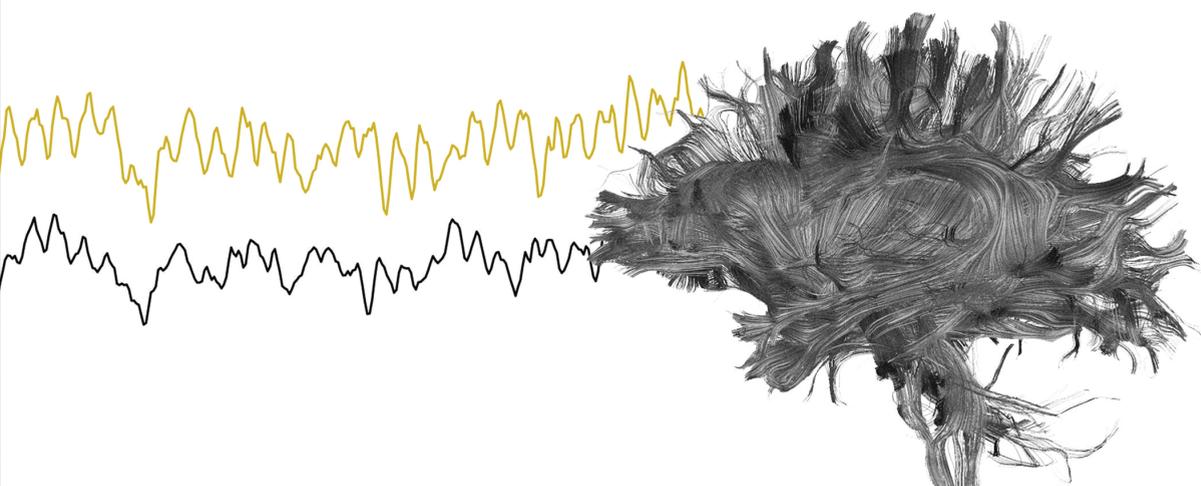


THE NEUROBIOLOGY OF INDIVIDUAL DIFFERENCES IN GRAMMAR LEARNING

Olga Kepinska



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The Neurobiology of Individual Differences in Grammar Learning

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PROMOTOR:

Prof. dr. N.O. Schiller

CO-PROMOTOR:

Dr. J. Caspers

COMMITTEE:

Dr. N.H. de Jong

Prof. dr. C.C. Levelt

Dr. S. Reiterer (University of Vienna)

Prof. dr. S.A.R.B. Rombouts

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Chapter 1

General introduction

1.1 Introduction

In their 2008 paper reporting on the results of a large-scale research programme ‘High-level Proficiency in Second Language Use’, Niclas Abrahamsson and Kenneth Hyltenstam examined the role of age and language aptitude in near-native proficiency levels of Swedish as a second language (L2). Age of onset of acquisition (AoA) accounts for the largest proportion of variation in the outcomes of L2 learning in that the later someone starts learning, the more effortful the learning process and the lower the ultimate attainment levels are (see e.g., DeKeyser, 2000; Johnson & Newport, 1989; Lenneberg, 1967; Long, 1990). The question asked by Abrahamsson and Hyltenstam was whether a high degree of language learning aptitude (i.e., a specific, measurable talent for learning foreign languages) could alleviate such age effects and enable adult learners to reach a level in an L2 that is comparable to that of native speakers. Not only did the study reveal that a high degree of language aptitude was crucial for late learners (AoA \geq 12) to attain a very high, near-native level of proficiency in L2, it also showed that it was an important factor influencing L2 proficiency of the early learners (AoA \leq 11).

This widely cited study was the starting point for the ideas and concepts explored in the present thesis. The robustness of aptitude effects in second language acquisition (SLA) was evident (see also e.g., DeKeyser, 2000; Granena & Long, 2013; S. Li, 2016), yet at the time of conception of the research proposal for the present study (late 2011) hardly any study investigating their neurobiological underpinnings was available¹. Indeed, such sentiment was also expressed by the authors, and time and again by other researchers from the field of SLA. In the words of Ioup, Boustagui, El Tigi and Moselle (1994) (as cited by Abrahamsson & Hyltenstam, 2008), “how the talented brain acquires language in comparison with the normal brain remains a mystery” (p. 93).

Human brains differ from each other almost as much as our faces do (Schumann, 2014). For example, the size of different brain structures, the number of neurons used to perform certain functions and the integrity of white matter (bundles of fibres connecting different parts of the cortex) vary from person to person. Although there is some debate as to

¹ But see e.g., Dogil and Reiterer (2009) for a noteworthy exception in the context of phonetic skills.

whether these parameters influence information processing, a growing body of research indicates that some of these inter-individual differences correlate with specific cognitive tasks, such as language learning (e.g., Coggins, Kennedy, & Armstrong, 2004; Golestani, Molko, Dehaene, LeBihan, & Pallier, 2007; López-Barroso et al., 2013; Mechelli et al., 2004).

Departing from the concept of a specific talent for learning foreign languages, and the idea that there are large differences in the way individual human brains work and are built, the main aim of this thesis is to advance the understanding of neural mechanisms and brain structures underlying individual differences in language acquisition.

The following sections of the General Introduction will, first, elaborate on previous language aptitude research, second, introduce the scope of the present investigations, and finally, present the methodology of the research.

1.2 Language aptitude research

Research into the phenomenon of language aptitude has been conducted in the context of individual differences in second language learning, other factors including learner's age, motivation, personality, anxiety and learning style. According to a recent meta-analytic study on aptitude effects (S. Li, 2016), general L2 proficiency and language aptitude measurements correlate strongly with each other ($r = .49$), making aptitude the best prognostic measure of language learning achievement (see also Dörnyei & Skehan, 2003; R. Ellis, 2008; Sawyer & Ranta, 2001).

Dörnyei and Skehan define language aptitude as “a specific talent for learning foreign languages, which exhibits considerable variation between learners” (2003, p. 613). It is viewed as a composite of general and specific abilities (R. Ellis, 2008). The question whether language aptitude is innate and remains stable throughout one's life, or depends upon past learning experience is still a matter of debate (see Grigorenko, Sternberg, & Ehrman, 2000; Sawyer & Ranta, 2001). Yet by no means has language aptitude been considered a prerequisite of mastering an L2, rather it serves in the form of a capacity which improves the rate and ease of learning (Carroll, 1981).

The concept of aptitude of any kind entails existence of some capabilities which enable an individual to perform particular tasks better than others do. In the case of second language learning, it is assumed that aptitude can be measured, thus providing information as to the individ-

ual's achievement even before the actual learning takes place. As early as the 1920s, attempts were made to develop tools for predicting one's success in language learning. However, as it was the case that L2 learning which was based on the popular grammar-translation method of the time was seen as a purely intellectual exercise, most of the early language aptitude tests correlated rather highly with intelligence tests (Carroll, 1981). For a long time, it has therefore been widely assumed that linguistic abilities are inseparable from general intelligence. Recent studies elucidated the relationship between intelligence and language aptitude, suggesting the two constructs overlap but are distinguishable from each other (Granena, 2013; S. Li, 2016). Similarly, language aptitude has been found to correlate with measures of executive functioning, in particular of working memory capacity (S. Li, 2016).

A methodology for studying language aptitude and its nature was developed by the American psychologist John Bissell Carroll, whose work laid the ground for the majority of current studies into the concept. The main motive for these early investigations of language aptitude was “the wish to identify those learners who could benefit most from language instruction” (R. Ellis, 2008, p. 659). In his research, Carroll administered a series of potential tests aiming at pinpointing the different components of language aptitude to learners starting a language course. Subsequently, these tests were correlated with each other, and with tests measuring language proficiency at the end of the course, which enabled Carroll (1981) to distinguish the following four components of language aptitude:

- (1) phonemic coding ability, or the capacity to code unfamiliar sounds so that they can be retained;
- (2) grammatical sensitivity, which refers to the ability to identify the functions that words fulfil in sentences;
- (3) rote learning ability, or the ability to learn associations between lexical forms and meaning rapidly and efficiently and to retain these associations (i.e. to easily learn and remember new words);
- (4) inductive language learning ability, which is the capacity to infer or induce the rules of a set of previously unknown language materials.

(See also Abrahamsson & Hyltenstam, 2008; Dörnyei & Skehan, 2003; R. Ellis, 2008; Sawyer & Ranta, 2001; Skehan, 2002 for further elaboration of these components.)

On the basis of the empirically established components of language aptitude Carroll, together with Sapon (1959), devised a commercially

available test battery, the Modern Language Aptitude Test (MLAT), consisting of five sub-tests. Notably, in the interest of the predictive validity of the test, there was no one-to-one correspondence between the sub-components of language aptitude and the sub-tests (Dörnyei & Skehan, 2003).

Carroll's findings concerning language aptitude almost completely shaped the way this subject was addressed within the SLA field, and although the results of post-MLAT research did not revolutionise the view of the nature of language aptitude outlined by Carroll, it certainly brought about a refinement of his initial theory. One important contribution was the development of a series of alternative language aptitude tests. The Pimsleur Language Aptitude Battery (PLAB) (Pimsleur, 1966) is a test developed as an alternative to the MLAT, targeted mostly at high school students. The Defense Language Aptitude Battery (DLAB) (Petersen & Al-Haik, 1976) aimed at discriminating learners at the high end of the aptitude range and has been used by the United States Department of Defence. Similarly, the recent Hi-LAB (Linck et al., 2013) also targets highly successful L2 learners. The Cognitive Ability for Novelty in Acquisition of Language (CANAL-F) is a dynamic test devised by Grigorenko et al. (2000), which underscores the role of coping with novelty in L2 acquisition. The Llama Language Aptitude Tests (LLAMA) (Meara, 2005) have been developed at the University of Wales Swansea through a series of research projects, including the development of the earlier version of the test – the Swansea Language Aptitude Test (LAT) v2.0 (Meara, Milton, & Lorenzo-Dus, 2003). The current LLAMA tests are based among others on the work of Carroll and Sapon (1959). The battery consists of the following four sub-tests: (1) LLAMA_B, a vocabulary learning task; (2) LLAMA_D, a test of phonetic memory; (3) LLAMA_E, a test of sound-symbol correspondence, and (4) LLAMA_F a test of grammatical inferencing. The tests can be used regardless of the linguistic background of the language learner. The sub-tests include linguistic materials from either artificial language systems or rare languages with which the participants are unlikely to be familiar. Furthermore, LLAMA is a freeware program, which is available online (through <http://www.lognostics.co.uk/>) and can be administered on a personal computer (see Section 1.4.1 below for further details concerning the LLAMA tests).

In terms of elaboration on the components of language aptitude in the post-MLAT research, Skehan (2002) proposed a more parsimonious structure of the construct, consisting of three instead of four components. Next to phonetic coding and rote learning, he suggested that

since grammatical sensitivity and inductive language learning ability are both associated with analytic aspects of aptitude, they can be both unified as language analytical ability (LAA). Furthermore, on the basis of his research with learners of colloquial Arabic within the British military, Skehan (1986, 2002) proposed that success in L2 learning may be a consequence of the learner's strength in only one of the components of language aptitude. In fact, he stated that "successful learners either achieved their success through strong involvement of language analytic abilities or through high memory, but surprisingly few students appeared to have high scores in each of these" (2002, p. 76). Another idea concerning the components of language aptitude put forward among others by Robinson (2005) is that they are dynamic in nature, in that different aspects of language aptitude may operate differently during the course of language learning (but see Granena (2013), and Section 1.4.1 below for data concerning the stability of aptitude measurements – i.e., the LLAMA tests – over time).

1.3 Scope of the present study

Following Skehan's (2002) suggestion indicating that successful L2 learning can be due to benefitting from either one's memory, or analytical abilities, this study set out to constrain its scope to LAA only. The analytic component of language aptitude has been shown to be best at predicting grammar learning, underscoring its link with learning of the morphosyntactic aspects of an L2 (S. Li, 2016). Since one of our main goals was to investigate the neural mechanisms coupled with high aptitude (and thus high LAA in particular), a grammar learning task was incorporated in our experimental design, in order to – as it were – observe the LAA effects for successful grammar learning "in action". Furthermore, since, as pointed out by Robinson (2005), aptitude levels can change over time, reliable neurobiological observations of the aptitude construct should either encompass a longitudinal design with a series of measurements, or be restricted to one stage of learning. Considering the limited time available within the present project, the latter option was chosen, and the beginning stage of the grammar learning process was investigated.

An added value of this approach was that it enabled a scrutinised exploration of the initial phase of novel grammar acquisition. Mastery of grammatical rules of a language is a complex and demanding task, in particular for adult L2 learners (Abrahamsson & Hyltenstam, 2009; Antoniou, Ettliger, & Wong, 2016). The experiments reported in the present thesis shed light on how the adult brain acquires new grammat-

ical rules and what mechanisms are typical of good performance. Moreover, effort was made to relate our findings to earlier studies concerned with novel grammar learning. To this end, an established experimental protocol was used (see below), and an attempt was made at reproducing and extending previous results reported in studies employing it (see in particular Chapter 2).

Experiments investigating the neural architecture behind language learning make frequent use of designs which are highly controllable, and tap into isolated aspects of an otherwise complex process. In case of research into the neurobiology of syntax acquisition, the so-called *artificial grammar learning* (AGL) paradigms (Reber, 1967) are commonly employed (e.g., Antonenko, Meinzer, Lindenberg, Witte, & Flöel, 2012; Brod & Opitz, 2012; Friederici, Steinhauer, & Pfeifer, 2002; Goranskaya, Kreitewolf, Mueller, Friederici, & Hartwigsen, 2016; Hauser, Hofmann, & Opitz, 2012; Opitz, Ferdinand, & Mecklinger, 2011; Opitz & Friederici, 2003, 2004, 2007). They offer a view on the neurobiological mechanisms of syntax acquisition in real time, without the interference of semantics, phonology or pragmatics. Moreover, due to the synthetic nature of the stimuli, strict control over prior exposure is guaranteed (cf. e.g., Petersson, Folia, & Hagoort, 2012; Petersson & Hagoort, 2012). Such an approach was also used in the present study (see Section 1.4.2 below for a further elaboration on the employed experimental design).

Understanding any cognitive phenomenon from the neurobiological perspective entails unravelling and integrating many layers of information. In this vein, in order to gain a comprehensive account of individual differences in grammar learning and language aptitude, the present study used a variety of neuroimaging data. Combining several analytical approaches to the data enabled us to investigate the phenomenon of language aptitude and grammar learning from a range of perspectives that complement each other, and – desirably – will improve the validity of the conclusions to be drawn.

1.4 Methodology

The workflow for the present study consisted of (1) a large-scale pre-test of language aptitude, (2) a multi-modal magnetic resonance imaging (MRI) paradigm consisting of several experiments, and (3) an electroencephalography (EEG) experiment. The following sections describe the distinct steps and elaborate on the methodology applicable to each of them.

1.4.1 LLAMA measurement

The first step of the present study consisted of administration of the LLAMA tests to a large sample of participants in order to choose participants for further experiments. The LLAMA tests (see also Section 1.2 above) and their earlier version, the Swansea Language Aptitude Tests (LAT) (Meara et al., 2003) have been widely used within the field of SLA, for example in studies of ultimate L2 attainment (Abrahamsson & Hyltenstam, 2008; Granena & Long, 2013) and effects of feedback during L2 instruction (Yilmaz, 2012). In a paper reporting on an exploratory validation study of the LLAMA tests, Granena (2013) presented results on its reliability: internal consistency, assessed by means of Cronbach's alpha, and test-retest reliability, derived from correlation of test scores obtained on two time points, two years apart. The LLAMA tests proved to have a good reliability, Cronbach's $\alpha = .77$ and to be stable over time ($r = .64$, $p = .002$).

The goal of the LLAMA measurement was to discriminate between learners with high and average language aptitude in one domain of language acquisition, namely grammar learning. To this end, the LLAMA_F test of grammatical inferencing was used, see Figure 1.1. In this test, twenty pictures are presented together with sentences in an unknown language that describe them. In the learning phase (lasting five minutes), participants are asked to discover grammatical rules (concerned mainly with agreement features) of this unknown language, and they are allowed to take notes. In the test phase, they are presented with a series of pictures, combined with two sentences and they have to decide which sentence is grammatically correct. Participants can score from 0 to 100, and according to the LLAMA manual, 80-100 is defined as outstandingly good and 25-45 as average (Meara, 2005). However, since the scores are awarded at intervals of 10, a slightly adjusted interpretation of the scores was used in the present study and an average score was defined as 30-50.

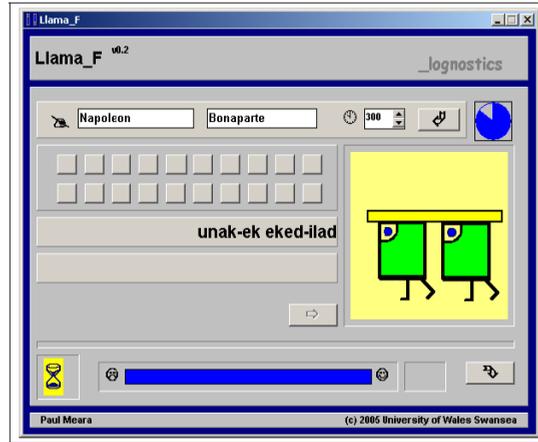


Figure 1.1 One of the items from the LLAMA_F test (Meara, 2005). The illustration on the right is described by a sentence (*unak-ek eked-ilad*) in a language unknown to the participant. On the basis of twenty such examples, participants discover grammatical rules which they are subsequently supposed to apply to new materials in the test phase of the experiment.

1.4.1.1 Procedure

The LLAMA test was administered on Personal Computers in a computer lab at the Faculty of Humanities at Leiden University. A maximum of 20 participants could take the test at the same time. Upon arrival, each participant was given a set of headphones and an instruction booklet (see Appendix 1) explaining the procedure.

Participants were asked to read the instructions and ask any questions before starting the tests. At least one experimenter was present at all times during the test. The order of the subtests was the same for all participants: they started with the LLAMA_B, followed by LLAMA_D, LLAMA_E and finished with the LLAMA_F. Following the language aptitude tests, the participants were asked to fill in an online questionnaire (see Appendix 2).

1.4.1.2 Participants

In total 307 participants were recruited at Leiden University through posters, flyers, email invitations and by word of mouth advertising. 239 of them completed all parts of the test and the biographical information

sheet, were native speakers of Dutch, and did not grow up bilingually. The statistics presented below pertain to the latter group. Participants' age ranged between 18 to 47 years ($M = 22.42$, $SD = 4.23$). The ratio between female and male participants was approximately 2:1 (168:71).

1.4.1.3 Results

The average scores (and standard deviations) on each of the LLAMA subtests are presented in Table 1.1.

| LLAMA subtest | Mean | SD |
|---------------|-------|-------|
| LLAMA_B | 64.98 | 20.33 |
| LLAMA_D | 34.46 | 14.73 |
| LLAMA_E | 89.21 | 15.44 |
| LLAMA_F | 65.10 | 25.53 |

Table 1.1 Average scores and standard deviations on each of the LLAMA subtests.

Participants for subsequent experiments were recruited from two groups of learners: those who scored within the average range (30-50), and those who obtained an “outstandingly good” score (80-100) per LLAMA manual. Figure 1.2 shows the distribution of scores on the LLAMA_F subtest; the two groups of learners are highlighted in the graph. In total, 67 participants scored within the average, and 93 within the high range. Only right-handed, healthy individuals with no contra-indications for an MRI scan (e.g., neurological disorders, metal implants) were approached to take part in the follow-up neuroimaging experiments. In total, 47 participants took part in the EEG, and 42 in the MRI experiments.

Additional psychometric measurements were collected from the participants of the MRI and EEG experiments. The tests were administered after the main part of the study (the grammar learning task, see Section 1.4.2 below) and included a nonverbal test of general fluid intelligence, the Raven Advance Progressive Matrices (RAPM, Hamel & Schmittmann, 2006) and a test of working memory span, Automated Operation Span Task (AOSPAN, Unsworth, Heitz, Schrock, & Engle, 2005). As expected on the basis of the previous research into the aptitude construct (see Section 1.2 above, and S. Li, 2016), the highly skilled learners had on average higher scores on both the reasoning abilities and working memory tests (RAPM: $M = 24.57$, $SD = 4.35$, and $M = 20.36$, $SD = 5.07$; AOSPAN: $M = 48.04$, $SD = 13.26$, and $M = 36.76$, $SD = 19.11$, for the high and average LAA participants, respectively).

The difference was statistically significant for the EEG cohort ($t(44) = 4.16$, $p < .05$, and $t(44) = 3.56$, $p < .05$, for RAMP and AOSPAN, respectively); the scores of highly and moderately skilled participants who took part in the MRI experiments did not differ significantly ($t(40) = 1.88$, $p = .07$, and $t(40) = 1.11$, $p = .27$, for RAMP and AOSPAN, respectively).

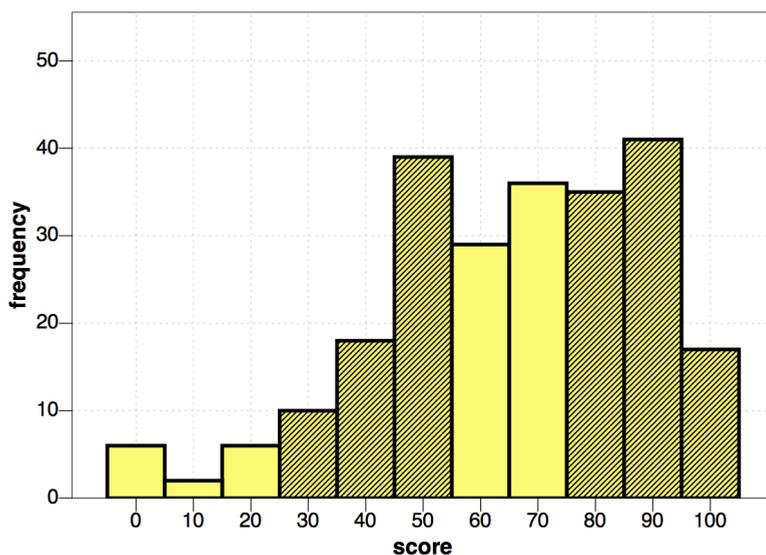


Figure 1.2 Distribution of scores on the LLAMA_F subtest. The shaded bars mark scores which were relevant for the later experiments, i.e. the average (30-50) and high (80-100) range.

1.4.2 Grammar learning task

For both MRI and EEG parts of the present study, the same paradigm was used: a study design enabling an investigation into rule learning in real time, in which learning is simultaneous to the recording of the data. The paradigm is based on the artificial language BROCANTO (Brod & Opitz, 2012; Friederici et al., 2002; Hauser et al., 2012; Opitz et al., 2011; Opitz & Friederici, 2003, 2004, 2007) comprising a set of pronounceable pseudo-words, combined in ways following rules found in many natural languages. The artificial grammar is presented to the participants over the course of several learning and test phases. During learning, correct grammatical sentences are shown one by one on the screen and participants are instructed to extract the underlying rules. The test phases consist of both grammatical and ungrammatical items

and participants' task is to assess the grammaticality of the sentences. The accuracy of these grammaticality judgements serves as an indication of the learning progress. See Chapter 3 and Chapter 4 for further details concerning the BROCANTO rules and the presentation of the task.

1.4.3 Neuroimaging methods

Brain imaging techniques can be divided into functional and structural methods. All methods directly (e.g., through electrophysiological measures) or indirectly (e.g., investigating levels of blood oxygenation) recording brain activity patterns fall under the umbrella of functional neuroimaging. Techniques dealing with the anatomical make-up of the central nervous system are referred to as structural. Both were used in the present study, and are shortly discussed hereunder (and in detail in Chapters 2-6).

1.4.3.1 fMRI

By detecting changes in blood oxygenation, functional magnetic resonance imaging (fMRI), together with its various applications, offers an indirect measurement of brain's activation levels. For example, the activation levels can be related to performance of a cognitive task (such as grammar learning) through a subtraction method utilised in event-related designs. At least two conditions of interest are presented to the participant, in our case, the grammatical and ungrammatical sentences comprising the test phases of the AGL experiment. The difference in the blood-oxygen-level dependent (BOLD) signal between them is then computed and localised, and can be taken as an indication of the brain's reaction to the particular stimulation. Moreover, inferences about how such localised activity patterns differ between groups of participants can be made by performing statistical comparisons, see Chapter 4.

Another possibility of approaching fMRI data is to explore correlated BOLD signal fluctuations of different brain areas, in order to visualise and quantify the brain's functional connectivity patterns at rest or during cognitive tasks. Here, at least two methods are available. First, insights concerning the cooperation between pre-defined regions of interest (ROIs) can be obtained from psychophysiological interaction (PPI) analysis (Friston et al., 1997). Such an approach aims at detecting regions in the brain whose activity levels can be explained by the activity pattern of the predefined ROI (during a specific cognitive process, such as novel grammar learning). Prior hypotheses about regions involved

are a prerequisite for performing such an analysis, hence the present study (see Chapter 2), utilised it in an effort to build on previous research concerning the functional interactions of Broca's region and the hippocampal system in the acquisition of grammar rules.

The connectivity question can also be approached in a data-driven manner, by investigating the intrinsic organisation of the brain as different networks without any spatial constraints. A method allowing for such an approach is the independent component analysis (ICA) of fMRI data. This technique allows for the detection of structured spatiotemporal processes in neuroimaging data (Beckmann et al., 2006) by means of their decomposition into a set of spatially independent activation maps (components) and their time courses. The components are seen as a representation of interconnected networks of brain regions that co-activate when certain types of tasks or cognitive processes are being performed, see Chapter 3. Moreover, inter-individual differences within the components can be assessed, providing information on brain's functional organisation coupled with, e.g., a certain trait (such as high language analytical abilities).

1.4.3.2 EEG

Electroencephalography measures repetitive neuronal firing (i.e., oscillations) of large populations of neurons. EEG signals recorded during a cognitive task, such as grammar learning, can be – among others – quantified by means of power spectrum and synchronisation analyses (cf. e.g., M. Siegel, Donner, & Engel, 2012; X.-J. Wang, 2010). Spectral power variations reflect the number of neurons discharging at the same time (Kiiski et al., 2012; Klimesch, 1999), thus indicating local neuronal activity. EEG also offers a view on functional cooperation between brain regions by means of coherence analyses. The premise of this approach is that brain areas activated by a particular cognitive task (e.g., learning of a novel grammar) exhibit increased coherence, and high coherence between two EEG signals is indicative of high cooperation (degree of information flow) and synchronisation between underlying brain regions within a certain frequency band (Weiss & Mueller, 2003), see Chapter 5.

1.4.3.3 DTI

Diffusion tensor imaging (DTI) is a structural neuroimaging technique based on MRI. Thanks to the magnetic gradient, it measures diffusivity of water along different directions. One of its applications, deterministic

tractography, offers visualisation of white matter pathways by inferring the movement of water molecules (Catani & Mesulam, 2008; see also Le Bihan, 2003). Brain images obtained with the DTI method can be quantified, offering a measure of the microstructural tissue properties underlying the white matter pathways. The technique thus enables comparisons between individuals (e.g., as determined with a language aptitude test), and establishment of functional correlates of particular anatomical structures, see Chapter 6.

1.5 The neurobiology of individual differences in grammar learning

The goal of the present thesis was to employ the above methodological approaches to neuroimaging data and produce a comprehensive – albeit undoubtedly not exhaustive – picture of the neural mechanisms and brain structures underlying individual differences in L2 grammar acquisition, with a special focus on language learning aptitude, viz. language analytical abilities.

Chapter 2 and Chapter 3 both report on the functional MRI data collected during the learning phases of the AGL task. In Chapter 2, an investigation into the functional architecture of the language learning brain following directly from previous studies employing the paradigm utilised in the present study is presented. PPI analysis was used in order to build upon previous findings (Opitz & Friederici, 2003) and to set the scene for further investigations involving the between-group comparisons of the highly and moderately skilled learners. In Chapter 3, whole-brain functional connectivity was investigated with the above-mentioned ICA approach. After decomposition of the fMRI data into maps representing separate cognitive processes, we explored whether the brain's networks were represented differently among participants with high and average language analytical abilities. Event-related fMRI was employed in the experiment reported in Chapter 4. Its goal was to establish where in the brain the novel grammar is processed, how the activity patterns differ between highly and moderately skilled learners, and how they change over the course of a task as a function of participants' behavioural performance. Chapter 5 reports on an EEG experiment, in which we investigated whether learners with different degrees of LAA exhibit different oscillatory patterns during acquisition of a novel grammar. The paper reports moreover on the dynamics of the learning process reflected in short- and long-range brain oscillations. Finally, Chapter 6 presents results of a structural imaging experiment employ-

Chapter 1

ing deterministic tractography of the main language-related white matter pathways. How the microstructure of these pathway relates to one's language analytical abilities was at the centre of this experiment.

Chapter 2

Connectivity of the hippocampus and Broca's area during acquisition of a novel grammar

This chapter is based on:

Kepinska, O., de Rover, M., Caspers, J., & Schiller, N. O. (*under review*). Connectivity of the hippocampus and Broca's area during acquisition of a novel grammar.

ABSTRACT

Following Opitz and Friederici (2003) suggesting interactions of the hippocampal system and the prefrontal cortex as the neural mechanism underlying novel grammar learning, the present fMRI study investigated functional connectivity of bilateral BA 44/45 and the hippocampus during an artificial grammar learning (AGL) task. Our results, contrary to the previously reported interactions, demonstrated parallel (but separate) contributions of both regions, each with their own interactions, to the process of novel grammar acquisition. The functional connectivity pattern of Broca's area pointed to the importance of coherent activity of left frontal areas around the core language processing region for successful grammar learning. Furthermore, connectivity patterns of left and right hippocampi (predominantly with occipital areas) were found to be a strong predictor of high performance on the task. Finally, increasing functional connectivity over time of both left and right BA 44/45 with the right posterior cingulate cortex and the right temporo-parietal areas points to the importance of multimodal and attentional processes supporting novel grammar acquisition. Moreover, it highlights the right-hemispheric involvement in initial stages of L2 learning. These latter interactions were found to operate irrespective of the task performance, making them an obligatory mechanism accompanying novel grammar learning.

2.1 Introduction

Acquisition of a new language is a dynamic and multi-layered process. It encompasses various aspects, from developing the lexicon, through mastering the phonology and pronunciation, to acquiring the syntactic and pragmatic competences. Combining linguistic units to form either phonologically, morphologically, or syntactically correct utterances is necessary to achieve proficiency in a second language (L2). However, particularly in case of adult L2 learners, such mastery of the grammatical rules of a language is often burdened by difficulties, and characterised by a great deal of differences between individuals, both in terms of learning rate and the ultimate levels achieved (cf. e.g., Abrahamsson & Hyltenstam, 2009; Antoniou, Ettliger, & Wong, 2016). Investigating the neural aspects of the process of novel grammar acquisition could help in understanding the different learning paths, and provide insights enabling proper training methodologies.

Research into the neural architecture behind grammar acquisition often employs highly controllable paradigms modelling an isolated aspect of language learning. The so-called *artificial grammar learning* (AGL) paradigms (Reber, 1967) can, for example, offer a view on the neurobiological mechanisms of syntax acquisition in real time, without the interference of semantics, phonology or pragmatics, and warrant strict control over prior exposure (cf. e.g., Petersson et al., 2012; Petersson & Hagoort, 2012).

In this line of research, Opitz and Friederici (2003) investigated how the brain modulates the initial stages of acquisition of a new artificial grammar. In a functional magnetic resonance (fMRI) experiment, they employed an AGL paradigm consisting of a number of vocabulary items forming different word categories, combined in ways following rules found in many natural languages. Participants in the study learned this artificial grammar over the course of several learning and test phases. During learning, they were presented with correct sentences formed on the basis of the grammar and were instructed to extract the underlying rules. The test phases consisted of presentation of both grammatical and ungrammatical sentences and participants were asked to assess their grammaticality. The accuracy of these grammaticality judgements served as an indication of the learning progress. Over the course of learning, Opitz and Friederici (2003) found decreasing activity of the left hippocampus; later stages were coupled with increased activation of Broca's area (left inferior frontal gyrus, left IFG). The authors interpreted these results as supporting the importance for hippocampal-

prefrontal interactions during acquisition of language-like rules and suggested that a transition of the roles of the different brain structures critically underlies the process of novel grammar learning. In particular, they argued that hippocampal involvement supporting general, similarity-based learning at the outset of grammar acquisition, with time shifts to the processing system specialised for language localised in the left ventrolateral prefrontal cortex. This process is accompanied by increasing proficiency in the novel grammar, which ultimately results in permanent cortical representations independent of the hippocampal contributions.

As a corollary to this proposal, several studies have provided evidence for contributions of two learning systems to AGL, as well as identified the underlying neural systems. Experiment reported by Opitz and Friederici (2004) tapped directly into the neural signatures of the two learning systems: similarity-based and rule-based learning, during AGL and established that they are supported by the left hippocampal system, and the left ventral premotor cortex respectively. Hauser, Hofmann and Opitz (2012) extended the study by accounting for individual differences in performance on both rule types and showed that development of similarity knowledge during an AGL task depended on the hippocampus and the right IFG, while activity of the left ventral premotor cortex was related to rule processing. On the other hand, however, Musso et al. (2003) proposed Broca's area to be involved in the acquisition of language rules, and its right-hemisphere homologue to underlie rule acquisition more generally. The role of the right Brodmann area (BA) 44/45 therefore seems to deserve more elaboration in the context of grammar learning. More recently, in a study concentrating on behavioural measurements, Opitz and Hofmann (2015) underscored the hybrid (rule- and similarity-driven) account of AGL, proposing an interaction of the two learning processes and suggesting a direct link between them to be established in future research. To the best of our knowledge, whether, and, if so, how the two learning systems might interact with each other during AGL remains thus far unclear.

On the neural level, interactions between the hippocampal formation and cortical regions are particularly important for memory encoding, consolidation and storage, as put forward by the hippocampal/neocortical interactions theory of memory formation by Morris (2006) (see also S.-H. Wang & Morris, 2010). Simons and Spiers (2003) suggested interactions between prefrontal cortex and the medial temporal lobe to be vital for long-term memory. In the domain of language, apart from the studies referred to above, contributions of the hippocam-

pal system and the prefrontal cortex to the initial stages of learning a second language (L2) have also been established for the acquisition of new vocabulary items (e.g., Breitenstein et al., 2005; Davis & Gaskell, 2009); intensive L2 acquisition was further shown to induce cortical (in the left IFG, middle frontal gyrus and superior temporal gyrus) and (right) hippocampal structural plasticity (Mårtensson et al., 2012).

However, relative levels of involvement of different brain structures in a task do not *per se* constitute a functional interaction between them. The question arising is whether the hippocampal and prefrontal contributions to novel grammar learning follow from a direct functional link between them, or whether they are independent from each other in terms of functional connectivity. Interactions between brain regions during a cognitive task (such as those proposed by Opitz & Friederici, 2003) can be explored by investigating temporal correlations between the hemodynamic activity of different brain areas obtained with fMRI. In particular, having prior hypotheses about regions involved, insights into whether and how they are coupled together in performing specific functions can be derived from psychophysiological interaction (PPI) analysis (Friston et al., 1997). Such an approach has been successfully applied to, for example, recent investigations into hippocampal – medial prefrontal interactions during memory integration (Schlichting & Preston, 2016). PPI analyses detect regions whose activity levels can be accounted for by the activation pattern of a predefined seed region in conjunction with a specific cognitive or sensory process. The premise of such investigations is that the MRI signal correlations potentially reveal functional connectivity between regions (Rogers, Morgan, Newton, & Gore, 2007), thus providing information on their common involvement in a task. Interregional correlations of hemodynamic signal fluctuations can moreover be dependent on behavioural measures and thus indicative of skill and performance. For example, Hampson et al. (2006) showed that individuals' reading abilities were associated with their functional connectivity between Broca's area and BA 39.

To the best of our knowledge, no study has tapped directly into the possible interactions between frontal and hippocampal structures during a grammar learning task, by investigating their functional connectivity patterns. The goal of the present experiment was therefore to extend the previous research on the learning-related changes in hemodynamic activity during novel grammar acquisition (Opitz & Friederici, 2003), by employing a PPI analysis and focusing on functional coupling of the crucial hubs in language processing and learning, viz. the hippocampus and Broca's area. Based on previous research (Hauser et al., 2012;

Mårtensson et al., 2012), our analysis involved both left and right hippocampal regions, together with Broca’s area proper and its right-hemisphere homologue. The present study used fMRI to explore the initial stages of L2 acquisition, employing a paradigm adapted from Opitz and Friederici (2003), and a different, complementary analytical approach to the collected data. Specifically, we asked whether there is a direct functional coupling between Broca’s area (left BA 44/45) and the hippocampus during the process of acquisition of novel grammar rules. Furthermore, we set out to explore whether the learning-related connectivity strength of the contributing brain systems can predict how well participants acquire the novel grammar. Based on the previous literature (in particular Opitz & Friederici, 2003), we expected a pronounced functional coupling between Broca’s area (left BA 44/45) and the hippocampus during the whole task. Decreasing levels of hippocampal connectivity (with regions other than the ventrolateral prefrontal cortex), along with increasing functional links of the prefrontal cortex over the course of the task, should also be present. Since the left prefrontal cortical activity was suggested to arise with increasing proficiency in the novel grammar and with the formation of permanent cortical representations, we expect its connectivity patterns to be predictive of the ultimate performance.

