ms, inversion time = 1100 ms, FA = 7°, FoV = 256 x 256 mm, 176 slices and voxel size = 1 mm^3.

6.2.4 MRI DATA ANALYSES

Standard SPM12 (Penny et al., 2011) preprocessing routines and analysis methods were employed. Images were first corrected for differences in timing of slice acquisition and then realigned to the first volume to the first and mean volumes using rigid-body registration. Each subject's functional volumes were spatially smoothed with a 4-mm full-width half-maximum (FWHM) Gaussian kernel. Next, motion parameters obtained from realignment were used to inform a volume repair procedure (ArtRepair, Mazaika et al., 2009) that identified bad volumes on the basis of scan-to-scan movement (>1 mm) and signal fluctuations in global intensity (>1.3%), and corrected bad volumes via interpolation between the nearest non-repaired scans. Data from two subjects requiring more than 20% of their volumes to be repaired were discarded. The number of corrected volumes was similar between groups ($p=0.43$). After volume repair, functional volumes were co-registered to the T1 images using 12-parameter affine transformation and spatially normalised to the MNI space by applying non-linear transforms estimated by deforming the MNI template to each individual's structural volume. During normalisation, the volumes were sampled to 3-mm cubic voxels. The resulting volumes were then spatially smoothed with a 7-mm FWHM Gaussian kernel. Finally, time series were temporally filtered to eliminate contamination from slow frequency drift (high-pass filter with cut-off period of 128 s).

Statistical analyses were performed on individual subject data using the general linear model (GLM). fMRI time series data were modelled by a series of impulses convolved with a canonical haemodynamic response function. Six motion parameters for translation (x, y, z) and rotation (yaw, pitch, roll) were included as covariates of non-interest in the GLM. Each trial was modelled as an epoch of 15s each, time-locked to either the beginning or the middle of the presentation of each block. The remaining functions were used as covariates in the 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. Brain coordinates throughout the text, as well as in tables and figures, are reported in MNI atlas space (Cocosco et al.,, 1997).

All fMRI analyses were performed with *a priori* neuroanatomical regions of interest (ROI) chosen in line with standard neuroanatomical models of language (e.g., Hagoort, 2013) and language control (Abutalebi and Green, 2007). We chose six language ROIs: inferior frontal gyrus (IFG) *pars orbitalis*, IFG *pars triangularis*, IFG *pars opercularis*, inferior parietal cortex (IPC), superior temporal gyrus (STG), and ventral occipito-temporal cortex (vOTC), using the AAL atlas (Tzourio-Mazoyer et al., 2002). For language control, we chose two ROIs: anterior cingulate cortex (ACC) and dorsolateral prefrontal cortex (dLPFC). Since these two regions were not sufficiently sub-divided in the AAL atlas, we extracted the caudal ACC and rostral middle frontal gyrus respectively from the Desikan-Killiany atlas (Desikan et al., 2006).

Due to the hypothesised dual nature of the verbal fluency task, we divided each semantic block into two equal parts, A and B (15s each), and used this as a factor in the three fMRI analyses described below.

ROI ANALYSIS

To test changes in activation as the task progressed, we ran mixed model ANOVAs on the parameter estimates (% signal change) of the eight left hemisphere ROIs for the contrast Semantics>Rest in each language condition, with Group (intermediate, advanced) as a between-subjects factor, with Language (L1, L2) and Part (A, B) as within-subjects factors. P-values were corrected for multiple comparisons using false discovery rate (FDR). To further examine the course of functional activation during the task, we performed time course analysis of activation in the same ROIs. BOLD signal time-series were extracted from each ROI by averaging time-series across all voxels in each ROI. Condition-wise task blocks were each modelled as 30s windows of activity and their time-series averaged together to construct mean time courses for each language. These condition-averaged time courses were then averaged across functional runs.

LATERALISATION

To test changes in lateralisation of activation during the verbal fluency task, we calculated the laterality indices of activation in each language in the first and second parts (i.e. A and B) of the task. We then ran mixed model ANOVAs on the laterality indices of the eight bilateral ROIs, with Group (intermediate, advanced) as a between-subjects factor, with Language (L1, L2) and Part (A, B) as within-subjects factors. P-values were corrected for multiple comparisons using FDR. Laterality is calculated by dividing the difference between activation in each hemisphere by the sum, resulting in an index between –1 (fully right-lateralised activation) and +1 (fully left-lateralised activation). In line with the latest recommendations (Bradshaw et al., 2017), we used a threshold-independent method to calculate the index (LI-Toolbox, Wilke and Lidzba 2007).

FUNCTIONAL CONNECTIVITY

To test changes in functional coupling between regions as the task progressed, we assessed functional connectivity using the beta-series correlation method (Rissman et al., 2004) implemented in SPM12 with custom MATLAB scripts. The canonical HRF in SPM was fitted to each occurrence of each condition and the resulting parameter estimates (beta values) were sorted according to the study conditions to produce a condition-specific beta series for each voxel. Pairwise connectivity was calculated between selected ROIs in the bilateral language networks and control regions for each participant and condition. Since the correlation coefficient ranges from –1 to +1, an arc-hyperbolic tangent transform (Fisher, 1922) was applied to these beta-series correlation values to make its null hypothesis sampling distribution approach that of the normal distribution. The normally distributed Fisher's Z values for each of the eight left hemisphere ROIs were submitted to mixed model ANOVAs, with Group (intermediate, advanced) as a between-subjects factor, with Language (L1, L2) and Part (A, B) as within-subjects factors. P-values were corrected for multiple comparisons using FDR.

6.3 RESULTS

6.3.1 IN-SCANNER BEHAVIOURAL PERFORMANCE

A mixed-model ANOVA was conducted on the behavioural performance in the fMRI task, with Group (intermediate, advanced) as a between-subjects factor and with Language (L1, L2) and Part (A, B) as within-subjects factors. This revealed a Group x Language interaction in participants' fluency scores (F(1,23)=4.49, p=0.05), as well as a Group x Part interaction (F(1,23)=6.96, p=0.015). Post-hoc simple-effect analyses showed that the intermediate and advanced learners exhibited no difference in fluency in their L1 (t(24.99)=0.99, p=0.332), but a significant difference in L2 (t(22.96)=2.48, p=0.021), with the advanced group showing significantly higher L2 fluency than the intermediate group. Both groups displayed significant differences between their two languages (intermediate group: t(17.56)=6.85, p=0.000002, and advanced group: t(13.44)=4.69, p=0.0003), with higher performance in L1 than L2 (Figure 1a). Both groups displayed significant drop in performance from first to second halves of the task, i.e. Part A to Part B (intermediate group: t(24.51)=2.25, p=0.033, and advanced group: t(16.47)=5.10, p=0.00009). The difference between groups was significant in Part A (t(24.5)=4.76, p=0.00007), but not in Part B (t(24.66)=0.72, p=0.481), with the advanced group performing better than the intermediate group in Part A (Figure 1b). For illustrative purposes, we also plotted the time course of behavioural performance for each Group and Language (Figure 6.1c).

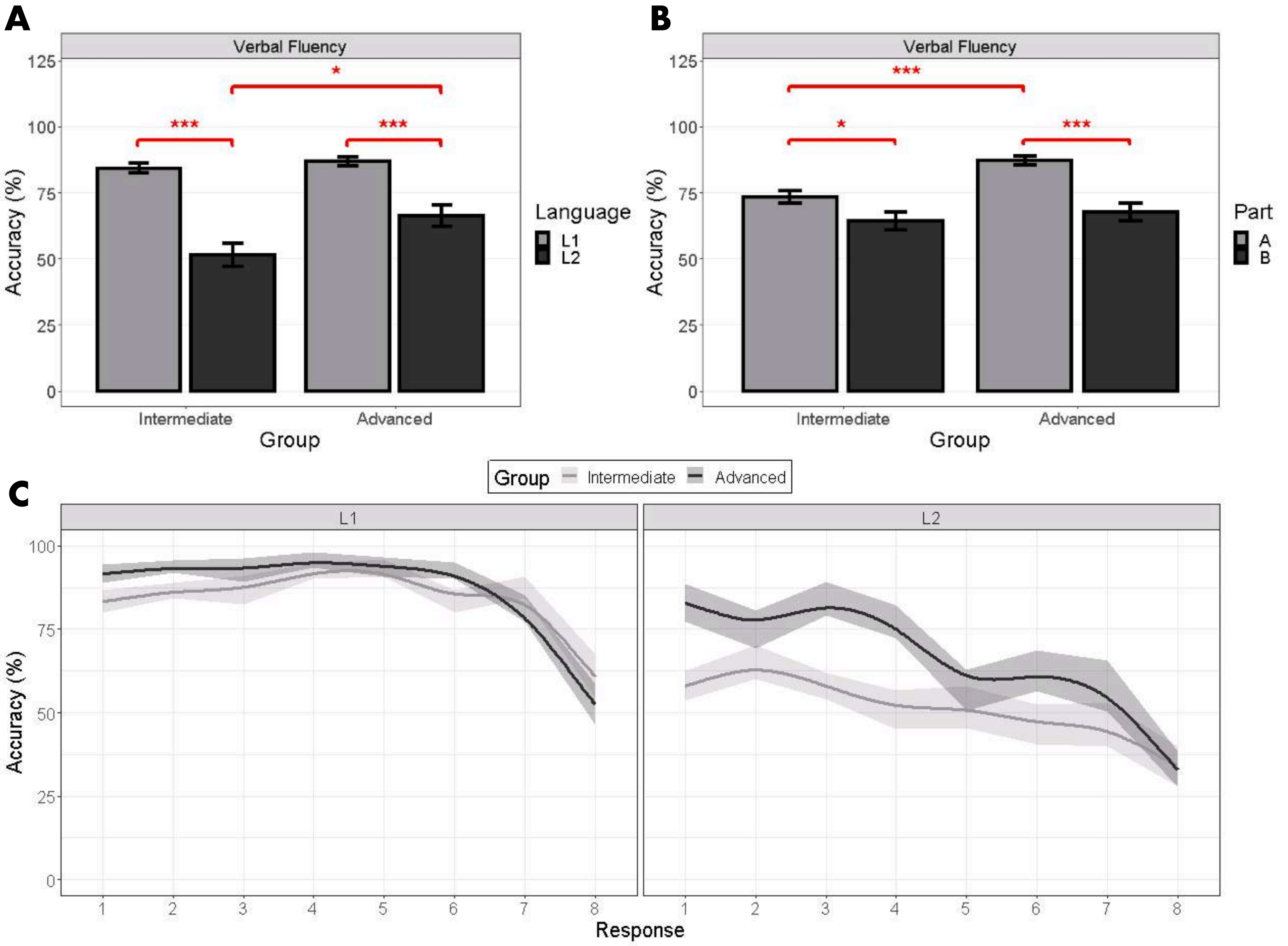


Figure 6.1 Behavioural results of the verbal fluency task inside the scanner revealed (A) Group x Language interaction in percent of correct responses, (B) Group x Part interaction in percent of correct responses. (C) Time course of behavioural performance for each Group and Language was plotted for illustrative purposes. Error bars represent standard deviation and asterisks statistically significant differences: *p<0.05 ***p<0.001.

To test our hypothesis about the hybrid nature of the verbal fluency task, we ran multiple regression analyses with task performance as the response variable and L1 proficiency, L2 proficiency, and executive control (ANT RTs) as explanatory variables. We found that across languages, task performance in the first half of the task was predicted by L2 proficiency (ß=0.39, p=0.0019), but not L1 proficiency (p=0.72) or executive control (p=0.59). On the other hand, task performance in the second half of the task was significantly predicted by executive control (ß=0.07, p=0.010), but not by L1 or L2 proficiency (p=0.71 and p=0.26 respectively). Further, we found significant correlations (Pearson's *r*) between task performance in Part A and L2 proficiency (Figure 6.2a), and task performance in B and executive control (Figure 6.2b).