2.2 Methods

Data from part of this experiment are also described in Chapter 3 (and in Kepinska, de Rover, Caspers, & Schiller, 2017) examining data-driven functional connectivity networks during AGL and how language learning predispositions influence the whole-brain connectivity patterns. The two studies differ in the analytical approach, in that in Chapter 3 we used an Independent Component Analysis approach to investigate brain’s networks present during novel grammar learning, whereas here we use a PPI approach to investigate how the hippocampi, Broca’s area and its right hemisphere homologue are engaged during the learning experience, and how the connectivity patterns of these predefined ROIs modulate the grammar learning success.

2.2.1 Participants

Forty-two participants took part in the study. Two data-sets had to be discarded due to technical issues. The remaining 40 participants (10 male) were all right-handed native-speakers of Dutch and with normal or corrected-to-normal vision. They were 19-43 years of age ($M = 23.33$).

The Medical Ethical Committee of the Leiden University Medical Centre (LUMC) (Leiden, the Netherlands) approved the protocol of the MRI experiment; behavioural testing was also conducted according to the Ethics Code of the Faculty of Humanities at Leiden University. Participants gave written informed consent prior to the experiment and were remunerated for their time.

2.2.2 Stimuli and design

The stimulus material was an adapted version of the materials used in Opitz and Friederici (2003), i.e. the BROCANTO AGL paradigm (see Section 2.1). In short, the task consisted of three alternating learning and test phases in which grammatical (learning phases), and grammatical and ungrammatical (test phases) sentences were presented. Six days after the scanning, participants performed a delayed transfer test. For a full description of the design see Chapter 3 and Chapter 4. As in the case of Chapter 3 and Kepinska et al. (2017), the present experiment focused on the consecutive learning phases of the AGL task.

2.2.3 Neuroimaging data acquisition and pre-processing

Imaging data were acquired using a Philips 3T MR-system (Best, The Netherlands) located at the Leiden University Medical Centre (LUMC) equipped with a SENSE-32 channel head coil. Three fMRI sequences were acquired for every participant, each during the consecutive learning phase of the AGL task. We obtained echo-planar images (EPI) using a T2*-weighted gradient echo sequence (repetition time [TR] = 2200 ms, echo time [TE] = 30 ms, matrix size: 80 x 80, 38 axial slices, 2.75 x 2.75 x 2.75 mm (+ 10% slice gap) voxel size). EPIs were scanned parallel to the anterior–posterior commissure plane. The length of each scan sequence was 200 volumes and lasted 7.5 minutes. Anatomical imaging included a 3D gradient-echo T1-weighted sequence (TR = 9.755 ms, TE = 4.59 ms; matrix 256 x 256; voxel size: 1.2 x 1.2 x 1.2 mm; 140 slices) and a high-resolution T2-weighted image (TR = 2200 ms, TE = 30 ms; matrix 112 x 112; voxel size: 2.0 x 2.0 x 2.0 mm; 84 slices).

Imaging data from two participants were discarded from further analyses due to technical issues. The remaining forty data sets acquired during the learning phases of the AGL task were processed using FSL software Version 5.0.7 (FMRIB's Software Library, <http://www.fmrib.ox.ac.uk/fsl>, Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012). FEAT (fMRI Expert Analysis Tool) Version 6.00 (<http://www.fmrib.ox.ac.uk/fsl>), implemented in MELODIC (Multi-

variate Exploratory Linear Decomposition into Independent Components) Version 3.14, was used for pre-processing. The following pre-statistics processing was applied: motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002), non-brain removal using BET (Smith, 2002), spatial smoothing using a Gaussian kernel of FWHM 5 mm, grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor, high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma=50.0s$).

The functional images were registered to MNI-152 standard space (T1-standard brain averaged over 152 subjects; Montreal Neurological Institute, Montreal, QC, Canada) using a three-step registration from functional to high-resolution structural T2-image (rigid body, 6 degrees of freedom) to T1-image (rigid body, 6 degrees of freedom) to MNI-template (affine registration, 12 degrees of freedom). Registration was carried out using FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001).

2.2.4 Data analysis

2.2.4.1 Behavioural data

The behavioural performance data gathered in the three test phases of the AGL task performed in the MRI scanner served as an indication of learning progress, and the delayed transfer test scores as an indication of the retention of the acquired rules and the degree of grammar learning success. For the analysis, the individual hit- and false-alarm rates for each participant were first transformed into d' scores in order to account for response bias (Macmillan & Creelman, 2005). Following previous studies employing similar experimental designs (Brod & Opitz, 2012; Friederici, Steinhauer, & Pfeifer, 2002; Hauser, Hofmann, & Opitz, 2012; Opitz, Ferdinand, & Mecklinger, 2011; Opitz & Friederici, 2003, 2004, 2007), the d' scores were then analysed with a repeated measures ANOVA (alpha level = 0.05) with learning phase (first phase, second phase, last phase, and transfer test) as a within-subject factor. The analysis was performed in SPSS version 22 (IBM SPSS, 2012). Mauchley's test showed violations of sphericity against the factor phase, $\chi^2(5) = 27.310$, $p < .001$, therefore Greenhouse-Geisser correction for non-sphericity was applied ($\epsilon = 0.730$).

2.2.4.2 First-level analysis of imaging data

We conducted a PPI analysis to examine the functional interaction between specific ROIs (seed ROIs) and the rest of the brain. Four seed ROIs were defined anatomically. Masks of left BA 44/45 (Broca's area) and right BA 44/45 were defined using the Juelich Histological Atlas, as implemented within FSLVIEW, part of FSL (<http://www.fmrib.ox.ac.uk/fsl>). The probabilistic maps of BA 44 and BA 45 in each hemisphere were thresholded at 50%, summed and binarised (cf. Flöel, de Vries, Scholz, Breitenstein, & Johansen-Berg, 2009). Masks of left and right hippocampus were defined on the basis of the Harvard-Oxford Subcortical Structural Atlas as implemented within FSLVIEW, part of FSL (<http://www.fmrib.ox.ac.uk/fsl>). Again, the probabilistic maps of the left and right hippocampus were thresholded at 50% and binarised.

Each ROI was projected on the pre-processed functional images (three data sets per participant). The time series of BOLD activity was extracted using *fslmeans* utility by averaging across all voxels within each ROI, for each individual data set. The PPI analysis was conducted for every ROI separately using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library, <http://www.fmrib.ox.ac.uk/fsl>). The design matrix of the first-level statistical analysis comprised of three regressors: the first two were the psychological variable (task design) convolved with a double gamma hemodynamic response function, and the physiological variable (the time-course of the seed ROI); the interaction between the physiological and psychological variables (PPI) was the third regressor. Brain regions showing significant PPI effects were determined by testing for a positive slope of the PPI regressor. Time-series statistical analysis was carried out using FILM (Woolrich, Ripley, Brady, & Smith, 2001).

2.2.4.3 Subject-level analysis of imaging data

Individual contrast images (corresponding to the three learning phases of the AGL task performed during the MRI) were entered into the subject-level analysis. Two separate subject-level analyses were performed: in the first, mean functional connectivity maps of the three phases of the task per subject were calculated; in the second analysis, we tested for significant linear increases and decreases in functional connectivity over the course of the task. In both cases, data were processed with FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library, <http://www.fmrib.ox.ac.uk/fsl>). The three phases of

the experiment were not enough for a mixed effects model, hence a fixed effects model was used, by forcing the random effects variance to zero in FLAME (FMRIB's Local Analysis of Mixed Effects) (Beckmann, Jenkinson, & Smith, 2003; Woolrich, 2008; Woolrich, Behrens, Beckmann, Jenkinson, & Smith, 2004). Again, both subject-level analyses were performed separately for each seed ROI.

2.2.4.4 Group-level analysis of imaging data

Finally, the contrast images generated on the two subject-level analyses were entered into group-level statistical analyses. Following the subject-level analyses, two separate analyses were performed. In the first the mean, i.e. time-invariant functional connectivity of the four seed ROIs during the whole task was investigated. Additionally, we examined whether the magnitude of functional connectivity during the AGL task predicts individual attainment of the presented grammar rules (operationalized by the transfer test scores).

Data processing was carried out using FEAT (fMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library, <http://www.fmrib.ox.ac.uk/fsl>). The analysis was carried out using FLAME (FMRIB's Local Analysis of Mixed Effects) stage 1 (Beckmann et al., 2003; Woolrich, 2008; Woolrich et al., 2004). Pre-threshold masking was applied and a grey matter mask was used to mask out non-grey matter regions. Subsequently, the Z (Gaussianised T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $p = 0.05$ (Worsley, 2001), with a Bonferroni correction for the number of investigated ROIs.

The second analysis explored whether the functional connections strengthened or weakened progressively as participants learned the task, and whether the changes in connectivity were coupled with the individual performance. The same analysis steps were taken as in the case of the time-invariant functional connectivity analysis described above, the difference being the subject-level contrast images processed.

2.3 Results

2.3.1 Behavioural data

The analysis of the behavioural data revealed that the d' scores on the AGL task increased over the course of the experiment (see Figure 2.1): there was a main effect of learning phase, $F(2.189, 85.386) = 34.898$,

$p < .001$, $\eta_p^2 = .472$, and a significant difference between the mean d' scores on the first and second phase ($F(1, 39) = 32.417$, $p < .001$, $\eta_p^2 = .454$), and second and third phase ($F(1, 39) = 22.197$, $p < .001$, $\eta_p^2 = .363$). The difference between the d' scores on the third phase and the subsequent transfer test was not significant ($F(1, 39) = 3.196$, $p = .082$, $\eta_p^2 = .076$).

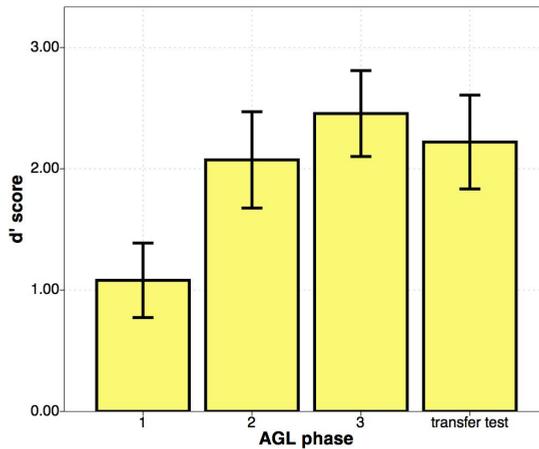


Figure 2.1 Performance (d' scores) across all participants during the three AGL test phases (performed in the scanner) and the subsequent transfer test. Error bars stand for 95% Confidence Intervals.

2.3.2 PPI results

Two separate analyses were performed. The first, concentrated on mean, i.e. time-invariant functional connectivity of the four seed ROIs during the whole task. Apart from group mean connectivity, modulation of the strength of the functional connections of each ROI by the individual attainment of the presented grammar rules (operationalized by the transfer test scores) was investigated. The results of this analysis are described in Section 2.3.2.1 and presented in Table 2.1 and Figure 2.2.

The second analysis examined whether the functional connections strengthened or weakened progressively as participants learned the task, and whether the changes in connectivity predicted the individual performance, see Section 2.3.2.2, Table 2.2 and Figure 2.3.

2.3.2.1 Time-invariant functional connectivity

During the whole AGL task, functional connectivity for the whole group, irrespective of task performance was found for only one of the four investigated seed ROIs, namely the left BA 44/45. The cluster exhibiting functional connectivity with the left BA 44/45 was localised in the occipital lobe, with a peak in the left occipital pole, see Figure 2.2a (in green) and Table 2.1, Section (a). Furthermore, the pattern of functional coupling of Broca's area also modulated the task performance, see Figure 2.2a (in red) and Table 2.1, Section (a). The higher the ultimate rule knowledge, the more functionally connected the left BA 44/45 was during the task with areas immediately adjacent to it. The peak of this effect was localised in the middle frontal gyrus, and the voxels forming the cluster extended further to the paracingulate, precentral, and the superior frontal gyri.

The strength of functional coupling of both left and right hippocampi was greatest for participants who performed best on the transfer test. The left hippocampal connectivity modulating the task performance was found in the occipital cortex, with a peak in the contralateral (right) occipital fusiform gyrus, and voxels localised in the left occipital fusiform gyrus, see Figure 2.2b and Table 2.1, Section (c). The right hippocampus exhibited increased functional connectivity with three clusters: (1) the right precuneus/cuneal cortex, extending to the right occipital pole and the lateral occipital cortex; (2) the contralateral (left) occipital fusiform gyrus extending to the right occipital fusiform gyrus, right lateral occipital cortex, and the left lingual gyrus; and (3) the temporal occipital fusiform cortex extending to the cerebellum (left crus I, II and left VI), see Figure 2.2c and Table 2.1, Section (d).

TIME-INVARIANT FUNCTIONAL CONNECTIVITY

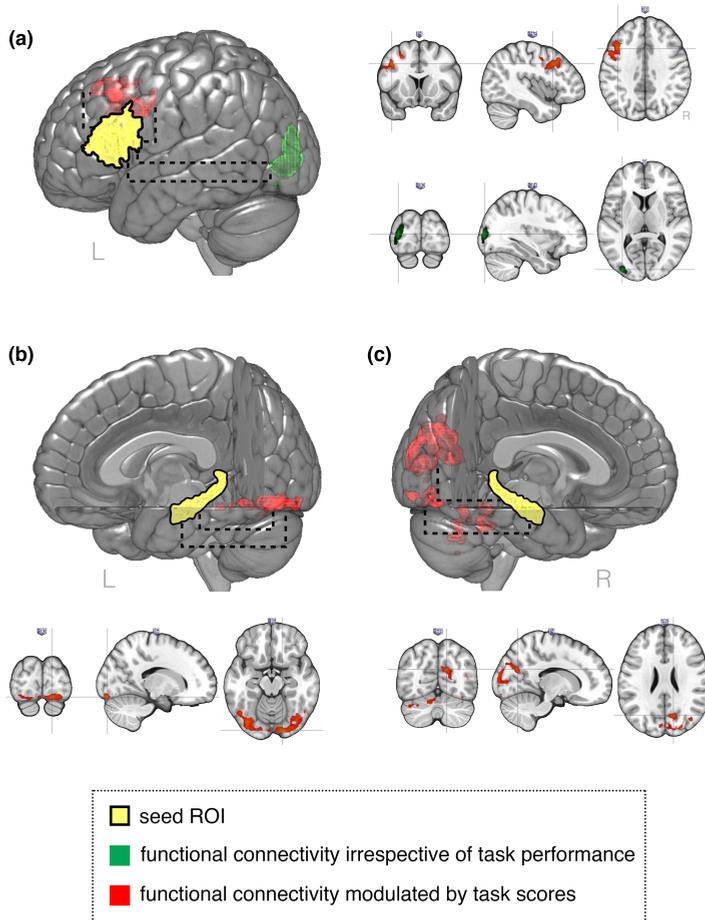


Figure 2.2 Results of the PPI analysis investigating time-invariant functional connectivity of the four seed ROIs. Represented are the mean connectivity maps (Z (Gaussianised T/F) statistic images) of each seed ROI: a) Left BA 44/45 (Broca's region), (b) Left Hippocampus, (c) Right Hippocampus; the seed ROI localised in the right BA 44/45 did not yield any significant clusters. Results are displayed at $p < .05$, Bonferroni-corrected. In yellow, the seed ROIs are marked; in green results of the contrast testing for mean functional connectivity of the whole group irrespective of task performance; in red, the connectivity modulated by the task performance is shown. Brain activations are displayed using MRIcroGL (<http://www.mccauslandcenter.sc.edu/mricrogl/>).

| Cortical region (peak) | Size (voxels) | p -value | Z_{\max} | L/R | Peak location (mm) | | |
|--|---------------|------------|------------|-----|--------------------|-----|-----|
| | | | | | X | Y | Z |
| (a) Seed ROI: Left Broca's region | | | | | | | |
| Connectivity irrespective of performance (group mean): | | | | | | | |
| Occipital Pole / Lateral Occipital Cortex, superior division | 610 | $p=0.005$ | 4.99 | L | -34 | -90 | 8 |
| Performance-related connectivity: | | | | | | | |
| Middle Frontal Gyrus | 1370 | $p<.001$ | 4.41 | L | -42 | 14 | 38 |
| (b) Seed ROI: Right Broca's region | | | | | | | |
| Connectivity irrespective of performance (group mean): | | | | | | | |
| - | - | - | - | - | - | - | - |
| Performance-related connectivity: | | | | | | | |
| - | - | - | - | - | - | - | - |
| (c) Seed ROI: Left Hippocampus | | | | | | | |
| Connectivity irrespective of performance (group mean): | | | | | | | |
| - | - | - | - | - | - | - | - |
| Performance-related connectivity: | | | | | | | |
| Occipital Fusiform Gyrus | 1089 | $p<.001$ | 4.44 | R | 16 | -90 | -16 |
| (d) Seed ROI: Right Hippocampus | | | | | | | |
| Connectivity irrespective of performance (group mean): | | | | | | | |
| - | - | - | - | - | - | - | - |
| Performance-related connectivity: | | | | | | | |
| Precuneus Cortex / Cuneal Cortex | 1432 | $p<.001$ | 3.95 | R | 14 | -68 | 26 |
| Occipital Fusiform Gyrus | 860 | $p<.001$ | 3.69 | L | -18 | -86 | -16 |
| Temporal Occipital Fusiform Cortex | 698 | $p<.01$ | 3.53 | L | -32 | -58 | -20 |

Table 2.1 Brain areas exhibiting functional connectivity during the three learning phases of the AGL task with the four ROIs: (a) Left BA 44/45 (Broca's region), (b) Right BA 44/45, (c) Left Hippocampus, (d) Right Hippocampus. Per each ROI, functional connectivity both irrespective of performance (group mean), and modulated by the ultimate task performance are reported. The x, y and z coordinates (in mm) are in MNI space, regions were labelled according to Harvard-Oxford Cortical and Subcortical Structural Atlases and Juelich Histological Atlas (all implemented within FSLVIEW, part of FSL).

2.3.2.2 Time-varying functional connectivity

Functional connections of both left and right BA 44/45 strengthened progressively as participants learned the task. These changes in connectivity were not affected by task performance, see Figure 2.3 and Table 2.2. Over the course of the AGL task the left BA 44/45 increased its functional coupling with two clusters: (1) a right parieto-temporal cluster with its peak in the angular gyrus/supramarginal gyrus, encompassing the superior and middle temporal gyri as well; (2) the right posterior cingulate gyrus extending to the left anterior cingulate gyrus and the right precuneus, see Figure 2.3 (in red), and Table 2.2, Section (a). The right BA 44/45 exhibited increasing functional connectivity with the following areas: (1) a cluster with a peak in the juxtapositional lobule (supplementary motor cortex) with voxels extending to the left paracingulate gyrus and the right posterior cingulate gyrus; (2) right

temporal areas encompassing middle temporal gyrus, lateral occipital cortex, planum temporale and supramarginal gyrus, see Figure 2.3 (in green), and Table 2.2, Section (b). No time-varying effects on the hippocampal connectivity were found.

INCREASING FUNCTIONAL CONNECTIVITY OVER TIME

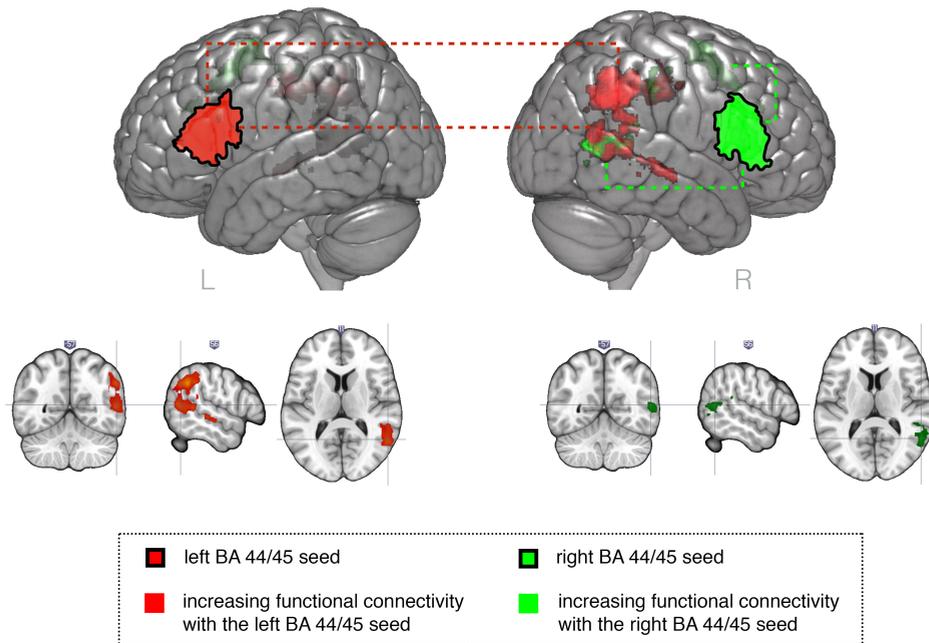


Figure 2.3 Results of the analysis investigating changes in functional coupling of the four seed ROIs over time: both left and right areas BA 44/45 increased their functional connectivity over the course of the task. The Z (Gaussianised T/F) statistic images displayed at $p < .05$, Bonferroni-corrected. In red, areas whose functional connectivity progressively increased during the three learning phases of the AGL task with the left BA 44/45 (Broca's region) are shown, in green with the right BA 44/45. Brain activations are displayed using MRICroGL (<http://www.mccauslandcenter.sc.edu/mricrogl/>).

2.4 Discussion

The main goal of the present study was to investigate whether there are direct functional links between the hippocampus, and Broca's area and its right-hemisphere homologue during acquisition of grammar rules. To this end, an fMRI experiment was performed in which participants were exposed to a novel grammar (BROCANTO, Opitz & Friederici,

2003) and were instructed to extract its rules on the basis of example sentences presented one by one over the course of three learning phases. Participants' progress was measured by means of test phases (following each learning phase) in which they were providing grammaticality judgements to both correct and incorrect sentences. Their sensitivity to the grammatical structure of BROCANTO (operationalised by means of d' scores) increased over the course of the task and did not significantly decrease until a delayed transfer test performed six days after the initial learning task.

| Cortical region (peak) | Size (voxels) | p -value | Z_{\max} | L/R | Peak location (mm) | | |
|--|---------------|------------|------------|-----|--------------------|-----|----|
| | | | | | X | Y | Z |
| (a) Seed ROI: Left Broca's region | | | | | | | |
| Increasing connectivity over time: | | | | | | | |
| Angular Gyrus / Supramarginal Gyrus, posterior division | 2326 | $p < .001$ | 5.09 | R | 56 | -48 | 36 |
| Cingulate Gyrus, posterior division | 873 | $p < .001$ | 3.95 | R | 6 | -26 | 38 |
| Decreasing connectivity over time: | | | | | | | |
| - | - | - | - | - | - | - | - |
| (b) Seed ROI: Right Broca's region | | | | | | | |
| Increasing connectivity over time: | | | | | | | |
| Juxtapositional Lobule Cortex (Supplementary Motor Cortex) | 930 | $p < .001$ | 4.26 | - | 0 | 2 | 62 |
| Middle Temporal Gyrus | 526 | $p = .01$ | 3.69 | R | 56 | -58 | 10 |
| Decreasing connectivity over time: | | | | | | | |
| - | - | - | - | - | - | - | - |
| (c) Seed ROI: Left Hippocampus | | | | | | | |
| Increasing connectivity over time: | | | | | | | |
| - | - | - | - | - | - | - | - |
| Decreasing connectivity over time: | | | | | | | |
| - | - | - | - | - | - | - | - |
| (d) Seed ROI: Right Hippocampus | | | | | | | |
| Increasing connectivity over time: | | | | | | | |
| - | - | - | - | - | - | - | - |
| Decreasing connectivity over time: | | | | | | | |
| - | - | - | - | - | - | - | - |

Table 2.2 Brain areas whose functional connectivity progressively changed during the three learning phases of the AGL task with the four ROIs: (a) Left BA 44/45 (Broca's region), (b) Right BA 44/45, (c) Left Hippocampus, (d) Right Hippocampus. The x, y and z coordinates (in mm) are in MNI space, regions were labelled according to Harvard-Oxford Cortical and Subcortical Structural Atlases and Juelich Histological Atlas (all implemented within FSLVIEW, part of FSL).

Previous research suggested that over the course of an AGL task hippocampal involvement shifts to brain areas specialised for language processing in Broca's region (Opitz & Friederici, 2003). Following this proposal, we performed a set of analyses on the fMRI data collected during

the three successive learning phases of the BROCANTO task, tapping directly into the functional couplings of four pre-defined regions of interest. The premise of our approach was that correlated time-courses of BOLD activity of two or more regions during a cognitive task point to their functional integration in performing the task in question (Friston, 2011; Friston et al., 1997). We thus investigated the functional connectivity patterns of the left and right hippocampi, and left BA 44/45 (Broca's area) and right BA 44/45. We expected Broca's area to be functionally coupled with the hippocampus during the learning process. Since L2 learning is a dynamic process, we furthermore examined the changes in functional connectivity of the seed ROIs over time. Here, our prediction was that since hippocampal contributions are most prevalent in the initial stages of learning, and the ventrolateral prefrontal cortex activity arises with increasing proficiency in the novel grammar, the functional connectivity patterns of both should be modulated by time. In particular, we expected a decrease in hippocampal connectivity (with regions other than the prefrontal cortex) over time, and an increase of the connectivity of the left BA 44/45. The delayed transfer test scores were predicted to be modulated by the connectivity patterns of Broca's region.

2.4.1 Interactions of the hippocampal system and the prefrontal cortex?

The expected interactions, i.e. functional coupling, of the hippocampal system and the prefrontal cortex in learning novel grammar have not been borne out by the present results. Our data suggest that the processes governed by Broca's region and the hippocampus seem to operate in parallel and complement each other, but not in a direct way to be functionally connected with one another. As such these results are in line with the notion of two separate learning systems present during grammar learning: the similarity-based and rule-based learning mechanisms as proposed by Opitz and Friederici (2004), and Hauser, Hofmann and Opitz (2012). On the basis of our experiment, such a hybrid model accounting for involvement of both surface knowledge and knowledge of grammatical rules in AGL could be extended, by underscoring the autonomous nature of these mechanisms. We note that null effects in neuroimaging analyses should be interpreted with great caution, and that the possibility of a direct functional coupling of the hippocampus and Broca's area during acquisition of novel grammar rules merits further investigations. One possibility of investigating the existence of such direct interactions would be a later stage of learning, past

the initial encoding phase (cf. e.g., Tambini, Ketz, & Davachi, 2010). Another way of approaching the question of a functional coupling between Broca's region and the hippocampus during AGL would be an investigation into interactions between subparts of the regions in question. Smaller ROIs might have the advantage of capturing more localised BOLD signal fluctuations, albeit introducing the risk of neglecting the region's activation peak for some subjects, due to inter-individual variations.

2.4.2 Connectivity of the hippocampus and Broca's area during the whole task

Over the course of the task we observed functional connections of left and right hippocampi, and Broca's region to modulate the grammatical knowledge acquired by the participants. Additionally, Broca's connectivity was found to be present irrespective of the performance: the region was functionally coupled with left occipital areas (see Figure 2.2a). Since the stimuli in the current experiment were presented visually, a coupling of the core syntactic processing area (cf. Friederici, 2006; Musso et al., 2003) with regions underlying visual processing seems necessary for attending to the task at hand. Furthermore, such a functional connection most probably follows from structural connectivity of the left inferior frontal areas, in particular in the form of the inferior fronto-occipital fasciculus (IFOF) (Anwander, Tittgemeyer, von Cramon, Friederici, & Knösche, 2007). This fibre track runs ventrally between the frontal regions and the posterior temporal and occipital lobe (Catani, Howard, Pajevic, & Jones, 2002) and has been implicated in, among others, such functions as reading (Epelbaum et al., 2008), and semantic processing of language (Duffau, Moritz-Gasser, & Mandonnet, 2014; Wu, Sun, Wang, & Wang, 2016). Whether and how the IFOF is directly involved in novel grammar learning, deserves additional examination.

The strength of functional connectivity of Broca's area was also correlated with the transfer test scores, thereby confirming our hypothesis concerning its connectivity patterns to be predictive of the ultimate performance. Participants who scored highest on the delayed transfer test, exhibited the strongest functional coupling of the left BA 44/45 with areas immediately adjacent to it, in the posterior, superior, as well as medial direction (see Figure 2.2a). Previous research has provided evidence for the importance of activity of regions bordering on Broca's area to the acquisition of novel grammar rules (e.g., Bahlmann, Schubotz, & Friederici, 2008). Moreover, the sites found to be functionally linked

with the left BA 44/45 in our study have been previously implicated in executive functions, including working memory (superior frontal gyrus, cf. du Boisgueheneuc et al., 2006), executive attention (middle frontal gyrus, cf. Andersson et al., 2009), verbal fluency and spatial working memory abilities (paracingulate gyrus, cf. Fornito et al., 2004). The results point to the conclusion that involvement of a broader network surrounding Broca's area in an AGL task is advantageous to the learning process. Such a coherence of activity of left frontal areas extending outside the traditionally defined core linguistic processing region results in a higher retention of the newly acquired grammar rules. This dense interconnectivity is further in line with investigations into the structural organisation of the region in the form of the frontal aslant tract and short U-shaped fibres connecting adjacent gyri (Catani et al., 2012; Ford, McGregor, Case, Crosson, & White, 2010; Lemaire et al., 2013). Whether the microstructure of these tracts would reflect the behavioural performance in a similar way as the functional connectivity patterns established in our data do, remains open to further investigations.

Successful learning of the grammatical rules of BROCANTO was further modulated by the functional connectivity patterns during the task of both left and right hippocampi (see Figure 2.2b and c). Hippocampal interactions with cortical regions seem critical for declarative memory formation, as the region has been proposed to underlie the initial binding of new associations formed from various aspects of an event processed in different neocortical areas (cf. Breitenstein et al., 2005; Eichenbaum & Cohen, 2004). Indeed, functional connectivity of the hippocampus has been shown to drive successful memory formation in previous studies (Gagnepain et al., 2011; Ranganath, Heller, Cohen, Brozinsky, & Rissman, 2005). Furthermore, the fact that the majority of areas exhibiting a functional connectivity with the hippocampal ROIs were localised in the occipital cortex, highlights the role the hippocampus plays in similarity-based learning mechanisms. Interestingly, the right hippocampus exhibited a pattern of connectivity more dispersed than the left. Apart from with left occipital areas, it was functionally linked with the precuneus, a region implicated in a number of highly integrated tasks, such as mental (visuo-spatial) imagery, episodic memory retrieval, self-processing and consciousness (Cavanna & Trimble, 2006). Moreover, hippocampal connectivity modulating the ultimate task performance was found for cerebellar structures, previously put forward to underlie spatial memory (Iglói et al., 2015) and spatial and temporal processing (Yu & Krook-Magnuson, 2015). Since both areas (precuneus and cerebellum) bear significance for visuo-spatial processing, these results seem to further emphasise the importance of the

development of surface knowledge for successful learning and memorisation of novel grammar rules.

2.4.3 Dynamics of functional connectivity during novel grammar learning

Contrary to our expectations, the hippocampal connectivity with regions other than the prefrontal cortex did not decrease over the course of the task. In terms of time-related effects, the consecutive stages of encoding of the new grammatical rules of BROCANTO were found to be associated with increasing functional connectivity of both left and right BA 44/45. The fact that this time effect was not modulated by task performance, might point to the obligatory nature of the involvement of Broca's area and its right-hemisphere homologue to the grammar learning process, extending the idea that syntax processing in the left IFG is automatic and involuntary (Musso et al., 2003). In other words, it seems to be the case that attending to AGL stimuli will over time increase the functional links of the ventrolateral prefrontal cortex bilaterally, no matter the actual level of attainment. Furthermore, the increasing functional connectivity of both our prefrontal regions of interest is in line with the view that the rule-based processing in AGL evolves gradually over time (Opitz & Hofmann, 2015). In addition, given the common topography of the connectivity patterns of both ROIs, it seems to be the case that both areas subserve similar rule-related processing systems.

The areas with which both left and right BA 44/45 progressively strengthened their functional coupling were partly overlapping and were localised in the right hemisphere and in the medial cortex. The sites in which the time-dependent functional links of both left and right BA 44/45 converged was the right posterior cingulate gyrus, along with the right middle temporal gyrus, extending to the right angular and supramarginal gyri, corresponding to the right temporo-parietal junction (TPJ) (cf. e.g., Mars et al., 2012).

These results point to the importance of both intra- and inter-hemispheric functional connectivity of the prefrontal cortex with the right parieto-temporal areas and the posterior cingulate gyrus during novel grammar learning. The latter has been previously proposed to be involved in controlling attentional focus (Leech & Sharp, 2014), memory consolidation of complex events (Bird, Keidel, Ing, Horner, & Burgess, 2015), and binding semantic representations on a multi-modal level (Jessen et al., 1999). Our data suggest that the region can also be seen as a site underlying encoding of grammatical rules, be it through its in-

volvement in attentional processes or memory consolidation. The regions in and surrounding the right TPJ are particularly important for multimodal processing. The importance of the inferior parietal lobule for language learning has been previously established by our group (Kepinska, de Rover, Caspers, & Schiller, 2016, see Chapter 4), as well as by others (Barbeau et al., 2016; Goranskaya et al., 2016; Prat, Yamasaki, Kluender, & Stocco, 2016). The TPJ itself has been associated with reorienting of attention, theory of mind (Krall et al., 2015) and in more general terms, with updating internal models of the environment (Geng & Vossel, 2013). The importance of attentional and multimodal processing in acquisition of novel grammar rules seems to be emphasised by the results of the present experiment. Moreover, the findings support claims of Kirchoff, Wagner, Maril and Stern (2000) who postulated that prefrontal modulation of posterior cortical representations is central to encoding. In more general terms, Jung & Haier (2007) have proposed the interactions between frontal and parietal cortices to underpin individual differences in reasoning abilities in humans. Viewed in the context of their Parieto-Frontal Integration Theory of Intelligence, the present results might also suggest increasing reasoning demands over the course of the task.

Finally, it remains to be noted that the patterns of increasing connectivity over time of both left and right BA 44/45 were constrained to the right hemisphere. We argued elsewhere (Kepinska et al., 2016, or Chapter 4) that engagement of the right hemisphere in adult L2 learning seems advantageous for the learning process, contrary to the idea that suppression of contralateral activity benefits language performance (Antonenko et al., 2012; Thiel et al., 2006). The findings of the present experiment appear to highlight the supporting role the right hemisphere might play in processes related to language learning, especially in its initial stage.

2.5 Conclusion

The present study examining the functional connectivity of bilateral BA 44/45 and the hippocampus aimed at exploring the possible interactions between the medial temporal and prefrontal cortex. Our results, instead of the expected interactions, rather demonstrated parallel contributions of both regions to the process of novel grammar acquisition. The functional connectivity pattern of Broca's area underscores the importance of coherent activity of left frontal areas around the core language processing region for successful grammar learning. Furthermore, the encoding of novel linguistic rules driven by the interplay of the visual (oc-

capital lobe) and memory (hippocampus) hubs of the brain seems to be a strong predictor of successful grammar acquisition. Finally, increasing functional connectivity over time of both left and right BA 44/45 with the right posterior cingulate cortex and the right temporo-parietal areas points to the importance of multimodal and attentional processes supporting novel grammar acquisition. Moreover, it highlights the right-hemispheric involvement in initial stages of L2 acquisition. These latter interactions seem to operate irrespective of the task performance, making them an obligatory neural mechanism accompanying novel grammar learning.

2.6 Acknowledgements

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Chapter 3

Whole-brain functional connectivity during acquisition of novel grammar: distinct functional networks depend on language learning abilities

This chapter is based on:

Kepinska, O., de Rover, M., Caspers, J., & Schiller, N. O. (2017). Whole-brain functional connectivity during acquisition of novel grammar: distinct functional networks depend on language learning abilities. *Behavioural Brain Research*, 320 (2017) 333–346. <http://dx.doi.org/10.1016/j.bbr.2016.12.015>

ABSTRACT

In an effort to advance the understanding of brain function and organisation accompanying second language learning, we investigate the neural substrates of novel grammar learning in a group of healthy adults, consisting of participants with high and average language analytical abilities (LAA). By means of an Independent Components Analysis, a data-driven approach to functional connectivity of the brain, the fMRI data collected during a grammar-learning task were decomposed into maps representing separate cognitive processes. These included the default mode, task-positive, working memory, visual, cerebellar and emotional networks. We further tested for differences within the components, representing individual differences between the High and Average LAA learners. We found high analytical abilities to be coupled with stronger contributions to the task-positive network from areas adjacent to bilateral Broca's region, stronger connectivity within the working memory network and within the emotional network. Average LAA participants displayed stronger engagement within the task-positive network from areas adjacent to the right-hemisphere homologue of Broca's region and typical to lower level processing (visual word recognition), and increased connectivity within the default mode network. The significance of each of the identified networks for the grammar learning process is presented next to a discussion on the established markers of inter-individual learners' differences. We conclude that in terms of functional connectivity, the engagement of brain's networks during grammar acquisition is coupled with one's language learning abilities.

Abbreviations: AGL, artificial grammar learning; BOLD, blood-oxygenation-level-dependent; DMN, default mode network; EPI, echo-planar images; FEAT, FMRI Expert Analysis Tool; fMRI, functional magnetic resonance imaging; IC, independent component; ICA, independent component analysis; IFG, inferior frontal gyrus; L2, second language; LAA, language analytical ability; MELODIC, Multivariate Exploratory Linear Decomposition into Independent Components; PCA, principal component analysis; ROI, region of interest; SLA, second language acquisition; TE, echo time; TFCE, threshold-free cluster enhancement approach; TR, repetition time; VWFA, visual word form area

3.1 Introduction

The knowledge of a second language (L2) in today's globalised world seems more and more indispensable. High levels of proficiency in an L2 play an important role in many people's economic, social and private lives. No matter its importance however, language acquisition can be characterised by a great deal of variability in the rate, efficiency and ultimate success. Understanding the factors contributing to such variability can aid the efforts to describe the theoretical foundations of second language acquisition (SLA) and - from an applied point of view - in improving the outcomes of learning and instruction.

Like other high-level cognitive functions, language is governed by synchronized activity of distributed areas (cf. e.g., Bressler, 1995; Bressler & Menon, 2010; Friederici & Singer, 2015; Mesulam, 1998; W. Singer, 1993; Weiss & Mueller, 2003). How different brain areas interact with each other, and what networks arise from those interactions is a question posed in more and more investigations into the neural architecture behind language processing and acquisition. Insights into the connectivity of the brain, both in terms of its structural (e.g., Catani et al., 2007; García-Pentón, Pérez Fernández, Iturria-Medina, Gillon-Dowens, & Carreiras, 2014; López-Barroso et al., 2013; Loui, Li, & Schlaug, 2011; Mohades et al., 2012; Stein et al., 2012; Xiang, Dediu, Roberts, Norris, & Hagoort, 2012) and functional networks (e.g., Antonenko et al., 2012; Cordes et al., 2000; Dodel et al., 2005; Ghazi Saidi et al., 2013; Pérez, Gillon Dowens, et al., 2015; Reiterer, Pereda, & Bhattacharya, 2009, 2011; Ventura-Campos et al., 2013; Veroude, Norris, Shumskaya, Gullberg, & Indefrey, 2010; Yang, Gates, Molenaar, & Li, 2015), keep advancing our understanding of the neural foundations of human communication.

One powerful tool for exploring the connectivity of the brain is functional magnetic resonance imaging (fMRI). It offers a view on temporal correlations between the hemodynamic activity of different brain areas and can be used for visualising and quantifying functional connectivity patterns at rest or during cognitive tasks (cf. Beckmann, DeLuca, Devlin, & Smith, 2005; Biswal, Yetkin, Haughton, & Hyde, 1995; Damoiseaux et al., 2006; Rissman, Gazzaley, & D'Esposito, 2004; Smith et al., 2009; van Diessen, Diederer, Braun, Jansen, & Stam, 2013; Veroude et al., 2010).

With this paper, we wanted to explore the functional connectivity patterns during initial phases of L2 acquisition and networks' characteris-

tics responsible for successful acquisition of a new language: a theme that has recently attracted interest in other studies in the context of language acquisition, which we briefly review below.

3.1.1 Functional networks of the brain and individual differences in L2 acquisition

Functional networks associated with vocabulary learning in a new language were investigated by Veroude et al. (2010). Functional connectivity of brain regions involved in phonological processing was measured during rest, before and after exposure to a new language. The authors showed that the recorded connectivity patterns differ between ‘good’ and ‘bad’ learners determined on the basis of their performance on a word recognition task after the scanning. Before the exposure to a new language, stronger connectivity between two sets of regions: the left supplementary motor area and the left precentral gyrus, and between the left insula and the left rolandic operculum was observed for ‘good’ compared to ‘bad’ learners. The authors interpreted this stronger connectivity as representing “a favourable disposition for the processing of the unknown language input” (p. 25). Furthermore, at the end of the task, good learners exhibited stronger functional connectivity between the left and right supramarginal gyrus, which was interpreted as an effect of exposure to the language itself and not a pre-existing difference between learners.

In a study investigating brain connectivity patterns in a group of Persian speakers learning new vocabulary in French, Ghazi Saidi et al. (2013), showed that network integration levels decreased as proficiency for L2 increased, thus reflecting more automatic processing of the L2. Furthermore, Yang et al. (2015) recently investigated the development of brain networks as a function of short-term tonal L2 learning experience and reported functional connectivity results relating to successful acquisition of novel words. The successful learners in their study were identified on the basis of behavioural performance after the training, but due to their high accuracy on the sound discrimination task prior to training, they were hypothesized to be “well suited to learning a vocabulary in which lexical tones make up the critical information” (p. 45). At the level of brain connectivity, the successful learners demonstrated more integrated networks both before and after the training: in comparison to the non-learners, their frontal-temporal network was stronger at the first time-point, whereas at the second, they could be characterized by strong global, as well as local connectivity, and automatic lexical

processing of acquired word knowledge driven by the inferior parietal lobule.

Learning novel words is undeniably one of the most important building blocks of acquisition of a new language. The brain's functional connectivity underlying another crucial subcomponent of language learning, namely the acquisition of grammatical rules, was investigated by Antonenko et al. (2012), and Dodel et al. (2005). In their study, Antonenko et al. (2012) used an artificial grammar learning (AGL) task to explore the ability to extract grammatical rules from new material in healthy older adults and found an opposite relationship between AGL task performance and resting-state functional connectivity of left and right BA 44/45: lower performance was tied to stronger inter-hemispheric functional coupling. Processing of syntax in L2 by bilinguals was explored by Dodel et al. (2005) who showed that regions associated with syntax and language production – left inferior frontal gyrus (IFG), putamen, insula, precentral gyrus, and the supplementary motor area – were more functionally connected in L2 than in L1. The strength of this functional connectivity was modulated by participants' syntactic proficiency: the functional connectivity network was less present in less proficient bilinguals.

With the present experiment, we aimed at concentrating on novel grammar learning, and capturing whole-brain functional connectivity correlates of the process of new syntax acquisition in its initial phase. Similarly to Antonenko et al. (2012), we employed an AGL paradigm in order to ensure that our data represent the neurobiology of syntax acquisition and processing, without the interference of semantics, phonology or pragmatics, and are not influenced by prior exposure (cf. e.g., Petersson et al., 2012; Petersson & Hagoort, 2012; Reber, 1967). In particular, we chose a paradigm enabling an investigation into rule learning in real time, in which learning is simultaneous to the recording of fMRI data. The chosen artificial language BROCANTO (Brod & Opitz, 2012; Friederici et al., 2002; Hauser et al., 2012; Opitz et al., 2011; Opitz & Friederici, 2003, 2004, 2007) is based on a set of pronounceable pseudo words, combined in ways following rules found in many natural languages. The paradigm can thus be seen as a model for language learning, though a highly controlled one (see Section 3.2.2 for a further description of the paradigm).

3.1.2 Language aptitude and language analytical ability

Next to investigating the functional connectivity patterns present during the acquisition of novel grammar, we wanted to explore more fully,

what in previous language acquisition connectivity studies was interpreted as a “favourable disposition” (Veroude et al., 2010) of L2 learners, or being “well suited” to learn a particular aspect of an L2 (Yang et al., 2015). Within the field of second language acquisition, a bulk of research has been dedicated to investigating pre-existing differences between learners, and L2 learning success has repeatedly been linked to the notion of language aptitude (cf. e.g., Dörnyei & Skehan, 2003; R. Ellis, 2008; Sawyer & Ranta, 2001).

Language aptitude is defined as an individual, relatively immutable cognitive ability particular to language learning, which is a combination of skills that are fairly independent from each other. The multi-componential nature of language aptitude can be found in tests measuring it. For example, the Llama Language Aptitude Test (LLAMA) (Meara, 2005), consists of four parts: (1) a vocabulary learning task, (2) a test of phonetic memory, (3) a test of sound-symbol correspondence and (4) a test of grammatical inferencing, being a measure of language analytical ability (LAA). LAA is relevant for pattern identification during SLA, which involves analysing and processing new linguistic input (Skehan, 2002). Arguably, LAA is the most important of the language aptitude components for grammar learning: learners with high degrees of LAA are sensitive to the grammatical structure of new languages and are able to make linguistic generalisations easily. According to SLA research, LAA plays an important role in L2 acquisition in a variety of settings, such as immersion (Harley & Hart, 1997), classroom (Erlam, 2005) and lab (Yilmaz, 2012).

With our study, instead of defining successful learners *post-hoc*, on the basis of their behavioural performance in the task at hand, we wanted to concentrate on neural substrates of the pre-existing differences between learners, diagnosed prior to the task, by means of a standardised test instrument, and in this way explore the neural underpinnings of a “favourable disposition” (cf. Veroude et al., 2010) for novel grammar learning. We manipulated the language analytical abilities of our participants by recruiting them on the basis of the LLAMA sub-test measuring LAA. Two groups participated in the experiment: with high and average LAA.

3.1.3 Whole-brain functional connectivity approach

Functional connectivity of the brain – temporal correlations between the hemodynamic activity of different areas – can be investigated in various ways by means of fMRI. For example, the studies cited in Sec-

tion 3.1.1 above, resorted to an approach employing a set of pre-defined regions of interest (ROIs). Though such a method is undoubtedly informative as to the insights concerning the cooperation between the given brain areas, it also limits the observations to the regions examined. The goal of the current study was therefore to approach the connectivity question in a data-driven manner and look for the intrinsic organisation of the brain as different networks without *a priori* spatial constraints.

A method allowing for such an approach is the independent component analysis (ICA) of fMRI data. This data-driven technique allows for detection of structured spatiotemporal processes in neuroimaging data (Beckmann et al., 2006) by decomposing the data into a set of spatially independent activation maps (components) and their time courses. The components can reflect meaningful neuronal signal sources (i.e., networks), as well as noise or artefacts. The meaningful components are seen as a representation of interconnected networks of brain regions that co-activate when certain types of tasks or cognitive processes are being performed. Several well-established and highly reproducible (Damoiseaux et al., 2006) functional networks are typically reported in the functional neuroimaging literature, both in resting-state (see e.g., Beckmann et al., 2005; Damoiseaux et al., 2006; Fox et al., 2005; Smith et al., 2009) and task-related investigations (see e.g., Smith et al., 2009; van Tol et al., 2013). They represent e.g., the default mode network (DMN) of the brain, motor processing, visual processing, cognition, perception, attention, and emotional processing (cf. Beckmann et al., 2005; De Luca, Beckmann, De Stefano, Matthews, & Smith, 2006; Smith et al., 2009; van Den Heuvel & Hulshoff Pol, 2010).

After extraction, components of interest are subject to identification and interpretation by the researcher and inter-individual differences within each component can be assessed statistically. For a detailed description of the applied ICA methodology, see Section 3.2.2, and e.g., Beckmann and Smith (2005), Beckmann et al. (2006; 2005), and Veer (2015).

3.1.4 Hypotheses

The aim of this study was to examine the characteristics of networks present during the grammar learning process and their features representing pre-existing differences between learners. It remains to be noted that previous studies investigating language learning concentrated predominantly on predefined regions of interest and their (mutual) connectivity, thus not fully profiting from the wealth of information present in such data. We approached the question in a data-driven way, adopt-

ing an exploratory approach by investigating whole-brain functional connectivity during the process of learning.

Based on current functional connectivity literature, we expect that the spatiotemporal characteristics of grammar learning on the neural level can be distinguished by several substrates, both typical to the type of the received input, as well as representing the highly reproducible intrinsic organisation of the brain found in resting-state and task-related investigations.

In terms of the differences between groups of learners chosen on the basis on their language analytical abilities, on the whole stronger functional connectivity patterns are expected in case of the highly skilled learners. In particular, we expect the syntax-related regions such as left IFG, putamen, insula, precentral gyrus, and the supplementary motor area to contribute more to the networks driven by the type of input in case of the highly skilled learners. Following from Antonenko et al.'s (2012) study, we further expect bilateral contribution from the Broca's area and its contra-lateral homologue in case of the moderately skilled learners.

3.2 Materials and methods

Data for this experiment were collected together with data reported in Chapter 2, Chapter 4 or Kepinska et al. (2016), and Chapter 6. As in the case of the experiment reported in Chapter 2, the present experiment focused on the consecutive learning phases of the AGL task, but utilised a different analytical approach (see Section 2.2). Participants' demographic details and task details remain the same for all studies. For reasons of clarity they are shortly presented hereunder.

3.2.1 Participants

Two groups of participants (with high and average LAA) were determined by administering a language aptitude test, the Llama Language Aptitude Test (LLAMA) (Meara, 2005), to a large group of participants ($N = 307$). On the basis of the test, forty-two healthy adults with no contra-indications for an MRI scan were chosen to take part in the MRI experiment.

There were 20 participants in the Average LAA group (16 female)¹, age 19-39 years ($M = 23.60$ years) and 22 participants in the High LAA group (16 female), age 19-43 years ($M = 23.18$ years). All participants were native speakers of Dutch, right-handed and had normal or corrected-to-normal vision.

The Medical Ethical Committee of the Leiden University Medical Centre (LUMC) (Leiden, the Netherlands) approved the protocol of the MRI experiment; behavioural testing was also conducted according to the Ethics Code of the Faculty of Humanities at Leiden University. Participants gave written informed consent prior to the experiment and were remunerated for their time.

3.2.2 Stimuli and design

The stimulus material was created on the basis of the artificial grammar of BROCANTO (Brod & Opitz, 2012; Friederici et al., 2002; Hauser et al., 2012; Opitz et al., 2011; Opitz & Friederici, 2003, 2004, 2007), the schematic representation of which can be found in Figure 3.1. The AGL task was administered in the scanner and consisted of three blocks of learn and test phases. Six days after the fMRI experiment, participants performed a delayed transfer test. The stimulus material consisted of both grammatical and ungrammatical sentences. The grammatical ones were used in the learning phases of the experiment, the test phases and the transfer test contained both grammatical and ungrammatical sentences. The learning phases, during which the neuroimaging data reported in this paper were collected, consisted of forty grammatically correct sentences. The sentences were presented in a random order, for 8 seconds each, preceded by a fixation cross (3 seconds). Participants were instructed to discover the grammatical rules of the language by analysing the correct sentences in the learning phases, and to give a grammaticality judgment in the test phases. Visual feedback was provided for the grammaticality judgements.

For a further description of the version of BROCANTO used in this experiment and technical presentation details see Chapter 4 or Kepinska et al. (2016).

¹ Although a comparison of highly skilled learners against a group of low aptitude learners would probably yield more clear-cut results, the low aptitude LAA learners were very infrequent in our sample. Only 8 Dutch-speaking participants scored within low range (0-15, according to the manual of the LLAMA test (Meara, 2005)) on the LLAMA_F test. Hence, the group of learners with high LAA was compared to a group who scored within average range.

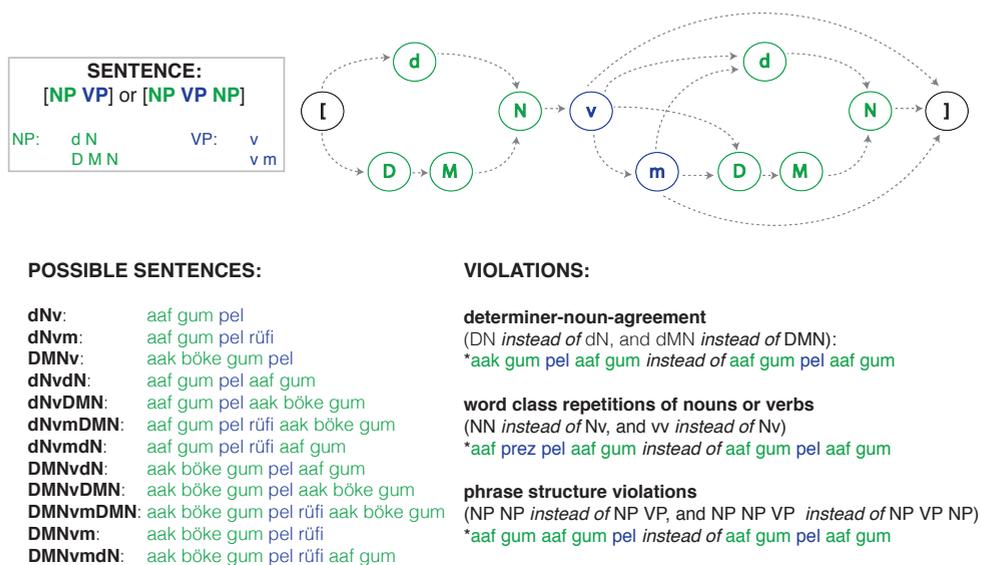


Figure 3.1 Representation of the artificial grammar of BROCANTO and its possible sentences. The graph in the top panel summarises the grammatical rules according to which the sentences were created: the nodes specify word classes (N = noun (“gum”, “trul”), v = verb (“pel”, “prez”), M = adjective (“böke”), m = adverb (“rüfi”), d (“aaf”) and D (“aak”) = determiner), and the arrows represent possible transitions between nodes. The green elements form noun phrases, the blue ones verb phrases. A grammatical sentence is formed by a transition from beginning ([) to end (]), cf. (Brod & Opitz, 2012; Friederici et al., 2002; Hauser et al., 2012; Opitz et al., 2011; Opitz & Friederici, 2003, 2004, 2007). The bottom panel lists all types of the sentences built according to the rules together with examples. On the left, three types of violations are exemplified.

3.2.3 Data acquisition

For a description of neuroimaging data acquisition parameters see Chapter 2.

3.2.4 Data analysis

3.2.4.1 Behavioural data

Based on the individual hit- and false-alarm rates, the responses on the AGL task for each participant were transformed into d' scores. Within the framework of Signal Detection Theory (Macmillan & Creelman, 2005) d' scores are used to represent a measure of sensitivity that accounts for response bias. The d' scores were calculated by subtracting

the normalised false-alarm rates from normalised hit rates (see Macmillan & Creelman, 2005 for details).

Following previous studies employing similar experimental designs (Brod & Opitz, 2012; Friederici et al., 2002; Hauser et al., 2012; Opitz et al., 2011; Opitz & Friederici, 2003, 2004, 2007), the d' scores were then analysed with a repeated measures ANOVA (alpha level = 0.05) with group as a between-subject factor (High LAA vs. Average LAA) and learning phase (first phase, second phase, last phase and transfer test) as a within-subject factor. As imaging data from two subjects had to be discarded due to technical reasons (see Section 3.2.4.2 below), the behavioural data report on the same sample of 40 participants. The analysis was performed in SPSS version 22 (IBM SPSS, 2012). Mauchley's test showed violations of sphericity against the factor phase, $\chi^2(5) = 19.957$, $p < .01$, therefore Greenhouse-Geisser correction for non-sphericity was used ($\epsilon = .772$).

3.2.4.2 Pre-processing of imaging data

Imaging data from one subject from the High LAA group were discarded from further analyses due to an artefact in one of the scans; another was rejected due to excessive motion. For a detailed description of the pre-processing parameters see Chapter 2, Section 2.2.3.

3.2.4.3 Extraction of functional connectivity networks

Group ICA was carried out using multi-session Tensor-ICA (Beckmann et al., 2005) as implemented in MELODIC Version 3.14. Tensor-ICA allowed for a model-free fMRI analysis of the three AGL phases by means of a three-way data decomposition into independent components (ICs), representing signal or artefacts in the data in terms of time courses, spatial maps and session/subject modes (see Beckmann & Smith, 2005 for a detailed description of Tensor-ICA).

The following default ICA processing steps were applied: masking of non-brain voxels, voxel-wise de-meaning of the data and normalisation of the voxel-wise variance. Subsequently, the data set was projected into a 10-dimensional subspace using principal component analysis (PCA): in order to approximate earlier studies (Beckmann et al., 2005; Smith et al., 2009), the dataset was decomposed into 10 sets of vectors, which describe signal variation across the temporal domain (time-courses), the session/subject domain and across the spatial domain (maps) by optimising for non-Gaussian spatial source distributions using a fixed-point iteration technique (Hyvärinen, 1999). Estimated com-

ponent maps were divided by the standard deviation of the residual noise and thresholded by fitting a mixture model to the histogram of intensity values (Beckmann & Smith, 2004). Finally, a grey matter mask was used to mask out non-grey matter regions in each of the 10 obtained IC maps. FSL Cluster tool was subsequently used to define significant clusters comprising the ICs, with the threshold of $Z > 2.3$.

Prior to the higher-level statistical analysis, the ten IC maps were inspected visually in order to distinguish anatomically and functionally task-relevant networks. Four out the ten components were identified as artefacts resulting from head motion, fluctuations in cerebrospinal fluid, and physiological or scanner noise. Visual maps of the noise components are presented in the supplementary data. The first three visual maps all show activity at the edges of the brain, which is typical for motion and scanner drift artefacts. The fourth one, in addition to showing activity on the edges of the brain, depicts activation that is dispersed and does not form a coherent network from an anatomical point of view. One task-relevant IC map represented a visual processing network (see component (d) in Table 3.2 and Figure 3.2), not relevant for our research questions. In order to maximise the statistical power of the group comparisons, only five components of interest were included in the between-group analysis².

3.2.4.4 Statistical analysis

Subject-specific versions of the spatial maps, and associated timeseries were created on the basis of the spatial maps from the group-average analysis in order to test for differences between the High and Average LAA groups in the identified components. We adopted a dual regression procedure (Beckmann, Mackay, Filippini, & Smith, 2009; Filippini et al., 2009) which uses the network time-course in a temporal and spatial regression against individual fMRI data. First, each component was spatially masked with a binary representation of the group main effects image. Then, for each subject, the group-average set of spatial maps was regressed (as spatial regressors in a multiple regression) into the subject's 4D space-time dataset. This resulted in a set of subject-specific timeseries, one per group-level spatial map. Subsequently, those timeseries were regressed (as temporal regressors, again in a multiple

² An exploratory independent sample t-test (implemented in FSL's Randomise tool, Version 2.9) performed with permutation testing with 5,000 permutations, revealed, however, that the two groups did not differ in the degree of engagement of the visual processing network ($p > .05$, Bonferroni corrected, for both High LAA > Average LAA and Average LAA > High LAA contrasts).

regression) into the same 4D dataset, resulting in a set of subject-specific spatial maps, one per group-level spatial map.

The resulting spatial maps represented a measure of the degree to which blood-oxygenation-level-dependent (BOLD) signal fluctuations in each voxel co-varied with each IC time series for each subject separately. In other words, each participant's spatial map for a given IC was seen as a voxelwise map of the strength of functional connectivity with that IC. The spatial maps were then used in voxelwise analysis to assess differences between the Average and the High LAA groups in connectivity strength within the identified ICs. FSL's Randomise tool, Version 2.9, was used to perform non-parametric permutation testing with 5,000 permutations. The resulting contrast maps for each task-relevant independent component were thresholded with a threshold-free cluster enhancement approach (TFCE) (Smith & Nichols, 2009), a standard and conservative approach for correcting for multiple comparisons with regard to the number of voxels in the brain (at $p < .05$). Subsequently we corrected for the number of investigated components (using a Bonferroni correction).

3.3 Results

3.3.1 Behavioural data

The d' scores on the test phases of the AGL task in both High LAA and Average LAA groups increased over the course of the experiment, see Table 3.1. A repeated-measures ANOVA showed a main effect of learning phase, $F(2.316, 88.018) = 38.224$, $p < .001$, $\eta_p^2 = .501$, and a significant effect of group, $F(1, 38) = 14.318$, $p = .001$, $\eta_p^2 = .274$. The High LAA group performed better than the Average LAA group, and there was a significant interaction between group and phase, $F(2.316, 88.018) = 4.896$, $p < .01$, $\eta_p^2 = .114$.

| AGL phase: | Mean (SD) | |
|------------|-------------|-------------|
| | High LAA | Average LAA |
| 1 | 1.20 (0.83) | 0.79 (0.89) |
| 2 | 2.52 (1.02) | 1.43 (1.28) |
| 3 | 2.88 (0.86) | 1.90 (1.10) |
| transfer | 2.92 (0.86) | 1.45 (1.0) |

Table 3.1 Proportion correct responses (and standard deviations) for the three phases of the AGL task and the subsequent transfer test for High and Average LAA groups.

3.3.2 Functional connectivity networks involved in learning language rules

Six functionally relevant functional connectivity networks were found using the group Independent Components Analysis. A summary of the cluster peaks in each of the networks can be found in Table 3.2; Figure 3.2 presents the results of the analysis overlaid on the MNI-152 standard brain. The final thresholded maps can be classified as follows:

- (a) *Task-positive/language network*: containing seven clusters (peaks described in Table 3.2). These clusters were extending into the set of areas consistent with the task-positive network (cf. Fox et al., 2005), with the addition of task-specific, i.e. language network activations. Moreover, the regions constituting this IC largely overlap with the set of areas described by Dodel et al. (2005) as syntax-related. The areas found in the task-positive network are the superior and middle prefrontal cortices, paracingulate gyrus and ventrolateral prefrontal cortex (Beckmann et al., 2005). Also involved in the task-positive network are the activated parietal structures (supramarginal and angular gyrus). The bilateral activation of caudate nuclei can be attributed to their role in learning and memory (cf. Grahn, Parkinson, & Owen, 2008; Seger & Cincotta, 2005), and to their role as a centre for language control (cf. Abutalebi & Green, 2008; Crinion et al., 2006; Hervais-Adelman, Moser-Mercer, Michel, & Golestani, 2014). Furthermore, there was activity in the insula, which, having direct connections to Broca's area and other speech and language centres, is implicated in coordinating higher-order cognitive aspects of speech and language production (Oh, Duerden, & Pang, 2014). Note that the activations in this network were mostly bilateral (see Figure 3.2), with asymmetry to the left hemisphere.
- (b) *Default-mode network*: activity was found in the anterior and posterior cingulate gyrus, in the frontal pole, frontal orbital cortex, superior parietal and temporal region and in the hippocampus - areas described as belonging to the DMN (Beckmann et al., 2005; Damoiseaux et al., 2006; Greicius, Krasnow, Reiss, & Menon, 2003; Greicius, Srivastava, Reiss, & Menon, 2004; Raichle, 2015; Raichle et al., 2001). In addition, there was activation in the cerebellum, which in a number of resting-state functional connectivity studies was shown to participate in higher-order networks such as the DMN (Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011; Habas et al., 2009; Krienen & Buckner, 2009; O'Reilly, Beckmann, Tomassini, Ramnani, & Johansen-Berg, 2010; L. Wang et al., 2014). Also observed was the contribution of the subcallosal cortex.

- (c) *Working memory network*: activations were consistent with the working memory network as described by Owen, McMillan, Laird and Bullmore (2005). These included: bilateral frontal pole and prefrontal cortex, cingulate gyrus, premotor cortex and posterior parietal cortex, including precuneus. Moreover, there was activity in the superior parietal lobule, which has been shown to be critically important for the manipulation of information in working memory (Koenigs, Barbey, Postle, & Grafman, 2009); the supramarginal gyrus (here activated bilaterally), has been reported to be involved in verbal working memory (Deschamps, Baum, & Gracco, 2014). Similarly, the bilateral activation of the thalamus can be related to its enhanced activation in verbal working memory tasks (Owen et al., 2005). Additionally, the network comprised of the left temporal occipital fusiform cortex, the activation of which corresponded to the localisation visual word form area (VWFA), shown to be involved in the recognition of words and letters from simple shape images (Dehaene & Cohen, 2011; McCandliss, Cohen, & Dehaene, 2003).
- (d) *Visual areas*: including activations in the lateral occipital cortex and occipital pole.
- (e) *Cerebellar network*: cerebellum was found to interact with the right IFG and the basal ganglia structures, pallidum and putamen. This assembly of structures has been described as part of the procedural learning system by Ullman (2004) (see also De Smet, Paquier, Verhoeven, & Mariën, 2013; Nicolson & Fawcett, 2011). Also observed was activation of the thalamus, the right temporal pole and the left temporal fusiform gyrus.
- (f) *Emotional network*: activity was found in the subcortical structures of brainstem (including the inferior olivary nucleus and the red nucleus), amygdala and the left hippocampus; cortically, the right temporal pole, bilateral parietal operculum, anterior cingulate gyrus, right precentral gyrus, the left posterior middle temporal gyrus and the subcallosal cortex were activated. This pattern of functional connectivity largely overlaps with the regions together forming “the emotional brain” circuitry, dedicated to processing and regulating emotions (Pessoa, 2008; Veer et al., 2012).

Chapter 3

| Cortical region (peak) | L/R | Size (voxels) | Peak location | | | Z_{\max} |
|--|-----|------------------|---------------|-----|-----|------------|
| | | | X | Y | Z | |
| (a) Task-positive/Language Network | | | | | | |
| (1) Lateral Occipital Cortex, superior division / Superior Parietal Lobule | L | 18874 | -30 | -62 | 46 | 7.67 |
| (2) Precentral Gyrus / Middle Frontal Gyrus | L | 6758 | -40 | 4 | 32 | 7.67 |
| (3) Middle Frontal Gyrus / Frontal Pole | R | 5076 | 50 | 32 | 26 | 7.27 |
| (4) Paracingulate Gyrus | L | 1237 | -6 | 16 | 46 | 6.12 |
| (5) Insular Cortex / Frontal Orbital Cortex | R | 205 | 32 | 24 | -2 | 4.84 |
| (6) Caudate | L | 151 | -16 | 6 | 8 | 2.91 |
| (7) Caudate | R | 49 | 16 | 6 | 14 | 2.77 |
| (b) Default-mode Network | | | | | | |
| (1) Frontal Pole | - | 10339 | 0 | 58 | 0 | 6.48 |
| (2) Cingulate Gyrus, posterior division / Precuneus Cortex | L | 5065 | -6 | -54 | 28 | 6.29 |
| (3) Frontal Orbital Cortex | R | 1981 | 44 | 26 | -14 | 4.09 |
| (4) Angular Gyrus / Lateral Occipital Cortex, superior division | R | 1828 | 56 | -58 | 28 | 4.88 |
| (5) Lateral Occipital Cortex, superior division | L | 1658 | -48 | -72 | 32 | 5.46 |
| (6) Middle Temporal Gyrus / Superior Temporal Gyrus, posterior division | L | 1300 | -62 | -16 | -12 | 4.59 |
| (7) Frontal Orbital Cortex | L | 255 | -40 | 24 | -18 | 3.82 |
| (8) Subcallosal Cortex | R | 209 | 2 | 12 | -6 | 3.98 |
| (9) Cerebellum | L | 161 | -28 | -82 | -34 | 3.77 |
| (10) Cerebellum | R | 140 | 32 | -82 | -34 | 3.62 |
| (11) Hippocampus | R | 57 | 28 | -22 | -18 | 3.4 |
| (12) Hippocampus | L | 43 | -24 | -22 | -20 | 3.02 |
| (13) Occipital Pole / Cuneal Cortex | R | 37 | 8 | -88 | 28 | 2.79 |
| (14) Parahippocampal Gyrus / Temporal Fusiform Cortex, posterior division / Lingual Gyrus / Temporal Occipital Fusiform Cortex | L | 33 | -26 | -40 | -14 | 2.88 |
| (c) Working Memory Network | | | | | | |
| (1) Supramarginal Gyrus, anterior division / Parietal Operculum Cortex / Planum Temporale | R | 17452 | 60 | -30 | 28 | 5.11 |
| (2) Supramarginal Gyrus, anterior division / Parietal Operculum Cortex / Postcentral Gyrus | L | 5263 | -62 | -28 | 22 | 4.42 |
| (3) Precuneus Cortex/ Intracalcarine Cortex / Supracalcarine Cortex | R | 4143 | 16 | -60 | 12 | 3.73 |
| (4) Frontal Pole | R | 584 | 32 | 40 | 22 | 3.88 |
| (5) Frontal Pole / Middle Frontal Gyrus | L | 568 | -30 | 40 | 30 | 3.6 |
| (6) Lateral Occipital Cortex | L | 333 | -56 | -68 | 8 | 3.04 |
| (7) Thalamus | R | 282 | 10 | -16 | 6 | 3.95 |
| (8) Thalamus | L | 109 | -6 | -18 | 6 | 3.23 |
| (9) Superior Parietal Lobule / Postcentral Gyrus | R | 72 | 26 | -44 | 60 | 2.66 |
| (10) Superior Frontal Gyrus | L | 53 | -20 | -2 | 62 | 2.74 |
| (11) Frontal Pole / Inferior Frontal Gyrus, pars triangularis | R | 39 | 46 | 36 | 4 | 2.72 |
| (12) Temporal Occipital Fusiform Cortex | L | 30 | -28 | -58 | -18 | 2.52 |
| (13) Postcentral Gyrus / Superior Parietal Lobule | R | 27 | 34 | -36 | 56 | 2.45 |

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| Cortical region (peak) | L/R | Size (voxels) | Peak location | | | Z_{\max} |
|--|-----|------------------|---------------|-----|-----|------------|
| | | | X | Y | Z | |
| (d) Visual Network | | | | | | |
| (1) Occipital Pole / Lateral Occipital Cortex, superior division | L | 17372 | -18 | -90 | 18 | 3.7 |
| (2) Lateral Occipital Cortex, superior division / Superior Parietal Lobule | L | 15 | -16 | -60 | 54 | 2.39 |
| (e) Cerebellar Network | | | | | | |
| (1) Cerebellum | L | 28906 | -4 | -64 | -22 | 6.36 |
| (2) Temporal Pole | R | 108 | 52 | 10 | -20 | 3.07 |
| (3) Pallidum / Putamen | L | 81 | -26 | -16 | -2 | 3.11 |
| (4) Temporal Fusiform Cortex, anterior division / Temporal Fusiform Cortex, posterior division | L | 36 | -34 | -6 | -38 | 2.79 |
| (5) Inferior Frontal Gyrus, pars opercularis | R | 13 | 62 | 14 | 4 | 2.66 |
| (6) Thalamus | L | 10 | -4 | -2 | -4 | 2.5 |
| (f) Emotional Network | | | | | | |
| (1) Brain-Stem | L | 14571 | -14 | -28 | -28 | 9.85 |
| (2) Temporal Pole | R | 881 | 44 | 10 | -16 | 6.1 |
| (3) Parietal Operculum Cortex | R | 90 | 42 | -30 | 20 | 3.18 |
| (4) Postcentral Gyrus / Precentral Gyrus | R | 49 | 52 | -10 | 32 | 2.7 |
| (5) Cingulate Gyrus, anterior division | - | 23 | 0 | -8 | 30 | 2.65 |
| (6) Middle Temporal Gyrus, posterior division | L | 17 | -48 | -28 | -10 | 2.75 |
| (7) Parietal Operculum Cortex / Planum Temporale | L | 12 | -52 | -34 | 18 | 2.65 |

Table 3.2 Six functionally relevant Independent Components distinguished by the group Tensor-ICA analysis. Each IC represents an assembly of regions associated with distinct cognitive processes at play during AGL. Only clusters of 10 or more voxels are reported; x, y and z coordinates are in MNI space, regions labelled according to Harvard-Oxford Cortical and Subcortical Structural Atlases and the Juelich Histological Atlas (all implemented within FSLVIEW, part of FSL).

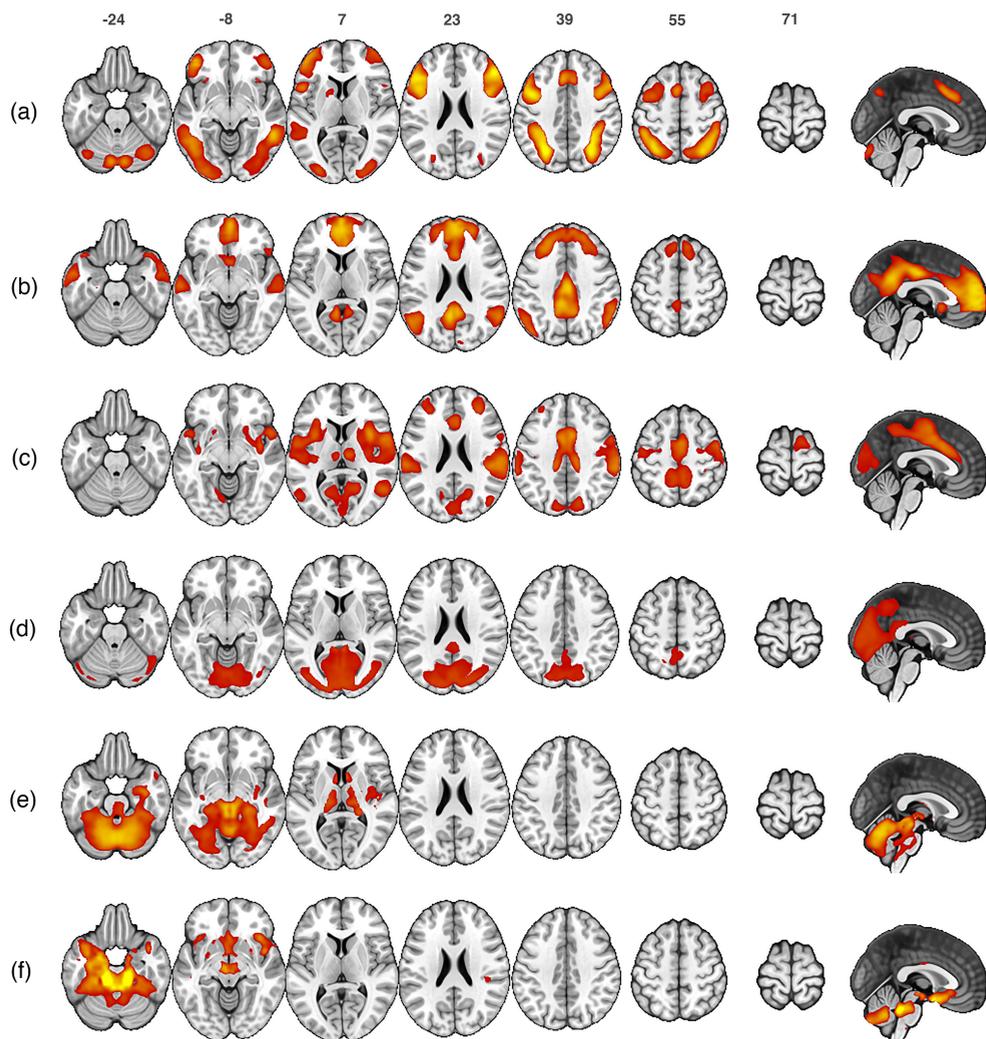


Figure 3.2 Group ICA networks. Depicted here are the six functional connectivity networks resulting from the group ICA step carried out on the concatenated data sets from both High and Average LAA groups. Images are z-statistics, ranging from 2.3 (red) to 7 (yellow), overlaid on the MNI-152 standard brain. The left hemisphere of the brain corresponds to the left side in the image. Brain activations are displayed using MRICroGL (<http://www.mccauslandcenter.sc.edu/mricrogl/>).