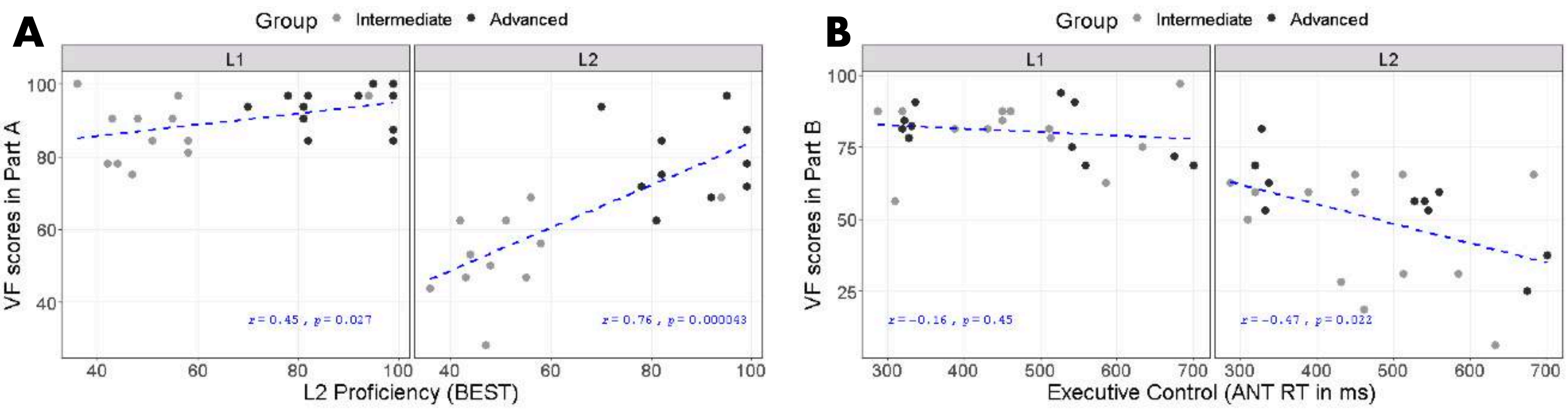


Figure 6.2 Pearson's correlations revealed (A) positive correlation between VF score in Part A and L2 proficiency, and (B) negative correlation between VF score in Part A and ANT RT

6.3.2 ROI ANALYSIS

Mixed model ANOVAs of the activation in each of the eight left hemisphere ROIs revealed a main effect of Language in the ACC and dlPFC, and the IFG *pars orbitalis, triangularis,* and *opercularis*, with significantly higher L1 activation than L2 activation in each of these (Figure 6.3a). We also found significant Group x Part interactions in the ACC, dlPFC, IFG *pars triangularis,* IFG *pars opercularis,* and the STG, with significant increases in activation from Part A to B of the task in the advanced but not the intermediate group. Additionally, the dlPFC, IFG *pars triangularis,* IFG *pars opercularis* displayed significant group differences in the second half of the task, but not the first (Figure 6.3b). The ANOVA results were corrected for multiple comparisons using FDR. We plotted the time courses for these ROIs, and after an initial peak, we found a steep dip in activation around 12s into the task (Figure 6.3c). After the dip, the advanced group's activation peaked again, while the intermediate group's activation remained around baseline.

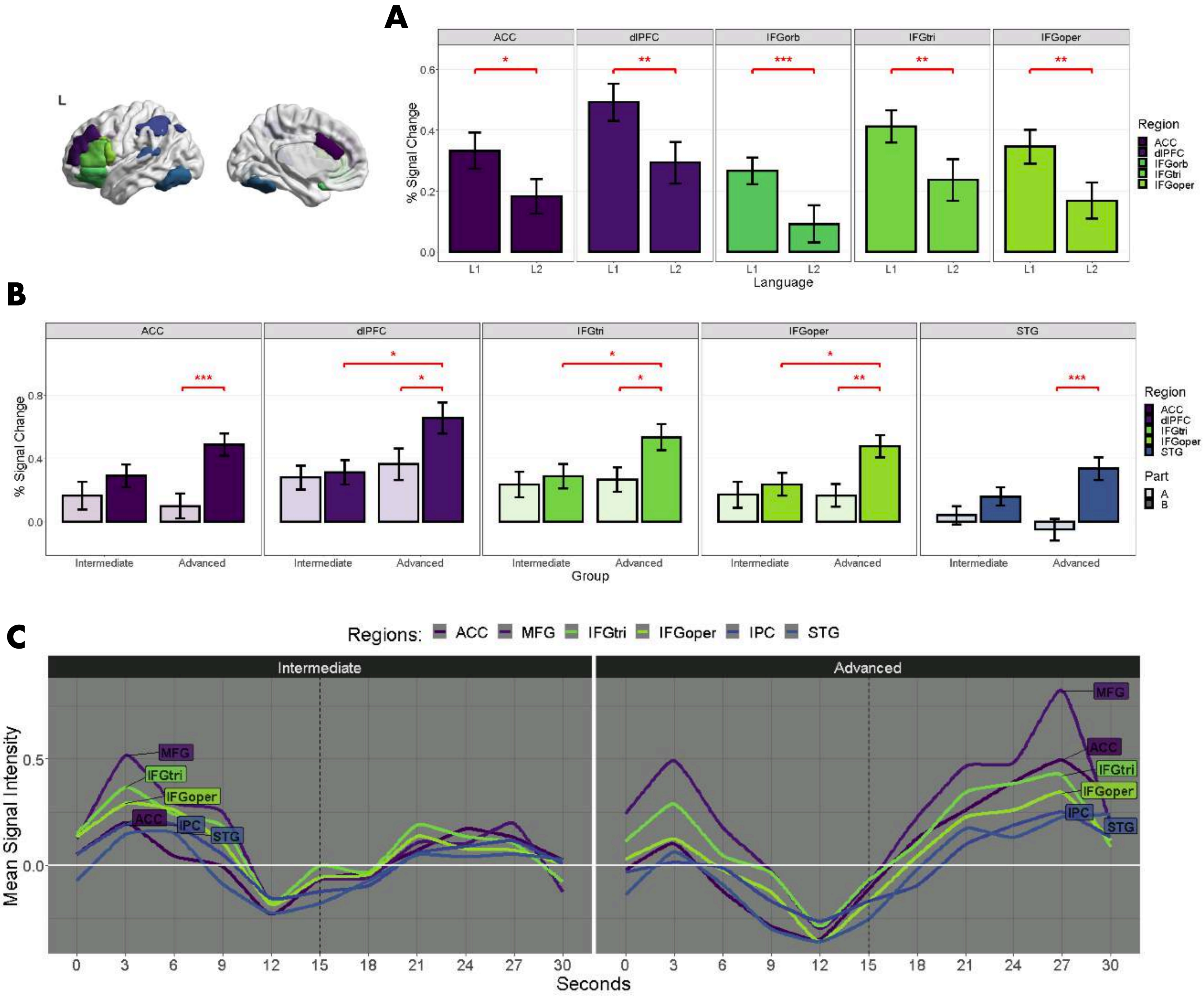


Figure 6.3 ROI analysis of the left hemisphere *a priori* ROIs during the verbal fluency task revealed (A) main effect of Language in frontal regions, and (B) Group x Part interaction in language and language control regions. (C) The Group x Part interaction was further illustrated with plots of the time courses for each Group. Language control regions=purple, IFG=green, and posterior regions=blue. Error bars represent standard error and asterisks statistically significant differences: *p<0.05 **p<0.01 ***p<0.001.

6.3.3 LATERALISATION

Mixed model ANOVAs of the laterality indices in each of the eight bilateral ROIs revealed a main effect of Language in the IFG *pars triangularis* and the STG, with significantly greater left lateralisation in L1 than in L2 (Figure 6.4a). We also found a main effect of Part in the IFG *pars orbitalis, triangularis,* and *opercularis*, IPL and STG, with significantly greater left lateralisation in the first half of the task, i.e. Part A (Figure 6.4b). The ANOVA results were corrected for multiple comparisons using FDR.

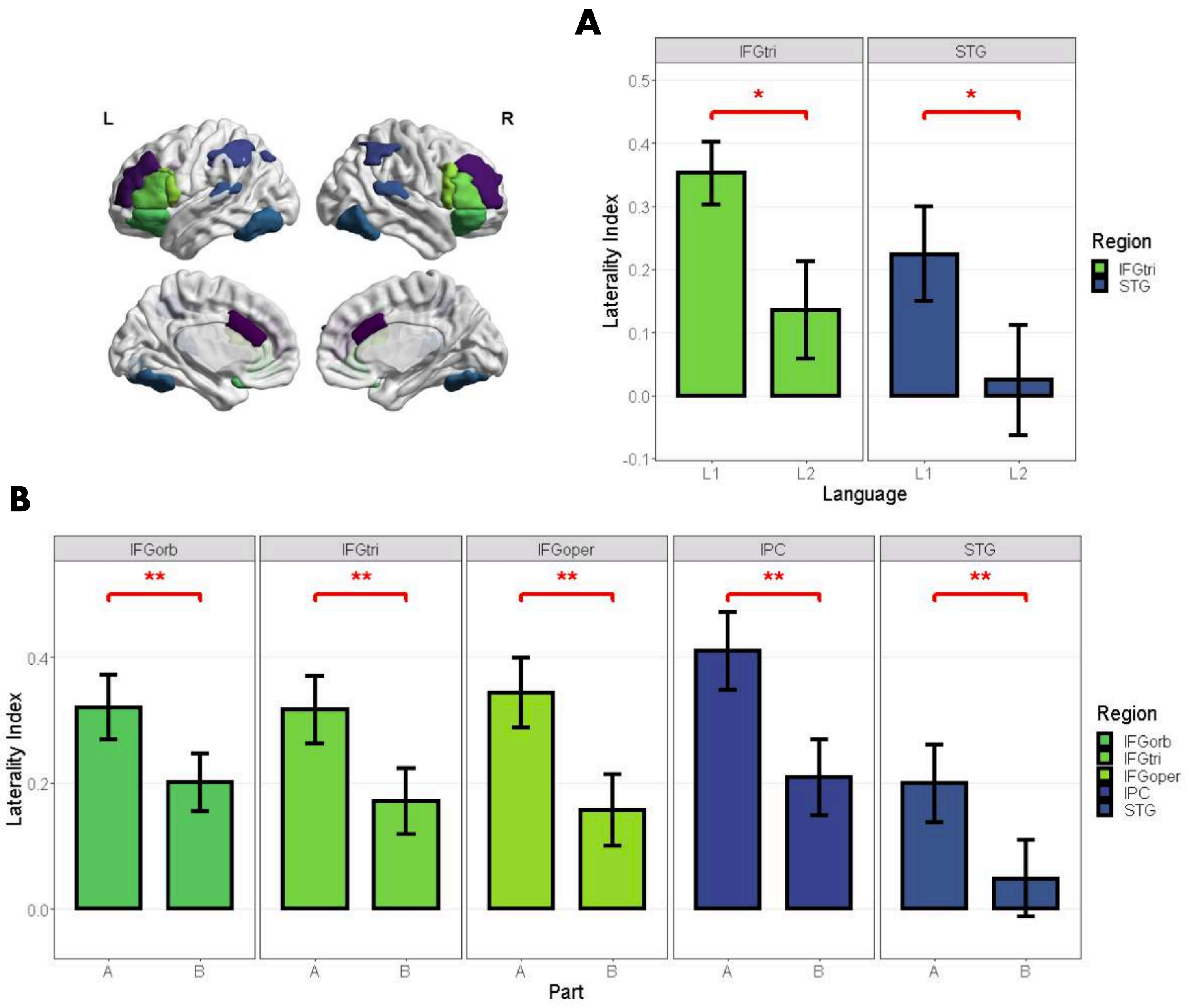


Figure 6.4 Laterality analysis of the bilateral *a priori* ROIs during the verbal fluency task revealed (A) main effect of Language and (B) main effect of Part in the language regions. Language control regions=purple, IFG=green, and posterior regions=blue. Error bars represent standard error and asterisks statistically significant differences: $*p<0.05$ $**p<0.01$

6.3.4 FUNCTIONAL CONNECTIVITY

Mixed model ANOVAs of the functional connectivity between the eight left hemisphere ROIs revealed a main effect of Language in the connectivity between the IFG *pars triangularis* and *opercularis,* with significantly higher connectivity in L2 than in L1 (Figure 6.5a). We also found a main effect of Group in the connectivity between the ACC and IFG *pars triangularis*, with significantly higher connectivity in the advanced group (Figure 6.5b). The ANOVA results were corrected for multiple comparisons using FDR.