3.3.3 Group differences

Five IC networks were subject to a between-group analysis: since no differences between the groups were expected in visual processing, the component (d) (see Table 3.2 and Figure 3.2) was excluded from the analysis in order to maximise the statistical power of the group comparisons. All investigated networks were significantly represented in both Average and High LAA groups (mean connectivity maps per group, showing a significant representation of each IC in the two groups are presented in the supplementary material). Between-group differences in the voxel-wise spatial distribution of the functional connectivity maps were revealed in four out of five ICs, which were subject to two-sample unpaired t-tests, corrected for multiple comparisons (at $p < .05$, TFCE-corrected) and for the number of investigated components, thus resulting in $p < .01$ (see Table 3.3).

In the first IC (the *task-positive* or *language network*), the Average LAA group displayed stronger functional connectivity in comparison with the High LAA in two clusters: (1) the right precentral gyrus bordering on pars opercularis in the IFG and (2) right occipital fusiform gyrus. The High LAA group displayed stronger connectivity within this network bilaterally, in two clusters adjacent to Broca's area and its right-hemisphere homologue: (1) left middle frontal gyrus, precentral gyrus and IFG, pars opercularis and (2) right IFG, pars opercularis and middle frontal gyrus (see Figure 3.3a).

Three clusters of activity were found to have a stronger contribution to the *default-mode* network for the Average as compared to the High LAA group. They were localised in (1) the posterior cingulate gyrus, (2) paracingulate gyrus and anterior cingulate gyrus and in the (3) right frontal pole and middle frontal gyrus (Figure 3.3b).

Central opercular cortex in the right hemisphere was found to have and increased functional connectivity for the High as compared to the Average LAA group in the third component (*working memory network*) (Figure 3.3c). Similarly, the High LAA group displayed increased connectivity in the *emotional network* component in two clusters: (1) the right amygdala and (2) mammillary body in the right hemisphere (Figure 3.3d).

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| Cortical region (peak) | L/R | Size (voxels) | Peak location | | | <i>p</i> -value |
|--|-----|------------------|---------------|-----|-----|------------------|
| | | | X | Y | Z | |
| (a) Task-positive/Language Network | | | | | | |
| Average LAA > High LAA | | | | | | |
| (1) Precentral Gyrus / Inferior Frontal Gyrus, pars opercularis | R | 57 | 50 | 4 | 22 | <i>p</i> < 0.001 |
| (2) Occipital Fusiform Gyrus / Lateral Occipital Cortex, inferior division | R | 24 | 36 | -78 | -18 | <i>p</i> < 0.01 |
| High LAA > Average LAA | | | | | | |
| (1) Middle Frontal Gyrus / Precentral Gyrus / Inferior Frontal Gyrus, pars opercularis | L | 11 | -42 | 8 | 34 | <i>p</i> < 0.01 |
| (2) Inferior Frontal Gyrus, pars opercularis / Middle Frontal Gyrus | R | 3 | 42 | 16 | 26 | <i>p</i> < 0.01 |
| (b) Default-mode Network | | | | | | |
| Average LAA > High LAA | | | | | | |
| (1) Cingulate Gyrus, posterior division | L | 29 | -2 | -36 | 32 | <i>p</i> < 0.01 |
| (2) Paracingulate Gyrus / Cingulate Gyrus, anterior division | R | 11 | 6 | 34 | 28 | <i>p</i> < 0.01 |
| (3) Frontal Pole / Middle Frontal Gyrus | R | 4 | 30 | 40 | 42 | <i>p</i> < 0.01 |
| High LAA > Average LAA | | | | | | |
| - | - | - | - | - | - | - |
| (c) Working Memory Network | | | | | | |
| Average LAA > High LAA | | | | | | |
| - | - | - | - | - | - | - |
| High LAA > Average LAA | | | | | | |
| (1) Central Opercular Cortex / Secondary somatosensory cortex | R | 109 | 46 | -12 | 20 | <i>p</i> < 0.01 |
| (d) Emotional Network | | | | | | |
| Average LAA > High LAA | | | | | | |
| - | - | - | - | - | - | - |
| High LAA > Average LAA | | | | | | |
| (1) Amygdala | R | 58 | 16 | -8 | -14 | <i>p</i> < 0.01 |
| (2) Mamillary body | R | 13 | 2 | -10 | -16 | <i>p</i> < 0.01 |

Table 3.3 Brain areas exhibiting increased functional connectivity for Average or High LAA group within the Independent Components distinguished by the group Tensor-ICA analysis; x, y and z coordinates in MNI space, regions labelled according to Harvard-Oxford Cortical and Subcortical Structural Atlases and Juelich Histological Atlas (all implemented within FSLVIEW, part of FSL).

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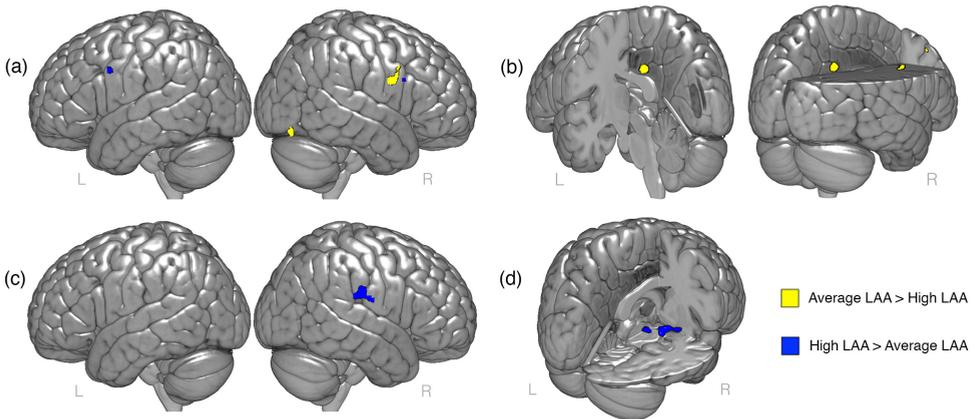


Figure 3.3 Results of the between-group analysis in the voxel-wise spatial distribution of the functional connectivity maps showing differences between High and Average LAA participants within the (a) task-positive/language network, (b) default mode network, (c) working memory network, and (d) emotional network. Results of two-sample unpaired t-tests are displayed at $p < .01$, TFCE-corrected. In blue, the results of the contrast testing for stronger connectivity for the High as compared to Average LAA participants are shown; in yellow, for the Average as compared to High LAA participants. Brain activations are displayed using MRIcroGL (<http://www.mccauslandcenter.sc.edu/mricrogl/>).

3.4 Discussion and conclusions

In an effort to advance the understanding of brain function and organisation coupled with second language learning, the present study set out to describe brain connectivity patterns in a group of adults learning novel grammar. Furthermore, we aimed at identifying neural mechanisms underlying individual variability in language acquisition by investigating network characteristics responsible for high abilities in grammar learning (operationalised by means of pre-testing participants' language analytical abilities). We collected functional connectivity data simultaneous to the learners acquiring new grammar rules and applied a data-driven analysis, looking for whole-brain connectivity patterns during the process of learning. It was expected that several distinct networks would be found: pertaining to the type of received input as well as representing intrinsic organisation of the brain found in resting-state and task related investigations alike (see e.g., Beckmann et al., 2005; Damoiseaux et al., 2006; Fox et al., 2005; Fox & Raichle, 2007; Smith et al., 2009). We further investigated differences between two groups of participants recruited on the basis of their language analytical abilities and expected that the highly skilled learners would be characterised by stronger functional connectivity patterns, especially of

syntax-related regions. Bilateral contribution from Broca's area and its right-hemisphere homologue were predicted for the moderately skilled learners.

By extracting and identifying six independent components in the collected fMRI data, we showed multiple processes being present during acquisition of novel grammar, thus providing insight into the intricate and multi-layered nature of learning new language rules. Indeed, we found networks reproducing earlier resting-state investigations, such as the *task-positive* and the *default mode network*, as well as correlated activations, which we assume were driven by the type of input received by the participants. Those included a *working memory network*, a set of co-activated visual areas, a *cerebellar* and an *emotional network*. In the following sections, we will discuss the possible significance of each of the identified networks for the grammar learning process, and the established markers of inter-individual learners' differences.

3.4.1 Task-positive/language network

The first of the extracted ICs, the *task-positive* or *language network*, comprised of regions related to language processing and could - typical for language-related activations - be distinguished by asymmetry from the left hemisphere. The component's map was consistent with the task-positive network (cf. Beckmann et al., 2005; Fox et al., 2005) and showed overlap with the set of regions described by Dodel et al. (2005) as syntax-related, but also extended it. We noted more frontal activations, in the frontal pole and middle frontal gyrus, with the addition of activity in language areas in the parietal and temporal lobes and in the occipital lobe and cerebellum.

One of our hypotheses, formulated on the basis of Antonenko et al.'s (2012) findings (see Sections 3.1.1 and 3.1.4 above), assumed bilateral contributions from Broca's area and its right-hemisphere homologue in case of the moderately skilled learners. The observed group differences in this component indicated increased involvement in the network from areas extending from the traditionally defined Broca's area to the more posterior structures of the ventrolateral prefrontal cortex. In terms of lateralisation of these prefrontal contributions to the network, the observed results were opposite to the findings of Antonenko et al.'s (2012): bilateral contributions were observed only among participants with high analytical abilities. The Average LAA group in our study demonstrated stronger functional connectivity within this network from the right precentral gyrus bordering on pars opercularis in the IFG and the

right occipital fusiform gyrus (see Figure 3.3a). One possible explanation for this discrepancy in lateralisation effects might be the fact that Antonenko et al. (2012) investigated the ability to acquire grammatical rules among older adults, who previously have been shown to process information differently from young people: bilateral activations of the prefrontal cortex have been found on a number of tasks where young adults display unilateral activations (Greenwood & Parasuraman, 2010). Antonenko et al. (2012) suggested that the explanation for the increased functional correlation between bilateral prefrontal areas in their study, lay in the a lack of inhibition between those functionally connected brain regions. Our data suggest, that among young adults the engagement of areas surrounding Broca's region and its right-hemisphere homologue to the network do not reflect a lack of predisposition to acquire novel grammar (which could be expected on the basis of Antonenko's study). Rather, the learning skills of the High LAA group were reflected in stronger contributions of both the left and the right frontal regions.

In terms of the exact localisation of the clusters in the prefrontal cortex, in the context of syntax processing, the areas immediately posterior to IFG have been previously established to be activated during phonological processing (Petersson & Hagoort, 2012), to reflect increased perceptual demands (Friederici, 2011), or to underlie general structural/sequential processing of input (Hoen, Pachot-Clouard, Segebarth, & Dominey, 2006). Indeed, they have also been shown to be involved in artificial grammar learning experiments (Bahlmann et al., 2008). They seem then to have a supporting role for the core syntactic areas localised in BA 44 (Goucha & Friederici, 2015). Friederici (2006b) suggested further that in comparison with BA 44/45, the ventral premotor cortex regions are phylogenetically older, hence they are more likely to be involved in syntactic processing on a lower level (i.e. based on local probabilities vs. hierarchical structures). Since our participants were in an initial phase of processing the presented input syntactically, it seems understandable that the regions exhibiting increased connectivity within the task-positive network were not yet localised within the core area underlying syntactic processing. Note that the highly skilled participant, in comparison with the average, exhibited increased contributions from areas closer to the traditionally defined Broca's region. It might thus be the case, that one's analytical abilities determine the involvement of the prefrontal cortex during language learning: the closer to the core, the easier it might be to learn the new syntactic rules. On the other hand, what seems to underlie lower analytical abilities, is the en-

agement of areas typical to lower level processing (word recognition), as was observed among the Average LAA participants.

Another possible explanation for such differences in network engagement between the High and the Average LAA participants might be their utilising different strategies for the learning task. Previous research has pointed to rule-based and memory-based learning as two possible mechanisms underlying acquisition of novel grammar rules (Domangue, Mathews, Sun, Roussel, & Guidry, 2004; Mathews et al., 1989; Opitz & Friederici, 2004; Opitz & Hofmann, 2015), with memory-based strategies being most prevalent in initial stages of learning (Opitz & Hofmann, 2015). In particular, the finding of stronger functional connectivity of the right occipital fusiform gyrus to the task positive network of the Average LAA group might suggest that one's analytical abilities play a role in determining the strategies employed and thus brain structures involved in novel grammar learning.

3.4.2 Default mode network

The default mode network was first discovered as a set of cortical areas increasing their activation levels during rest as opposed to performance of cognitive tasks (Shulman et al., 1997, cf. Raichle, 2015), thus reflecting a default state of neuronal activity of the human brain (Gusnard & Raichle, 2001; Raichle, 2015; Raichle et al., 2001; Raichle & Snyder, 2007; van Den Heuvel & Hulshoff Pol, 2010). Further investigations suggested the DMN to underpin internally-directed processes, such as internal attention (Fox et al., 2005), integration of cognitive and emotional stimuli (Greicius et al., 2003), mind wandering (Mason et al., 2007) and representation of the world around us (Gusnard & Raichle, 2001). A network reproducing the set of regions traditionally described as belonging to the DMN was also observed in our data, with the contribution of the subcallosal cortex. Since the subcallosal cortex has been described as a part of motivation/drive circuit of the brain (Volkow et al., 2010), its contribution to the DMN derived from data acquired during a learning task, is not entirely surprising (see also the discussion on the *emotional network* in Section 3.4.6 below). One possible explanation for this finding is that our acquisition paradigm (data were collected simultaneously to the task, and not during rest) might cause a shift in the balance between the task-positive and default mode network (cf. Marchetti, Koster, Sonuga-Barke, & De Raedt, 2012), resulting in additional areas contributing to the DMN. However, considering the fact that the subcallosal cortex has previously been reported to contribute to the DMN uniquely in clinically depressed individuals (Greicius et al.,

2007), its role in task-related functional connectivity merits further investigation.

When it comes to differences in the DMN between the High and Average LAA participants, we observed stronger contributions to the network for the Average as compared to the High LAA group. The difference was localised in three regions: the posterior cingulate gyrus, the paracingulate gyrus bordering on anterior cingulate and in a cluster in the right frontal pole and middle frontal gyrus (see Figure 3.3b). This finding of increased connectivity within the DMN only among the Average LAA participants, and in regions marking on-going execution of cognitive processes (cf. e.g., Fornito et al., 2004; Owen et al., 2005), might point to the conclusion that intrinsic characteristics of one's DMN determine the predispositions to efficiently acquire novel languages. During the language learning task at hand, the Average LAA participants engaged more neural resources for internally-directed processes, such as mind wandering, instead of utilising them for the resolution of cognitive operations demanded by the task.

3.4.3 Working memory network

The set of areas identified as the next component was consistent with the working memory network as described by Owen et al. (2005) with the addition of activations in the superior parietal lobule, the supra-marginal gyrus and the thalamus. All those areas show increased activity in cognitively demanding tasks, in particular verbal ones (Deschamps et al., 2014; Koenigs et al., 2009; Owen et al., 2005). Working memory capacity, defined as the ability to build, maintain and update information (Wilhelm, Hildebrandt, & Oberauer, 2013), is undeniably critical for a learning task in which rules have to be continuously discovered and revised (see de Diego-Balaguer & Lopez-Barroso, 2010; N. C. Ellis, 1996; Martin & Ellis, 2012 for additional support for the links between working memory and rule learning). Interestingly, besides the working memory activations we noted activity in the left temporo-occipital fusiform cortex, the localisation of which corresponds to the visual word form area (cf. Dehaene & Cohen, 2011; McCandliss et al., 2003). This collaboration between the fronto-parietal working memory system and the VWFA can be traced back to the type of input employed in the task: building, maintaining and updating the grammar rules driven by the fronto-parietal working memory system most likely proceeds on the basis of the recognition of letters and words driven by the VWFA.

Within the *working memory* IC, the central opercular/secondary somatosensory cortex in the right hemisphere was found to exhibit increased functional connectivity for the High as compared to the Average LAA group (see Figure 3.3a). The fact that the engagement of a network consistent with working memory related processes, differed as a function of pre-tested analytical abilities, does not come as a surprise. Language analytical abilities can be seen as domain-specific proxy for fluid intelligence (since the latter is defined as variation in general reasoning and the ability to solve novel problems) (cf. Burgess, Gray, Conway, & Braver, 2011) and the links between fluid intelligence and working memory are well established in the literature (e.g., Ackerman, Beier, & Boyle, 2005; Burgess et al., 2011; Duncan, Schramm, Thompson, & Dumontheil, 2012; Shelton, Elliott, Matthews, Hill, & Gouvier, 2010). Increased connectivity within this IC in the right central opercular/secondary somatosensory cortex can be seen as advantageous when it comes to determining one's abilities to acquire new languages, in particular since the role of the secondary somatosensory cortex has been described to consist of perception, integration and categorisation of incoming input (Crystal & Varley, 2013).

3.4.4 Visual areas

A network responsible for lower-level processes present during grammar learning comprised of areas specialised for visual processing. Since the stimulus material in our study was presented visually, the presence of a network including activations in the lateral occipital cortex and occipital pole seems clear to interpret. Moreover, the network reproduces findings from resting-state studies employing analytical approaches similar to ours (e.g., Beckmann et al., 2005; Damoiseaux et al., 2006; Smith et al., 2009), where visual areas were consistently forming separate components identified by the analyses. Contrary to some investigations though, the ICA in our study produced one visual component map, whereas Beckmann et al. (2005), Damoiseaux et al. (2006), and Smith et al. (2009), report two visual maps separating more lateral and more medial visual areas. The explanation for this difference may lie in our analysis employing a smaller number of pre-set components: ICA decompositions with higher numbers of components produce higher separation of the functional sub-networks (Smith et al., 2009).

3.4.5 Cerebellar network

Cerebellar involvement in language functions is one of coordination and automatisisation. For example, by means of the “cerebellar deficit framework”, Nicolson et al. (1995) explain dyslexia: such a deficit might cause problems with automatisisation of learned skills (such as articulation and spelling) and result in impairments of reading and writing (see Nicolson & Fawcett, 2011 for a review). Moreover, the cerebellum has important function for – among others – working memory during processing (Marien, Engelborghs, Fabbro, & De Deyn, 2001) and meta-linguistic and higher-level language abilities (Cook, Murdoch, Cahill, & Whelan, 2004; Whelan & Murdoch, 2005; cf. De Smet et al., 2013)

In our data, the cerebellar activations were coupled with a set of regions (right IFG and the basal ganglia structures, pallidum and putamen) previously put forward to form the procedural learning system (Ullman, 2004). Additionally, we observed activity in the thalamus, which is the node connecting the cerebellum to the cortex (cf. De Smet et al., 2013), and in the right temporal pole. Note that the structural connectivity of the temporal pole, as shown by tractography, suggests its role as a convergence centre, with important implications in language and multimodal semantic processing (Binney, Parker, & Lambon Ralph, 2012). The contribution of the left temporal fusiform gyrus (involved in the recognition of written words) (cf. Kirchoff et al., 2000; Weiner & Zilles, 2016) can be related to the type of received input during the task (strings of written words). Taken together, the connectivity between the temporal pole and temporal fusiform gyrus might point to the process of assignment of semantic features to letter strings, which are then taken up by the procedural learning system in order to be processed as a grammar in a more holistic way.

No group differences were found in a comparison between High and Average LAA participants in this network. In other words, when it comes to coordination and automatisisation processes, both groups exhibited brain activity of similar profiles, making the cerebellar involvement not being driven by the participants’ language analytical abilities.

3.4.6 Emotional network

The last of the identified components comprised of areas corresponding to the regions together forming “the emotional brain” circuitry, dedicated to processing and regulating emotions (Pessoa, 2008; Veer et al., 2012). This finding is in accordance with the view that emotion and cognition, by means of strong interaction and integration, together con-

tribute to behaviour (Pessoa, 2008). Furthermore, the activations found within this network extended to such structures as the inferior olivary nucleus and the red nucleus, which (through their connectivity with the cerebellum via the climbing fibres system) play an important role in procedural learning (cf. A. Siegel & Sapru, 2011).

In the context of language learning, the emotional circuits seem in particular crucial for the control of motivation and (intrinsic) reward mechanisms (cf. Ripollés et al., 2014). The presence of an emotional network in our data could mean that acquisition of new grammatical rules in part relies on subcortical, emotional circuits. The group differences in this network were found for the High as compared to Average LAA participants. The learners with higher language analytical abilities showed stronger contributions within this network from the right amygdala and mammillary body in the right hemisphere (see Figure 3.3d). The amygdalar involvement during the task can be explained by its role in encoding and retrieving of emotionally significant information (e.g., Sarter & Markowitsch, 1985). Furthermore, the amygdala seems to enable memory consolidation of emotionally salient information through its interactions with the hippocampus (McGaugh, 2004; Veer, 2015), which also contributed to the network in question. Mammillary bodies, and their projections to the anterior thalamus, are important for episodic memory (Vann, 2010). Taken together, these increased contributions to the emotional network from the High LAA participants suggest that highly skilled learners might have associated more emotional valence with the material being learned. It might also be the case that the subcortical emotional brain circuitry of individuals with higher language abilities exhibits a more integrated organisation in the presence of a language learning task.

3.4.7 The interconnected brain during novel language rule learning

By investigating functional connectivity during a novel grammar-learning task by means of a data-driven, unbiased whole-brain approach, we found a set of networks bearing significant importance for such a process of learning. The collected data were decomposed into maps, each representing a separate putative cognitive process present during the task. We found both internally oriented (*default mode network*) activations next to externally, task-oriented ones. The information with which the participants were confronted had to be continuously manipulated and updated, by means of working memory. At the same time the learning process was coordinated by the cerebellum; all this in the presence of emotional activity, driving the will to learn.

Apart from decomposing the learning process into several cognitive sub-processes, we investigated differences between participants with varying degrees of language analytical abilities. The obtained results did not corroborate our first hypothesis, predicting bilateral contribution from Broca's area and its right-hemisphere homologue for the moderately skilled learners. Instead, we found contributions from areas adjacent to Broca's right-hemisphere homologue for both groups, stronger involvement from the right occipital fusiform gyrus in case of Average LAA participants and stronger contribution of the areas adjacent to left Broca's area in case of the High.

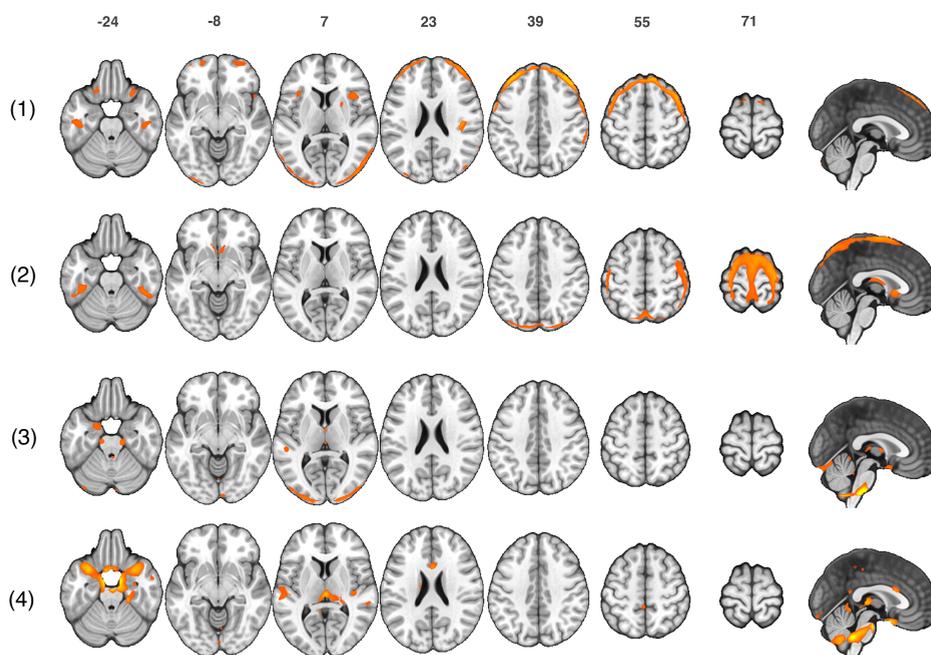
We further hypothesised that the highly skilled learners would be distinguished by stronger functional connectivity patterns, especially of syntax-related regions. Examination of the results of the between-group analyses lets us conclude that this hypothesis is confirmed: the majority of the results pointed to stronger connectivity within networks for High LAA participants. Average LAA participants exhibited stronger functional connectivity in the default mode network, which makes us believe that since DMN is normally deactivated during a task, the stronger connectivity of this network during a task is not advantageous for the demands of the task at hand. In sum, we demonstrated that in terms of functional connectivity, the engagement of brain's networks during grammar acquisition is coupled with one's language learning abilities.

Although informative as to the nature of distinct processes being present during acquisition of language-like rules, there are still open questions deriving from this research. For example, the matter of interactions and collaborations between different networks present during learning awaits further investigation. Although extracted as Independent Components, the networks are indeed connected to each other and by means of other methodological approaches, the interactions between them can be brought to light (cf. e.g., Smith et al., 2009). Furthermore, it merits to be explored how other building blocks of language learning (such as acquisition of new vocabulary items (cf. e.g., López-Barroso et al., 2015) and inter-individual differences in rote learning memory) are represented at the neural level, employing the same or similar methodologies. Also, research should try to elucidate whether the connectivity strength within various networks, as found in our study, bears consequence for structural connectivity measures and other indexes of anatomical variability.

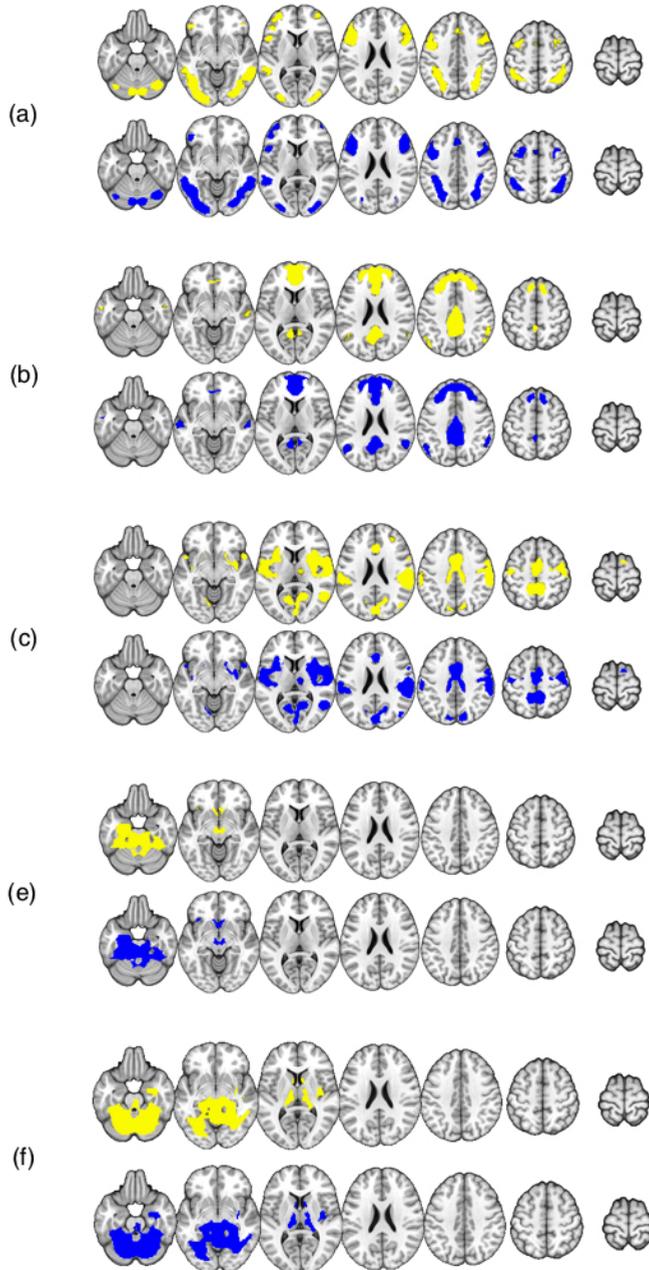
3.5 Acknowledgements

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3.6 Supplementary material



Supplementary Figure 3.1 Four noise components distinguished by the group ICA analysis. Images are z-statistics, ranging from 2.3 (red) to 7 (yellow), overlaid on the MNI-152 standard brain. The left hemisphere of the brain corresponds to the left side in the image. Brain activations are displayed using MRICroGL (<http://www.mccauslandcenter.sc.edu/mricrogl/>).



Supplementary Figure 3.2 Mean connectivity maps per group, showing a significant representation of each IC in the two groups (yellow maps represent mean connectivity maps for the Average LAA participants, blue, for the High): (a) *task-positive/language network*; (b) *default-mode network*; (c) *working memory network*; (e) *cerebellar network*; (f) *emotional network*. The left hemisphere of the brain corresponds to the left side in the image. Brain activations are displayed using MRICroGL (<http://www.mccauslandcenter.sc.edu/mricrogl/>).

Chapter 4

On neural correlates
of individual differences in novel
grammar learning: an fMRI study

ABSTRACT

We examine the role of language analytical ability, one of the components of language aptitude - a specific ability for learning languages - during acquisition of a novel grammar. We investigated whether the neural basis of artificial grammar learning (AGL) differs between populations of highly and moderately skilled learners. Participants performed an AGL task during an fMRI scan and data from task's test phases were analysed. Highly skilled learners performed better than moderately skilled ones and engaged during the task more neural resources in the right hemisphere, i.e. in the right angular/supramarginal gyrus and superior frontal and middle frontal gyrus and in the posterior cingulate gyrus. Additional analyses investigating the temporal dynamics of brain activity during learning revealed lateralisation differences in the modulation of activity in the parietal and temporal cortex. In particular, the left angular gyrus BOLD activity was coupled with high performance on the AGL task and with a steep learning curve.

4.1 Introduction

It is a commonly observable fact that individuals learning foreign languages differ from each other both in terms of acquisition rate and the ultimate attainment of the languages. Some people are believed to have a so-called “knack” for languages, or to possess a set of special abilities, which enable them to communicate in any given foreign language successfully both faster and more proficiently than others. The question arising is what neural mechanisms are responsible for such differences between individual learners.

As language acquisition is a complex process consisting of various aspects (i.e., building up the mental lexicon, acquisition of grammatical rules, phonological regularities and pragmatic competence), capturing the neural architecture behind individual variability between learners poses important methodological challenges. Although it is possible to investigate language learning in a holistic way, employing natural language input (see e.g., Musso et al., 2003; Veroude, Norris, Shumskaya, Gullberg, & Indefrey, 2010), most neuroimaging studies on language acquisition resort to highly controllable stimuli representing only one of the facets of language learning. Acquisition of novel vocabulary items for example, is often investigated without the involvement of their morphosyntactic features (e.g., Breitenstein et al., 2005; Freundlieb et al., 2012; Hultén, Laaksonen, Vihla, Laine, & Salmelin, 2010).

The focus of this study is how new language is *ab initio* processed by the brain and how individual differences in performance are reflected in brain functionality. As a proxy for the language acquisition process, we chose to concentrate on the acquisition of new grammatical rules. We believe the grammar to be one of the most important building blocks of (second) language learning. Our aim is to capture the process of new syntax acquisition in isolation from other aspects of language learning and control for earlier exposure.

4.1.1 High cognitive skills for grammar learning

Within the field of second language acquisition (SLA) success in language learning has been ascribed to various factors, such as learner’s age, language aptitude, motivation, personality and learning style. Besides the age factor, language aptitude is the most robust predictor of achievement in a second language (L2) (Dörnyei & Skehan, 2003; R. Ellis, 2008; Sawyer & Ranta, 2001). This individual, relatively immuta-

ble factor, plays an important role in SLA, when language is acquired by means of instruction (i.e. in a formal setting, where it is explicitly reflected upon) (de Graaff, 1997), under incidental learning conditions (Hamrick, 2015), and naturalistically, i.e. without formal instruction (Abrahamsson & Hyltenstam, 2008; DeKeyser, 2000; Robinson, 1997; Sawyer & Ranta, 2001). Language aptitude has traditionally been operationalised by means of standardised test instruments that aim at capturing learners' abilities underlying L2 acquisition. Such tests typically consist of a number of different parts, each aiming to measure a putative separate component of the larger construct of aptitude. Most aptitude tests thus underscore its multi-componential nature (i.e., this specific talent is a combination of skills that are fairly independent from each other). Four sub-components of language aptitude are traditionally distinguished: rote learning memory, phonemic coding ability, inductive language learning ability and language analytical ability (LAA) (cf. Abrahamsson & Hyltenstam, 2008; Carroll, 1981; Dörnyei & Skehan, 2003; Ellis, 2008; Sawyer & Ranta, 2001; Skehan, 2002).

Despite the recent technological advances available for neurolinguistic research, it remains unclear how these language aptitude components can be accounted for in terms of their neural correlates (cf. Hu et al., 2013; Reiterer, Pereda, & Bhattacharya, 2011; Xiang, Dediu, Roberts, Norris, & Hagoort, 2012). With this functional magnetic resonance imaging (fMRI) study, we therefore wanted to gain insight into the neural mechanisms underlying language aptitude, in particular, one of its components, viz. language analytical ability. We aimed to capture the neural correlates of LAA during the process of acquisition of a novel grammar. LAA, being relevant for pattern identification during SLA which involves analysing and processing new linguistic input (Skehan, 2002), is arguably the most important of the aptitude components when it comes to grammar learning: learners with a high degree of LAA are sensitive to grammatical structure of new languages and are able to make linguistic generalisations easily. SLA research has shown that LAA plays an important role in second language acquisition in a variety of contexts, including immersion (Harley & Hart, 1997), classroom (Erlam, 2005) and lab (Yilmaz, 2012) settings.

A number of studies investigating individual differences in cognitive abilities in relation to brain function have focussed on the neural efficiency hypothesis in order to explain the mechanisms underlying high cognitive skills (Haier et al., 1988; Neubauer & Fink, 2009; Nussbaumer, Grabner, & Stern, 2015; Prat, 2011; Prat & Just, 2011; Prat, Long, & Baynes, 2007; Reichle, Carpenter, & Just, 2000). Neural

efficiency is understood as using fewer mental resources, in a more focused and goal-directed way, while dealing with demands of the task at hand (Neubauer & Fink, 2009). For example, within the domain of language abilities, Prat et al. (2007) showed that high-capacity readers (as per a reading span test), exhibited higher neural efficiency during sentence comprehension than low capacity readers.

To date, however, we are not aware of any studies investigating high skills for particular L2 learning sub-processes - such as acquisition of novel grammar rules - either corroborating or contradicting the neural efficiency hypothesis. By investigating the neural correlates of LAA during new grammar learning, we aim to contribute to understanding of neural mechanisms behind successful foreign language learning in general, as well as to the discussion on neural efficiency as the underlying mechanism behind high cognitive skills. Does neural efficiency drive successful and efficient L2 learning?

4.1.2 The artificial grammar learning paradigm

In our approach, we employed a methodology previously used in studies investigating neural mechanisms behind the acquisition of novel grammar rules, i.e. *artificial grammar learning* (AGL). Even though AGL paradigms do not offer a comprehensive model of language acquisition, they are often used in laboratory settings in order to gain insight in the neurobiology of syntax processing and acquisition, without the interference of semantics, phonology or pragmatics (Petersson et al., 2012; Petersson & Hagoort, 2012; Reber, 1967) and with the advantage of being highly controllable. Also, contrary to the use of natural language stimuli, AGL excludes any interference of prior exposure. Neuroimaging investigations into the neurobiology of AGL have shown that such tasks involve the same neural resources as in case of processing and acquisition of natural languages, i.e. the left inferior frontal gyrus (LIFG) (Petersson & Hagoort, 2012). Moreover, Ettlinger, Morgan-Short, Faretta-Stutenberg and Wong (2015) have recently provided evidence for a strong relationship between performance on an artificial language learning task and L2 learning.

Although most AGL studies require an acquisition period of several days (e.g., Friederici et al., 2002; Petersson et al., 2012), on-line learning of an artificial grammar in an MRI scanner was employed in our experimental design in order to enable observation of the neural mechanisms behind the learning process in real time. Another difference between our study and traditional AGL experiments has to do with artifi-

cial grammar systems being often learnt implicitly (e.g., Petersson et al., 2012; Reber, 1967), solely on the basis of examples and without instruction or feedback. Our aim was to guide participants' attention towards discovering the grammatical rules by providing instructions to do so. Also, we wanted to include feedback as part of the learning process. Such procedure has previously been adopted in a series of experiments where the artificial language BROCANTO was used to investigate the learning mechanisms underlying grammar acquisition (Brod & Opitz, 2012; Friederici et al., 2002; Hauser et al., 2012; Opitz et al., 2011; Opitz & Friederici, 2003, 2004, 2007; Opitz & Hofmann, 2015). BROCANTO studies consist of learning and test phases. During learning, participants are presented with grammatically correct sentences and are instructed to extract the underlying grammatical rules. In test phases, both grammatical and ungrammatical sentences are presented and participants are asked to give a grammaticality judgement on the sentences.

The neural architecture responsible for acquiring the BROCANTO structure has been shown to involve a dynamic interaction between left hippocampal formation and the left inferior frontal area: during the task, activity in the hippocampus decreased as a function of time (and performance); the reverse was observed in the LIFG (Opitz & Friederici, 2003). Hauser et al. (2012) investigated the underpinnings of two types of knowledge acquired in the course of AGL: rule and similarity knowledge. They confirmed the earlier findings of Opitz & Friederici (2003) and proposed that hippocampus and right IFG support grammar learning when the acquired knowledge is based on similarity; left ventral premotor cortex was found to be responsible for rule knowledge (Hauser et al., 2012; Opitz & Friederici, 2004).

The goal of this study is then twofold: first, we want to find mechanisms responsible for processing novel grammar that are representative of individual cognitive traits measured prior to the fMRI experiment, namely the language analytical ability. Second, we are interested in the way successful learning of a novel grammar is supported by the brain and how it is represented in the neural data over time. On the basis of previous findings, we expect to observe an interaction of the hippocampal system and the prefrontal cortex when concentrating on time effect. In line with the neural efficiency hypothesis (Haier et al., 1988; Neubauer & Fink, 2009), less distributed activity networks are expected in the case of highly skilled learners, especially in the inferior frontal region.

4.2 Methods

4.2.1 Pre-test

A language aptitude test was administered to a large group of participants ($N = 307$). We used the Llama Language Aptitude Test (LLAMA) (Meara, 2005), which is a computer-based test battery with automated scoring, suitable for participants with various language backgrounds. The test consists of four parts: (1) a vocabulary learning task, (2) a test of phonetic memory, (3) a test of sound-symbol correspondence and (4) a test of grammatical inferencing (LLAMA_F), being a measure of LAA. Recruitment of participants for this study was based on the scores on the LLAMA_F test.

In this test, twenty pictures are presented together with sentences in an unknown language that describe them. In the learning phase (lasting five minutes), participants are asked to discover grammatical rules (primarily concerned with agreement features) of this unknown language, and they are allowed to take notes. In the test phase, they are presented with a series of pictures, combined with two sentences and they have to decide which sentence is grammatically correct. Participants can score from 0 to 100, where 80 - 100 is defined as outstandingly good and 25 - 45 as average (Meara, 2005).

4.2.2 Participants

After taking the LLAMA test, forty-two healthy adults with no contraindications for an MRI scan were invited for the second part of the study, i.e. the fMRI experiment. On the LLAMA_F test, the participants received either an “average score” (i.e. 30-50)¹ (henceforth Average LAA), or an “outstandingly good” score (i.e. 80-100) (henceforth High LAA).

There were 20 Average LAA participants (16 female), age 19-39 years ($M = 23.60$ years) and 22 High LAA participants (16 female), age 19-43 years ($M = 23.18$ years). All were native speakers of Dutch, right-handed and had normal or corrected-to-normal vision.

The Medical Ethical Committee of the Leiden University Medical Centre (LUMC) (Leiden, the Netherlands) approved the protocol of the MRI

¹ Although the LLAMA manual defines “average score” as 25-45, a score of 50 was also included as average in this study. The scores are awarded at intervals of 10 and a score of 45 is not possible to obtain. Therefore, there were no participants who scored 25, either.

experiment; behavioural testing was also conducted according to the Ethics Code of the Faculty of Humanities at Leiden University. Participants gave written informed consent prior to the experiment and were remunerated for their time.

4.2.3 Stimuli and design

The stimulus material was created on the basis of the artificial grammar of BROCANTO (Brod & Opitz, 2012; Friederici et al., 2002; Hauser et al., 2012; Opitz et al., 2011; Opitz & Friederici, 2003, 2004, 2007). The AGL task was administered in the scanner and consisted of three blocks of learn and test phases, and a subsequent transfer test. The stimulus material consisted of both grammatical and ungrammatical sentences. The grammatical ones were used in the learning phases of the experiment, the test phases (and the transfer test) contained both grammatical and ungrammatical sentences. In this study, only the fMRI data acquired during the test phases are reported.

The grammar of BROCANTO follows rules found in many natural languages: a sentence (S) consists of a noun phrase (NP) and a verb phrase (VP). A version of the BROCANTO language with 8 vocabulary items was used in this experiment. Words forming a particular word class (nouns, verbs, etc.) could be distinguished by a particular vowel, e.g., ‘u’ specified a noun and ‘e’ a verb. The items were categorised into nouns (“gum”, “trul”), verbs (“pel”, “prez”), adjectives (“böke”), adverbs (“rüfi”) and determiners (“aaf”, always followed by a noun and “aak”, always followed by a modifier). The sentences contained three to eight words and had a subject-verb[-object] structure. The following possible sentence structures were included: dNv² (e.g., *aaf gum pel*), dNvm (e.g., *aaf gum pel rüfi*), DMNv (e.g., *aak böke gum pel*), dNvdN (e.g., *aaf gum pel aaf gum*), dNvDMN (e.g., *aaf gum pel aak böke gum*), dNvmDMN (e.g., *aaf gum pel rüfi aak böke gum*), dNvmdN (e.g., *aaf gum pel rüfi aaf gum*), DMNvdN (e.g., *aak böke gum pel aaf gum*), DMNvDMN (e.g., *aak böke gum pel aak böke gum*), DMNvmDMN (e.g., *aak böke gum pel rüfi aak böke gum*), DMNvm (e.g., *aak böke gum pel rüfi*) and DMNvmdN (e.g., *aak böke gum pel rüfi aaf gum*). In total, we constructed 80 sentences according to the above rules.

The ungrammatical sentences were constructed on the basis of the 80 grammatical ones. They contained syntactic violations and were created by substituting words from one category by words from a different cate-

² N = noun, v = verb, M = adjective, m = adverb, d = determiner (followed by a noun) and D = determiner (followed by a modifier)

gory. The violations were either determiner-noun-agreement violations (i.e., DN instead of dN and dMN instead of DMN, e.g., **aak gum pel aaf gum* instead of *aaf gum pel aaf gum*), word class repetitions of nouns or verbs (e.g., **aaf prez pel aaf gum* instead of *aaf gum pel aaf gum*) and phrase structure violations (i.e., NP NP and NP NP VP rather than NP VP and NP VP NP, respectively, e.g., **aaf gum aaf gum pel* instead of *aaf gum pel aaf gum*). For each grammatical item there were three ungrammatical versions (according to the three violation types). From the pool of 80 grammatical and 240 ungrammatical items, we chose items for the learning and test phases of the experiment and the subsequent transfer test.

4.2.3.1 Presentation

The task was created and presented in E-Prime 2.0.10 software (Psychology Software Tools, 2012). Stimuli were presented on a projection screen reflected to a mirror attached to the head coil above participants' eyes. All stimuli were presented in E-Prime 'silver' letters (Courier New, size 22) on an E-Prime 'black' background.

In the learning phases of the experiment, participants were instructed to discover the grammatical rules of the language. They saw forty sentences in each of the three learning phases; these were presented for 8 seconds and proceeded by a fixation cross (3 seconds). Each of the three test phases included 20 samples of grammatical and 20 samples of ungrammatical sentences, presented in a random order, for 6 seconds each. The exact details of the stimulus selection algorithm and a complete list of all sentences used can be found in the Supplementary material.

Participants were instructed to give a grammaticality judgment by a button press within the 6 seconds of presentation of the sentence. After 6 seconds, visual feedback was provided (a green tick indicating a correct response or a red cross for wrong answers). The feedback screen was presented for 1 second. After the feedback screen, a fixation cross was presented. The duration of the fixation cross was jittered (2-6 seconds of inter-trial interval) in order to ensure that the feedback presentation would not influence the brain activation to the following sentence. Figure 4.1 contains an example trial from the test phase.

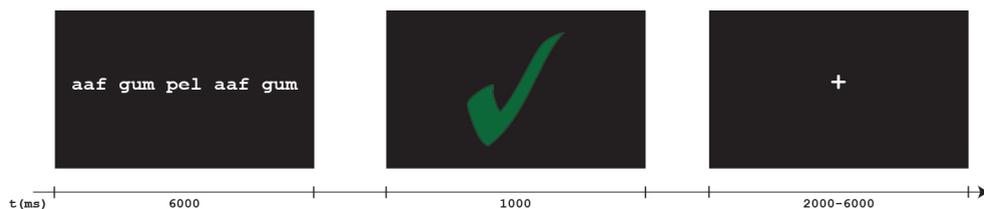


Figure 4.1 An example of a trial from the test phase of the AGL task: a grammatical test item is correctly classified by the participant.

Six days after the fMRI experiment, participants performed a delayed transfer test, with 40 new sentences (half of which grammatical, half ungrammatical) presented in random order. The task was performed on a desktop computer or online, in 3 cases where participants could not be present in the lab six days after the fMRI scan. The online version was prepared and administered in Qualtrics (Qualtrics, 2013). In order to prevent further learning, no feedback was provided in the transfer test.

4.2.4 Data acquisition

Imaging data were acquired using a Philips 3T MR-system (Best, The Netherlands) located at the Leiden University Medical Centre (LUMC) equipped with a SENSE-32 channel head coil. For each subject, changes in blood oxygen level dependence (BOLD) were measured three times; each scan was acquired during the consecutive test phases of the AGL task. We obtained echo-planar images (EPI) using a T2*-weighted gradient echo sequence (repetition time [TR] = 2200 ms, echo time [TE] = 30 ms, matrix size: 80 x 79, 38 axial slices, 2.75 x 2.75 x 2.75 mm voxel size). EPI's were scanned parallel to the anterior–posterior commissure plane. The length of each scan sequence was 209 volumes and lasted 7.5 minutes. Anatomical imaging included a 3D gradient-echo T1-weighted sequence (TR = 9.755 ms, TE = 4.59 ms; matrix 256 x 256; voxel size: 1.2 x 1.2 x 1.2 mm; 140 slices) and a high-resolution T2-weighted image (TR = 2200 ms, TE = 30 ms; matrix 112 x 112; voxel size: 2.0 x 2.0 x 2.0 mm; 84 slices).

4.3 Behavioural data

4.3.1 Effect of LAA

The responses on the AGL task for each participant were first transformed into d' scores in order to correct for response bias (Macmillan &

Creelman, 2005). The data were then analysed with the goal of establishing the learning effect and differences between High and Average LAA participants distinguished by the LLAMA_F test. Following previous studies employing similar experimental designs (Brod & Opitz, 2012; Hauser, Hofmann, & Opitz, 2012; Opitz, Ferdinand, & Mecklinger, 2011; Opitz & Friederici, 2003, 2004, 2007), a repeated measures ANOVA (alpha level = 0.05) was employed. We used SPSS version 22 (IBM SPSS, 2012). The analysis was performed with LAA as a between-subject factor (High LAA vs. Average LAA) and learning phase (first phase, second phase, last phase and transfer test) as a within-subject factor. Mauchley's test showed violations of sphericity against the factor phase, $\chi^2(5) = 21.408$, $p < .01$, therefore Greenhouse-Geisser correction for non-sphericity was used ($\epsilon = 0.769$).

The analysis revealed that the d' scores on the AGL task both among the High LAA and Average LAA participants increased over the course of the experiment (see Figure 4.2): there was a main effect of learning phase, $F(2.308, 92.301) = 38.236$, $p < .001$, $\eta_p^2 = .489$. Furthermore, the High LAA participants performed better than the Average LAA participants which was reflected in a significant effect of LAA, $F(1, 40) = 16.762$, $p < .001$, $\eta_p^2 = .295$, and an interaction between LAA and phase, $F(2.308, 92.301) = 4.469$, $p = .011$, $\eta_p^2 = .10$.

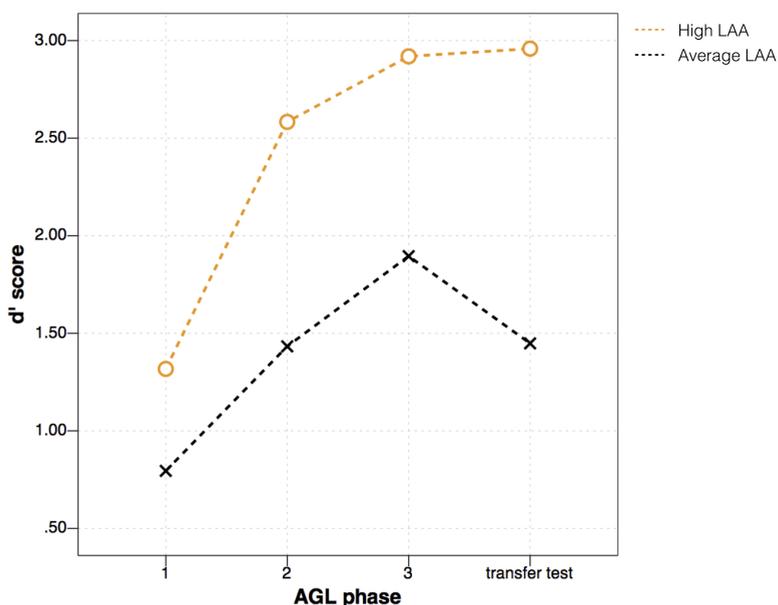


Figure 4.2 Performance (d' scores) across participants with High and Average LAA during the three AGL test phases and the subsequent transfer test.

4.3.2 Learning patterns over time

Apart from establishing whether, and to what degree (as a function of the pre-tested analytical abilities) the participants were able to acquire the grammar rules, we were interested in gaining more insight into the various ways the learning of a novel grammar proceeded in time. Individual participants exhibited various learning curves, which can arguably be coupled with different neural mechanisms of learning (cf. Karuza, Emberson, & Aslin, 2014). Therefore, we aimed to classify the behavioural AGL data sets into groups with similar learning patterns, thus taking into account the effect of time and participants' actual performance. To this end, we chose to perform a procedure enabling objective identification of relatively homogeneous groups of participants, namely a *k*-means cluster analysis (Aldenderfer & Blashfield, 1984, cf. Catani et al., 2007). The analysis was performed in R (R Development Core Team, 2015).

The *k*-means cluster analysis was run on standardized *d*' scores from the three AGL test blocks using 1 to 6 clusters with 1000 starts (i.e., running the analysis 1000 times, each time with a different initial clustering of the subjects and retaining the best clustering found across the 1000 analyses (see Steinley & Brusco, 2007). We determined the optimal number of clusters by using a scree-plot-like procedure (Cattell, 1966). In this procedure, the proportion explained variance per clustering solution is plotted against the number of clusters (see Figure 4.3) and an optimal number of clusters is determined by looking for an elbow (Thorndike, 1953) in this plot (see also Wilderjans, Ceulemans, & Meers, 2013). Looking at Figure 4.3, a clear elbow was found for the solution with two clusters and a smaller, but still substantial, elbow for the three cluster-solution. The two cluster-solution explained almost 60% of the variance, whereas adding a third cluster substantially increased the proportion explained variance of the solution (from 58.8% to 73.5% respectively). However, adding more clusters, which makes the solution more complex, did not result in a much better solution (i.e., 79.7%, 85.3% and 87.5% explained variance for the four, five and six cluster-solution, respectively). In particular, in Figure 4.3 one can see that the increase in percentage explained variance levels off when using more than three clusters.

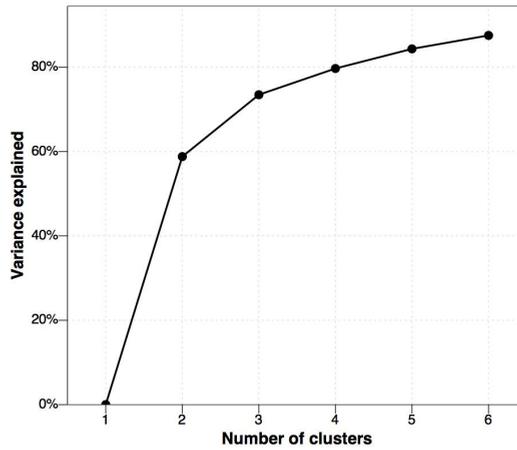


Figure 4.3 Graphical representation of the number of clusters versus the amount of explained variance.

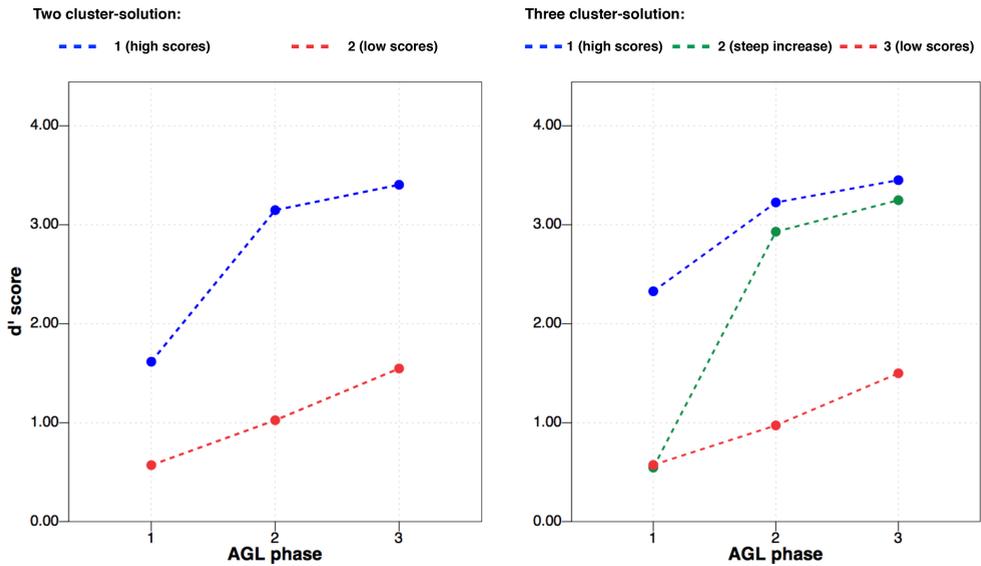


Figure 4.4 Results of the *k*-means cluster analysis on the behavioural data from the AGL task. Two solutions of the analysis are presented: the two cluster-solution on the left, and the three cluster-solution on the right. Points represent the mean d' score per identified cluster of participants per AGL task phase.

The two cluster-solution classified learners into two almost equally sized groups: one group ($N = 20$) with high learners (i.e., larger d' scores in each AGL phase) and one group ($N = 22$) with low learners (i.e., lower scores in each phase). The three cluster-solution demonstrated that the cluster of high learners in fact consisted of two types of high learners: those who achieved high d' scores already in the first AGL test phase ($N = 12$), and those who had started with low scores but were able to quickly improve their performance, thus displaying a steeper increase in the obtained d' scores ($N = 9$) (see Figure 4.4).

When it comes to the way the original LAA scores were represented in the groups of learners determined by the analysis, the high learners, no matter whether obtaining high scores only at the end of the task, or also right from the beginning, were in both instances coupled with (on average) high analytical abilities. An independent samples t-test on the LLAMA_F scores for the high and low learners according to the two cluster-solution was significant ($t(40) = 3.39$, $p = .002$, $r = .472$); the effect of group was also significant for a three-clusters solution ($F(2, 39) = 6.38$, $p = .004$, $\eta^2 = .247$). A Games-Howell post-hoc test revealed that learners with low d' scores on the AGL task had significantly lower LAA scores ($M = 55.71$, $SD = 5.05$) than the “steep learners” ($M = 80.00$, $SD = 6.00$, $p = .015$), and the learners with high d' scores ($M = 79.17$, $SD = 6.09$, $p = .017$). There were no statistically significant differences between the “steep learners” and the learners with high d' scores ($p = .995$). A summary of the results of the analysis including mean d' scores per AGL task phase per group and mean scores on the pre-test and the LLAMA_F test are presented in Supplementary Table 4.2.

4.4 Imaging data

4.4.1 Pre-processing

Imaging data acquired during the test phases of the AGL task were processed using FSL software Version 5.0.7 (FMRIB’s Software Library, <http://www.fmrib.ox.ac.uk/fsl>; Jenkinson et al., 2012). Pre-processing was carried out using FEAT (FMRI Expert Analysis Tool) Version 6.00. The following pre-statistics processing was applied: motion correction using MCFLIRT (Jenkinson et al., 2002); non-brain removal using BET (Smith, 2002); spatial smoothing using a Gaussian kernel of 5 mm FWHM; grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor; and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma = 50.0$ s).

The functional images were registered to MNI-152 standard space (T1-standard brain averaged over 152 subjects; Montreal Neurological Institute, Montreal, QC, Canada) using a three-step registration from functional to high-resolution structural T2-image (rigid body, 6 degrees of freedom) to T1-image (rigid body, 6 degrees of freedom) to MNI-template (affine registration, 12 degrees of freedom). Registration was carried out using FLIRT (Jenkinson et al., 2002; Jenkinson & Smith, 2001). Time-series statistical analysis was carried out using FILM with local autocorrelation correction (Woolrich et al., 2001). The hemodynamic response function (HRF) was computed as a double gamma function. The design matrix for each participant included grammatical and ungrammatical sentences as events of interest. Events of non-interest were not modelled. The contrasts tested for differential BOLD-response in grammaticality, i.e. for greater activity during grammatical than ungrammatical items and in ungrammaticality, i.e. for greater activity during ungrammatical than grammatical items.

4.4.2 Higher level analyses

4.4.2.1 Effect of LAA

A multi-session and multi-subject (repeated measures – three level) analysis was conducted with the aim of detecting BOLD-response differences and modulations between participants with different degrees of LAA (High LAA vs. Average LAA). The goal of this analysis was to establish brain activations typical for participants with high and average analytical abilities, as measured prior to the experiment, during novel grammar learning. The analysis consisted of the following steps: First, mean activation maps of the three phases per subject were calculated. The three phases of the experiment were not enough for a mixed effects model, hence a fixed effects model was used, by forcing the random effects variance to zero in FLAME (FMRIB's Local Analysis of Mixed Effects) (Beckmann et al., 2003; Woolrich, 2008; Woolrich et al., 2004). Z (Gaussianised T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a cluster corrected significance threshold of $p = 0.05$ (Worsley, 2001). The results of this analysis were subsequently used as input for a two-sample unpaired t-test which was carried out using FLAME stage 1 (Beckmann et al., 2003; Woolrich, 2008; Woolrich et al., 2004). Pre-threshold masking was applied and a grey matter mask was used to mask out non-grey matter regions. Z (Gaussianised T/F) statistic images were thresholded using clusters determined by

$Z > 2.3$ and a cluster-corrected significance threshold of $p = 0.05$ (Worsley, 2001).

4.4.2.2 Learning patterns over time

Beside exploring brain activity distinguishing highly from moderately skilled learners as determined by the LLAMA_F test, we were interested in investigating the neural architecture behind the successful grammar learning process in time. The analysis revealing the heterogeneous learning patterns in our behavioural data (see Section 4.3.2 above) enabled us to further explore the neural underpinnings of differently realised learning curves. This approach thus facilitated an analysis integrating both behavioural responses and time with brain activity (cf. Karuza, Emberson, & Aslin, 2014).

Of interest for the further analysis of the fMRI data were the differences in activation between the first and last test phase (run) and a comparison of that effect across the groups identified in the k -means clusters analysis. Only the first and last time point was included in the analysis in order to observe the largest contrast in terms of the increase in correct responses.

Based on the two outcomes of the k -means clusters analysis, we conducted two group analyses of the fMRI data. The first analysis was based on the two cluster-solution (a 2 x 2 between-subjects ANOVA), the second on the three cluster-solution (a 2 x 3 between-subjects ANOVA). Both analyses were conducted using FEAT Version 6.00, part of FSL (FMRIB's Software Library, <http://www.fmrib.ox.ac.uk/fsl>). Pre-threshold masking was applied and a grey matter mask was used to mask out non-grey matter regions. Z (Gaussianised T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a cluster corrected significance threshold of $p = 0.05$ (Worsley, 2001). The goal of these analyses was to examine the main effect of time (phase of the AGL task) and group (cluster) and an interaction effect between them.

4.4.3 Results

4.4.3.1 Effect of LAA

A general linear model was used in the first level fMRI analysis to test for differential BOLD-responses to grammatical and ungrammatical items. Data from the three runs were averaged per participant and subsequently a two-sample unpaired t-test was conducted in order to compare mean activations between the High and Average LAA participants.

On group level, only the contrast testing for differential BOLD-response in ungrammaticality, i.e. for greater activity during ungrammatical than grammatical items, yielded significant activation clusters for both High and Average LAA participants (see Table 4.1 and Figure 4.5). Grammaticality (greater activity during the presentation of grammatical than ungrammatical items) did not produce significant activation clusters.

| Cortical region (peak) | L/R | BA | Size (voxels) | Peak location | | | Z_{\max} | p -value |
|--|-----|-----------|---------------|---------------|-----|-----|------------|-------------|
| | | | | X | Y | Z | | |
| High LAA (group mean) | | | | | | | | |
| (1) Supplementary Motor Cortex / Superior Frontal Gyrus | L | 6 | 35783 | -6 | 8 | 62 | 5.35 | $p < 0.001$ |
| (2) Hippocampus | R | 28 | 641 | 26 | -22 | -16 | 3.81 | $p = 0.002$ |
| Average LAA (group mean) | | | | | | | | |
| (1) Paracingulate Gyrus / Superior Frontal Gyrus | R | 8 | 6797 | 0 | 36 | 40 | 4.86 | $p < 0.001$ |
| (2) Frontal Orbital Cortex / Inferior Frontal Gyrus, pars triangularis | L | 45 | 2537 | -48 | 30 | -10 | 4.54 | $p < 0.001$ |
| (3) Angular Gyrus | R | 39 | 1159 | 54 | -54 | 32 | 4.25 | $p < 0.001$ |
| (4) Middle Temporal Gyrus | R | 37 | 918 | 64 | -46 | -8 | 3.97 | $p < 0.001$ |
| (5) Middle Temporal Gyrus | L | 21 | 579 | -54 | -42 | 0 | 3.94 | $p = 0.004$ |
| (6) Angular Gyrus / Supramarginal Gyrus | L | 40 | 481 | -54 | -54 | 34 | 3.9 | $p = 0.011$ |
| Average LAA > High LAA | | | | | | | | |
| - | - | - | - | - | - | - | - | - |
| High LAA > Average LAA | | | | | | | | |
| (1) Supramarginal Gyrus / Angular Gyrus | R | 39/ 40 | 867 | 56 | -44 | 30 | 3.7 | $p < 0.001$ |
| (2) Cingulate Gyrus, posterior division | L | 23 | 695 | 0 | -42 | 24 | 3.73 | $p = 0.001$ |
| (3) Superior Frontal Gyrus / Middle Frontal Gyrus | R | 6 | 647 | 28 | 2 | 62 | 3.3 | $p = 0.002$ |

Table 4.1 Brain areas exhibiting greater activity for ungrammatical than grammatical items as a function of Average LAA and High LAA group; x, y and z coordinates in MNI space, regions labelled according to Harvard-Oxford Cortical and Subcortical Structural Atlases.

The greater activity for ungrammatical items among the High LAA participants (group mean) could be attributed to two clusters of activity: (1) a widespread, bilateral fronto-parieto-temporal activation, with its peak in the left supplementary motor cortex bordering on superior frontal gyrus, including superior frontal gyrus, IFG and right angular gyrus; (2) a cluster encompassing subcortical areas of the right hippocampus and right thalamus. The Average LAA participants displayed a network of activity smaller in size, but similar in topography. It included six

clusters, both in the left and right hemisphere, covering the following areas: (1) bilateral frontal areas including the paracingulate gyrus, middle and superior frontal gyri; (2) left IFG and left frontal orbital cortex; (3) right temporo-parietal areas including right angular and supramarginal gyri; clusters in (4) right and (5) left temporal lobe, including middle and superior temporal gyri and (6) a left temporo-parietal cluster encompassing the angular and supramarginal gyri and stretching out to the lateral occipital cortex.

The High LAA participants displayed significantly more activity than the Average LAA participants, and the difference was observed in (1) the right superior temporal lobe in the supramarginal and angular gyri, stretching to the middle temporal gyrus, (2) the left cingulate gyrus and (3) the right superior and middle frontal gyri, see Table 4.1 and Figure 4.5.

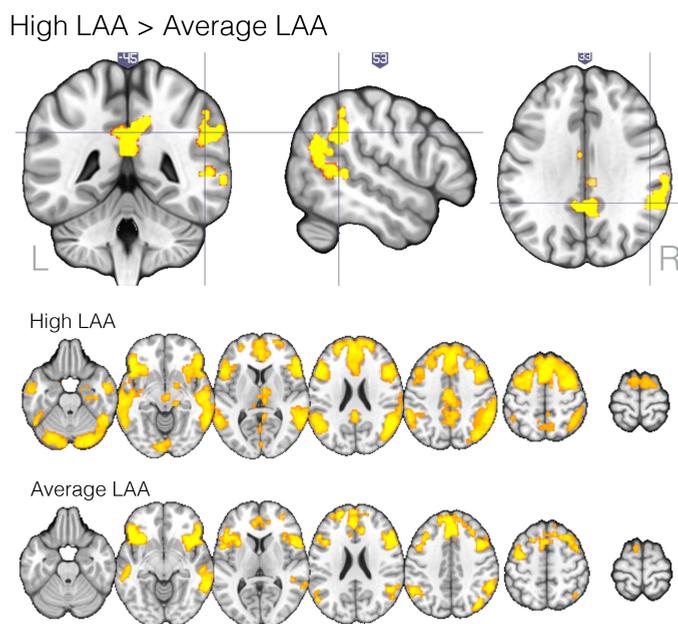


Figure 4.5 Brain activation in response to ungrammatical as compared to grammatical items significantly greater for the High than for the Average LAA participants (top panel) and group mean activation maps for High and Average LAA participants separately. Z (Gaussianised T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a cluster corrected significance threshold of $p = 0.05$ (Worsley, 2001).

4.4.3.2 Learning patterns over time

The second set of fMRI analyses concentrated on the different patterns of increase in correct responses on the task (as distinguished by the analysis of learning patterns in the behavioural data, see Section 4.3.2), and two time points of the experiment: the first and last AGL task phase.

For each of the analyses two factors were distinguished in FEAT: Time (two levels: first and third phase) and Group (learners with high and low d' scores on the task as identified on the basis of the k -means cluster analysis described in Section 4.3.2). The analysis was run twice, with the factor Group consisting of two, and three levels. Each time, we tested for the main effect of Time, main effect of Group and an interaction effect (Time x Group).

In each of the analyses, there was a significant effect of the factor Time. The factor Group yielded significant results only in the case of the 2 x 2 ANOVA analysis; there was no evidence of a group effect, or interaction between Group and Time when the groups were determined on the basis of the three cluster-solution of the k -means clusters analysis. Since the results for the factor Time are the same for both analyses, only the 2 x 2 ANOVA analysis is reported, see Table 4.2.

Five clusters of activity were determined in the 2 x 2 FEAT analysis as being significantly modulated by the factor Time. They were localised in (1) the left frontal pole; (2) right and (3) left angular gyrus and lateral occipital cortex; (4) left and (5) right superior and middle temporal gyri. The factor Group yielded one significant activity cluster localised in the left angular and supramarginal gyri, with voxels in the lateral occipital cortex, see Figure 4.6. There was no significant interaction between the factors Time and Group.

| Cortical region (peak) | L/R | BA | Size (voxels) | Peak location | | | Z_{\max} | p -value |
|--|-----|-------|------------------|---------------|-----|----|------------|-------------|
| | | | | X | Y | Z | | |
| Time | | | | | | | | |
| (1) Frontal Pole | L | 9 | 2346 | -18 | 54 | 34 | 4.68 | $p < 0.001$ |
| (2) Angular Gyrus / Lateral Occipital Cortex | R | 39/40 | 1278 | 52 | -62 | 38 | 4.43 | $p < 0.001$ |
| (3) Angular Gyrus / Lateral Occipital Cortex | L | 39/40 | 1247 | -52 | -58 | 34 | 4.87 | $p < 0.001$ |
| (4) Superior Temporal Gyrus | L | 21 | 797 | -60 | -30 | 0 | 3.23 | $p < 0.001$ |
| (5) Middle Temporal Gyrus | R | 21 | 566 | 66 | -40 | -4 | 2.24 | $p = 0.006$ |
| Group | | | | | | | | |
| (1) Angular Gyrus | L | 39 | 540 | -52 | -58 | 30 | 4.17 | $p = 0.008$ |
| Interaction (Time x Group) | | | | | | | | |
| - | - | - | - | - | - | - | - | - |

Table 4.2 Brain areas exhibiting a significant differential modulation of BOLD signal for grammatical and ungrammatical items, as a function of time and performance on the AGL task (as determined by the analysis of learning patterns in the behavioural data, where two groups of learners, with high and low d' scores on the AGL task were identified); x, y and z coordinates are in MNI space, regions labelled according to Harvard-Oxford Cortical Structural Atlas.

FSL Featquery tool was used to further investigate the effects of Group and Time. First, we explored the lateralisation differences in the activity of parietal and temporal regions, established to be significantly modulated by the factor Time. Four Region of Interest (ROIs) were determined: clusters of activity in the left and right temporal and parietal cortex distinguished as significantly modulated by the factor Time (see Table 4.2, Time). Subsequently, we extracted values for the ungrammatical > grammatical contrast from the ROI for each participant, and per each time-point and converted them into percentage signal change values. Figure 4.6 shows that the BOLD signal values were higher for the third AGL task phase for all ROIs, and for both groups. However, the magnitude of this effect was the strongest for the learners with high scores in the left parietal region.

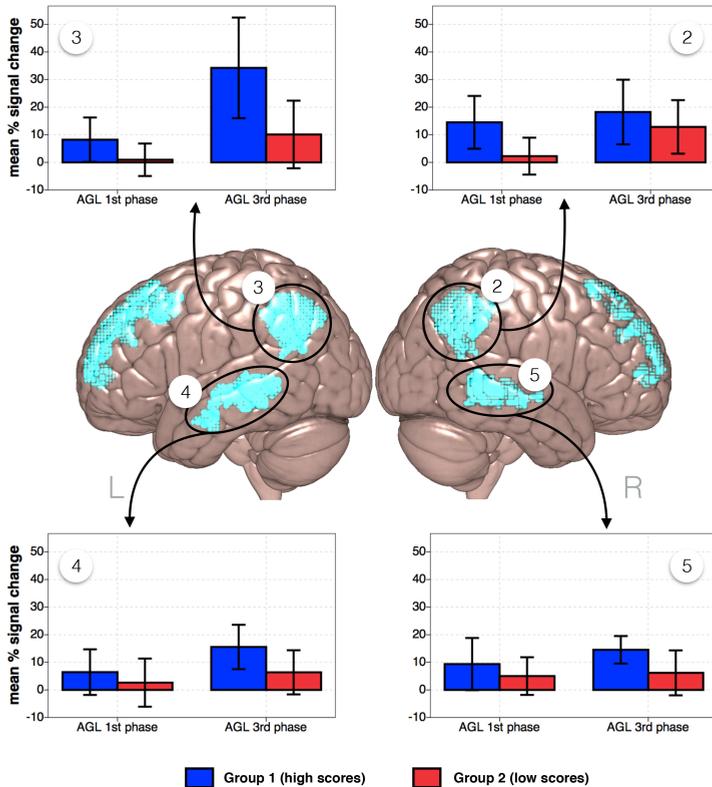


Figure 4.6 Time effect in the FEAT analysis investigating two time points of the experiment (first and last AGL task phase) and two groups (as determined by the analysis of learning patterns in the behavioural data): presented in the middle of the figure are the brain areas exhibiting a significant differential modulation of BOLD signal for grammatical and ungrammatical items, as a function of time, clusters 2 - 5 in Table 4.2. Graphs show the percentage signal change values for the ungrammatical > grammatical contrast, for each group distinguished in the analysis of learning patterns in the behavioural data, two time-points of the AGL task, and each ROI. Colours of the bars correspond to the colours of the group marking in Figure 4.4 (blue bars represent the mean values for learners with high scores, and red bars for learners with low scores). Error bars stand for 95% Confidence Intervals.

A more detailed account for how the activity in the left parietal region reflected participants' proficiency in the AGL task was further obtained by investigating the effect of Group and extracting the contrast values from the ROI determined to be significantly modulated by the factor Group (see Table 4.2). After extracting the percentage signal change values for each participant, per each time-point, we correlated them with the respective d' scores. The results show that there was a significant positive correlation between the contrast values and the d' scores, but only in the 3rd phase of the AGL task ($r(40) = .144$, $p = .36$ and $r(40) = .400$, $p = .009$, for the 1st and 3rd AGL task phase respectively), see Figure 4.7.