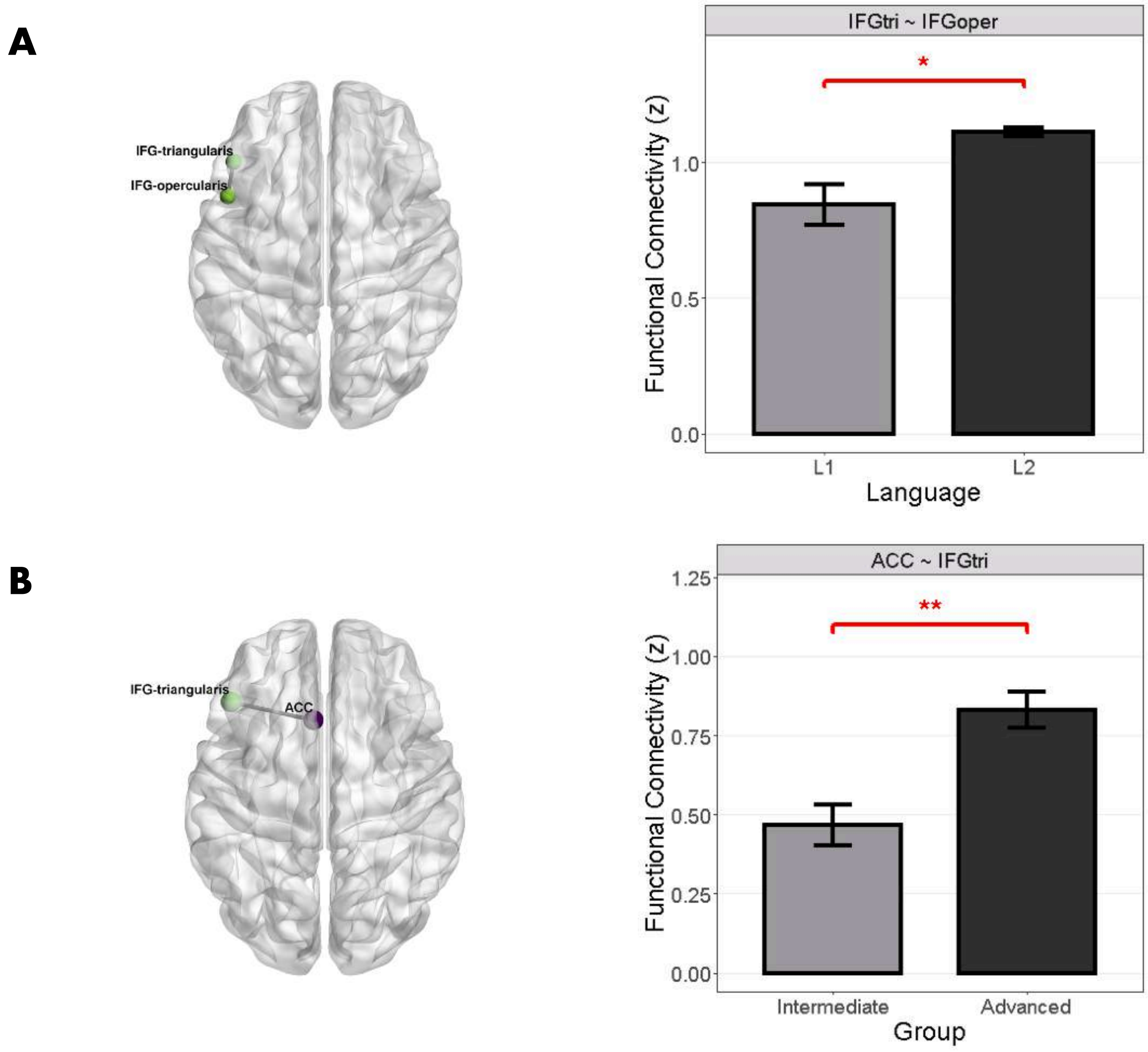


Figure 6.5 Functional connectivity analysis of the left hemisphere *a priori* ROIs during the verbal fluency task revealed (A) main effect of Language in functional coupling in the IFG and (B) main effect of Group in functional coupling of language and language control regions. Error bars represent standard error and asterisks statistically significant differences: $^{*}p<0.05$ $^{**}p<0.01$

6.4 DISCUSSION

In the current experiment, we examined functional differences between adult intermediate and advanced language learners with two goals: (i) to investigate the effect of second language learning on the neural substrates of language production, and (ii) to examine the neural dynamics of verbal fluency and dissociate the contributions of language knowledge (i.e. vocabulary) and executive control. While structural and functional changes have previously been observed in young adults learning completely new languages, functional correlates of neural changes in higher proficiency adult language learners had yet to be investigated. Additionally, the interaction between language and proficiency groups allowed us to test our hypothesis about the neural correlates of verbal fluency. We hypothesised that such a design would be well suited to examine effects in the second language that might be too small to be detected in the native language. To ensure sufficient proficiency differences, we used a cross-sectional design and studied two groups of adult language learners from intermediate and advanced level classes at the same language school. All participants were studying a local language with very different morphology and syntax, but similar phonology and the same writing system and a transparent orthography as in their native language, thus controlling for extra-linguistic factors such as immigration or foreignness, as well as linguistic factors such as motor learning of phonology and articulation. Inside the MRI scanner, participants performed semantic verbal fluency tasks in their native and new languages. The overt, paced task was carefully designed to allow investigation of its time course, and all analyses were performed by partitioning the task into two parts. We first confirmed our hypothesis using behavioural in-scanner task performance and measures from linguistic and cognitive assessments. Our fMRI analytical approach included ROI analyses of functional activation, lateralisation analyses, and analyses of functional connectivity between regions. We found that (i) significant learning-related changes in functional correlates of verbal fluency, (ii) no significant learning-related changes in lateralisation, but increasing recruitment of right hemisphere regions with increasing task difficulty, and (iii) functional coupling between language and language control regions increased with second language proficiency and exposure. Collectively, our results point to significant functional differences between adult language learners in the intermediate and the advanced stages of learning, and also support our hypothesis about the neural dynamics of verbal fluency.

In the time course of verbal fluency performance, we found that performance in the first half of the task was predicted by L2 proficiency (but not executive control), while performance in the second half was predicted by executive control component of the ANT (but not L2 proficiency), supporting our hypothesis that early word generation is associated with linguistic knowledge and later word generation with executive control. Language proficiency was measured by a standardised picture naming task, and participants had uniformly high performance in L1, but displayed a significant group difference in L2. Participants exhibited the same language-by-proficiency-group interaction in verbal fluency task performance. However, multiple regression analysis revealed that in both languages, verbal fluency performance in the first and last parts of the task were separately and exclusively predicted by L2 proficiency and executive control, respectively. While L2 proficiency was significantly correlated with initial verbal fluency performance in both languages, executive control was significantly correlated with later task performance in L2, but not L1. We hypothesised that the effect is relatively muted in L1 since the task was relatively easy, but the higher task difficulty in L2 allowed us to observe the role of executive control in L2.

In the ROI analyses, we found significant main effect of language and group x time interaction. Overall activation patterns were identical in both languages, but the

IFG and control regions, i.e. ACC and dlPFC, displayed greater activation in L1 than in L2. The difference in activation between the intermediate and advanced groups was negligible in the first half of the task, but pronounced in the second half. This difference was significant in the dlPFC, IFG *pars triangularis* and *pars opercularis*. Less expectedly, this group difference was found in both languages; time course analyses revealed that both groups displayed an initial peak in activation at the beginning of the task and a dip midway through the task, but while the advanced group's activation peaked again, the intermediate group's activation remained around baseline and did not pick up again in the latter half of the task. The advanced group also exhibited strong task progression effects, with significant differences between activation in the first and second parts of the task in the both language and language control regions.

The lateralisation of activation during the verbal fluency task exhibited no effects of proficiency, but task difficulty decreased left lateralisation, i.e. right hemisphere homologues were recruited with increasing task difficulty. This was seen in two instances: (i) the IFG *pars triangularis* and posterior STG were significantly more left-lateralised in L1 than in L2 in both groups and throughout the task, (ii) the frontal, temporal, and parietal language regions displayed significantly higher left-lateralisation of activation at the beginning of the task compared to the end of the task. Thus, results indicate that task difficulty, but not proficiency, modulates lateralisation of activation during verbal production.

In our final analysis, we examined the functional coordination between the language and language control regions. Pairwise functional connectivity analyses revealed differential functional coupling of the ACC with IFG *pars triangularis*. We found that advanced L2 learners exhibited significantly stronger coupling than did the intermediate L2 learners, indicating that coordination between the left ACC and IFG was significantly higher in language production across languages. Additionally, and contrary to the direction of activation, functional coupling between the IFG *pars triangularis* and *pars opercularis* was higher in L2 than in L1 in both groups throughout the verbal fluency task.

In conclusion, we found that across languages, advanced learners showed significantly greater activation in the later stages of verbal fluency and that functional connectivity between language and language control regions increased with L2 proficiency and exposure, indicating that language learners well into adulthood display functional plasticity of language networks that is not specific to the second language. Results further indicated that language proficiency and executive control play dissociable roles in semantic verbal fluency. ■

CHAPTER 7

HEMISPHERIC SPECIALISATION AND PLASTICITY

In this chapter, we compared and contrasted language comprehension and production, with a focus on hemispheric lateralisation. Here we present Experiment III, which consists of two parts: (A) data from the previously presented cross-sectional study, and (B) a second longitudinal study in which participants performed the same comprehension and production tasks. We performed comprehensive analyses of language lateralisation and its experience-dependent plasticity in order to examine how language background and language learning affect language lateralisation in reading, speech comprehension, and verbal production. The following work has been published in The Journal of Neuroscience (Gurunandan et al., 2020).

7.1 INTRODUCTION

Functional specialisation in the brain is a well-established principle of neural organisation, but studies of atypical development suggest dramatic potential for neural plasticity (Payne and Lomber 2001; Bavelier and Neville 2002). While the capacity for neural reorganisation decreases with age, it does not disappear completely, and adult neural plasticity is essential for learning and maintaining new information or behaviours (Kleim and Jones 2008). The human propensity for language requires a delicate balance between neural specialisation and capacity for re-organisation, making language learning the ideal candidate for examination of specialisation and plasticity in the human brain.

Language typically activates a fronto-temporo-parietal network (Skeide and Friederici, 2016; Hagoort, 2019), and has long been thought to be predominantly left-lateralised (Broca, 1863; Dax, 1863). However, the right hemisphere appears to be capable of taking over or supporting language function if needed, as seen in cases of language recovery after left-hemisphere damage (Papanicolaou et al., 1987; Boatman et al., 1999; Duffau et al., 2002, 2003; Hope et al., 2017) and in language learning (Vingerhoets et al., 2003; Park et al., 2012). It is thus unclear whether the left hemisphere is indeed specialised for language as is broadly accepted, with the right hemisphere playing at best a supporting role (Vigneau et al., 2010), or whether hemispheric dominance is more variable across individuals, as suggested by the larger than expected prevalence of language deficits following right hemisphere brain surgery (Vilasboas et al., 2017).

Language is a complex construct involving multi-level representations that can be processed visually (reading), auditorily (listening) or by motor production (speaking/writing), and cumulative evidence points to these functions lateralising differently. Auditory language has been found to be bilateral in infants (Dehaene-Lambertz et al., 2002; Perani et al., 2011), with either no increase in lateralisation from childhood to adulthood (Lidzba et al., 2011), increasing left-lateralisation (Ahmad et al., 2003), or increasing right-hemisphere involvement (Booth et al., 2000), and a meta-analysis of auditory comprehension studies suggested that any left-lateralisation from childhood to adulthood increases more slightly and gradually than previously thought (Enge et al., 2020). On the other hand, there is little evidence to suggest that language production is anything but left-lateralised (Gaillard et al., 2003; Szaflarski et al., 2006; Lidzba et al., 2011).

Language learning is known to change the pattern of neural activation for language. Studies comparing bilinguals and monolinguals consistently find differences in activation between them, with bilinguals typically exhibiting greater right hemispheric involvement in comprehension tasks (e.g. Kovelman et al., 2008; Horowitz-Kraus et al., 2015). However, it is uncertain whether this increased right hemispheric involvement merely modulates the magnitude of left-lateralisation, or whether it is significant enough to constitute a change in hemispheric dominance. Further, are differences in lateralisation between monolinguals and bilinguals due to developmental differences or is hemispheric dominance in fact plastic even into adulthood? Few neuroimaging studies have looked into ecologically-valid adult language learning, but findings indicate that language learning in adults involves structural changes in cortical thickness and connectivity that could indeed support shifts in lateralisation (Mårtensson et al., 2012; Schlegel et al., 2012; Xiang et al., 2015), suggesting that lateralisation, at least for comprehension, may be susceptible to learning-dependent changes.

The variegated nature of the available neuropsychological, neuroimaging, and psycholinguistic evidence has made it difficult to extract the underlying principles of language organisation, and language is still largely considered a unitary left-lateralised function, with serious consequences for clinical populations (Vilasboas et al., 2017). The mixed findings across studies using different language tasks strongly suggest that there are critical differences in organisation and plasticity between different language systems such as reading, speech comprehension, and verbal production, and that testing these concurrently is of vital research importance. To this end, we conducted two fMRI experiments, one cross-sectional and one longitudinal, with immersed late language learners, and examined lateralisation of reading, speech comprehension, and verbal production in their native (L1) and non-native (Ln) languages, and how this changed with increasing Ln proficiency. To test both replicability and generalisability of findings, the two experiments were contrasted on several factors such as early language experience of the participants (monolingual vs bilingual) and the language currently being learnt, and the L1-Ln pairs in the two experiments had contrasting degrees of overlap in language families, phonology, and orthography. We hypothesised that (i) lateralisation of comprehension would be more variable across individuals but production would be left-lateralised, and (ii) with increasing language proficiency, comprehension may display changes in hemispheric dominance, while production would remain left-lateralised. We further expected that L1-Ln associations would change with increasing Ln proficiency, and that the pattern of changes would differ across the language systems.