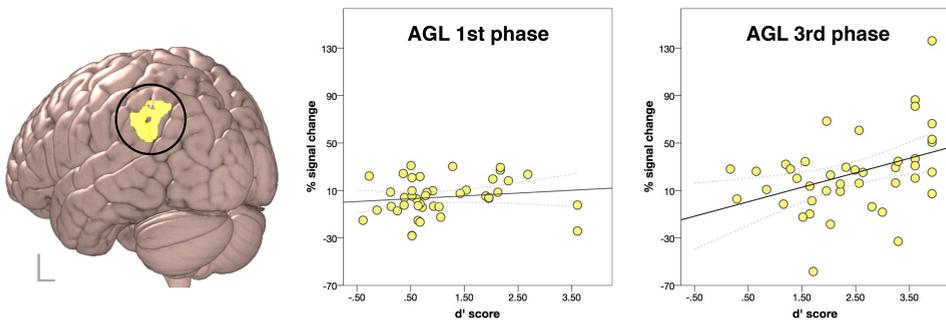


Figure 4.7 Group effect in the FEAT analysis investigating two time points of the experiment (first and last phase) and two groups (as determined by the analysis of learning patterns in the behavioural data): presented on the left is the brain area exhibiting a significant differential modulation of BOLD signal for grammatical and ungrammatical items, as a function of performance on the task. Graphs on the right show the percentage signal change values for the ungrammatical > grammatical contrast, in relation to the respective d' scores on the 1st and 3rd phase of the task.

Lastly, looking back at the analysis of learning patterns in the behavioural AGL task data (see Figure 4.4), we were interested in exploring the steep learning curve of participants who in the 1st AGL task phase obtained low scores but were able to quickly improve their performance and score highly in phase 3. We then ran additional exploratory analyses on the fMRI data of participants classified in the three groups in order to gain insight into the neural mechanism behind the differently realised learning curves. However, due to the fact that this effect was not strong enough to reach statistical significance in the 2 x 3 FEAT analysis, we wish to make only cautious observations concerning these results.

Data from two runs of the experiment of the participants classified in each group were entered in three separate paired sample t-tests. The analysis was carried out using FLAME stage 1 (Beckmann et al., 2003; Woolrich, 2008; Woolrich et al., 2004). It revealed that for the “steep learners” group, the left angular gyrus (at coordinates -48, -54, 24) exhibited more activity at the end of the task than at the beginning ($Z_{\max} = 3.14$, $p = 0.026$); no brain areas were significantly more active at the beginning of the task than at the end, see Figure 4.8. This effect was specific to the “steep learners” group; analyses of the other two groups of learners showed that learners with low scores exhibited a difference in activity between the third and the first phase in bilateral parietal and frontal regions; learners scoring highly from the beginning of the task showed a cluster of activity localised in the left frontal regions, see Supplementary Figure 4.1.

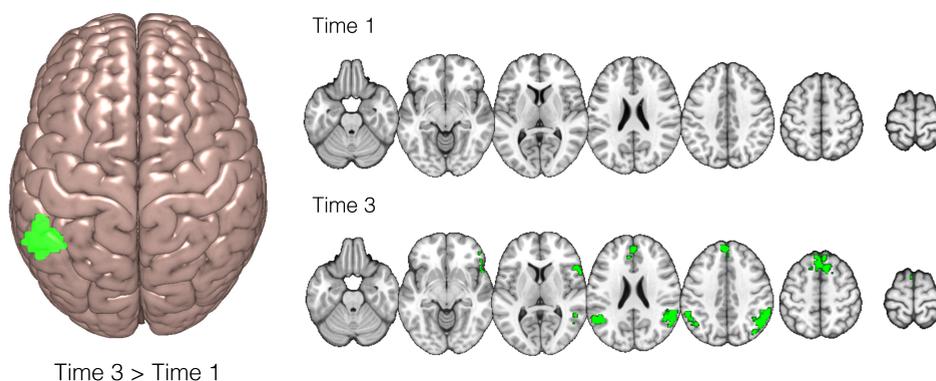


Figure 4.8 Brain activations in response to ungrammatical as compared to grammatical items for the group of participants determined by the analysis of learning patterns in the behavioural data as showing the most pronounced difference in scores on the AGL task between the first and the last phase. Z (Gaussianised T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a cluster corrected significance threshold of $p = 0.05$ (Worsley, 2001). On the left, brain activation cluster significantly greater in phase 3 than in phase 1 of the AGL task; two mean activation maps per time point are shown on the right. The left hemisphere of the brain corresponds to the left side in the image.

4.4.3.3 Summary of the results

In summary, the obtained results indicated that participants with high language analytical abilities outperformed moderately skilled learners on the AGL task (see Figure 4.2). This difference observed on the behavioural level, was coupled with increased activity on the neural level among High LAA participants. The difference was localized predominantly in the right hemisphere (see Figure 4.5). Moreover, our design enabled a further investigation of the different ways the learning of a novel grammar proceeded over time, both behaviourally (see Figure 4.4), and on the neural level. We found that activity in the bilateral temporal and parietal regions increased over the course of the task and that the left parietal region displayed the biggest modulation of BOLD activity at the end of the task, especially among successful learners (see Figure 4.6). The amount of activity in the left angular gyrus correlated with the behavioural performance, but only in the last AGL task phase (see Figure 4.7). Additionally, we saw that a steep learning curve in the AGL task (starting out with low scores and quickly improving the performance) could be traced back to the modulation of BOLD activity in the left angular gyrus. Participants displaying such a pronounced difference in performance between the first and the last phase of the task, showed only one cluster of brain activation significantly greater in phase 3 than in phase 1 of the AGL task localised in the left angular gyrus (see Figure 4.8).

4.5 Discussion and conclusions

The present study set out to investigate the neural correlates of individual differences in artificial grammar learning. We wanted to examine both the correlates of cognitive abilities measured independently from the fMRI task, i.e. the language analytical abilities, and task-specific activations representing the learning process over time.

Our results suggest that individuals learning an artificial grammar who were chosen on the basis of high or average score on a language aptitude test, not only differ when it comes to behavioural data on an AGL task, but also on the level of brain activity. Both groups of participants showed an increase in the amount of correct responses, but at the end of the task only the High LAA participants were on average able to correctly classify more than 90% of the items.

In the analyses of the imaging data, only the contrast testing for differential BOLD-response in ungrammaticality, i.e. greater activity during

ungrammatical than grammatical items, yielded significant activation clusters for both High and Average LAA participants. Comparable findings illustrating response to violations of newly acquired grammatical rules were reported by e.g., Forkstam, Hagoort, Fernandez, Ingvar and Petersson (2006), and Petersson, Forkstam and Ingvar (2004), and interpreted (Petersson et al., 2004) in terms of a model of learning through negative evidence (cf. Karuza et al., 2014). In our analyses of imaging data, we aimed at investigating such process of learning and pinpointing the mechanisms responsible for individual differences.

We showed that participants with high analytical abilities, contrary to our expectations, formulated on the basis of the neural efficiency hypothesis, did not exhibit less distributed activity networks when compared to the moderately skilled ones. We believe this result to be coupled with the task's complexity and clear differences in performance between the High and Average LAA participants. As argued by Neubauer and Fink (2009), neural efficiency can be most clearly applicable to tasks where high and low ability individuals perform on a similar level (see also Nussbaumer et al., 2015). However, the two groups did not perform on the same level, most probably due to the task being more challenging than expected and the training in the paradigm being rather short (45 minutes). According to Neubauer and Fink (2009), in cases where higher ability individuals perform much better than lower ability individuals, the high performance is coupled with a stronger brain activation, and the neural efficiency hypothesis is not applicable. In other words, “[w]hen it comes to difficult tasks it seems that brighter individuals [...] invest more cortical effort than individuals with lower ability may do” (p. 1014). In particular, the difference between the High and Average LAA participants lay in the High LAA participants displaying more activity in the brain areas traditionally described as belonging to the language network (cf. Hagoort, 2014; Joseph, 1982), but localised in the right hemisphere, i.e. the right angular/supramarginal gyrus and superior frontal and middle frontal gyrus and in the posterior cingulate gyrus.

Although language processing has been repeatedly reported to activate a left-hemisphere focused network (Gernsbacher & Kaschak, 2003), and despite the notion present in the literature that suppression of contralateral activity can benefit language performance (Antonenko et al., 2012; Thiel et al., 2006), our study showed a bilateral network of regions involved in the AGL task. The engagement of regions in the right hemisphere, in our view, might reflect the difference between proficient language processing and language learning, in a similar way to which

bilateral language-related activity is found in young children during L1 processing (cf. e.g., Everts et al., 2009; Holland et al., 2001; Ressel, Wilke, Lidzba, Lutzenberger, & Krägeloh-Mann, 2008). Successful acquisition of new grammatical information in adults might thus be governed by parallel engagement of additional neural resources. Engagement of broader networks seems advantageous for the ultimate outcome of the learning process and the activity in the right homologue areas to the classically left-lateralised language regions might cause the learning to be more efficient.

In addition to examining the correlates of pre-tested language analytical ability, in an analysis integrating behavioural responses and time with brain activity, we found that modulation of angular gyrus activity could be tied to differences in participants' performance on the task. Angular gyrus, middle temporal gyrus (both bilaterally) and the frontal pole were modulated when we investigated the effect of time. Furthermore, effort was made to identify the mechanisms involved in the progress of the learning process. By correlating the BOLD contrast values extracted from the left angular gyrus with the d' scores on respective AGL task phases, we believe to have underscored the importance of this region for successful learning of a novel grammar and rule acquisition.

The behavioural data on the AGL task increased steeply over the course of the experiment among a sub-group of the participants. A learning curve of such shape has been previously interpreted within the framework of Skill Acquisition Theory as typical for proceduralisation of newly acquired knowledge (DeKeyser, 1997, 2015) As argued by DeKeyser, L2 knowledge typically develops along three stages: declarative, procedural, and automatic. Declarative knowledge, acquired through observation and memorisation can turn into procedural knowledge rather quickly, and at fairly early stages of learning, especially among high-aptitude adult learners³. One of the clearest manifestations of such a shift is a decrease in error rates, most noticeably present among participants classified as "steep learners" in our data set (see Figure 4.4). DeKeyser's skill acquisition perspective on L2 development is also compatible with Ullman's (2004) declarative/procedural model, proposing distinct neural circuits for each type of knowledge, with - among others

³ We limit our interpretation of the results to the notion of "proceduralisation", since according to DeKeyser (2015) automaticity can be achieved much later in L2 development: the shift from declarative to procedural knowledge is "followed by a much slower process of automatization of procedural knowledge" (p. 96) and depends on a large amount of practice.

- the parietal cortex making up the procedural memory system⁴. By comparing two runs of the experiment among participants with the steepest learning curve on the task, we then believe to have tapped into the process of proceduralisation of the acquired knowledge. However, as pointed out in Section 4.4.3.2, this particular set of findings should be seen as a trend and investigated further in future studies in order for the results to be inarguably robust.

Support for our interpretations comes nevertheless from recent studies establishing similar qualitative differences in the neural substrates of second language grammar processing associated with learning. In their study, Morgan-Short and colleagues (2015) employed an adapted version of BROCANTO, BROCANTO2, with the aim of investigating how an implicit learning context may mediate the neural representation of L2. The authors showed some learners to be able to quickly rely on neural circuits associated with L1 grammar and procedural memory (in this case, the LIFG and basal ganglia). Other learners increasingly used neural circuits possibly tied to extralinguistic processing (e.g., the left middle frontal gyrus). Moreover, the behavioural analysis of their data provided evidence for relationships between declarative and procedural learning abilities and L2 development (Morgan-Short, Faretta-Stutenberg, Brill-Schuetz, Carpenter, & Wong, 2014). The authors established a role for declarative memory at early, and for procedural memory at later stages of syntactic development. That early grammar learning relies on declarative memory and later, on procedural, has also been recently established by Tagarelli (2014). Comparable individual differences in recruitment of neural resources were also shown in natural L2 processing: early stage L2 learners were observed to progress through distinct stages of learning, with a varying rate of progression across learners (Tanner, McLaughlin, Herschensohn, & Osterhout, 2013).

Successful acquisition of a new grammar appears to highly depend upon the engagement of the parietal cortex and in particular, the angular and supramarginal gyri. Due to its location at the intersection of parietal, occipital and temporal lobes, the angular gyrus has been characterised as a cross-modal integrative hub bringing together information

⁴ An alternative, but congruent interpretations of L2 knowledge development has been recently offered by Opitz & Hofmann (2015) who present rule- and similarity-based learning mechanisms as the basis of AGL. In our understanding, the similarity-based learning can be interpreted on a par with the declarative knowledge in DeKeyser's and Ullman's account of L2 learning; the rule-based learning, with the procedural knowledge.

from different modalities and processing subsystems (see Seghier, 2013 for review). Moreover, already in the early 1900s, the left lower parietal region was delineated as the “language talent area” by the German neurologist Pötzl (1925), who pointed it out to be the site underlying the exceptionality of the brains of multilinguals (Della Rosa et al., 2013). His findings seem to converge with recent neuroimaging investigations: the inferior parietal cortex has been shown to play a crucial role in complex language functions and memory processes, phonological representation, semantic integration, and second language vocabulary learning (Della Rosa et al., 2013; P. Li, Legault, & Litcofsky, 2014; Mechelli et al., 2004; Yang et al., 2015). More specifically, O’Connor, Han, & Dobbins (2010) have found the angular and supramarginal gyri to act as markers of violations in memory expectations, where a violation is a sign of contradiction between retrieval outcomes and expectations, and argued for the importance of both superior and inferior aspects of the lateral parietal regions for noting a lack of correspondence between what is anticipated from memory retrieval, and what is unusual. The inferior parietal cortex has furthermore been argued to form part of the attention and memory systems in that it is part of a “bottom-up” attentional subsystem facilitating the automatic allocation of attention to task-relevant information (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010), particularly to retrieved memories (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; cf. Seghier, 2013). More recently, in the effort to explore the computational characteristics of sentence processing regions, the angular gyrus has been implicated in the combinatorial network participating in the construction of complex meaning (Poeppel, 2014).

In the current study, right angular and supramarginal gyri activity differentiated highly from moderately skilled learners who were presented with grammatical and ungrammatical sentences of a newly acquired artificial language. The regions were more active during presentation of ungrammatical sentences among the High LAA than in the Average LAA participants, pointing to the fact that High LAA learners reacted more strongly to violations in sentences in a newly acquired language than the Average LAA learners, either due to allocating more attention to the stimuli or by having formed better knowledge representations of the acquired material, or both. Since the materials used in this study did not have a semantic component, the activations of angular gyrus present in our data suggest that its role in the construction of complex meaning (as proposed by Poeppel, 2014) might be predominantly combinatorial in nature. Moreover, as pointed out above, modulation of activity in the left angular gyrus seems to be tied to the proceduralisation

process of new rules - rules determining ways in which a number of unknown words can be combined and form sentences.

Another neural marker of high analytical abilities in our data was the posterior cingulate gyrus, which has previously been shown to be modulated by working memory tasks (Greicius et al., 2003), binding semantic representations on a multi-modal level (Jessen et al., 1999), to be implicated in successful episodic memory retrieval (Cabeza & Nyberg, 2000) and recently in memory consolidation of complex events (Bird et al., 2015). Morgan-Short et al. (2015) found the activity in left cingulate gyrus to increase over time during the AGL task and suggested increased engagement of attentional processes as an interpretation for this finding. The posterior cingulate activations in our study might help understand the nature of the skill in question: LAA seems to depend on good working memory, attention abilities and episodic memory and future studies employing neuropsychological testing and SLA diagnostic instruments might be able to elucidate the way these constructs interact with each other.

Interestingly, the previous findings concerning artificial grammar learning and the interactions of the hippocampal system and the prefrontal cortex (Opitz & Friederici, 2003) were only partially replicated in this study. Hippocampus activity was only observed among the High LAA participants and was not part of the significant activation clusters revealed by the Time by Group analysis. The role of the hippocampus in learning language rules and its involvement in language analytical abilities remains unclear on the basis of present results.

In terms of its neural correlates, success in foreign language learning has so far been linked to, among others, an anatomically larger primary auditory cortex (Golestani et al., 2007), increased white matter integrity (Flöel et al., 2009; Loui et al., 2011), differences in the functionality of the hippocampus (Breitenstein et al., 2005), as well as differences in structural (Xiang et al., 2012) and functional connectivity (Reiterer et al., 2011; Veroude et al., 2010) of the brain (see also Erard, 2012). With this study, we aimed at extending these results and gaining more insights into the neural mechanisms underlying individual differences in second language acquisition, with particular focus on novel grammar learning. We have shown that activity of the higher order associative brain areas (i.e. angular gyrus, cingulate gyrus) plays a crucial role in successful acquisition of a new grammar. In particular, we found that the activity of the right angular and supramarginal gyri during learning of a new grammar might be seen as a marker of high analytical skills, and the left angular gyrus as a site marking progress in acquir-

ing language-like rules. In other words, our results point to the conclusion that engagement of right parietal regions is crucial for efficient learning, but in order to process the newly acquired rules proficiently, the language specialised left-hemisphere activations must be present. The sooner they occur, the better the task performance.

The present study has at least two theoretical implications. First it brings nuance to the neural efficiency hypothesis by showing that its predictions could not be borne out in a demanding AGL task focussing on initial stages of learning. Predictions of neural efficiency are yet to be tested in future studies investigating L2 learning in more advanced stages, or in contexts where learners' behavioural performance is equal, but the underlying skills vary. Secondly, the present study suggests that the neural mechanisms supporting L2 syntax abilities differ as a function of proficiency in the task. Whether these mechanisms can unequivocally be coupled with distinct stages of knowledge development (i.e., declarative, procedural and automatic as proposed by DeKeyser, 2015), or engagement of distinct memory systems (i.e., declarative and procedural, as put forward by Ullman, 2004), should be investigated further. A conclusive test for the predictions of the Skill Acquisition Theory and the neural underpinnings of development of L2 knowledge along the declarative, procedural, and automatic stages would in any case require a longitudinal design tracking learners over a period of L2 acquisition considerably longer than the 45 minutes offered by the present design.

Further questions deriving from this research concern inter-individual differences at the network level, such as differences in connectivity networks active during similar tasks. Also, research should try to elucidate the nature of structural correlates of LAA and explore whether the involvement of the right hemisphere in the task employed in this study, could also be characterised by weaker lateralisation of e.g. the arcuate fasciculus (cf. Catani et al., 2007; López-Barroso et al., 2013). Other subcomponents of language aptitude await further neurolinguistic investigations. Furthermore, it remains an open question whether results obtained by this or any other study on individual differences in SLA, such as language aptitude levels, are also due to individual's personal experiences, or only their innate qualities.

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4.7 Supplementary material

4.7.1 Stimulus material

A list of twenty-four unique grammatical sentences was compiled for the learning phases. Each possible sentence structure described in Section 4.2.3 of the manuscript was represented twice in the list. From this list, in each learning phase, forty samples were selected (without repetitions within one cycle of 24 items) and presented to the participants in a randomised order.

The list of twenty-four grammatical sentences used in the learning phases was extended by a further 41 sentences with different sentence structures for the test phases. Again, samples were selected from this list of 65 items without repetitions (within one cycle of 65 sentence structure items) and presented to the participants in a randomised order. Furthermore, in one phase no more than two samples of one sentence structure could be presented. The ungrammatical items included in the test phases were counterbalanced over all possible violation types and the different (grammatical) sentence structures.

For technical (display-related) reasons, the longest (eight-word long) sentences (belonging to both grammatical and ungrammatical conditions) could not be presented in the test phases and had to be omitted from the selection. The final list of items for the test phases consisted therefore of 59 unique grammatical and 65 ungrammatical sentences.

The Supplementary Table 4.1 below lists all items and specifies in which part of the experiment they were used. In sum, each participant received a different list of the items, counterbalanced over the possible types of sentence structures and violations, in a randomised order.

Chapter 4

| Learning Phases | |
|--------------------------------|--------------------------------------|
| sentence structure | item |
| dNv | aaf gum prez |
| | aaf trul pel |
| dNvdN | aaf trul prez aaf gum |
| | aaf gum pel aaf trul |
| dNvDMN | aaf gum pel aak böke gum |
| | aaf trul prez aak böke gum |
| dNvmDMN | aaf trul pel rüfi aak böke gum |
| | aaf gum prez rüfi aak böke trul |
| dNvm | aaf gum pel rüfi |
| | aaf trul prez rüfi |
| dNvmdN | aaf gum pel rüfi aaf trul |
| | aaf trul prez rüfi aaf trul |
| DMNv | aak böke gum prez |
| | aak böke trul pel |
| DMNvdN | aak böke trul pel aaf gum |
| | aak böke gum pel aaf trul |
| DMNvDMN | aak böke trul prez aak böke gum |
| | aak böke gum pel aak böke trul |
| DMNvmDMN | aak böke gum prez rüfi aak böke trul |
| | aak böke trul pel rüfi aak böke trul |
| DMNvm | aak böke gum pel rüfi |
| | aak böke trul prez rüfi |
| DMNvmdN | aak böke gum prez rüfi aaf gum |
| | aak böke trul prez rüfi aaf gum |
| Test Phases: grammatical items | |
| sentence structure | item |
| dNv | aaf gum pel |
| | aaf gum prez |
| | aaf trul pel |
| | aaf trul prez |
| dNvdN | aaf gum pel aaf gum |
| | aaf gum prez aaf gum |
| | aaf trul prez aaf gum |
| | aaf gum pel aaf trul |
| | aaf gum prez aaf trul |
| | aaf trul pel aaf trul |
| dNvDMN | aaf trul prez aaf trul |
| | aaf gum pel aak böke gum |
| | aaf trul pel aak böke gum |
| | aaf trul prez aak böke gum |
| | aaf gum pel aak böke trul |
| dNvmDMN | aaf gum prez aak böke trul |
| | aaf trul pel aak böke trul |
| | aaf gum prez rüfi aak böke gum |
| | aaf trul pel rüfi aak böke gum |
| | aaf gum pel rüfi aak böke trul |
| | aaf gum prez rüfi aak böke trul |
| dNvm | aaf trul prez rüfi aak böke trul |
| | aaf gum pel rüfi |
| | aaf gum prez rüfi |
| | aaf trul pel rüfi |
| dNvmdN | aaf trul prez rüfi |
| | aaf gum pel rüfi aaf gum |
| | aaf gum prez rüfi aaf gum |
| dNvmdN | aaf gum pel rüfi aaf gum |
| | aaf gum prez rüfi aaf gum |
| | aaf trul prez rüfi aaf gum |

Neural correlates of individual differences in novel grammar learning

| | |
|---------|----------------------------------|
| | aaf gum pel rüfi aaf trul |
| | aaf trul pel rüfi aaf trul |
| | aaf trul prez rüfi aaf trul |
| DMNv | aak böke gum pel |
| | aak böke gum prez |
| | aak böke trul pel |
| | aak böke trul prez |
| DMNvdN | aak böke gum pel aaf gum |
| | aak böke gum prez aaf gum |
| | aak böke trul pel aaf gum |
| | aak böke trul prez aaf gum |
| | aak böke gum pel aaf trul |
| | aak böke trul pel aaf trul |
| | aak böke trul prez aaf trul |
| DMNvDMN | aak böke gum prez aak böke gum |
| | aak böke trul pel aak böke gum |
| | aak böke trul prez aak böke gum |
| | aak böke gum pel aak böke trul |
| | aak böke gum prez aak böke trul |
| | aak böke trul prez aak böke trul |
| DMNvm | aak böke gum pel rüfi |
| | aak böke trul pel rüfi |
| | aak böke trul prez rüfi |
| DMNvmdN | aak böke gum pel rüfi aaf gum |
| | aak böke gum prez rüfi aaf gum |
| | aak böke trul prez rüfi aaf gum |
| | aak böke gum pel rüfi aaf trul |
| | aak böke gum prez rüfi aaf trul |
| | aak böke trul pel rüfi aaf trul |

Test Phases: ungrammatical items

| sentence structure | item |
|---|---------------------------------|
| <i>determiner-noun-agreement violations</i> | |
| DMNv | aaf böke gum prez |
| | aaf böke trul pel |
| DMNvDMN | aaf böke trul prez aak böke gum |
| | aak böke gum pel aaf böke trul |
| DMNvdN | aaf böke trul prez aaf gum |
| | aak böke gum pel aak trul |
| DMNvm | aaf böke gum pel rüfi |
| | aaf böke trul prez rüfi |
| DMNvmdN | aak böke gum pel rüfi aak trul |
| | aaf böke trul prez rüfi aaf gum |
| dNv | aak gum pel |
| | aak trul prez |
| dNvDMN | aak trul pel aak böke gum |
| | aaf gum prez aaf böke trul |
| dNvdN | aaf trul pel aak trul |
| | aaf trul prez aak gum |
| dNvm | aak gum pel rüfi |
| | aak trul prez rüfi |
| dNvmDMN | aak trul pel rüfi aak böke gum |
| | aaf gum prez rüfi aaf böke trul |
| dNvmdN | aaf gum pel rüfi aak trul |
| | aak gum prez rüfi aaf gum |
| <i>word class repetitions of nouns or verbs</i> | |
| DMNv | aak böke gum trul |
| | aak böke pel prez |
| DMNvDMN | aak böke prez pel aak böke gum |

Chapter 4

| | |
|---|---|
| | aak böke pel prez aak böke trul |
| DMNvdN | aak böke pel prez aaf trul aak böke prez pel aaf gum |
| DMNvm | aak böke gum trul rüfi aak böke pel prez rüfi |
| DMNvmdN | aak böke trul gum rüfi aaf gum aak böke prez pel rüfi aaf gum |
| dNv | aaf gum trul aaf pel prez |
| dNvDMN | aaf pel prez aak böke gum aaf prez pel aak böke trul |
| dNvdN | aaf prez pel aaf gum aaf pel prez aaf trul |
| dNvm | aaf prez pel aaf trul gum |
| dNvmDMN | aaf prez pel rüfi aak böke gum aaf gum trul rüfi aak böke trul |
| dNvmdN | aaf trul gum rüfi aaf gum aaf prez pel rüfi aaf trul |
| <i>phrase structure violations</i> | |
| DMNv | aak böke gum aaf trul aak böke trul aaf gum |
| DMNvDMN | aak böke gum aak böke trul prez aak böke trul aak böke trul pel |
| DMNvdN | aak böke trul aaf gum pel aak böke gum aaf trul prez |
| DMNvm | aak böke trul aak böke gum |
| DMNvmdN | aak böke trul aaf trul prez rüfi aak böke gum aaf gum pel rüfi |
| dNv | aaf gum aaf trul aaf trul aaf gum |
| dNvDMN | aaf trul aak böke gum prez aaf gum aak böke trul pel |
| dNvdN | aaf gum aaf gum prez aaf trul aaf gum pel |
| dNvm | aaf gum aak böke trul aaf trul aak böke gum |
| dNvmDMN | aaf trul aak böke trul prez rüfi aaf trul aak böke gum prez rüfi |
| dNvmdN | aaf trul aaf trul prez rüfi aaf gum aaf gum pel rüfi |
| Transfer Test: grammatical items | |
| sentence structure | item |
| DMNvDMN | aak böke trul pel aak böke trul aak böke gum pel aak böke gum |
| DMNvdN | aak böke gum prez aaf trul aak böke trul prez aaf gum |
| DMNvm | aak böke gum prez rüfi aak böke trul pel rüfi aaf gum |
| DMNvmdN | aak böke trul prez rüfi aaf trul aak böke gum pel rüfi aaf trul aaf trul prez aak böke trul |
| dNvDMN | aaf gum prez aak böke gum aaf gum pel aak böke trul |
| dNvdN | aaf trul pel aaf gum aaf gum pel aaf gum |
| dNvm | aaf trul pel rüfi |
| dNvmDMN | aaf gum pel rüfi aak böke gum |

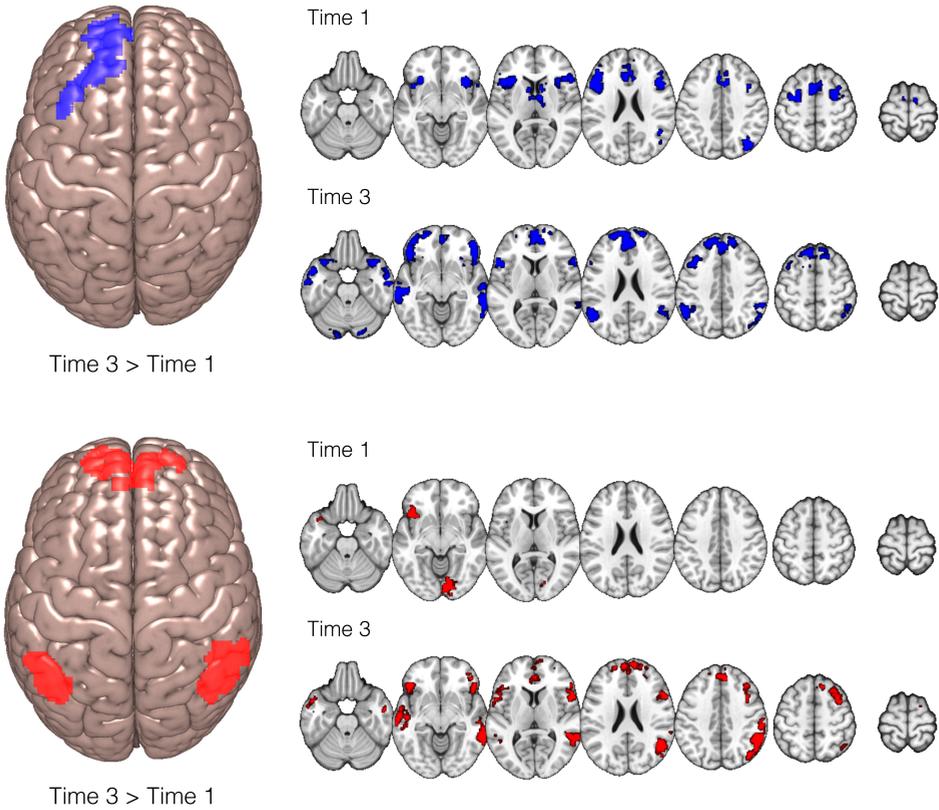
| | |
|---|---------------------------------|
| | aaf trul prez rüfi aak böke gum |
| | aaf trul pel rüfi aak böke trul |
| | aaf trul pel rüfi aaf gum |
| dNvmdN | aaf gum prez rüfi aaf trul |
| | aaf trul prez rüfi aaf gum |
| Transfer Test: ungrammatical items | |
| sentence structure | item |
| <i>determiner-noun-agreement violations</i> | |
| DMNvDMN | aaf böke trul pel aak böke gum |
| DMNvdN | aak böke trul pel aak trul |
| DMNvmdN | aaf böke trul pel rüfi aaf gum |
| dNvDMN | aaf gum pel aaf böke trul |
| | aak gum pel aaf gum |
| dNvdN | aak trul pel aaf gum |
| | aaf trul prez rüfi aak trul |
| dNvmdN | aaf gum prez rüfi aak trul |
| <i>verbs and phrase structure violations</i> | |
| DMNvm | aak böke gum aak böke trul |
| DMNvDMN | aak böke trul aak böke gum pel |
| DMNvmdN | aak böke gum aaf trul prez rüfi |
| dNvDMN | aaf trul aak böke trul prez |
| dNvdN | aaf gum aaf trul prez |
| dNvmdN | aaf trul aaf gum prez rüfi |
| <i>word class repetitions of nouns or verbs</i> | |
| DMNvDMN | aak böke pel prez aak böke gum |
| DMNvdN | aak böke trul gum aaf gum |
| dNvDMN | aaf prez pel aak böke gum |
| dNvdN | aaf gum trul aaf trul |
| | aaf prez pel rüfi aak böke trul |
| dNvmdN | aaf pel prez rüfi aak böke gum |

Supplementary Table 4.1 A complete list of BROCANTO sentences used in the learning phases, test phases and the transfer test of the experiment.

4.7.2 Results

| | Two clusters solution | | Three clusters solution | | |
|---------------------------------|-----------------------|-------------------|-------------------------|-----------------------|-------------------|
| | 1 (high scores) | 2 (low scores) | 1 (high scores) | 2 (steep increase) | 3 (low scores) |
| <i>number of cases:</i> | 20 | 22 | 12 | 9 | 21 |
| AGL 1st phase | 1.62 | 0.57 | 2.33 | 0.54 | 0.57 |
| AGL 2nd phase | 3.15 | 1.02 | 3.22 | 2.93 | 0.97 |
| AGL 3rd phase | 3.40 | 1.55 | 3.45 | 3.24 | 1.50 |
| LLAMA_F | 79.50 | 56.82 | 79.17 | 80.00 | 55.71 |

Supplementary Table 4.2 Results of the k -means cluster analysis on the behavioural data from the AGL task, presenting number of participants classified in each group and the mean d' score per AGL task phase per group. Two solutions of the analysis are presented: two clusters solution on the left, and three clusters solution on the right. Additionally, the mean scores on the pre-test, the LLAMA_F test are included.



Supplementary Figure 4.1 Brain activations in response to ungrammatical as compared to grammatical items for the groups of participants determined by the analysis of learning patterns in the behavioural data as scoring highly on the AGL task from the first phase (top panel), and obtaining low scores on the task (bottom panel). Z (Gaussianised T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a cluster corrected significance threshold of $p = 0.05$ (Worsley, 2001). On the left, brain activation cluster significantly greater in phase 3 than in phase 1 of the AGL task; two mean activation maps per time point are shown on the right.

Chapter 5

Neural oscillatory mechanisms during novel grammar learning underlying language analytical abilities

Kepinska, O., Pereda, E., Caspers, J., & Schiller, N. O. (*under review*) Neural oscillatory mechanisms during novel grammar learning underlying language analytical abilities.

ABSTRACT

The goal of the present study was to investigate the initial phases of novel grammar learning on neural level, concentrating on mechanisms responsible for individual variability between learners. Two groups of participants, one with high and one with average language analytical abilities, performed an artificial grammar learning (AGL) task consisting of learning and test phases. During the task, EEG signals from 32 cap-mounted electrodes were recorded and epochs corresponding to the learning phases were analysed. We investigated spectral power modulations over time, and functional connectivity patterns by means of a bivariate, frequency-specific index of phase synchronisation termed Phase Locking Value (PLV). Behavioural data showed learning effects in both groups, with a steeper learning curve and higher ultimate attainment for the highly skilled learners. Moreover, we established that cortical connectivity patterns and profiles of spectral power modulations over time differentiated L2 learners with various levels of language analytical abilities. Over the course of the task, the learning process seemed to be driven by whole-brain functional connectivity between neuronal assemblies achieved by means of communication in the beta band frequency. On a shorter time-scale, increasing proficiency on the AGL task appeared to be supported by stronger local synchronisation within the right hemisphere regions. Finally, we observed that the highly skilled learners might have exerted less mental effort, or reduced attention for the task at hand once the learning was achieved, as evidenced by the higher alpha band power.

5.1 Introduction

Second language (L2) learning can be characterised by a great deal of variability in the rate, efficiency and ultimate success. For some individuals, it requires strenuous efforts, whereas, for others, high levels of proficiency in an L2 can be attained with relative ease and little time investment. Understanding what factors are responsible for such variability among learners is important both for second language acquisition (SLA) theory building, and the applied efforts for learning and instruction improvements.

From a neurophysiological point of view, high-level cognitive functions such as language, necessarily depend on synchronised activity both between and within specific neural assemblies (Bressler, 1995; Bressler & Menon, 2010; Friederici & Singer, 2015; Maguire & Abel, 2013; Mesulam, 1998; W. Singer, 1993; Varela, Lachaux, Rodriguez, & Martinerie, 2001; Weiss & Mueller, 2003). Investigations into interactions taking place in different brain areas and the networks arising from them are invaluable for understanding the neural underpinnings of human communication. One possible way of exploring such interactions is to study the rhythms of the brain, their topographical properties, task- and state-dependent development, and dynamics. Such neural oscillations lie at the centre of coordinated activity of the brain and are seen as one of the fundamental mechanisms enabling learning and neural plasticity (Benchenane et al., 2010; Uhlhaas & Singer, 2010).

The goal of this paper is to investigate the initial phases of learning a new language, when completely new linguistic input is identified, analysed, processed, and – with various levels of success and different degrees of efficiency – learned. We are interested in the way such a learning process is reflected in neural oscillations over time and in the mechanisms responsible for variability between the learners. A technique well suited for investigating brain oscillatory architecture during language learning is electroencephalography (EEG) (cf. De Diego-Balaguer, Fuentemilla, & Rodriguez-Fornells, 2011; Reiterer, Pereda, & Bhattacharya, 2009; Wang, 2010). It offers a view on the nature of brain rhythms in different frequencies during information processing, and coherence or synchronisation analyses can be used to visualise the functional cooperation between cortical regions.

EEG signals recorded during a cognitive task can be indicative of synchronisation of local and distant cortical networks; the signal can be quantified by means of, for example, power spectrum or synchronisation

analyses (cf. e.g. Siegel, Donner, & Engel, 2012; Wang, 2010). Spectral power variations reflect the number of neurons discharging at the same time (Kiiski et al., 2012; Klimesch, 1999), and are thus seen as a measure of local neuronal activity. Employing coherence analyses, EEG offers a view on functional cooperation between cortical regions: brain areas activated by a particular cognitive task exhibit increased coherence, and high coherence between two EEG signals is indicative of high cooperation (degree of information flow) and synchronisation between underlying brain regions within a certain frequency band (Weiss & Mueller, 2003).

Furthermore, there are various putative roles assigned to different frequency bands (see e.g. Uhlhaas & Singer, 2010 for an overview). For example, the beta band frequency (13–29 Hz) has been linked to long-range synchronisation (Kopell, Ermentrout, Whittington, & Traub, 2000), and within the language domain, to underlie such higher-order functions as semantic memory and syntactic binding (Bastiaansen, Magyari, & Hagoort, 2010; Weiss & Mueller, 2012). Gamma band frequency (30–40 Hz) is believed to be tied to for example perceptual processing, attention, and episodic memory formation (cf. Herrmann, Munk, & Engel, 2004; Reiterer et al., 2009). In the context of learning, Miltner, Braun, Arnold, Witte and Taub (1999) found the development of gamma band coherence to be a signature of associative learning. They put forward that an increase in coherence in the gamma band “could fulfil the criteria required for the formation of Hebbian cell assemblies, binding together parts of the brain that must communicate with one another in order for associative learning to take place” (Miltner et al., 1999, p. 434) and suggested it could be the case for other types of learning as well.

The different EEG frequency bands can also reflect various strategies employed for learning. De Diego-Balaguer et al. (2011) investigated the dynamics of synchronisation properties of the EEG signal during auditory language learning. In a study employing exposure to an artificial language, they found that increased long range gamma band phase coherence between frontal, temporal, and parietal regions accompanied successful learning of rules embedded in the presented speech stream. On the other hand, poor rule learners exhibited greater local synchrony in the gamma range and increased theta-band (4–8 Hz) coherence over the course of the task. Different learning strategies for the two groups were thus suggested based on both behavioural and neurophysiological data. Whereas successful learning was driven by rule extraction (and coupled with long range gamma band coherence), the poor learners

seemed to apply a more memory-oriented, template-matching strategy during learning, reflected in local gamma power and theta-band coherence increases.

Within the framework of SLA, coherence of the EEG signals was investigated by Reiterer, Pereda and Bhattacharya (2009; 2011) who explored differences in EEG synchronisation measures in the gamma band range between second language speakers of English with high and low proficiency who were listening to first (L1, German) and second language input. The authors reported different patterns of synchronisation for the two groups, involving more extensive networks in the right hemisphere for participants with low L2 proficiency during processing of English input, and an inverse relationship between L2 proficiency and synchronisation density: high proficiency was coupled with lower synchronisation (Reiterer et al., 2009). Further investigation into the gamma band phase synchrony (Reiterer et al., 2011) by means of coarse-graining of Markov chains (Allefeld & Bialonski, 2007) and phase lag index (Stam, Nolte, & Daffertshofer, 2007) revealed differences between low and high L2 proficiency participants during second language processing. The group with less L2 expertise displayed stronger and broader network patterns than the high proficiency group, especially in fronto-parietal areas of the left hemisphere. The authors noted that differences between the two groups of learners might have reflected pre-existing individual differences in the linguistic abilities of the participants, rather than differences in L2 proficiency only.

Within the field of SLA, such individual differences in linguistic abilities are referred to as language aptitude. Language aptitude is a relatively fixed ability of an L2 learner to acquire a language. It is a strong predictor of achievement in L2 (Dörnyei & Skehan, 2003; Ellis, 2008; Sawyer & Ranta, 2001) and plays an important role both in instructed (de Graaff, 1997) and naturalistic (Abrahamsson & Hyltenstam, 2008; DeKeyser, 2000; Harley & Hart, 2002; Robinson, 1997) language learning. Traditionally, language aptitude has been operationalised by means of standardised test instruments aiming at capturing learners' abilities underlying L2 acquisition. Such tests typically consist of a number of different parts, underscoring the multi-componential nature of language aptitude of which four sub-components are traditionally distinguished: rote learning memory, phonemic coding ability, inductive language learning ability and grammatical sensitivity, the two latter also referred to as language analytic ability (LAA) (cf. Abrahamsson & Hyltenstam, 2008; Carroll, 1981; Dörnyei & Skehan, 2003; Ellis, 2008; Sawyer & Ranta, 2001; Skehan, 2002). In recent years, the theoretical

construct of language aptitude has also been investigated from a neuroscientific perspective, with the aim of indicating the aspects of brain functioning that underlie the different aptitude components (Hu et al., 2013; Kepinska, de Rover, Caspers, & Schiller, 2016; Prat, Yamasaki, Kluender, & Stocco, 2016; Xiang, Dediu, Roberts, Norris, & Hagoort, 2012).

In this study, drawing on the construct of language aptitude, we wanted to *a priori* control for individual variability between the learners, and explore the neural mechanisms of language learning coupled with high and moderate abilities. In our approach, we focused on one of the most important elements of L2 acquisition, namely novel grammar learning. Our aim was to explore how the sub-component of language aptitude crucial for grammar acquisition (i.e. the LAA), influences initial phases of L2 learning and the properties of the EEG signal measured during such a task. To this end, we employed an experimental design previously used in research investigating the neurobiological basis of language acquisition, namely an *artificial grammar learning* (AGL) paradigm. The design of our experiment was based on the study of Opitz et al. (2011), where the artificial language BROCANTO was used (cf. Friederici et al., 2002; Opitz & Friederici, 2003). In studies employing the BROCANTO language (e.g. Brod & Opitz, 2012; Friederici et al., 2002; Hauser, Hofmann, & Opitz, 2012; Opitz, Ferdinand, & Mecklinger, 2011; Opitz & Friederici, 2003, 2004, 2007) participants are presented with sentences constructed according to its rules and are instructed to extract the underlying grammar. The paradigm consists of learning and test phases. During learning, participants are presented only with grammatically correct sentences. In the test phases, both grammatical and ungrammatical sentences are presented and participants are asked to give a grammaticality judgement on the sentences.

Previous fMRI studies employing this paradigm concentrated on temporal changes in brain activity, and on the underpinnings of two types of knowledge acquired over the course of AGL: rule and similarity knowledge. Opitz and Friederici (2003) reported decreasing activity of the hippocampus and increasing activity of the left inferior frontal gyrus as a function of time and performance during the task. Opitz and Friederici (2004) extended these results by suggesting that the hippocampus and right IFG support grammar learning when the acquired knowledge is based on similarity; the left ventral premotor cortex was coupled with rule knowledge (Hauser et al., 2012; Opitz & Friederici, 2004). Furthermore, a recent experiment from our group investigating individual differences in grammar learning (Kepinska et al., 2016)

pointed to right fronto-parietal involvement underlying superior skills for grammar learning. EEG studies using the BROCANTO task have concentrated on the event-related potentials (ERP) coupled with adult ‘native-like’ processing of the newly learned grammar (Friederici et al., 2002), and signatures of feedback processing during the learning task (Opitz et al., 2011).

In the current study, we investigated whether learners with different degrees of LAA exhibit different oscillatory patterns during acquisition of a novel grammar, as operationalized by the BROCANTO AGL paradigm. Furthermore, we are interested in the dynamics of the learning process of a novel grammar and in the way the learning process is represented on a neural level, namely in short- and long-range brain oscillations. Our analysis is based on the approach of Reiterer et al. (2011) and De Diego-Balaguer et al. (2011). Based on their work, our hypothesis is that synchronisation mechanisms play a key role during language learning and that those mechanisms are modulated by individual differences in pre-tested language learning abilities. On the basis of Miltner et al. (1999), we expect an increase in the gamma band phase synchrony values as the learning proceeds. Furthermore, following the results of De Diego-Balaguer et al. (2011), we expect stronger long-range gamma band synchrony among the highly skilled learners; lower analytical abilities are hypothesised to be coupled with local gamma synchrony and power. Due to the importance of the theta band for lower level memory processes during learning, we expect theta band synchrony to be tied with initial phases of grammar learning, with decreasing levels of synchronisation for this band as learning proceeds, especially among the participants with high analytical abilities.

5.2 Materials and methods

5.2.1 Pre-test

Two groups of participants (with high and average LAA) were determined by administering a language aptitude test to a large group of participants ($N = 307$). We used the Llama Language Aptitude Test (LLAMA) (Meara, 2005), a computer-based test battery with automated scoring, suitable for participants with various language backgrounds. The test consists of four parts: (1) a vocabulary learning task, (2) a test of phonetic memory, (3) a test of sound-symbol correspondence and (4) a test of grammatical inferencing (LLAMA_F), being a measure of LAA. Recruitment of participants for the study was based on the scores on the LLAMA_F test.

In this test, twenty pictures are presented together with sentences in an unknown language that describe them. In the learning phase lasting five minutes, participants learn the grammatical rules, while taking notes. In the test phase, they are presented with a picture and two sentences and have to judge which sentence is grammatically correct. Participants can score from 0 to 100, where 80 - 100 is defined as outstandingly good and 25 - 45 as average (Meara, 2005).

5.2.2 Participants

Having taken the LLAMA test, a total of 45 healthy, right-handed native speakers of Dutch were invited for the EEG experiment. Three participants were excluded due to technical difficulties. The remaining 42 participants (14 male) were 18-29 years old. On the LLAMA_F test, the participants scored either within average range (i.e. 20 - 50)¹ (henceforth Average LAA) or got the “outstandingly good” score (i.e. 80 - 100) (henceforth High LAA).

There were 20 participants in the Average LAA group (5 male), age 19-25 years ($M = 22$ years) and 22 participants in the High LAA group (9 male), age 18-29 years ($M = 23$ years). A chi-squared test of the male/female ratio across the two groups was not significant (Chi-squared = 1.1932, $df = 1$, $p = 0.27$). Groups did not differ significantly in terms of age ($t(40) = 1.92$, $p = 0.062$).

Testing was conducted according to the Ethical Code of the Faculty of Humanities at Leiden University. Participants gave written informed consent prior to the experiment and were remunerated for their time after the last visit in the lab.

5.2.3 Stimuli and design

The stimulus material was created on the basis of the artificial grammar of BROCANTO (Brod & Opitz, 2012; Friederici et al., 2002; Hauser et al., 2012; Opitz et al., 2011; Opitz & Friederici, 2003, 2004, 2007) which follows universal rules of natural languages; a sentence (S) consists of a noun phrase (NP) and a verb phrase (VP) and the different categories are represented by different members: nouns (“gum”, “trul”, “ploX”, “tok”), verbs (“pel”, “prez”, “glif”, “rix”), adjectives (“böke”), adverbs (“rüfi”) and determiners (“aaf”, always followed by a noun and

¹ Although the LLAMA manual defines “average score” as 20-45, a score of 50 was also included as average in this study. The scores are awarded at intervals of 10 and a score of 45 is not possible to obtain.

“aak”, always followed by a modifier). Twelve possible sentence structures were included, see Table 5.1.

The task consisted of 15 blocks of learn and test phases, all presented visually. Following the BROCANTO rules, 50 grammatical sentences were formed for the learning phases. A further 150 grammatical sentences were formed for the test phase. The ungrammatical sentences for the test phase contained syntactic violations and were created by substituting words from one category by words from a different category. The violations were either determiner-noun-agreement violations (i.e., DN instead of dN and dMN instead of DMN), word class repetitions of nouns or verbs and phrase structure violations (i.e., NP NP and NP NP VP rather than NP VP and NP VP NP, respectively).

| Sentence structure | Example sentence |
|--------------------|---|
| dNv ² | <i>aaf gum pel</i> |
| dNvdN | <i>aaf gum pel aaf gum</i> |
| dNvDMN | <i>aaf tok rix aak böke gum</i> |
| dNvmDMN | <i>aaf plox glif rüfi aak böke gum</i> |
| dNvm | <i>aaf gum prez rüfi</i> |
| dNvmdN | <i>aaf gum glif rüfi aaf trul</i> |
| DMNv | <i>aak böke plox pel</i> |
| DMNvdN | <i>aak böke trul pel aaf trul</i> |
| DMNvDMN | <i>aak böke gum pel aak böke gum</i> |
| DMNvmDMN | <i>aak böke plox pel rüfi aak böke plox</i> |
| DMNvm | <i>aak böke plox rix rüfi</i> |
| DMNvmdN | <i>aak böke tok glif rüfi aaf tok</i> |

Table 5.1 Twelve possible BROCANTO sentence structures included in the experiment.

During each learning phase, 20 sentences out of a pool of 50 that followed the BROCANTO rules were randomly presented for 7 seconds each. Over fifteen blocks, sentences were presented multiple times, but not within a block. During each test phase, 10 unique correct and 10 unique incorrect sentences were randomly presented. Each presentation lasted until the participant gave a response, or for a maximum of 7 seconds. Participants were asked to indicate by pressing a response box button (left or right) whether the sentence followed the BROCANTO rules or not. Assignment of buttons to grammatical/ungrammatical responses was counterbalanced. 500 ms after each response, participants received visual feedback lasting for 500 ms, which displayed either the word ‘correct’ in blue or the word ‘incorrect’ in red.

² N = noun, v = verb, M = adjective, m = adverb, d = determiner (followed by a noun) and D = determiner (followed by a modifier)

In order to observe the learning effects and retention of grammatical rules of BROCANTO, participants were asked to perform a transfer test seven days after the experiment. In the transfer test, they were presented with 200 sentences, half of which following the BROCANTO rules, the other half containing one of the three types of grammatical errors. Each sentence was presented for a maximum of 7 seconds, during which time participants were asked to indicate whether the sentence was grammatically correct or not. In order to prevent further learning, no feedback was provided. Participants' performance on the post-test is reported together with the results of the 15 test phases completed during the EEG recording. Two participants (one from each group) did not perform the post-test.

Both the acquisition task and transfer test were created in E-Prime 2.0.10 software (Psychology Software Tools, 2012) and performed on a desktop computer. Stimuli were presented on a 22" Philips Widescreen LCD monitor (1680x1050 at 60Hz). Participants were seated at a distance of approximately 60 cm from the screen. All stimuli were presented in black letters (Courier New, size 20) on an E-Prime 'silver' (192, 192, 192) background. Due to time constraints for the transfer test, one participant performed a web-based version of the transfer test using Qualtrics (Qualtrics, 2013).

5.2.4 EEG recording and pre-processing

The EEG signals were recorded continuously during the entire AGL task. Recording was performed through 32 Ag/AgCl cap-mounted electrodes using the Biosemi Active Two recording system (see Figure 5.1). Eye movement and blink artefacts were recorded as horizontal and vertical electrooculograms (HEOG and VEOG) using bipolar recording from electrodes situated above and below the left eye and outside the outer canthi of both eyes. EEG signals were recorded using ActiView software at 512 Hz. Low-pass filter was set to 100 Hz, high-pass filter to 0.16 Hz and the CMS was used as reference.

Pre-processing of the data was conducted in EEGLAB version 13.4.4b. Data were filtered in band-pass 0.3–48 Hz and re-referenced to mastoids. For further analysis, only epochs from the learning phases were selected. Artefact-free epochs were chosen manually after careful visual inspection. One data-set (from the Average LAA group) did not yield any artefact-free epochs and had to be discarded. Independent Component Analysis (ICA) was conducted on the epoched data and components corresponding mainly to vertical eye movements, heart rate vari-

ability and noise (≤ 3 components) were removed. The epochs used in the subsequent analysis corresponded to the presentation of BROCAN-TO sentences and were 7 seconds long (3,584 samples).

5.3 EEG data analysis

Our goal was to investigate the oscillatory mechanisms coupled with language analytical abilities during language learning representing both local and large-scale communication between neuronal assemblies. To this end, we investigated two aspects of the EEG signal: spectral power, reflecting local activations of large groups of neurons; and phase synchronisation between different EEG signals, indicating functional relationship between (distant) brain sites (cf. Pérez, Carreiras, Gillon Dowens, & Duñabeitia, 2015).

5.3.1 Power spectrum analysis

We estimated the power spectral density of each EEG channel by dividing each epoch in non-overlapping segments of 256 samples and tapered them with a Hamming window. We then calculated the discrete Fourier Transform (DFT) of the sum of these tapered segments and took the amplitude of the sum of the DFTs as the power of the signal in the whole frequency band analysed.

The power spectrum analysis was centred in four commonly studied frequency bands, namely theta (4–8 Hz), alpha (8–12 Hz), beta (13–29 Hz), and gamma (30–40 Hz). We decided not to define the alpha bands based on the individual alpha peaks but made sure that they fell within the range for this band as defined above. We then evaluated the changes in power by averaging the data of each frequency according to the bands described and analysed it as a function of the learning process.

5.3.2 Functional connectivity

Phase synchronisation (PS) between all possible electrode pairs $[(32 \times 31) / 2 = 336]$ different electrode pairs] was calculated in the same four frequency bands as for power spectrum analysis. To evaluate the degree of PS between pairs of electrodes, the epochs recorded during learning phases were analysed employing a bivariate, frequency-specific index of PS termed Phase Locking Value (PLV, (Mormann, Lehnertz, David, & Elger, 2000)).

The estimation of PLV is a two-step procedure that consists of first calculating the phases from the EEG electrodes and then using the relative phase between any two electrodes to estimate the degree of PS between them as well as the significance of the index itself (see Supplementary Material for details).

5.3.3 Defining electrode clusters from PLV values

In order to explore the variations in PS in each frequency band as a function of grammar learning, as well as the topographical distribution of these effects, we identified synchronisation clusters consisting of groups of electrodes displaying similar PS profiles. Different methods have been proposed for this aim, all of them based on algebraic manipulation of the matrix of PLV indices (Allefeld & Bialonski, 2007; Allefeld & Kurths, 2004). Here, we applied instead an efficient, data-driven clustering method termed affinity propagation (Frey & Dueck, 2007), which allows the estimation of clusters from the matrix of their bivariate similarities without the need of setting a priori the number of clusters. For this, we estimated the grand average (across participants and frequency bands) of the PLV matrices and used it to estimate the PS clusters, which resulted in six different groups of electrodes showed in Figure 5.1. Note that the regions so defined, while clearly resembling the usually defined scalp regions of interest based on brain topography (namely, frontal, central, etc.), also shows a certain hemispheric asymmetry, with central, parietal, temporal and occipital electrodes clustered differently in the two hemispheres.

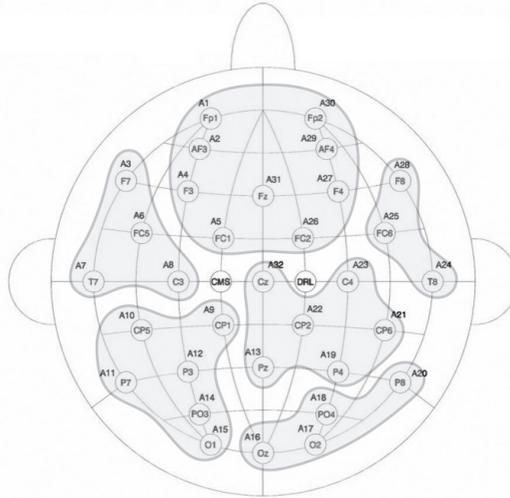


Figure 5.1 Clusters of electrodes with similar PS profiles used for subsequent analysis of the PLV values, overlaid on a schematic representation of the Biosemi Active Two recording system with 32 electrodes.

5.3.4 Statistical analysis

In order to trace the temporal changes in spectral power over the course of the artificial grammar learning process, we divided the AGL test blocks into four phases of three test blocks each (i.e., ± 60 sentence trials), and regarded the first block of the task as baseline activity. In order to keep the number of blocks per phase constant, and in order to avoid effects potentially driven by fatigue instead of the learning process itself, the last two blocks of the task were not subject to the analysis. Changes in global power values over the course of the task were analysed with a repeated measures ANOVA (alpha level = 0.05) with the between-subject factor group (High and Average LAA) and the within-subject factor learning phase (baseline, first, second, third, fourth phase). When necessary, degrees of freedom were corrected using the Greenhouse–Geisser epsilon value.

The statistical analysis including topographical effects in power and PS values between the two groups of participants concentrated on increases/decreases in power, or PS values across bands, clusters of electrodes and set of blocks (four phases of three blocks each, see above).

For the power and the PS values at the cluster/electrode level we used a paired t-test to detect, at the $p < 0.05$ level, the existence of significant within-group differences induced by the learning tasks by comparing the original (i.e., base level) block with the averages of blocks 2-4, 5-7 and 8-10 and 11-13 (see Figure 5.3 and Figure 5.5). Between-group differences were tested using a t-test for independent samples to compare, for these same blocks, the distribution of power and PS values for the High and Average LAA groups. Finally, we applied, in both cases, the type I false discovery rate (FDR) correction for multiple comparisons (Benjamini & Yekutieli, 2001) at the $q < 0.05$ level t . Of note, the effects we found were confirmed, in all cases reported, by applying also the Wilcoxon signed-rank and the U-Mann-Whitney nonparametric tests to analyse within and between group differences, respectively. The use of nonparametric tests along with the FDR correction guarantees that the effects we detect were robust.

Changes in global, whole brain PS values over time were investigated with a repeated measures ANOVA. Furthermore, in order to establish the relationship between the individual performance on the AGL task and the global PS values in the four frequency bands, we performed a regression analysis accounting for the fact that the measurements within the same participant were correlated, i.e. a multilevel analysis of change.

5.4 Results

5.4.1 Grammar learning task

Based on the individual hit- and false-alarm rates, the responses on the AGL task for each participant were transformed into d' scores (Macmillan & Creelman, 2005). The d' scores were calculated by subtracting the normalised false-alarm rates from normalised hit rates. Missing values in the behavioural data set in four instances (two post-test cases and instances of malfunction of the response buttons, in total 6 cells) were replaced with series means. Scores on the AGL task in both groups increased over the course of the experiment. A repeated-measures ANOVA on the d' scores on the consecutive test blocks and the subsequent post-test showed a main effect of block, ($F(7.99, 319.44) = 20.98, p < .001, \eta_p^2 = 0.34$). Furthermore, there was a significant effect of group, ($F(1, 40) = 18.36, p < .001, \eta_p^2 = 0.32$) and a significant interaction between group and block ($F(7.99, 319.44) = 3.25, p = .001, \eta_p^2 = 0.075$). The High LAA group performed better than the Average LAA group and showed a higher increase in the proportion of

the correct responses than the Average LAA group. Their learning curve was steeper, especially between the 5th and the 8th block of the task (see Figure 5.2).

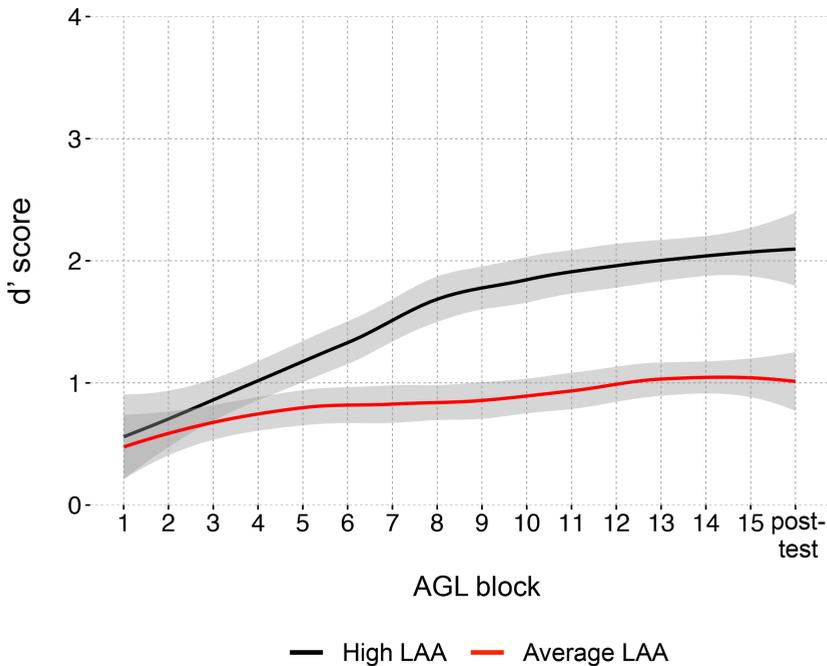


Figure 5.2 Performance (with 95% Confidence Intervals) across participants in High LAA and Average LAA groups during fifteen AGL test phases and the subsequent post-test.

5.4.2 Power spectra analysis

Analysis of power spectra in the theta (4–8 Hz), alpha (8–12 Hz), beta (12–29 Hz), and gamma (30–40 Hz) bands recorded during the consecutive phases of the learning task was aimed at detecting changes of local oscillatory activity and differences between the High and Average LAA groups.

The analysis revealed modulations with time for theta and alpha band and interactions between factors time and group for beta and gamma bands. A repeated measures ANOVA on global power values showed a main effect of Phase for theta ($F(1.54, 58.74) = 6.70, p = .005, \eta_p^2 = 0.15$)

and alpha ($F(2.39, 90.82) = 7.15, p = .001, \eta_p^2 = 0.16$) bands. Both theta and alpha bands significantly increased linearly ($F(1, 38) = 8.56, p = .006, \eta_p^2 = 0.18$ and $F(1, 38) = 13.76, p = .001, \eta_p^2 = 0.27$, respectively); a less pronounced but significant quadratic increase in alpha band was also observed ($F(1, 38) = 5.25, p = .028, \eta_p^2 = 0.12$).

There was no main effect of Phase for beta and gamma bands (in both cases $p > .05$). In both instances, however, a modulation of the increase by the factor group was observed. There was a significant quadratic increase in beta band power over time ($F(1, 38) = 5.42, p = .025, \eta_p^2 = 0.13$) and a cubic increase modulated by the factor group ($F(1, 38) = 6.58, p = .014, \eta_p^2 = 0.15$). Power in gamma band increased significantly in a cubic mode only in interaction with the factor group ($F(1, 38) = 4.09, p = .05, \eta_p^2 = 0.1$). The power increase in beta and gamma band over time modulated by the factor group can be clearly observed in Figure 5.3: in case of High LAA learners, the increase reached its maximum in the second phase of the task (blocks 2-4) and decreased afterwards, whereas, after an initial decrease among the Average LAA learners, it kept increasing until the end of the task.

We further performed a topographical analysis of the 32 electrodes using FDR- correction for multiple comparisons. The only significant difference between the High and the Average LAA groups (across bands, electrodes and set of blocks at the 0.05 level) was found in alpha band power values and was localised at the occipital electrodes. Corrected p -values for each group separately were obtained across bands, electrodes and set of blocks at the 0.05 level only for theta band power. Among the High LAA group, we observed an increase in theta power at the right parieto-occipital and frontal electrodes at the end of the task; significant increases in theta power among the Average LAA group were observed at the occipital electrodes at the beginning of the AGL task, and at the right frontal electrodes towards the end of the task. No significant interactions either with scalp locations (all $p > .05$) or power evolution during the learning process (interaction between block and topographical factors, in all cases $p > .05$) were observed for other bands. The topographical representation of each band power throughout the AGL task and average power evolution for all electrodes throughout the task is presented in Figure 5.3.

5.4.3 Phase synchrony analysis

5.4.3.1 Global PS values per band and behavioural performance

The global phase synchronisation values changed over the course of the AGL task. A repeated-measures ANOVA on the PLV values recorded during the consecutive blocks of the learning task showed a main effect of block for theta, alpha, and gamma bands ($F(8.40, 327.44) = 2.91$, $p = .001$, $\eta_p^2 = 0.07$, $F(7.64, 297.86) = 2.74$, $p = .007$, $\eta_p^2 = 0.07$, $F(2.71, 105.72) = 3.07$, $p = .036$, $\eta_p^2 = 0.07$, respectively). Furthermore, a set of exploratory analyses revealed that the amount of global PS in all frequency bands correlated with the performance on the AGL task. On the whole (across all participants), we observed a negative correlation between global PLV values of the slow frequency bands (theta, $r(13) = -.60$, $p = .001$, and alpha, $r(13) = -.68$, $p = .005$) and d' scores on the learning task, and a positive correlation between the high frequency bands (gamma, $r(13) = .77$, $p = .001$, and beta, $r(13) = .67$, $p = .007$) and the scores (see Supplementary Figure 5.1). According to a stepwise linear regression analysis, out of the four frequency bands, only the gamma band global PLV values proved predictive of the performance scores ($F(1,14) = 19.06$, $p < .001$, $R^2 = .595$).

SPECTRAL POWER DURING GRAMMAR LEARNING

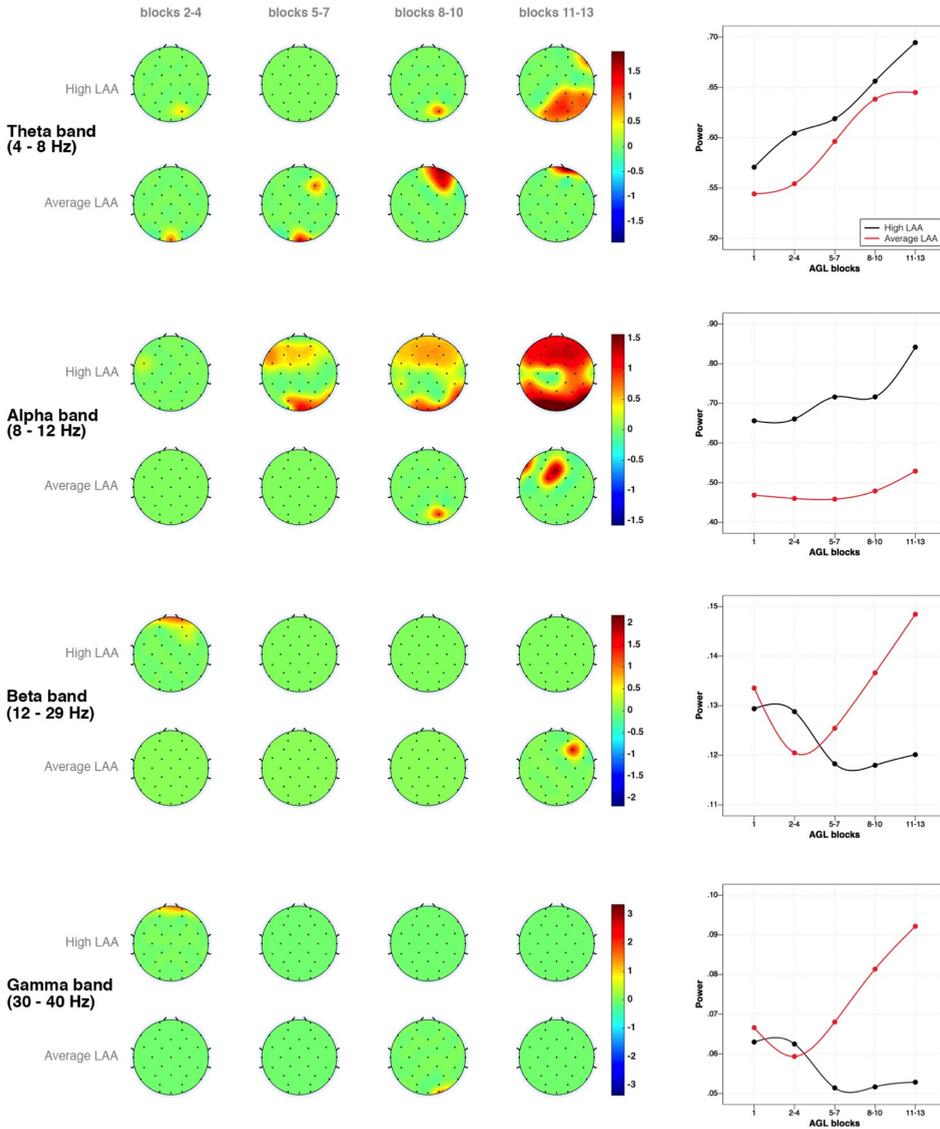


Figure 5.3 Spectral power modulations as a function of language exposure during the AGL task. The topographical plots on the left present differences between grand mean theta, alpha, beta, and gamma band scalp topography spectral power distribution at the selected blocks of the task and the first block. The graphs on the right present mean theta, alpha, beta, and gamma band power evolution throughout language learning for both groups of participants (in black and red colour for the High and Average LAA groups, respectively) measured at the selected blocks and averaged across all electrodes.

In order to gain a more fine-grained insight into the relationship between the individual performance on the AGL task and the PS values in the four frequency bands, we performed a regression analysis in which the evolution of AGL d' scores over time was studied as a function of group and the four frequency bands. As the data are longitudinal, measurements within the same subject are correlated. To account for this, a multilevel analysis of change (J. D. Singer & Willett, 2003) was conducted. For this analysis, our interest centred on the question of which frequency bands contributed most to the behavioural performance during learning, and whether the relationship between the synchronisation values and AGL d' scores differed between the two groups of participants.

The d' scores on the consecutive blocks of the AGL task served as a dependent variable for the analysis; time (block), group (High and Average LAA), and global PLV values in theta, alpha, beta and gamma bands were entered as predictors; we used a random intercept model. To identify a good fitting model, we pursued the following procedure. First, we fitted a model with the main effects of the six predictors, the two-way interactions between them, and the three-way interactions between the predictors (time, group and the four frequency bands). Next, we looked for a parsimonious model by, first, excluding the insignificant three-way interactions, and, next, further removing the insignificant two-way interactions, which were not involved in any significant three-way interaction. The last model resulted in the model with the best fit (as assessed by the Akaike's Information Criterion (AIC), (Akaike, 1973) and is presented in Table 5.2.

Out of the four frequency bands, only the PLV values in beta band proved to be significantly predictive of the AGL task scores over time. In other words, the magnitude of the change of the AGL d' scores over time depended on the global phase synchronisation in beta band. Moreover, the effect of global beta PLV values on the evolution of d' scores during the task was different for the two groups, as evidenced by the significant three-way interaction term between PLV values in beta band, time and group: The time-varying effect of global beta band phase synchronisation on AGL d' scores was larger for the High LAA participants than for the Average LAA participants.

| Parameter | Estimate | SE | df | t | SIG |
|----------------------------|-------------|------------|---------------|---------------|-------------|
| Intercept | -.27 | 1.83 | 250.17 | -.147 | .884 |
| Alpha | 1.15 | 1.93 | 563.85 | .597 | .551 |
| Beta | -.03 | 3.94 | 390.51 | -.007 | .994 |
| Gamma | -.52 | 1.43 | 567.38 | -.360 | .719 |
| Theta | .58 | 1.67 | 425.09 | .345 | .730 |
| Time | -.25 | .14 | 579.68 | -1.789 | .074 |
| Group | -2.59 | 2.43 | 308.14 | -1.066 | .287 |
| group * time | .46 | .19 | 586.54 | 2.238 | .026 |
| beta * group | 4.74 | 4.86 | 311.10 | .974 | .331 |
| beta * time | .74 | .28 | 580.99 | 2.646 | .008 |
| beta * group * time | -.96 | .37 | 587.66 | -2.574 | .010 |

Table 5.2 Summary of the results of the multilevel analysis of change: the significant predictors of the AGL task scores are printed in bold font.

This effect can be observed in Figure 5.4, where the PS values in the beta band recorded during consecutive blocks of the AGL task are plotted against the respective d' scores. The overall higher level of beta band PS values was recorded for the highly skilled learners. Moreover, the beta band synchronisation's relationship with d' scores varied more over time in case of the High LAA group: the coupling between the PS values and the respective d' scores was stronger in the second half of the task, when the behavioural performance was the highest.

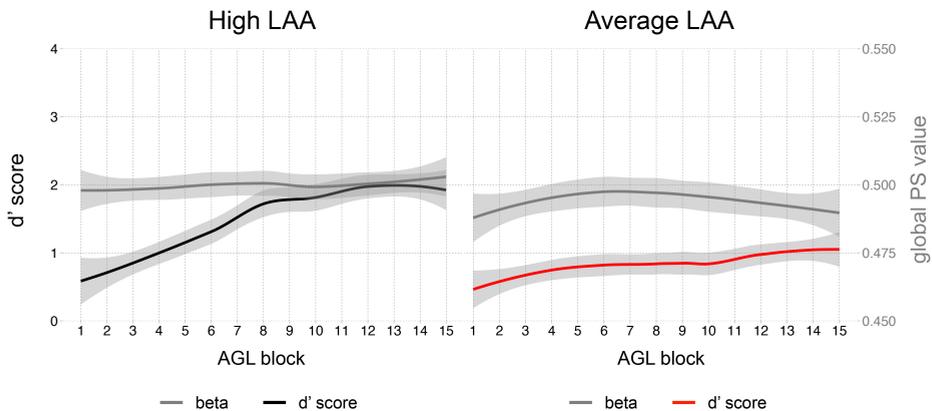


Figure 5.4 Global PS (PLV) values (surrounded by 95% Confidence Intervals) in the beta band frequency during the fifteen AGL task blocks plotted against the respective mean AGL task scores, separately for the High and the Average LAA groups.

5.4.3.2 PLV synchrony clusters

The topographical analysis of PS in the theta (4–8 Hz), alpha (8–12 Hz), beta (12–29 Hz), and gamma (30–40 Hz) bands recorded during the consecutive phases of the learning task was aimed at detecting both short range, i.e., intra-cluster connectivity, and long-range, i.e., inter-cluster connectivity. Our goal was to establish the modulation of synchronisation values by learning and the differences between the High and Average LAA groups.

The analysis of the PS within and between the six previously established clusters was performed using FDR-correction for multiple comparisons. For intra-cluster connectivity corrected p -values in between-group comparisons were obtained across bands, clusters of electrodes and set of blocks at the 0.05 level for alpha, theta and gamma bands, each time revealing an increase of intra-cluster PS in time larger for the High than for the Average LAA participants (see Figure 5.5). For theta band, the cluster consisted of right frontal electrodes (F8, FC6, T8), whereas both for alpha and gamma bands, the effect was localised in the right centro-parietal regions (Cz, Pz, CP2, C4, P4, CP6). Notably, in all cases of an increase of intra-cluster PS in time significantly larger for the High than for the Average LAA participants, the effect was observed in the same time-frame, namely in blocks 5-7.