7.2 METHODS

7.2.1 PARTICIPANTS

EXPERIMENT A: INTERMEDIATE VS ADVANCED LANGUAGE LEARNERS (CROSS-SECTIONAL)

The final experiment sample consisted of 29 right-handed native Spanish adults (mean age = 43.7 ± 9.7 years; 15 female) studying Basque in the same language school at either the intermediate (A2 level, n = 14) or advanced level (C1 level, n = 15). The proficiency levels correspond to those specified by the Common European Framework of Reference for Languages (CEFR). Participants were from the Basque Country, Spain; they grew up primarily exposed to Spanish at home and in school, with little early Basque exposure, and had limited knowledge of English or other languages (no difference between groups, p=0.83). The two groups of learners were matched on age, gender, IQ and Spanish proficiency (Table 7.1). Data from 5 other participants was discarded due to excessive head motion during MRI scanning and these were not counted in the final sample.

EXPERIMENT B: INTERMEDIATE LANGUAGE LEARNERS (LONGITUDINAL)

The final experimental group consisted of 19 right-handed native Spanish adolescents (mean age = 17.2 ± 0.6 years; 16 female) taking part in a 3-month English immersion-style after-school programme for B1 level students. Participants were from the Basque Country, Spain; they were native speakers of Spanish and acquired Basque in school (AoA = 2.6 ± 2.06 years). The medium of instruction in school was Spanish/ Basque; English was learnt as a foreign language, with little exposure outside of classes. The students had intermediate English proficiency (Table 7.1). Data from 5 other participants was discarded due to excessive head motion during MRI scanning and these were not counted in the final sample.

BOTH EXPERIMENTS

In both experiments, language proficiency was assessed using picture-naming tasks — an adaptation of the Boston Naming Test (Kaplan et al., 1983) controlled for cognates across Spanish, Basque and English. Participant groups in Experiment A differed significantly in their Basque proficiency, and participants in Experiment B exhibited significant increase in English proficiency after language training (Table 7.1). All participants had normal or corrected-to-normal vision, and no history of neurological or psychiatric disorders. In compliance with the ethical regulations established by the BCBL Ethics Committee and the guidelines of the Helsinki Declaration, all participants gave written informed consent prior to taking part in the experiment, and received monetary compensation for their participation.

Table 7.1: Participant demographics and linguistic scores

	Experiment A			Experiment B		
	Intermediate group	**Advanced group**	***p*-value**	**Before Training**	**After Training**	***p*-value**
Age	42.86 (10.10)	44.53 (10.51)	0.66	17.2 (0.6)		
Gender	7 female, 7 male	8 female, 7 male	0.86	16 female, 3 male		
L1 proficiency	99.35 (1.88)	99.64 (0.77)	0.61	99.11 (1.49)	99.26 (1.15)	0.56
L2 proficiency	52.6 (14.66)	87.96 (10.58)	0.00	58.00 (11.73)	62.89 (12.82)	0.01

Note: Values correspond to the mean with standard deviation in parentheses.

7.2.2 TASK DESIGN

Inside the MRI scanner, participants performed two tasks: a comprehension and a production task. The order of tasks was counter-balanced across participants.

LANGUAGE COMPREHENSION TASK

The participants performed semantic animacy judgement (living/non-living) with single-word text and speech stimuli in each of their languages. Participants were instructed to fixate on a white cross in the middle of a black screen, and on presentation of stimuli, to indicate their responses as quickly and as accurately as possible via button presses (counter-balanced across participants) using their dominant (right) hand. Stimuli were high frequency, concrete, imageable nouns (e.g. house, dog, table) with an even split between living and non-living items. Visual stimuli were presented in white letters on a black screen and were 5-8 letters long. Auditory stimuli were presented through headphones and lasted an average of 565 ms (s.d. = 86 ms).

Each run had 48 stimuli with inter-mixed reading and listening trials. The fMRI design was event-related with six/four runs (Experiment A: 2 languages x 3 runs; Experiment B: 2 languages x 2 runs). To avoid language-switching, the languages were separated and their order was counterbalanced across participants.

LANGUAGE PRODUCTION TASK

The participants performed a paced form of the semantic verbal fluency task in each language. Participants were instructed to fixate on a white cross in the middle of a black screen and respond overtly to semantic category words (e.g. fruits, animals, clothes) presented on the screen. Each word was displayed eight times, each requiring a novel response, or failing this, an overt response saying “pass” in the relevant language. Fluency was scored as the percentage of valid answers out of eight possible responses for each category. Repetitions, inflections of the same word and erroneous responses were removed, and responses were scored only for correctness and not accent or pronunciation. In the control condition, participants repeated the word presented on the screen. The task had a block design with two runs per language, each run containing eight semantic categories. To avoid language-switching, the languages were separated and their order was counterbalanced across participants.

7.2.3 MRI DATA COLLECTION

Whole-brain MRI data was acquired using a 3-T Siemens Magnetom Trio whole-body MRI scanner and a 32-channel head coil at the Basque Center on Cognition, Brain and Language (BCBL). Padded headphones were used to dampen background scanner noise and enable clear transmission of the auditory stimuli. Participants viewed the print stimuli on a screen via a mirror mounted on the head coil. To limit head movement, the head coil was padded with foam and participants were asked to remain as still as possible. Structural T1-weighted images were acquired with a MPRAGE sequence with TR = 2530 ms, TE = 2.97 ms, inversion time = 1100 ms, FA = 7°, FoV = 256 x 256 mm, 176 slices and voxel size = 1 mm^3.

LANGUAGE COMPREHENSION TASK

Functional MRI was acquired in the course of six/four separate runs using a gradient-echo echo-planar pulse sequence with the following parameters: TR 2000 ms, TE 30 ms, 32 axial slices with a 3.4 x 3.4 x 4 mm voxel resolution, 0% inter-slice gap, flip angle (FA) = 80°, field of view (FoV) = 220 mm, 64 x 64 matrix. 186 volumes were collected for each of the functional runs. Prior to each scan, four volumes were discarded to allow for T1-equilibration effects. To improve estimation of the resting baseline in functional analyses, functional runs contained three silent fixation periods of 20 s each. Within each functional run, the order of the trials (reading and listening conditions) and the inter-trial intervals of variable duration corresponding to the baseline MR frames (30% of total collected functional volumes) were determined by an algorithm designed to maximise the efficiency of the recovery of the blood oxygen level dependent response (optseq2; Dale, 1999).

LANGUAGE PRODUCTION TASK

Functional MRI was acquired in the course of four separate runs using a gradient-echo echo-planar pulse sequence with the following parameters: TR 3000 ms, TE 25 ms, 43 axial slices with a 3.0 x 3.0 x 3.0 mm voxel resolution, 10% inter-slice gap, flip angle (FA) = 90°, field of view (FoV) = 192 mm, 64 x 64 matrix. 240 volumes were collected for each of the functional runs. Prior to each scan, four volumes were discarded to allow for T1-equilibration effects.

7.2.4 MRI DATA ANALYSES

PREPROCESSING

Standard SPM8 (Penny et al., 2011) preprocessing routines and analysis methods were employed. Images were first corrected for differences in timing of slice acquisition and then realigned to the first volume using rigid-body registration. Each subject's functional volumes were spatially smoothed with a 4-mm full-width half-maximum (FWHM) Gaussian kernel. Next, motion parameters obtained from realignment were used to inform a volume repair procedure (ArtRepair; Mazaika et al., 2009) that identified bad volumes on the basis of scan-to-scan movement (>1 mm) and signal fluctuations in global intensity (>1.3%), and corrected bad volumes via interpolation between the nearest non-repaired scans. Data from subjects requiring more than 20% of volumes to be repaired were discarded. The number of corrected volumes was similar between groups (Experiment A: comprehension task p=0.34, production task p=0.63) and scans (Experiment B: comprehension task p=0.75, production task p=0.46). After volume repair, functional volumes were co-registered to the T1 images using 12-parameter affine transformation and spatially normalised to the MNI space by applying non-linear transforms estimated by deforming the MNI template to each individual's structural volume. During normalisation, the volumes were sampled to 3-mm cubic voxels. The resulting volumes were then spatially smoothed with a 7-mm FWHM Gaussian kernel. Finally, time series were temporally filtered to eliminate contamination from slow frequency drift (high-pass filter with cut-off period of 128 s).

SUBJECT-LEVEL ANALYSES

Statistical analyses were performed on individual subject data using the general linear model (GLM). fMRI time series data were modelled by a series of impulses convolved with a canonical haemodynamic response function. Six motion parameters for translation (x, y, z) and rotation (yaw, pitch, roll) were included as covariates of non-interest in the GLM. In the event-related-design comprehension task, each trial was modelled as an event, time-locked to the onset of the presentation of each stimulus, and error responses were modelled separately. In the block-design production task, each trial was modelled as an epoch of 31 s each, time-locked to the beginning of the presentation of each block. The remaining functions were used as covariates in the 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 experimental condition were used in pairwise contrasts.

LATERALITY ANALYSES

For every subject, lateralisation of activation in the classical language network regions was calculated for each task x language. Laterality is typically quantified as a normalised ratio of left and right hemisphere contributions, ranging between +1 (fully left-lateralised activation) and -1 (fully right-lateralised activation). Each subject's whole-brain t-maps were masked with anatomical language regions from the AAL atlas (Tzourio-Mazoyer et al., 2002) — six bilateral regions from standard language models (Friederici 2012; Hagoort 2013): inferior frontal gyrus (IFG) *pars orbitalis*, IFG *pars triangularis*, IFG *pars opercularis*, superior temporal gyrus (STG), middle temporal gyrus (MTG), and inferior parietal lobule (IPL). Since laterality indices are highly threshold-dependent, in line with the latest recommendations (Bradshaw et al., 2017), a threshold-independent bootstrapping method was used to calculate the laterality index using the LI-toolbox (Wilke and Lidzba, 2007), in which 10,000 indices were iteratively calculated at different thresholds, yielding a robust mean laterality index. Three analyses were carried out to examine proficiency-dependent plasticity of (i) L1-Ln correlation, (ii) hemispheric dominance, and (iii) modality clustering. L1-Ln correlations were calculated for each group x task, and Cohen's q was used to quantify the difference in L1-Ln correlation between intermediate/advanced proficiency and before/after training in each modality. To examine hemispheric dominance, a lateralised dissociation index was calculated such that:

$$Lateralised\, Dissociation\, Index \; = \left| \, LI_{L1} \; - \; LI_{Ln} \right| \; * \, hem$$

$$hem = \begin{cases} 1 \text{ if opposite lateralisation} \\ -1 \text{ if same lateralisation} \end{cases}$$

i.e. the absolute difference between laterality indices for each language and a factor to code whether the two languages were lateralised to the same or opposite hemispheres. Positive values indicated that languages were lateralised to opposite hemispheres, while negative values indicated that the languages were lateralised to the same hemisphere. Cohen's d was used to measure the magnitude of proficiency-dependent change in each modality: difference between medians in cross-sectional Experiment A, and difference in repeated measures in longitudinal Experiment B. To examine the modality-wise clustering of the joint L1-Ln distribution, 85% data ellipses were plotted for each modality and joint distribution difference (JDD) between any two modalities was calculated as:

$$Joint\, Distribution\, Difference = \frac{distance\; between\; centroids}{maximum\; distance} * \frac{angle\; between\; major\; axes}{maximum\; angle}$$

i.e. standardised difference between the bivariate L1-Ln group means and difference between joint spread of the data. This index lies between 0 and 1, with values closer to 1 indicating greater difference between modalities. The maximum Euclidean distance between centroids was considered to be 1 for laterality data, and maximum angle between the axes is 90°. Proficiency-group differences were measured in terms of percentage difference in the difference index.

7.3 RESULTS

7.3.1 IN-SCANNER BEHAVIOURAL PERFORMANCE

EXPERIMENT A: INTERMEDIATE VS ADVANCED LANGUAGE LEARNERS (CROSS-SECTIONAL)

A series of mixed-model analyses of variance (ANOVAs) were conducted on the behavioural measures of the fMRI tasks: comprehension task accuracy, production task fluency, and comprehension task reaction times (Figure 7.1A). The comprehension task accuracy ANOVA with between-subjects factor Proficiency (intermediate, advanced) and within-subject factors Language (L1, Ln) and Modality (reading, speech) showed a significant Proficiency x Language interaction ($F(1,26)=16.18$, $p=0.0004$). The production task fluency ANOVA with between-subjects factor Proficiency (intermediate, advanced) and within-subject factor Language (L1, Ln) also showed a significant Proficiency x Language interaction ($F(1,23)=31.36$, $p=0.00001$). Post-hoc simple-effect analyses (two-sample t-tests) of these Proficiency x Language interactions showed that the advanced proficiency group had significantly higher Ln task accuracy than the intermediate proficiency group in both comprehension ($t(18.08)=3.20$, $p=0.002$, one-sided) and production ($t(22.28)=5.502$, $p=0.000008$, one-sided), but there was no significant difference between groups in L1 task accuracy (comprehension: $t(25.48)=-0.93$, $p=0.360$, two-sided, production: $t(21.683)=1.03$, $p=0.31$, two-sided). Finally, the ANOVA for comprehension task reaction times showed a main effect of Language, with both groups significantly slower in their Ln than their L1 ($F(1,26)=40.41$, $p=0.000001$).

EXPERIMENT B: INTERMEDIATE LANGUAGE LEARNERS (LONGITUDINAL)

A series of repeated-measures ANOVAs were conducted on the behavioural measures of the fMRI tasks: comprehension task accuracy, production task fluency, and comprehension task reaction times (Figure 7.1B). The comprehension task ANOVAs with 3 within-subject factors Training (before, after), Language (L1, Ln), and Modality (reading, speech), showed main effects of Language (L1 > Ln, F(1,17)=338.64, p=0.000000000001) and Modality (reading > speech, F(1,17)=30.05, p=0.00004) on task accuracy. The production task fluency ANOVA with 2 within-subject factors Training (before, after), and Language (L1, Ln) showed a main effect of Language (L1

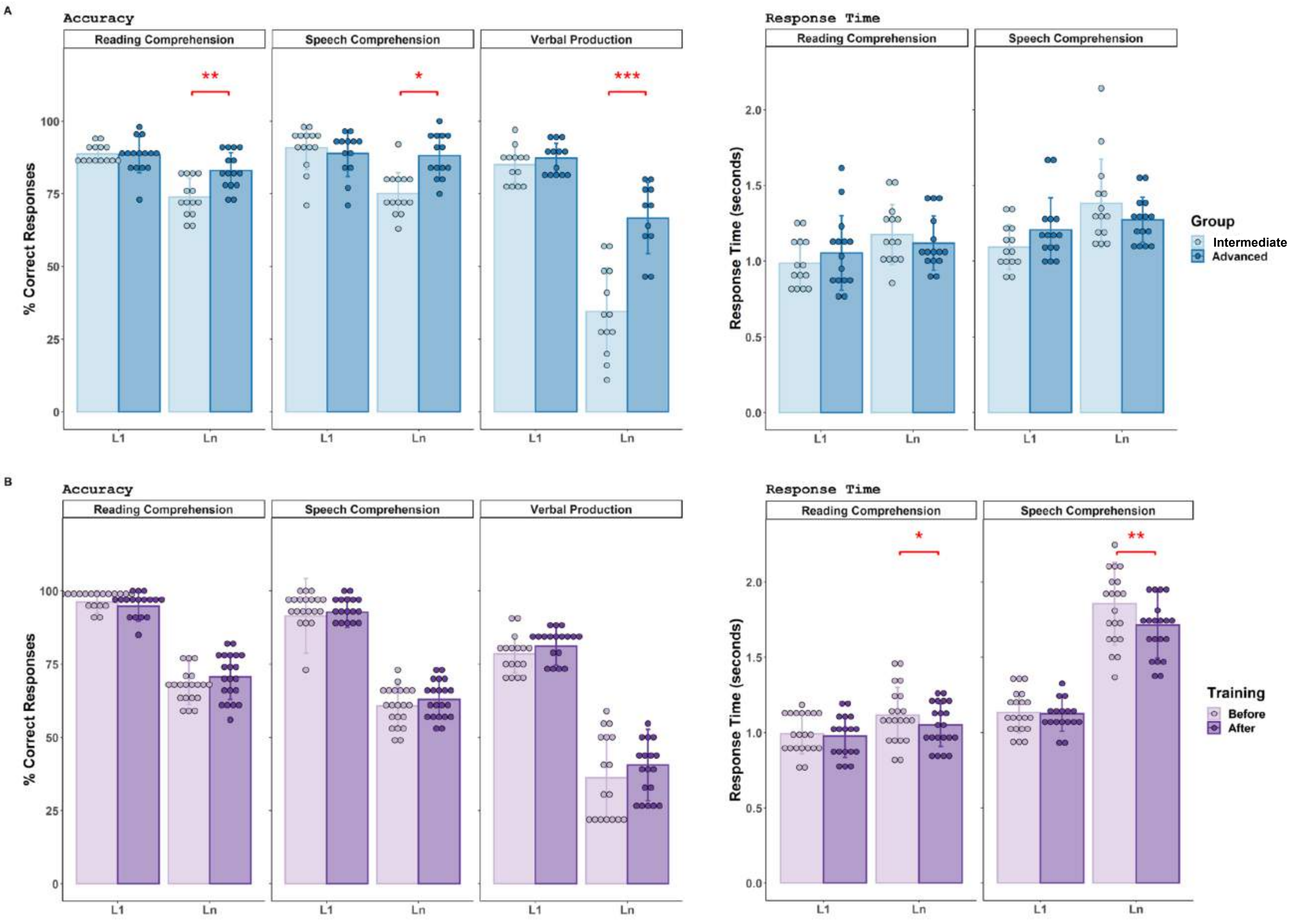


Figure 7.1 Behavioural measures Accuracy and Response Time for in-scanner semantic tasks plotted as a function of Group, Language, and Modality in Experiment A (A), and as a function of Training, Language, and Modality in Experiment B (B). Error bars represent standard deviation and asterisks statistically significant differences (*** p < 0.001, ** p<0.01, * p<0.05).

> Ln, F(1,15)=146.01, p=0.000000004). The comprehension task reaction times ANOVA revealed a significant Training x Language interaction (F(1,17)=5.48, p=0.031). Post-hoc simple-effect analyses (paired t-tests) showed that reaction times decreased significantly after training in Ln (t(17)=2.83, p=0.006, one-sided), but not in L1 (t(17)=0.21, p=0.836, two-sided).

7.3.2 LATERALISATION IN COMPREHENSION AND PRODUCTION

Laterality indices were calculated for the language network regions in each task and language using a threshold-free method, with values between +1 (left lateralisation) and -1 (right lateralisation). In both experiments, Wilcoxon signed-rank tests of paired samples (two-sided) revealed significant differences between each of the modalities. Comprehension and production displayed robust differences in lateralisation, with significant differences between both reading and verbal production (Experiment A: W = 421, *p* = 0.000000000006, Experiment B: W = 1099, *p* = 0.0000000004) as well as between speech comprehension and verbal production (Experiment A: W = 824, p = 0.000002, Experiment B: W = 729.5, p = 0.000000000000006). Reading and speech comprehension also differed significantly (Experiment A: W = 1998.5, p = 0.021, Experiment B: W = 3840, p = 0.012). In reading and speech comprehension, lateralisation was highly variable and indices spanned the full range of possible values between the two languages, while verbal production was clearly left-lateralised. At the group level, comprehension appeared bilateral and production was left-lateralised. This result was consistent across the cross-sectional and longitudinal experiments (Figure 7.2).

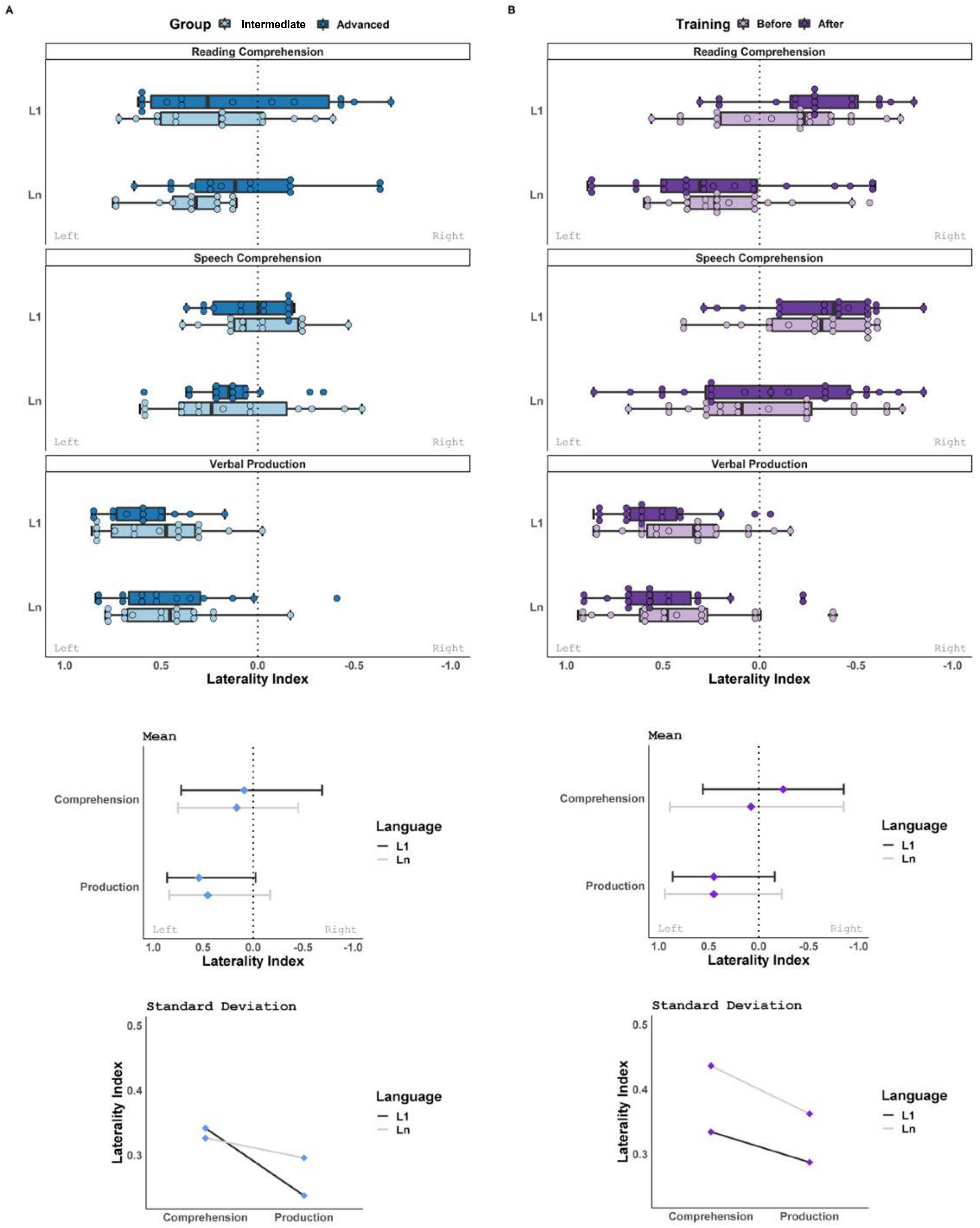
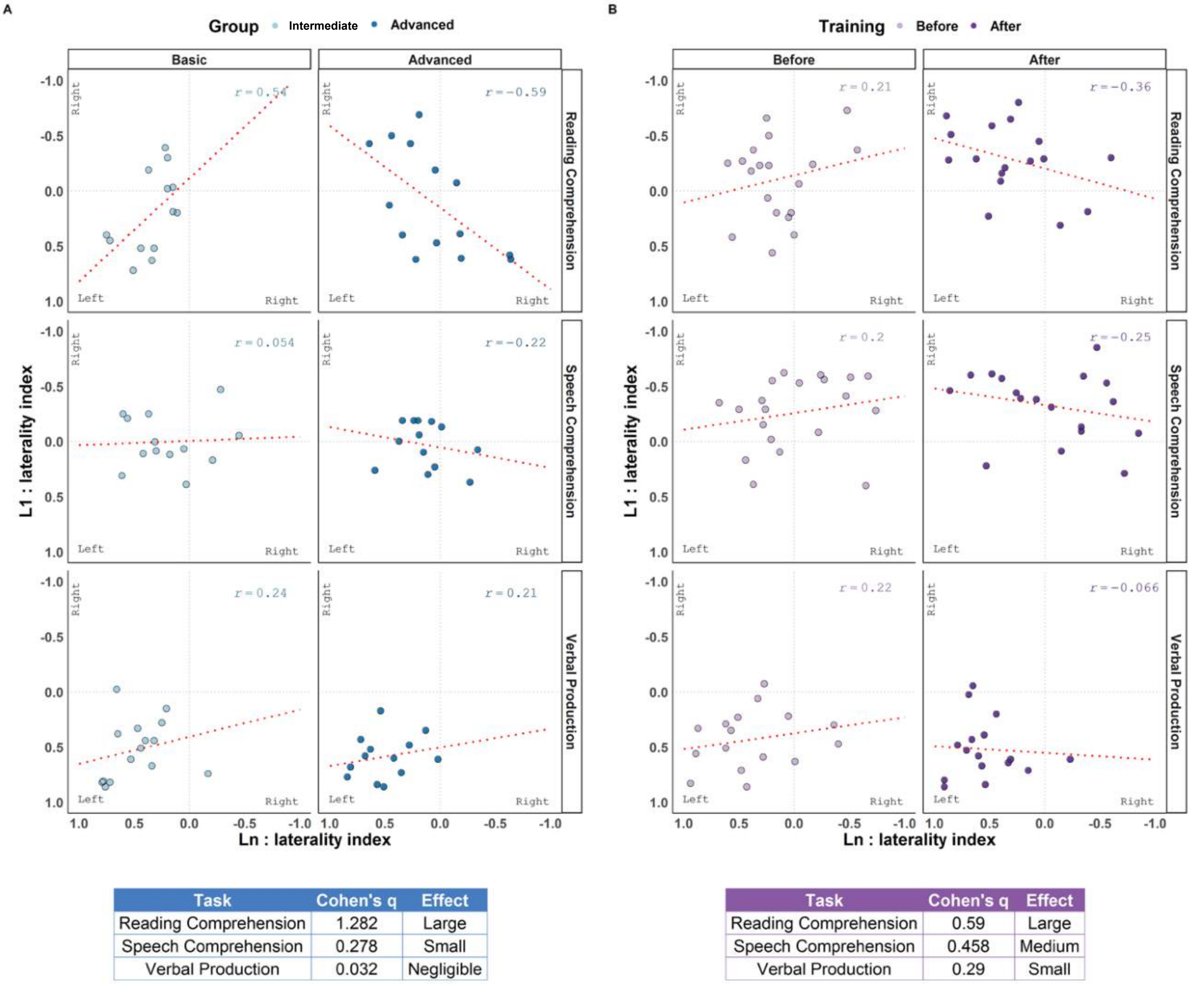


Figure 7.2 Laterality indices plotted as a function of Group, Language, and Modality in Experiment A (A), and Training, Language, and Modality in Experiment B (B). Laterality indices were obtained from individual whole brain activation in the neuroanatomical language network, and the respective line graphs display mean and standard deviation of laterality indices across participants in each Modality and Language.

7.3.3 LEARNING-DEPENDENT CHANGES IN LATERALISATION

To examine patterns of learning-dependent changes in lateralisation while accounting for the high inter-individual variability across tasks and languages, L1 lateralisation was used as a baseline for each subject's Ln lateralisation, and the linear association between L1 and Ln was assessed using Pearson's *r*. In lower proficiency learners, L1 and Ln lateralised similarly, regardless of left/right lateralisation. However, with increasing proficiency, this pattern reversed for comprehension, and L1 and Ln lateralised to opposite hemispheres. This learning-dependent change was not observed in verbal production (Figure 7.3). Cohen's *q* was used to quantify the proficiency-dependent change in L1-Ln correlation for each task, confirming that, across both studies, learning-dependent change in lateralisation was large in reading comprehension, medium in speech comprehension, and small in verbal production.

To examine whether increasing proficiency involved changes in hemispheric dominance for each modality, lateralised dissociation indices (LDI) were calculated for each subject such that absolute values indicated the magnitude of L1-Ln difference, and direction (i.e. positive or negative) indicated whether the languages were lateralised to same or opposite hemispheres (positive = opposite hemispheres, negative = same hemisphere). There was a significant proficiency-related increase in absolute dissociation between L1 and Ln lateralisation across modalities (Experiment A: Mann-Whitney U tests: across modalities: W = 584.5, $p = 0.013$; reading comprehension: W = 41, $p = 0.007$; speech comprehension: W = 88, $p = 0.579$; verbal production: W = 53.5, $p = 0.022$; Experiment B: Wilcoxon signed-rank tests: across modalities: V = 374.5, $p = 0.023$; reading comprehension: V = 15, $p = 0.004$; speech comprehension: V = 53, $p = 0.142$; verbal production: V = 78, $p = 0.330$), while Cohen's *d* quantified learning-dependent change in hemispheric dominance (i.e. LDI) for each modality,



Task	Cohen's q	Effect
Reading Comprehension	1.282	Large
Speech Comprehension	0.278	Small
Verbal Production	0.032	Negligible

Task	Cohen's q	Effect
Reading Comprehension	0.59	Large
Speech Comprehension	0.458	Medium
Verbal Production	0.29	Small

Figure 7.3 Linear associations between L1 and Ln lateralisation indices (Pearson´s r) as a function of Group and Modality in Experiment A (A) and of Training and Modality in Experiment B (B). Cohen's q quantified the learning-dependent changes in L1-Ln correlation in each Modality.

revealing the same pattern of changes in hemispheric dominance in both experiments: large effect of proficiency on reading comprehension, medium effect on speech comprehension, and small effect on verbal production (Figure 7.4).

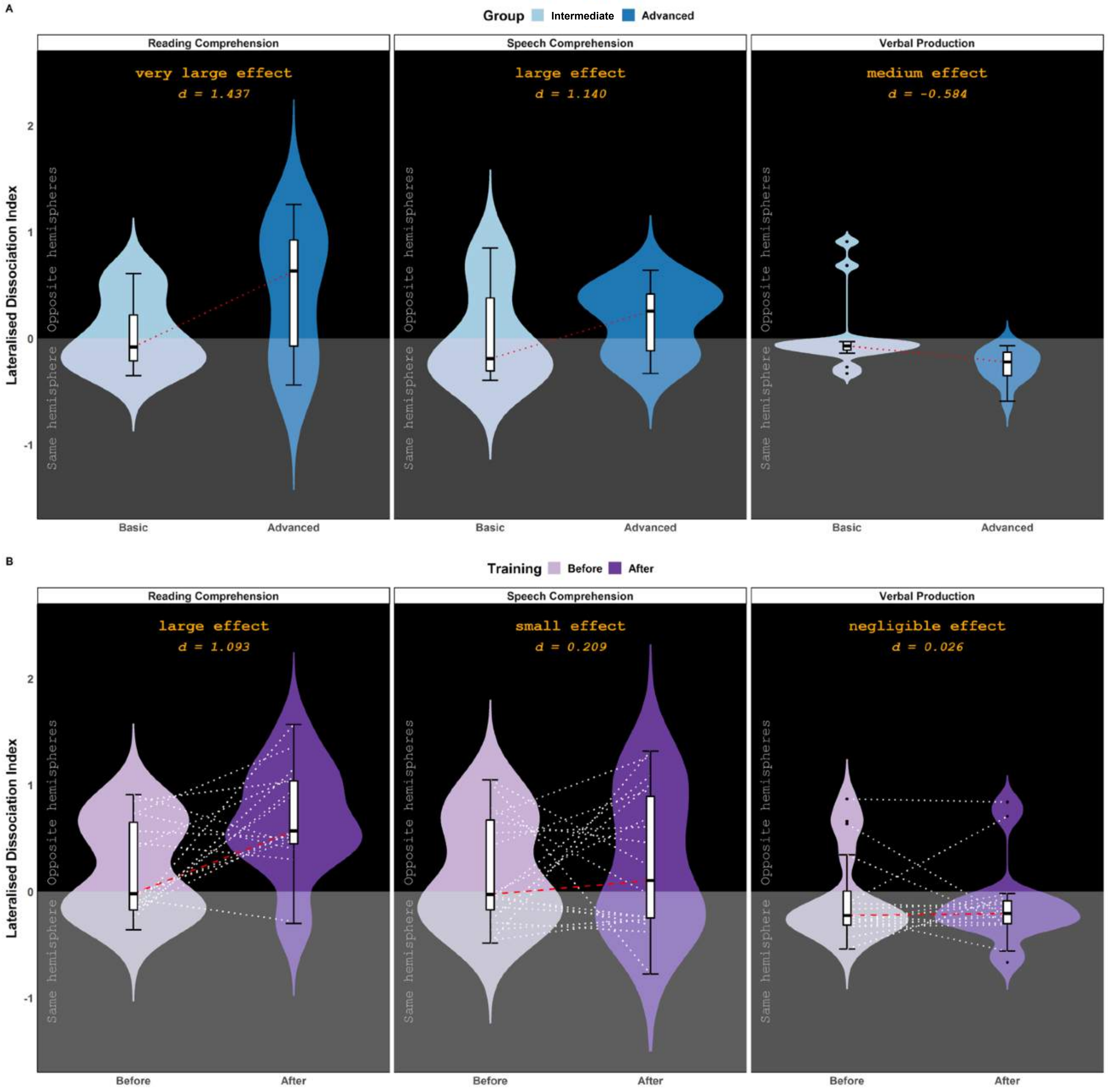


Figure 7.4 Lateralised dissociation indices (LDI) as a function of Group and Modality in Experiment A (A), and Training and Modality in Experiment B (B). Positive values indicate that L1 and Ln lateralised to opposite hemispheres, and negative values indicate that L1 and Ln lateralised to the same hemisphere. Cohen's d quantified the learning-dependent changes in LDI in each Modality.

Finally, modality-wise clustering of joint L1-Ln lateralisation was plotted using 85% data ellipses to examine overlap between modalities. Permutation one-way MANOVAs and a joint distribution difference (JDD) index were used to test and quantify the separation between: (i) comprehension (both reading and speech) and production (Figure 7.5-I), and (ii) reading and speech comprehension (Figure 7.5-II), and the effects of proficiency were tested using non-parametric two-sample/paired tests of difference/change in cluster separation between modalities (Euclidean distance) and quantified with percent change in the JDD. The one-way MANOVA modelled the joint L1-Ln distribution differences between modalities, and the index quantified this difference by taking into account the difference in both bivariate mean and spread of data, with values between 0 (overlapping distributions) and 1 (no similarities). MANOVAs revealed significant differences between comprehension and production (Experiment A: intermediate proficiency group: F (1.8, 65.2) = 11.73, p = 0.0005; advanced proficiency group: F (1.9, 63.8) = 22.96, p = 0.00000002; Experiment B: before training: F (1.7, 73.2) = 21.67, p = 0.0000002, after training: F (1.7, 70.7) = 38.94, p = 0.0000000000004) and with increasing proficiency, comprehension and production dissociated further (Experiment A: advanced proficiency group displayed 1042.35% greater comprehension-production dissociation than the intermediate proficiency group, Mann-Whitney U test of group difference in cluster separation: W = 67398, *p* = 0.000000000003; Experiment B: participants displayed 47.38% increase in comprehension-production dissociation after training, Wilcoxon signed-rank test of post-training change in cluster separation: V = 101769, *p* = 0.0000000000000002). There were no significant differences in L1-Ln joint distribution between reading and speech comprehension (Experiment A: Intermediate proficiency group: F (1.9, 45.5) = 1.84, p = 0.18; Advanced proficiency group: F (1.7, 41.4) = 0.32, p = 0.71; Experiment B: Before Training: F (1.9, 71.2) = 1.98, p = 0.15, After Training: F (1.8, 60.5) = 2.09, p = 0.13), and reading and speech comprehension converged further with increasing proficiency (Experiment A: the advanced group displayed 87.27% greater comprehension-production overlap than the intermediate group, Mann-Whitney U test of group difference in cluster separation: W = 18073, p = 0.177; Experiment B: participants displayed 27.13% increase in comprehension-production overlap after training, Wilcoxon signed-rank test of post-training change in cluster separation: V = 39306, p = 0.0005).

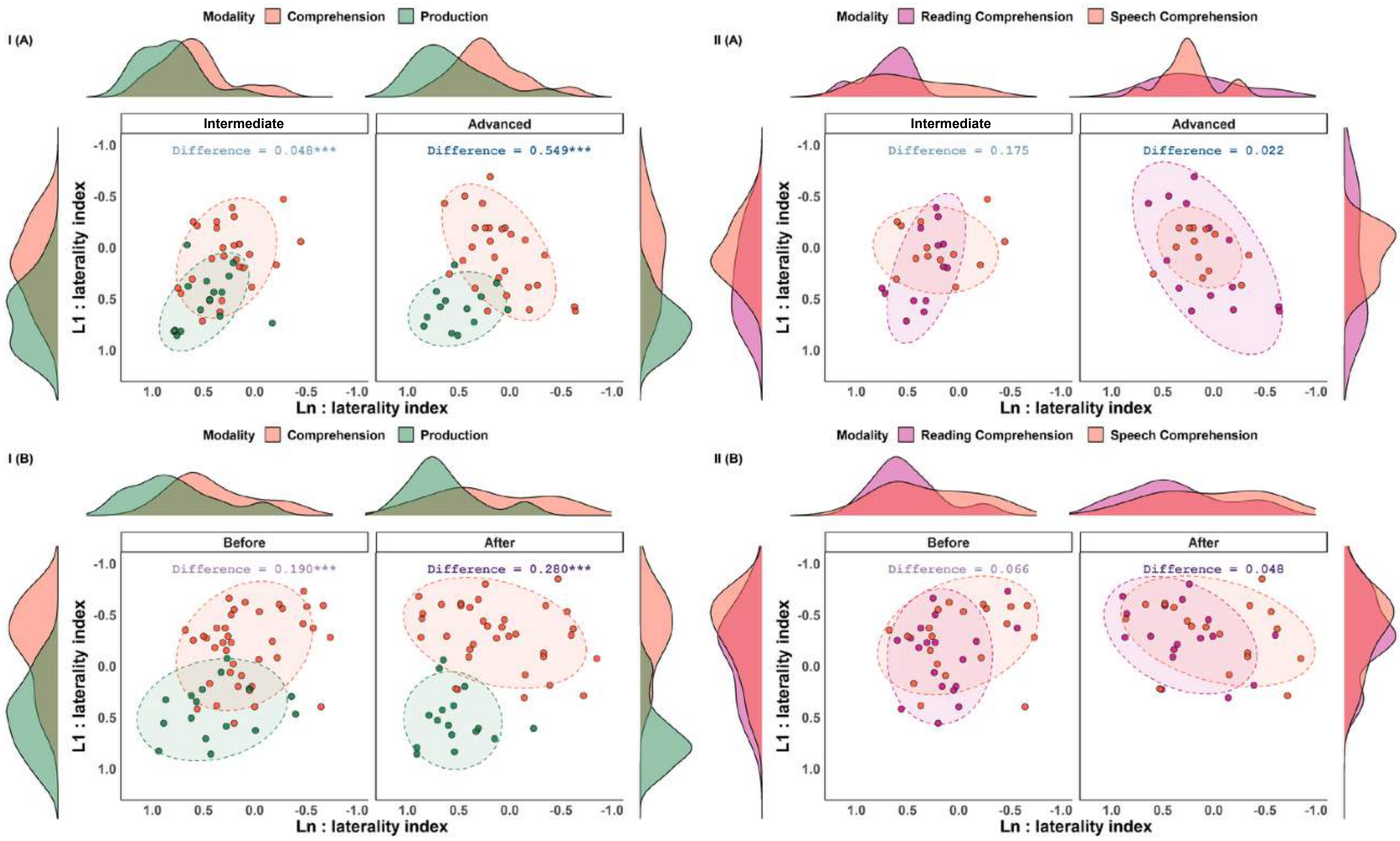


Figure 7.5. Modality-wise clustering (I: comprehension versus production, II: reading versus speech comprehension) in joint distributions of L1-Ln lateralisation indices plotted as a function of Group in Experiment A (A) and as a function of Training in Experiment B (B). A Joint Distribution Difference index with values between 0 and 1 quantified overlap in each group, with higher values indicating larger separation between modalities. Asterisks represent statistically significant differences (p < 0.001).

7.4 DISCUSSION

In the present work, we examined hemispheric specialisation and learning-dependent plasticity of the language network concurrently in three language systems:

reading, speech comprehension and verbal production. We conducted cross-sectional and longitudinal fMRI experiments in separate populations of immersed language learners. Both experiment samples had the same L1 (Spanish), but were contrasted in other factors: (i) early language experience: monolingual vs sequential bilingual, (ii) language being learnt: Basque vs English, (iii) phonological similarity with native language: high overlap vs low overlap, (iv) orthographic depth: transparent vs opaque. Across these contrasting experimental designs and participant groups, we found a highly consistent pattern of results in both experiments: (i) across native and non-native languages, lateralisation for language comprehension was variable but language production was strongly left-lateralised, and (ii) with increasing non-native language proficiency, reading and speech comprehension displayed significant changes in hemispheric dominance (reading > speech), while verbal production remained left-lateralised. The converging results from separate experiments provide unique insight into the long-standing debate on hemispheric specialisation of language and the effects of language experience (Gainotti, 1993; Price, 1998, 2012; Jung-Beeman, 2005; Hickok and Poeppel, 2007; Friederici, 2012; Hervé et al., 2013; Tzourio-Mazoyer et al., 2016).

The first result showing variably-lateralised (bilateral at the group-level) comprehension and left-lateralised verbal production across different languages suggested that comprehension is flexible while verbal production is hard-wired to be left-lateralised. In the second part, our analytic approach to examining learning-dependent changes in language lateralisation built on the observed inter-individual variability and used within-subject measures calculated with each subject's L1 as a baseline for their Ln. We used three measures — L1-Ln correlation, L1-Ln distance, and modality clustering — and quantified the change within each language system. These revealed that (i) L1 and Ln were similarly lateralised in lower-proficiency language learners and tended to dissociate with increasing Ln proficiency, (ii) the change was largest in reading, smaller in speech comprehension, and smallest in verbal production, and (iii) with increasing proficiency, comprehension and production dissociated, while reading and speech comprehension converged.

In conclusion, our study design with cross-sectional and longitudinal experiments in contrasting samples of real-world language learners, testing of different language systems, and a multi-pronged analytical approach revealed robust and converging patterns of modality-dependent lateralisation and plasticity of the language network. Our findings suggest that language lateralisation for reading and speech comprehension is plastic well into adulthood, while production shows strong left-hemisphere specialisation. Plasticity for reading was greater than for speech comprehension which was in turn greater than for verbal production. Taken together with previous evidence in the literature, we propose that hemispheric specialisation for language may arise from the sensorimotor cortices, and that the differential plasticity of language systems is tied to the plasticity of the associated sensorimotor systems. ■

DISCUSSION

CHAPTER 8

NEURAL PLASTICITY OF LANGUAGE SYSTEMS

Chapter 8 discusses the findings of this doctoral thesis, its limitations, and future work.

The current doctoral thesis asked two main questions: (1) Do large-scale neural changes accompany language learning in adulthood? and (2) Are these neural changes similar across different language systems such as reading, speech comprehension, and verbal production? We investigated these questions in three fMRI experiments with adult language learners. In Experiments I and II, we examined comprehension and production in 30-to-60-year-old intermediate and advanced language learners and comprehensively characterised functional learning-related changes in each modality. In Experiment III, we compared and contrasted hemispheric lateralisation of reading, speech comprehension, and verbal production, and extended the same analyses to a second longitudinal study with a contrasting participant sample. We found evidence for significant functional plasticity well into adulthood, and showed that different language systems exhibited different patterns of hemispheric specialisation and plasticity. The results have theoretical and practical implications for our understanding of fundamental principles of neural organisation of language, language learning in healthy populations, and language testing and recovery in patients.

8.1 PLASTICITY OF ADULT LANGUAGE SYSTEMS

In Experiments I and II, we found that significant functional changes were associated with language learning well into adulthood. Previous MRI studies of ecologically-valid language learning have been conducted in young adults in the early stages of learning a completely new foreign language, and to the best of our knowledge, this was the first study of intermediate and advanced language learners spanning a broad range of ages.

LANGUAGE COMPREHENSION

In Experiment I on functional plasticity of comprehension, we found that: (i) print-speech convergence was not significantly affected by second language proficiency, (ii) similarity between native and new languages declined with higher second language proficiency, and (iii) functional coupling between language and language control regions increased with second language proficiency and exposure.

In both L1 and L2, we found significant convergence of reading and speech comprehension in classical language areas. In monolinguals, print-speech convergence has been found to be a reliable and universal indicator of reading-related skills, invariant across age and languages (Shankweiler et al., 2008; Rueckl et al., 2015; Preston et al., 2016). In late bilingual-biliterates, participants displayed significantly more extensive print-speech convergence in frontal regions and less in parietal regions in L2 compared to L1, a finding considered to indicate more effortful reading in a new writing system (Brice et al., 2019). In these previous studies, participants had learnt to speak before they learnt to read in the same language, and their reading circuits were integrated with previously-established spoken language networks commensurate with their reading proficiency. Participants in Experiment I were skilled L1 readers learning an L2 with the same writing system as their L1 — reflecting the experience of many late bilinguals — and displayed no significant effect of L2 proficiency on print-speech convergence in either language. Thus we find that print-speech convergence is unaffected by overall language proficiency in skilled readers, at least when both languages have transparent orthographies.

The similarity of L1 and L2 activation in classical language areas was significantly higher in the intermediate group compared to the advanced group. Psycholinguistic theory has suggested that since late bilinguals acquire their L2 with reference to their L1, early stages of L2-learning entail dependency on the L1, which diminishes in later stages (Kroll and Stewart, 1994; Kroll et al., 2010). Consistent with this idea, a recent word-learning study found that lexical items in an artificial language showed high neural pattern similarity with the native language (Li et al., 2018). Examining later stages in the language learning process, we found a strong correlation between L1 and L2 language networks in the intermediate language learners but a dissociation in the advanced learners. Thus, we infer that, though L1 and L2 share common neural bases, L2 proficiency modulates the similarity of their activation patterns in language learners. In addition, we found a differential effect of L2-proficiency on the dorsal and ventral pathways across modalities. In both reading and speech comprehension, the dorsal pathway (IFG *pars opercularis*, STG, and IPL) is involved in phonological processing, i.e. graphene to phoneme conversion in reading, and sound to articulatory-based representation in speech comprehension, while the ventral pathway (IFG *pars orbitalis*, IFG *pars triangularis*, vOTC) is involved in mapping of either written or spoken stimuli to its meaning. The more consistent effect of L2-proficiency on the ventral compared to the dorsal pathway in both reading and speech comprehension could be attributed to the fact that our participants' L1 and L2 have similar phonology but different morphology. Thus, given the prominent role of the ventral pathway in semantic processing, it is reasonable that we found a substantial effect of L2-proficiency on L2 activation of the ventral pathway regions in both reading and speech comprehension.

Pairwise functional connectivity analyses revealed differential functional coupling of the language control region dlPFC with the language regions IFG *pars opercularis* and the STG during L2 reading. Language control is a crucial part of the language learning process, involving the recruitment of extra resources when comprehension and retrieval are effortful. Previous studies have found that lower L2 exposure between similarly proficient bilinguals was associated with more extensive prefrontal activation, particularly in the left hemisphere (Abutalebi et al., 2001; Perani et al., 2003; Indefrey, 2006). We hypothesised that a diffuse activation of prefrontal areas in lower proficiency/exposure bilinguals may go hand in hand with weaker functional connectivity between the language regions and language control regions, and that functional connectivity would increase with greater proficiency and exposure. We found that the advanced L2-learner group with higher proficiency and exposure displayed greater coupling with the dlPFC than did intermediate learners. Thus we see that language learners who have achieved a high level of L2-proficiency — but still find comprehension more effortful than in their L1 (as measured by reaction times) — exhibit higher connectivity with the left dlPFC, a region implicated in effort and conflict resolution (Mansouri et al., 2009), than do language learners with lower L2 proficiency.

LANGUAGE PRODUCTION

In Experiment II on functional plasticity of production, we found: (i) significant learning-related changes in functional correlates of verbal fluency, (ii) no significant learning-related changes in lateralisation, but increasing recruitment of right hemisphere regions with increasing task difficulty, and (iii) functional coupling between language and language control regions increased with second language proficiency and exposure.

The left dlPFC, IFG *pars triangularis* and *pars opercularis* each exhibited significant proficiency-related differences in the second half of the task, with the advanced group displaying significantly higher activation than the intermediate group. This effect was not specific to the L2, but was instead present in both languages, suggesting neural changes in the advanced group that were not restricted to the L2 but were instead associated with verbal production in both languages. At the behavioural level, the advanced group also exhibited higher performance across languages, though the difference was only significant in the first half of the task, and the advanced group exhibited a larger drop in performance from the first to second half of the task in both languages ($p<0.0001$). This effect is congruent with previous findings from Luo and colleagues (2010) who found similar trajectories in a behavioural study of verbal fluency in low and high vocabulary bilinguals. Post-hoc analyses revealed a significant correlation between performance in the first half of the task and activation in the second half in these three regions (dlPFC: $r=0.33$, $p=0.018$; IFG *pars triangularis*: $r=0.31$, $p=0.027$; IFG *pars opercularis*: $r=0.37$, $p=0.007$). This may indicate an effect of (unsuccessful) effort in the advanced group that is proportional to their initial performance. Thus we see clear global changes in the behavioural patterns and neural correlates of verbal fluency with increasing L2 proficiency that are coherent with previous studies which found that semantic verbal fluency is lower in bilinguals compared to monolinguals (Portocarrero et al. 2007; Luo et al., 2010). We propose that increasing L2 proficiency involves a change in retrieval strategies that in the current experiment are partially offset by the higher vocabulary of the advanced compared to the intermediate group.

The lateralisation of activation during the verbal fluency task exhibited no effects of proficiency, but right hemisphere homologues were recruited with increasing task difficulty. The IFG *pars triangularis* and posterior STG were significantly more left-lateralised in L1 than in L2, and the frontal, temporal, and parietal language regions displayed significantly higher left-lateralisation of activation at the beginning of the task compared to the end of the task. Thus, results indicate that task difficulty, but not proficiency, modulates lateralisation of activation during verbal production. Previous studies have found similar effects, with greater right hemisphere activation in more difficult language tasks (Buckner et al., 1995; Schnur et al., 2009). A few previous studies have hypothesised a non-language-specific role of the right hemisphere regions (e.g. Basho et al., 2007; Vigneau et al., 2011; Geranmayeh et al., 2014), but in the current experiment, we found no significant change in lateralisation of language control regions, and the drop in left-lateralisation was specific to the language regions, supporting the idea that the involvement of the right hemisphere regions at the end of the task is specific to language and not executive processes.

In our final analysis, we examined the functional coordination between the language and language control regions. Pairwise functional connectivity analyses revealed differential functional coupling of the ACC with IFG *pars triangularis*. We found that advanced L2 learners exhibited significantly stronger coupling than did the intermediate L2 learners, indicating that coordination between the left ACC and IFG was significantly higher in language production across languages. Additionally, and contrary to the direction of activation, functional coupling between the IFG *pars triangularis* and *pars opercularis* was higher in L2 than in L1 in both groups throughout the verbal fluency task. Previous studies have found that lower L2 exposure between similarly proficient bilinguals was associated with more extensive prefrontal activation, particularly in the left hemisphere (Abutalebi et al., 2001; Perani et al., 2003; Indefrey, 2006). In the current experiment, we showed that the direction of functional coupling was opposite to the direction of activation effects, and that the advanced L2-learner group with higher proficiency and exposure displayed greater coupling with the ACC than did intermediate learners. In Experiment I, we found a similar pattern, with advanced learners exhibiting higher connectivity between language and language control regions. Thus, higher proficiency and possibly exposure were associated with greater functional coupling between language and language control regions across languages and tasks.

8.2 HEMISPHERIC SPECIALISATION AND PLASTICITY

In Experiment III, we focused on language lateralisation. To the best of our knowledge, this was the first comprehensive study of the experience-dependent plasticity of hemispheric specialisation of language comprehension and production systems.

Language learning is a demanding task that entails neural changes at any age. Acquiring a language is thought to be particularly difficult after early childhood due to decreasing neural plasticity, and adult language learners are often able to accomplish a high level of comprehension in a new language, but achieving native-like language production becomes increasingly difficult as age of exposure increases (Walsh and Diller, 1981). Language production requires more sensorimotor elaboration than does comprehension (Bates, 1993), making production of native-like accents and grammar inherently more difficult than their comprehension. More unexpectedly, psycholinguistic studies found that vocabulary size in language learners also differed significantly between comprehension and production, with receptive vocabulary being substantially higher than expressive vocabulary (Gibson et al., 2012a, 2012b) —

suggesting that the greater sensorimotor demands of native-like production alone do not fully explain the comprehension-production asymmetry in language learners.

In Experiment III, we put together cross-sectional and longitudinal experiments involving distinct populations and languages, and examined hemispheric lateralisation and learning-dependent plasticity of reading, speech comprehension, and verbal production. We found a highly consistent pattern of results across the two experiments, showing that (1) in both native and non-native languages, while language production was left lateralised, lateralisation for language comprehension was highly variable across individuals; and (2) with increasing non-native language proficiency, reading and speech comprehension displayed substantial changes in hemispheric dominance, with languages tending to lateralise to opposite hemispheres, while production showed negligible change and remained left-lateralised.

The finding of variably-lateralised (bilateral at the group-level) comprehension and left-lateralised verbal production across different languages suggested that comprehension is flexible while verbal production is hard-wired to be left-lateralised. Previously, conflicting evidence from studies in monolinguals had led to a range of different conclusions and models of comprehension: from left-lateralised to partly-bilateral, bilateral, or right-lateralised function (Booth et al., 2000; Gaillard et al., 2000; Jung-Beeman, 2005; Hickok and Poeppel, 2007; Lidzba et al., 2011). Few studies have compared different modalities in the same participants, and though lateralisation was seen to be highly modality-dependent in the current experiment, it did not appear to depend on the exact task used, since lateralisation for the single-word overt tasks in the current experiment was consistent with results from far more complex discourse-level covert tasks in previous studies (Dehaene et al., 1997; Lidzba et al., 2011; Bhattasali et al., 2019). There were also subtle differences between the two experiments, with similar Ln lateralisation but differing central tendencies for L1 laterality. This pattern is consistent with the literature on the influence of early language experience: meta-analyses have found that early bilinguals (L2 acquired before age 6) typically show bilateral hemispheric involvement, while monolinguals and late bilinguals show greater left hemisphere dominance (Hull and Vaid, 2006, 2007; Bloch et al., 2009; Liu and Cao, 2016). Thus the convergent results in the present work indicate that inter-individual variability in lateralisation for language comprehension is not an artefact of task or methodology, but that instead, language comprehension is differently lateralised across individuals. Lesion studies in children have found dissociative effects of lesion side on comprehension and production: while lesions in the left hemisphere were associated with more severe delays in production compared to comprehension, comprehension delays were more common — but not universal — in children with right-hemisphere damage (Marchman, Miller and Bates, 1991; Thal et al., 1991; Bates, 1993). In line with these findings, developmental neuroimaging studies all found left-lateralised language production, but reached conflicting conclusions on comprehension, leading to a suggestion of differing maturational mechanisms for comprehension and production (Hervé et al., 2013). Clinical studies have recommended that both comprehension and production tasks be used in determining language lateralisation for clinical purposes (Wilke et al., 2010; Lidzba et al., 2011; Vilasboas et al., 2017; Woodhead et al., 2018). Modality-dependent lateralisation, i.e. variably-lateralised comprehension vs left-lateralised production, could explain the long-standing conflicts among previous studies that used tasks tapping into different modalities, and shed new light on the question of functional specialisation for language.

Cognitively, comprehension is a natural precursor to meaningful production, and is more developed from an early age (Fraser et al., 1963). The ability for comprehension remains higher than for production in adulthood: monolingual adults exhibit rapid adaptation to accented speech (Clarke and Garrett, 2004; Maye et al., 2008) and adult language learners exhibit high comprehension abilities (Walsh and Diller, 1981), but imitation of even native language accents is quite difficult (Markham, 1999). Psycholinguistic evidence has long supported life-long comprehension-production asymmetry in monolinguals and multilinguals that is not fully accounted for by task difficulty (Clark and Hecht, 1983; Bates, 1993; Gibson et al., 2012; Gershkoff-Stowe and Hahn, 2013; Keller et al., 2015), but this well-established cognitive phenomenon remained to be addressed in the neuroscientific field. Our first finding of high lateralisation variability in native language comprehension indicates that lateralisation for comprehension is highly susceptible to developmental and psycholinguistic factors, while production appears to be neurobiologically constrained to the left-hemisphere. Our second finding of increasing learning-dependent dissociation between hemispheric dominance of each language suggests that the ability to recruit either hemisphere for comprehension might be more advantageous than left-lateralised production. Together, these converging findings from our experiments could suggest that neural flexibility of comprehension and neurobiological fixedness of production may underlie the psycholinguistic comprehension-production asymmetry.

Convergence and dissociation of neural activation for different languages and language systems has been of considerable research interest. Neuroimaging studies of language have by and large come to the conclusion that all languages do indeed recruit the same language regions, and that language experience modulates the amount of overlap, leading to the “convergence hypothesis” (Perani and Abutalebi, 2005; Gurunandan et al., 2019). The current experiment built on this finding, and characterised lateralisation patterns for L1 and Ln within the common language network, finding that increasing Ln-proficiency led to increasing dissociation in lateralisation between the two languages. There has been much debate on whether language control in bilinguals is language-specific or domain-general, with mixed evidence (Hernández et al., 2013), and it is possible that, apart from any changes in the involvement of language control regions, the greater hemispheric separation of languages in more proficient non-monolinguals also contributes to their improved language control. Future studies looking concurrently at dissociation within the language network and recruitment of language control regions are needed to test this idea. Comprehension and production also dissociated with increasing Ln-proficiency. In lower proficiency learners, there was lower separation between modalities, possibly indicating variable strategies of Ln access and variable activation profiles (Dehaene et al., 1997), but as individuals attained higher proficiency, their activation profiles stabilised and became more uniform. Turning to the question of convergence between language systems, print-speech convergence has been considered a universal signature of native language proficiency (Shankweiler et al., 2008; Rueckl et al., 2015; Preston et al., 2016), but it is less well-studied in multilinguals. In the current experiment, we found increasing convergence of joint L1-Ln lateralisation for reading and speech comprehension with increasing language learning, suggesting that reading-speech convergence is also sensitive to increasing Ln-proficiency.

The pattern of plasticity differences between the language systems, i.e. plasticity for reading > speech comprehension > verbal production, was strikingly similar to their perceived difficulty in real-world language learning in adults. Two observations support the idea that the differential plasticity of language systems contribute to differential learning.

First, learners in the longitudinal study had switched languages from same to opposite hemispheres in reading within a relatively short time-frame, while fewer did so for speech comprehension, and none for production. Further, individuals who had L1 and Ln lateralised in opposite hemispheres maintained this dissociation post-training, and individuals who had L1 and Ln in the same hemisphere tended to dissociate post-training to varying degrees depending on the modality. This suggested that opposite hemispheric dominance of languages could be advantageous for language learning, and further, that shifts in hemispheric dominance are limited by the plasticity of the sensory/motor cortices corresponding to each language system. Neuropsychological evidence from stroke recovery patterns in adults who showed greater (but not complete) recovery in comprehension than in production (Lomas and Kertesz, 1978), as well as different reorganisation patterns for comprehension and production (Musso et al., 1999; Heiss and Thiel, 2006) further supports our conclusion. Though the visual, auditory and motor cortices are all bilateral, each of them exhibits hemispheric advantages for processing specific features (Benke and Kertesz, 1989; Deruelle and Fagot, 1997; Flinker et al., 2019; Albouy et al., 2020), and previous studies with monolinguals have found differences in visual lateralisation of different writing scripts (Tzeng et al., 1979; Kuo et al., 2001), asymmetrical sensitivity of the auditory cortices (Friederici and Alter, 2004; Boemio et al., 2005), and left-lateralisation of auditory and articulatory motor areas (Morillon et al., 2010), pointing to differential potential for post-critical-period plasticity of these sensory/motor regions that matches the converging pattern of language system plasticity found in the current experiment.

Second, the adolescent learners in the second experiment displayed substantial neural changes after just three months of training, while the adult learners in the first experiment displayed similar neural differences for a much larger proficiency difference between groups. This finding is compatible with age-related decrease in neural plasticity, and sheds further light on the source of the difficulty of late language learning. However, despite the convergence of the neural results in Experiments IIIA and IIIB, the modest behavioural effect in Experiment IIIB limited any further interpretation of the neural changes in relation to behavioural outcomes at the individual level in naturalistic language learning. In sum, taken together with previous evidence, the converging findings in the present work point to the sensorimotor cortices playing a large role in both the lateralisation of language as well as the asymmetric decrease in plasticity of the language network.

8.3 LIMITATIONS AND FUTURE WORK

The experiments in the current thesis had relatively small sample sizes. To address this issue, and in line with best statistical practices, we restricted the number of comparisons and used non-parametric statistics, within-subject measures, and effect sizes where appropriate. Methodological studies and reviews of language lateralisation have often warned against over-interpretation of results from a single task, small regions of interest, or non-robust analytical methods (e.g. Bradshaw et al., 2017a, 2017b; Bain et al., 2019). These were avoided in the current thesis and interpretations were based on robust patterns of results verified by corroborating analyses that were replicated in contrasting experiments. However, we used classical single word tasks, and while the results were consistent with the findings from far more complex comprehension tasks (Dehaene et al., 1997; Lidzba et al., 2011; Bhattasali et al., 2019), future studies are needed to establish whether the results presented in the current experiment would be as or possibly even more pronounced in sentence/discourse processing (Hagoort, 2019).

The experiments involved ecologically valid language learning, and the lateralisation results were sensitive to participants' real-world language-learning progress, i.e. CEFR level, rather than their performance or improvement on the in-scanner semantic tasks involving high-frequency stimuli. In fact, while performance on the tasks was relatively uniform across participants, lateralisation exhibited much larger variation in both languages, supporting the idea of multi-factorial modulation of hemispheric specialisation (Tzourio-Mazoyer et al., 2016). The replication of findings in language learners at different levels of proficiency suggested that the learning-dependent neural changes were not temporary, but further studies are necessary to disentangle the effects of learning vs proficiency, and test lateralisation of languages in early balanced bilinguals.

The current work also opened avenues for follow-up analysis and experiments. First, an open question from the current work is the mechanism underlying the observed differences between the language systems. We hypothesised that the pattern of differences may be due to the involvement of the sensorimotor systems, and plan to further explore the functional coupling of the language network regions and the sensory regions. Second, it was unclear whether the greater neural changes seen in Experiment IIIB was due to the lower age of the participants or whether being a bilingual facilitates later language learning, and further analyses of the modulatory effect of the second language might shed light on the effects of bilingualism on further language learning. Finally, the current work did not explore the role of subcortical structures, such as the caudate and putamen, which have been implicated in language control (e.g. Hervais-Adelman et al., 2015a, 2015b), and should be examined in future analyses.

8.4 CONCLUSION

Across three fMRI experiments with adult language learners across a broad range of ages, we found evidence for significant functional plasticity well into adulthood, and showed that different language systems exhibited different patterns of hemispheric specialisation and plasticity. Cross-sectional and longitudinal experiments in contrasting samples of real-world language learners, testing of different language systems, and a multi-pronged analytical approach revealed robust and converging patterns of modality-dependent lateralisation and plasticity of the language network. Our findings suggest that language lateralisation for reading and speech comprehension is plastic well into adulthood, while production shows strong left hemisphere specialisation. Plasticity for reading was greater than for speech comprehension, which was in turn greater than for verbal production. Finally, functional coupling between language and language control regions was found to increase with increasing second language proficiency and exposure. ■

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