INTRA-CLUSTER PS DURING GRAMMAR LEARNING

High LAA > Average LAA

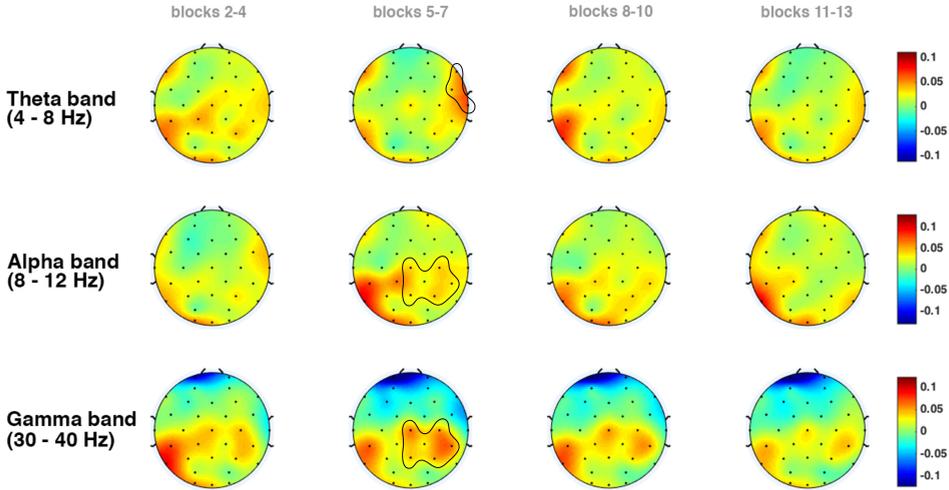


Figure 5.5 Topographical plots representing differences between mean theta, alpha, beta, and gamma scalp topography PS intra-cluster connectivity distribution at the selected blocks of the task and the first block as a result of a between group comparison (High vs. Average LAA groups). Clusters of electrodes showing increase of intra-cluster PS in time significantly larger for the High than for the Average LAA participants ($p < .05$, FDR-corrected) are indicated by the black line.

No group differences were observed for the long range, inter-cluster connectivity (all $p > .05$). However, the analysis revealed that the PS values were modulated by time in the alpha (both groups) and theta band (only the Average LAA group). In alpha band, for the High LAA group, we observed decreases in inter-cluster connectivity from baseline at the beginning of the task (blocks 2-4) at frontal electrodes (Fp1, AF3, F3, FC1, Fp2, AF4, F4, FC2 and Cz) and in the middle of the task (blocks 8-10) in the left frontal region (F7, FC5, C3, T7). The Average LAA group displayed decreases in inter-cluster connectivity from baseline in the middle of the task (blocks 8-10) in the left (CP1, CP5, P3, P7, PO3, O1) and right (P8, PO4, O2, Oz) parieto-occipital regions. In theta band, for the Average LAA group we observed a decrease in inter-cluster connectivity from baseline at the beginning of the task (blocks 2-4) in the left parieto-occipital electrodes (CP1, CP5, P3, P7, PO3, O1).

5.4.4 Summary of the results

In summary, the obtained results indicated that both groups of participants increased their performance in the grammar learning task, but the group with high language analytical abilities outperformed the moderately skilled learners (see Figure 5.2). This difference observed on the behavioural level, was coupled with several oscillatory mechanisms on the neural level. First, investigating local neural oscillations operationalised by the power spectra analysis, we noted a significant group difference in the alpha power at posterior electrodes towards the end of the task, and different profiles of development over time of the global power spectra in four frequency bands across the two groups (see Figure 5.3). Furthermore, our analysis of phase synchrony, revealed different contributions of the low and high frequency bands over the course of the task to learning. Whereas the theta and alpha bands decreased, as the learning proceeded, beta and gamma increased (see Supplementary Figure 5.1). What is more, the global PS values in the beta band proved to significantly predict the AGL d' scores over the course of the task as a function of language analytical abilities: the effect of global beta band phase synchronisation on AGL d' scores over time was larger for the High LAA participants (see Table 5.2 and Figure 5.4). Finally, we observed differences between the two groups of learners in short-range phase synchronisation in theta, alpha and gamma bands. The highly skilled learners exhibited larger increase of intra-cluster PS in time than the moderately skilled participants, each time in blocks 5-7 of the AGL task. The differences between the groups were localised in the right hemisphere, at the frontal electrodes for theta band, and centroparietal electrodes for alpha and gamma bands (see Figure 5.5).

5.5 Discussion and conclusions

The goal of this study was to establish whether different levels of language aptitude influence the process of novel grammar learning and whether the possible differences in attainment of a new language can be traced back to brain oscillatory mechanisms recorded by means of EEG. To the best of our knowledge, only a handful of studies have investigated the temporal dynamics of EEG power and synchronisation properties during language acquisition so far. Neural oscillations have been shown to play a critical role in language processing, underpinning such aspects of it as speech perception (e.g. Giraud & Poeppel, 2012; Pérez et al., 2015), syntactic operations (e.g. Bastiaansen et al., 2010) and semantic memory (e.g. Hanslmayr et al., 2016). Ubiquitous in the (human) brain,

oscillatory mechanisms also potentially differ between individuals and such inter-individual differences may be coupled with various behavioural manifestations. In the case of the present experiment, we indeed established that cortical connectivity patterns and different profiles of spectral power modulations over time differentiated L2 learners with various levels of language analytical abilities.

Based on previous literature investigating the oscillatory mechanisms coupled with (language) learning, we hypothesised increases in the gamma band phase synchrony values as the learning proceeds and decreasing levels of synchronisation for the theta band. For the highly skilled learners, we expected stronger long-range gamma band synchrony than for average skilled learners. Lower analytical abilities were hypothesised to be reflected in high local gamma synchrony and power. Our results provided only partial confirmation of these hypotheses. First, increasing levels of global synchronisation values with learning were found for high frequency bands, both for gamma and beta bands alike. On the other hand, the synchronisation in slow frequency bands decreased as the learning proceeded. These results point to the importance of the synchronisation in alpha and theta bands in initial stages of learning. Since low-frequency phase synchronisation has been proposed to underlie long-range transmission of information (Clayton, Yeung, & Cohen Kadosh, 2015; Weiss & Mueller, 2012), our results suggest that such long-range transmission of information seems to be more prominent at the beginning of novel grammar learning. The observed increases in gamma and beta global PS values point to their importance for later stages of learning, and thus increasing reliance on localised neuronal activity as the learning proceeds.

Support for this claim comes from the results obtained from the long-range (inter-cluster) connectivity analysis. Although we did not observe any differences between our two groups of learners (with High and Average LAA), we did note that synchronisation between distant regions decreased over the course of the task in alpha and theta bands. The lack of significant differences between the two groups of learners in long-range phase coherence coupled with learning is in contrast with De Diego-Balaguer et al.'s (2011) finding that long-range gamma band coherence between frontal, temporal, and parietal regions accompanies successful language learning driven by rule extraction. Contrary to our predictions formulated on the basis of these previous findings, successful learners in our study could rather be distinguished by increased short-range phase synchronisation. De Diego-Balaguer et al. (2011) argued that the finding of increased long-range gamma band coherence is

a marker of the process of binding neural representations to a global percept (i.e. not focussing attention on local features of the items). Since successful rule learning in our task similarly depended on attending to nonadjacent elements of the sequences, the lack of increased long-range gamma band phase synchrony among the highly skilled learners remains unclear.

By analysing global PS variations in four frequency bands using multi-level statistics, and within groups of electrodes chosen on the basis of their degree of bivariate PS, we showed that improving the task performance appears to be coupled with the development of whole-brain beta band coherence over time, and increases in local phase synchronisation values.

With regard to differences between the two groups of learners in global phase synchronisation values, the beta frequency band PS values proved to be predictive of the behavioural performance over time. This effect was modulated by the factor group: the behavioural scores of the highly skilled learners depended to a larger degree on their beta band synchronisation values over time than the behavioural scores of the average skilled learners. The oscillatory beta synchronization has been proposed to play an important role in language processing by - among others - underlying memory encoding and retrieval and supporting syntactically complex operations and high memory load demands (Weiss & Mueller, 2012). Moreover, it has been hypothesised to “bind distributed sets of neurons into a coherent representation of (memorized) contents during language processing” (Weiss & Mueller, 2012, p. 13) and to be suited to preserve neuronal activity (underlying the current sensorimotor or cognitive state) over time (Engel & Fries, 2010). Our results add to this body of research on beta band frequency coherence and suggest that L2 grammar learning outcomes might - at least in part - be driven by time-varying whole-brain synchronisation within beta frequency range. What seems to be the case, is that communication between distributed neuronal assemblies in the beta frequency range supports the learning process and reflects the ability to acquire novel grammar.

Simultaneously to such whole-brain oscillatory activity, also local synchronisation mechanisms contribute to successful and efficient learning. Differences between High and Average LAA learners in terms of connectivity strength within certain groups of electrodes (intra-cluster connectivity) were observed in blocks 5-7 of the AGL task (see Figure 5.5). Evaluation of the behavioural learning curves of the two groups (see Figure 5.2) reveals that precisely at this time during the task, the High and Average LAA participants differed most in their performance:

whereas both groups kept improving their performance in blocks 5-7, the scores obtained by the highly skilled learners increased notably more steeply. In terms of the differences between the groups on neural level in the time frame in question, they were localised in the right hemisphere, at the frontal electrodes for theta band, and centro-parietal electrodes cluster for alpha and gamma bands (see Figure 5.5).

Frontal theta band oscillations have been shown to be associated with plastic changes in learning and memory (cf. Voelker et al., 2016) and to be coupled with successful encoding of new information (cf. Begus, Southgate, & Gliga, 2015), including motivationally significant stimuli (Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013). Our data support these previous results and point to the importance of localised theta band oscillatory synchronisation for encoding of novel syntactic information. Furthermore, the localisation of this effect ties with results reported by De Diego-Balaguer & Lopez-Barroso (2010) which concern language rule learning performance being reflected in the amplitude of an ERP P2 component recorded on the right frontal electrodes. New grammar learning also appears to be tied to increased synchronisation at the right centro-parietal site, both in the slow, alpha band and in fast, gamma band frequency. Increased alpha band synchronisation of the High LAA participants can be traced back to its role in ‘top-down control’, information transfer and - possibly - the storage and retrieval of memory representations from long-term memory (cf. Klimesch, Sauseng, & Hanslmayr, 2007). As presented in section 1, gamma band has been shown to be involved in perceptual and attentional processing, episodic memory formation, and to play an important role in learning (cf. Herrmann et al., 2004; Miltner et al., 1999; Reiterer et al., 2009). Together, these results highlight the functional importance of the right regions for the grammar acquisition process and are in line with recent investigations into resting-state EEG power measurements prior to language learning by Prat, Yamasaki, Kluender and Stocco (2016). The authors found power in beta and low-gamma frequency ranges over right temporo-parietal regions to correlate positively with the rate of subsequent L2 learning and concluded that variability in functioning of the right hemisphere might relate to L2 learning rate. Such a conclusion is also consistent with results from our group concerning individual differences in grammar learning abilities investigated by means of fMRI (Kepinska et al., 2016). Employing a comparable design to the present one (adapted for MRI protocol), we found that during learning highly skilled learners could be distinguished from the average ones by increased activity localised in the right angular/supramarginal gyrus and right superior frontal and middle frontal gyri, and in the posterior cin-

gulate gyrus. These recent experiments thus underscore the supporting role of the right hemisphere in language learning and suggest that engagement of the right hemisphere (localised both in the frontal and parietal sites) might lie at the centre of individual differences in L2 skills and attained proficiency (see Kepinska et al., 2016, or Chapter 4, for a further discussion on the importance of the right hemispheric involvement in grammar acquisition). In particular, in the present study, compared to the average skilled learners, the highly skilled learners exhibited increased synchronisation in theta band in right frontal areas, and a higher degree of synchronous oscillations within the right centroparietal region. These mechanisms might possibly be underlying the differently realised learning curves by the two groups.

Although largely consistent with the localisation of neural activity coupled with L2 learning performance, the nature of the EEG signals recorded by our and Prat et al.'s (2016) study varies. Whereas Prat and colleagues reported values of spectral power in beta and low gamma frequency to correlate with L2 learning rate, our data provide information about localised synchronisation of the EEG signal marking increasing proficiency in a new language. As mentioned before, power within particular frequency bands measures the magnitude of oscillations over a specified time range, whereas coherence is an index of oscillatory coupling between two signals irrespective of their power (Kam, Bolbecker, O'Donnell, Hetrick, & Brenner, 2013). Since Prat et al.'s data were recorded during resting state, prior to L2 learning, the power values most probably reflect the default neuronal state and its suitability for subsequent language learning. Our data, on the other hand, show that when the learning is actually taking place, there needs to be functional connectivity within particular neural assemblies in order for the learning to be successful.

With regard to the spectral power variations recorded during our experiment, we observed a significantly higher increase of values in the alpha band at the posterior electrodes among the highly skilled learners towards the end of the AGL task (in blocks 11-13), see Figure 5.3. Notably, in terms of power spectra, it was the only significant difference between the two groups of learners. According to the standard view present in the neurophysiological literature, the alpha rhythm results from an idle, relaxed state (cf. Berger, 1929; Pfurtscheller, Stancák, & Neuper, 1996), and when recorded at posterior electrodes, it can reflect

reduced attention or distraction (Clayton et al., 2015)³. Considering the fact that the performance on the AGL task of the highly skilled learners in blocks 11-13 was stable and still better than Average LAA group's performance (see Figure 5.2), the possible reduced attention seems not have had adverse consequences for the learning process. It might be the case that, at the period in question, the highly skilled participants have learned enough to perform well on the task, and were no more actively engaged in the learning process as such. Analogous findings in the context of memory encoding were found by Park et al. (2014) who suggest that increase in alpha power during a memory task can reflect intentional inhibition and disengagement of task-irrelevant brain regions. Furthermore, such observations have also been made in the context of neural efficiency investigations by Jaušovec (1996, 2000). Neural efficiency theory – using fewer mental resources, in a more focused and goal-directed way, while dealing with demands of the task at hand (Neubauer & Fink, 2009) – has been repeatedly employed in investigations examining the nature of neural processing in gifted individuals. In Jaušovec's studies (1996, 2000), the gifted individuals in comparison with average ones were reported to exhibit higher alpha power during problem solving, which was interpreted as less mental effort and disengagement of brain areas not required for the problem at hand. Our data suggest that participants exhibiting increased alpha power might have already learned all the necessary information and did not need to further focus their attention on the presented stimuli – a view following the idea that high degrees of language aptitude enable learners to attain high levels of proficiency in an L2 with relative ease and little time investment. The neural efficiency perspective might also shed light on the different profiles of global power evolvment over time in the high frequencies (beta and gamma). As presented in Figure 5.3, where the values of power among the highly skilled learners remained virtually unchanged, the average learners exhibited high increases in the values.

It is important to note that, as mentioned in Section 3.1, we used a common range (8-12 Hz) for the alpha band for all participants as it is customary in many EEG language studies (e.g., De Diego-Balaguer et al., 2011), instead of defining it based on individual alpha peaks. The drawback of our approach might be that a fixed frequency band may be

³ As stated above (see the discussion on the interpretation of the increased alpha band coherence among the Highly skilled learners), reports also suggest that alpha activity plays an important role during active cognitive processes (cf. Klimesch et al., 2007). However, since the observed significant increase in the alpha power for the High as compared to Average LAA participants was constrained to posterior electrodes, our data rather seem to point to the classical 'cortical idling' interpretation.

unsuited to different individuals, due to age-related and/or participant-to-participant variability (see e.g., Hashemi et al., 2016). This could be solved by choosing participant or group-dependent frequency limits. However, this approach might have created an unwanted bias in our work, which targets group-level statistics, as different frequencies show different oscillatory characteristics. It might prove problematic to determine if the results are due to brain activity in the band of interest (e.g., alpha band) or due to differential background activity in different frequencies. In addition, both groups were age-matched, so age-related changes in alpha peaks are not an issue in our study. We did calculate the alpha peaks for all the individuals and made sure that in all cases they fell within the range we used. Thus, our approach can be regarded as an intermediate one: we selected the same frequency limits for all participants, rather than fixated these frequency limits to the true alpha range of our participant sample, which we believe is a reasonable trade-off between choosing the most realistic limits for the band of interest and ensuring comparability across groups.

A possible direction for future research concerns the way in which language aptitude, or the ease of acquiring new languages, can be modified. Such ideas have already been pursued in the context of semantic learning, where pharmacological substances such as levodopa have been shown to boost acquisition of novel lexicon and enhance consolidation of newly learned words (Knecht et al., 2004; Shellshear et al., 2015). Identification of brain regions related to language learning success, or increased efficiency in acquiring novel L2 materials, opens further possibilities for increasing learners' capabilities and offers foundations for probing the effects of non-invasive stimulation modulating neuronal activity patterns. As pointed out by Prat et al. (2016), power spectra of the EEG signal can indeed be modified. Simultaneously, there is increasing evidence for the possibility of non-invasive modulation of brain connectivity by means of transcranial current brain stimulation (see Luft, Pereda, Banissy, & Bhattacharya, 2014 for a review). The present data, together with other research identifying brain regions underlying successful performance on language learning tasks (cf. Kepinska et al., 2016; Prat et al., 2016), provide a suggestion for a possible target of such stimulation in the form of the right parietal regions, and to some extent right frontal regions. Such stimulation might prove particularly effective in cases where the learning concerns novel grammatical rules.

In sum, by analysing EEG data recorded during a learning task, we have provided evidence for the functional role of neural oscillations in novel grammar acquisition. Having combined different measurements

applied to the recorded signals, we offer a multi-layered picture of language learning and development of L2 knowledge on a neural level. In particular, on the basis of our results obtained with the global PS values and analyses investigating short- and long-range connectivity within the four frequency bands, we can conclude that oscillatory neural mechanisms underlying the grammar learning process and reflecting pre-tested analytical abilities operate on multiple levels, are topographically dispersed and dynamic in nature. Over the course of the task, the learning process seems to be driven by whole-brain functional connectivity between neuronal assemblies achieved by means of communication in the beta band frequency. On a shorter time-scale, increasing proficiency on a grammar learning task appears to be supported by stronger local synchronisation within the right hemisphere regions. Finally, we observed that the highly skilled learners might have exerted less mental effort, or reduced attention for the task at hand once the learning was achieved, as evidenced by the increasing alpha band power.

5.6 Acknowledgements

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5.7 Supplementary material

5.7.1 Details on the estimation of the PS indices

Henceforth we provide a detailed explanation of the steps involved in the estimation of the PLV between two EEG electrodes.

5.7.1.1 Estimation of the phases

As a necessary initial step to estimate the PLV, we calculated the phases of each EEG channel at each frequency. Thus, we filtered each EEG channel, $x(t)$, in non-overlapping narrow frequency bands of 2 Hz of bandwidth, and estimated the Hilbert Transform (HT) of each of these filtered signals, as follows:

$$x(t) = \frac{1}{\pi} p.v. \int \frac{x(\tau)}{t - \tau} d\tau \quad (1)$$

where p.v. stands for Cauchy's principal value. Then, the analytic, complex valued signal, is defined as

$$x_a(t) = x(t) + ix(t) \quad (2)$$

The phase of this complex-valued signal, $\phi_x(t)$, is then simply defined as:

$$\phi_x(t) = \arctag \frac{\hat{x}(t)}{x(t)} \quad (3)$$

5.7.1.2 Estimation of bivariate PS

For every pair of electrodes $x_l(t)$ and $x_k(t)$ ($l, k=1, \dots, 32$; $l \neq k$) and each narrow frequency band, one can estimate the degree of PS between the corresponding analytic signals by the following index, termed phase locking value (PLV), or mean phase coherence (Mormann et al., 2000):

$$PLV_{lk}(f) = \frac{1}{N} \left| \sum e^{-i\phi_{l,k,f}(t)} \right| \quad (4)$$

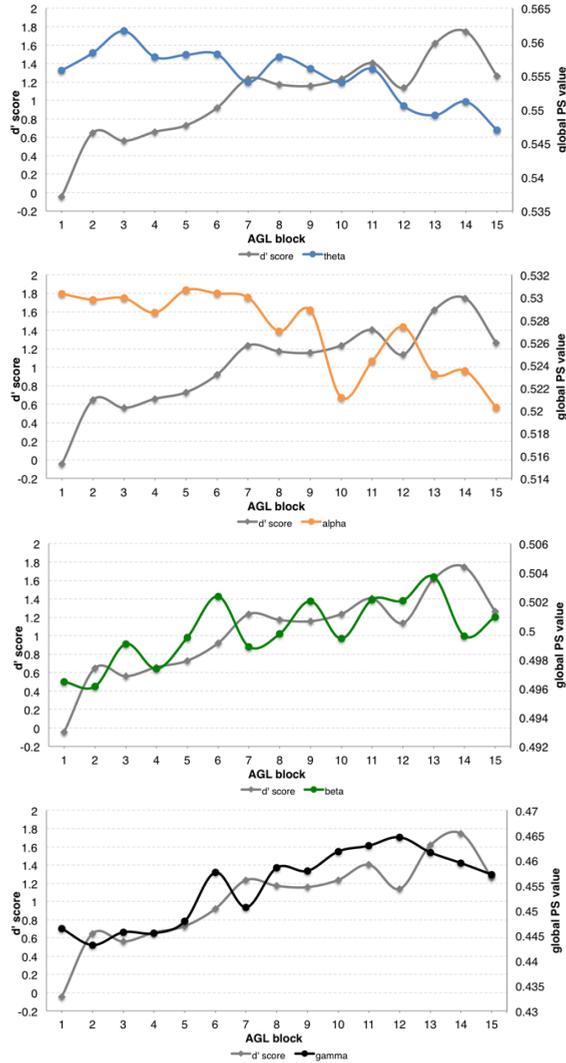
where N is the total number of phases, f is the centre frequency of each band and $||$ stands for the module of this complex number. Defined in this way, PLV ranges between 0 (no coherence) and 1 (perfect phase coherence). Yet, it is well-known (see, e.g., Daly, Sweeney-Reed, & Nasuto, 2013) that this index can be different from zero only due to properties of the individual signals such as its short length. Thus, we used the formula suggested by (Mardia & Jupp, 2000) to calculate the p value for the null hypothesis that (4) was actually not different from 0 and set to 0 if $p < 0.0001$ (i.e., at the $p > 0.05$ level after applying Bonferroni correction for multiple comparisons for every pair of electrode and frequency band). The MATLAB scripts for the estimation of the phases, the PLV and its significant level are publicly available, as described in (Niso et al., 2013; García-Prieto, Bajo & Pereda, 2017).

Of note, using more sophisticated strategies to estimate the significance of the PLV entails the construction of surrogate data from the original EEGs, namely time series that share with the original EEGs most of their individual features but are independent between them by construction (Daly et al., 2013; Schelter, Winterhalder, Timmer, & Peifer, 2007). The original PLV values are later compared to the distribution of “surrogated” PLVs, and the significance of the former is decided based on how different it is from the latter, using either parametric or non-parametric hypothesis test. Besides its computational complexity, there is no such thing as a perfect surrogate data in the literature, and the hypothesis tests provide p values that are no lower than $1/N_s$, where N_s is the number of surrogates. Thus we decided to use the formula above, which has also the advantage to provide an analytic estimation of the p value directly from the PLV.

Finally, PLV for each of the same four frequency bands as defined in the power spectral analysis was equally obtained by averaging across all the narrow frequency bands between the corresponding limits.

It may be argued that, for the case of scalp EEG data, PLV is known to be sensitive to volume conduction effects (Stam et al., 2007), so that other indices such as the phase lag index (PLI) or the imaginary part of the coherence function (Nolte et al., 2004) would be more appropriate in the present framework, as they disregard phase relationship with zero lag, as those due to volume conduction. Yet, on the one hand, recent results have shown that results from PLV are sometimes easier to interpret in neurophysiological terms than those from the PLI (Ioannou, Pereda, Lindsen, & Bhattacharya, 2015; Porz, Kiel, & Lehnertz, 2014). And, on the other hand, it is also known that a considerable amount of functionally relevant synchrony takes place with near zero or zero-phase lag (Finger et al., 2016; Gollo, Mirasso, Sporns, & Breakspear, 2014). Further, this index has been used successfully to study the oscillatory encoding of second language (Pérez et al., 2015; Reiterer et al., 2011).

5.7.2 Global PS values over time



Supplementary Figure 5.1 Global PS (PLV) values in the four frequency bands (theta, alpha, beta, gamma) recorded during the fifteen AGL task blocks plotted against the respective mean AGL task scores.

Chapter 6

The perisylvian language network and language analytical abilities

Kepinska, O., Lakke, E. A. J. F., Dutton, E. M., Caspers, J., & Schiller, N. O. (*under review*) The perisylvian language network and language analytical abilities.

ABSTRACT

Aiming at exploring the brain's structural organisation underlying successful second language learning, we investigate the anatomy of the perisylvian language network in a group of healthy adults, consisting of participants with high and average language analytical abilities. Utilising deterministic tractography, six tracts per participant (left and right long direct segment, left and right indirect anterior segment and left and right indirect posterior segment of the arcuate fasciculus) were virtually dissected and measurements pertaining to their microstructural organisation were collected. Our results obtained by means of linear discriminant analysis pointed to mean diffusivity (MD) values of three tracts (right anterior, left long and left anterior segments) as best discriminating between the two groups. By far the highest coefficient was obtained for the MD values of the right anterior segment, pointing to the role of the right white matter fronto-parietal connectivity for superior language learning abilities. The results imply the importance of attentional processes and reasoning abilities for successful L2 acquisition, and support previous findings concerning right-hemispheric involvement in language learning.

6.1 Introduction

The brain’s structural connectivity underpinning the uniquely human language function has in recent years gained increased attention in the field of cognitive neuroscience and neurobiology of language. The anatomical organisation of language-specific white matter connections (e.g., Catani et al., 2007; Catani, Jones, & Ffytche, 2005), their development (e.g., Mohades et al., 2015), and functional contributions (e.g., López-Barroso et al., 2013; Vaquero, Rodríguez-Fornells, & Reiterer, 2016) have been studied with the overarching aim of producing a coherent understanding of how the brain networks shape our communicative behaviour. Central to such studies is the perisylvian language network (also referred to as the arcuate fasciculus) comprising of three white matter fibre tracts: the long segment running dorsally from the frontal lobe (“Broca’s region”) to temporal structures comprising Wernicke’s area, the anterior segment connecting “Broca’s region” with the inferior parietal cortex (in particular the angular gyrus), and the posterior segment connecting the inferior parietal lobe to “Wernicke’s territory” (Catani et al., 2005).

Adult second language (L2) learning is an aspect of our linguistic behaviour characterised by a lack of uniformity in results. Although when acquiring languages as children we tend to reach universally high levels of proficiency, mastering an L2 after the onset of puberty seems virtually unattainable (Abrahamsson & Hyltenstam, 2009). One factor mitigating this age effect is language aptitude (Abrahamsson & Hyltenstam, 2008; DeKeyser, 2000), a specific talent for L2 learning, exhibiting considerable variation between learners (Dörnyei & Skehan, 2003). Language aptitude consists of several components, tapping into various sub-processes of language learning. For example, rote-learning memory underlies lexico-semantic processing, and language analytical abilities (LAA) determine successful morphosyntactic and grammatical processing (see e.g., S. Li, 2016). In terms of neural correlates of the different components of language aptitude, previous research from our group suggests that engagement of the right hemisphere (through activity localised both in the frontal and parietal sites) might lie at the centre of individual differences in abilities for L2 grammar learning (Chapter 4, or Kepinska et al., 2016; Chapter 5, or Kepinska, Pereda, Caspers, & Schiller, under review).

The goal of the present study is to investigate the structure of the perisylvian language network in participants who differ in their language

analytical abilities. We aim to employ diffusion tensor imaging (DTI) and deterministic tractography in order to reproduce anatomical features of the language pathways of the participants. DTI tractography measures diffusivity of water along different directions, and offers visualisation of white matter pathways by inferring the movement of water molecules exposed to a magnetic gradient (Catani & Mesulam, 2008, see also Le Bihan, 2003). Moreover, it quantifies the microstructural tissue properties underlying the distinguished pathways, enabling comparisons between individuals and establishment of functional correlates of the particular anatomical structures.

Our approach is partly based on a recently proposed neuroanatomical model for Social Communication And Language Evolution and Development (SCALED), in which Catani and Bambini (2014) outline how the hierarchically organised aspects of social communication map onto the major structural networks of the human brain. The model distinguishes five levels of language and communicative functions: (1) informative actions, (2) communicative intentions, (3) lexical and semantic processing, (4) syntactic analysis and (5) pragmatic integration, and couples each function with a separate anatomically defined network. The perisylvian language pathways are the core anatomical structures behind the identified processes, and according to the model, syntactic analysis is proposed to be supported by the direct fronto-temporal long segment pathway. If this particular tract plays a prominent role in successful syntactic processing, its structure should correspond with individuals' abilities for acquiring novel morphosyntactic information. On the other hand, our previous functional neuroimaging and neurophysiological (fMRI and EEG) results point to the right anterior structures as possibly underlying the differences in language analytical abilities. By investigating the brain anatomy of participants with different levels of LAA, we aim at gaining insights into the brain's structural connectivity correlates of successful L2 learning.

6.2 Methods

6.2.1 Participants

Forty-two healthy adults (32 female, age 19-43, $M = 23.38$ years) with no contra-indications for an MRI scan took part in the study. They were recruited on the basis of a test of language analytical abilities (LLAMA_F, Meara, 2005) administered to a large group of participants ($N = 307$). The study cohort comprised two groups based on the LLAMA_F

scores: participants who gained an “average score” (i.e., 30-50¹; Average LAA group), and participants who gained an “outstandingly good” score (i.e. 80-100; High LAA group). See Chapter 4, or Kepinska et al. (2016) for a full description of the study cohort.

The Medical Ethical Committee of the Leiden University Medical Centre (LUMC) (Leiden, the Netherlands) approved the protocol of the MRI experiment; behavioural testing was also conducted according to the Ethics Code of the Faculty of Humanities at Leiden University. Participants gave written informed consent prior to the experiment and were remunerated for their time.

6.2.2 DTI data acquisition and processing

DTI images were acquired on a Philips 3T MR-system (Best, The Netherlands) located at the Leiden University Medical Centre (LUMC) equipped with a SENSE-32 channel head coil. Each scan consisted of 32 diffusion-weighted images, and one non-diffusion weighted volume (b-value 1000 s/mm²). Matrix size was 112 x 112 x 60; voxel size was 2 x 2 x 2.1 mm. The data were pre-processed and corrected for eddy current and motion artefacts using ExploreDTI (<http://www.exploredti.org>). Whole-brain deterministic tractography was performed from all brain voxels with fractional anisotropy >0.2. Streamlines were propagated with a step-size of 0.5 mm. The maximum curvature threshold was set to 35°. Where fractional anisotropy was <0.2 or when the angle between two consecutive tractography steps was >35°, tractography stopped. Finally, diffusion tensor maps and whole brain tractography were exported to Trackvis (R. Wang, Benner, Sorensen, & Wedeen, 2007) for virtual manual dissection of the tracts.

Tractography dissections were obtained for the three perisylvian language networks in both hemispheres (six tracts per dataset were virtually dissected²). All dissections were performed in participants’ native space with a two regions of interest (ROIs) approach as described by Catani, Howard, Pajevic and Jones (2002) and Catani et al. (2005), and adopted by e.g., Catani et al. (2007), Forkel et al. (2014), López-Barroso et al. (2013) and Vaquero et al. (2016). Additionally, since detailed in-

¹ Although the LLAMA manual defines “average score” as 25-45, a score of 50 was also included as average in this study. The scores are awarded at intervals of 10 and a score of 45 is not possible to obtain. Therefore, there were no participants who scored 25, either.

² With the exception of the right long segment in case of two participants, whose direct white matter connection between the frontal and temporal ROIs was fully left-lateralised (see e.g., Catani et al., 2007 for similar findings).

structions are available for a one ROI approach for tractography dissection of the whole arcuate fasciculus (AF) (Catani & Thiebaut de Schotten, 2008), we further guided the placement of the frontal and temporal ROIs by first dissecting the whole AF with a one ROI approach. Visualising all its fibres enabled us to accurately determine the position of the frontal and temporal ROIs in such a way that as many relevant fibres as possible were included in the dissected tracts. The parietal ROI was drawn as last. Here, first fibres originating in the frontal and temporal ROI were visualised, ensuring that all fibres passing between the frontal and the parietal ROIs, and between the temporal and the parietal ROIs were included in the distinguished tracts. Finally, artefactual fibres were removed using exclusion ROIs. All datasets were carefully inspected by two dissectors, with special care taken for consistency of the distinguished tracts across all participants. The individual dissections for all data sets are presented in the Supplementary Material.

6.2.3 Statistical analysis

Per tract three measurements were used in the subsequent statistical analysis: fractional anisotropy (FA), mean diffusivity (MD) and volume (in cm^3). FA and MD are diffusion parameters describing the average microstructural tissue properties along the segmented tracts. FA is used as a measure of microstructural integrity of white matter, putatively following from the degree of myelination or axonal density (Johansen-Berg & Behrens, 2009); the higher the FA values, the denser the given tract. MD describes microscopic water movement without directional preferences; the higher its values, the more free water diffusion along a tract (Soares, Marques, Alves, & Sousa, 2013), and the less dense the tissue.

Our aim in the statistical analysis was to investigate how the microstructure of the perisylvian language network differs in participants with average language analytical ability versus those with high language analytical ability. Given the study cohort comprising two distinguished groups regarding their LAA scores, we conducted a linear discriminant analysis using the MASS package (Venables & Ripley, 2002) in R (R Development Core Team, 2015), treating the different tract measurements (FA, MD and volume) as predictors (i.e., 6 tracts \times 3 measurements = 18 predictors) and LAA group as the outcome variable. Linear discriminant analysis (LDA) derives the linear combination of predictors that best separates the groups (i.e., small difference within but large differences between groups in the given measurement) that

are given by the outcome variable and provides discriminant weight, which are coefficients that indicate the strength of the contribution of each predictor to the linear function.

In the first pre-processing stage for the analysis, all values at each of the six tracts were standardized to have zero mean and unit variance over all participants. In order to maximise the availability of data for LDA, we imputed mean scores for four cells which had missing data values (MD and FA values in case of the absent right long segment in two data sets).

| AF segment | Measure | Linear discriminant coefficient |
|-----------------|---------|---------------------------------|
| Left Long | FA | 0.18 |
| | MD | -1.49 |
| | Volume | -0.42 |
| Left Anterior | FA | -0.11 |
| | MD | -0.96 |
| | Volume | -0.17 |
| Left Posterior | FA | 0.00 |
| | MD | -0.32 |
| | Volume | 0.73 |
| Right Long | FA | -0.28 |
| | MD | 0.03 |
| | Volume | -0.03 |
| Right Anterior | FA | -0.44 |
| | MD | 2.29 |
| | Volume | -0.20 |
| Right Posterior | FA | -0.49 |
| | MD | 0.52 |
| | Volume | 0.31 |

Table 6.1 Results of the LDA listing the linear discriminant coefficients for all measures (FA, MD and volume) of the six dissected tracts.

6.3 Results

The linear discriminant function, when evaluated on the same data set, displayed a mean classification accuracy of 78% (78% correctly classified as High LAA and 79% correctly classified as Average LAA). Table 6.1 shows the discriminant weights for each predictor included in the LDA. As can be seen in the list of coefficients, the MD measures contributed most to discrimination between average and high LAA groups. The most influential predictor in the linear discriminant function is Right Anterior MD (2.29), followed by Left Long MD (-1.49) and Left Anterior MD (-0.96). All other predictors had coefficients between -0.49 and 0.73. Figure 6.1 compares MD measurements between the two LAA groups in each of the six tracts.

6.4 Discussion

The goal of the present experiment was to investigate the structure of the perisylvian language networks of participants with different levels of language analytical abilities. DTI images of two groups (High and Average LAA) were collected and deterministic tractography of three segments of the AF was performed bilaterally. Per participant six tracts were dissected: left and right long direct segment, left and right indirect anterior segment and left and right indirect posterior segment. Each tract was quantified by means of three measurements: FA, MD and volume. Our statistical analysis aimed at determining the best predictors of the group membership among the collected measurements, and at pointing to the structural network bearing most importance for one's analytical abilities for language learning. On the basis of the SCALED model (Catani & Bambini, 2014), we expected the long direct segment of the AF to be the strongest group membership predictor; meanwhile, our previous fMRI and EEG data suggested the right anterior indirect pathway as a possible white matter correlate of different LAA levels.

Out of all tractography-based measurements of the dissected pathways, the MD values of the right indirect anterior segment of the arcuate fasciculus predicted the group membership of our participants the strongest. They were followed by MD values of the left long and anterior segments. The linear discriminant analysis thus offered support for the predictions based on our previous functional data (Chapter 4, or Kepinska et al., 2016; Chapter 5, or Kepinska et al. under review), and to some extent to the predictions of the SCALED model (Catani & Bambini, 2014).

MD is a measure of the overall amount of water diffusion, and has been associated with the degree of myelination, coherence of fibres and the amount of crossing fibres from other bundles (Jones, Knösche, & Turner, 2013). Kronfeld-Duenias, Amir, Ezrati-Vinacour, Civier and Ben-Shachar (2016) interpreted lower MD values as underlying faster transmission between cortical regions, a view following from studies relating low MD to enhanced processing speed. The present results indicate that MD values of three segments of the perisylvian language network were best at differentiating between highly and moderately skilled language learners. Overall lower MD values for the High LAA as compared to the Average LAA participants in our study suggest that better language analytical abilities can be associated with a more coherent organisation and/or denser tissue microstructure of the given tracts, possibly resulting in a more efficient information transfer between the sep-

arate cortical regions. What exact biological factors underlie this result, is – given the available methodology – an open question.

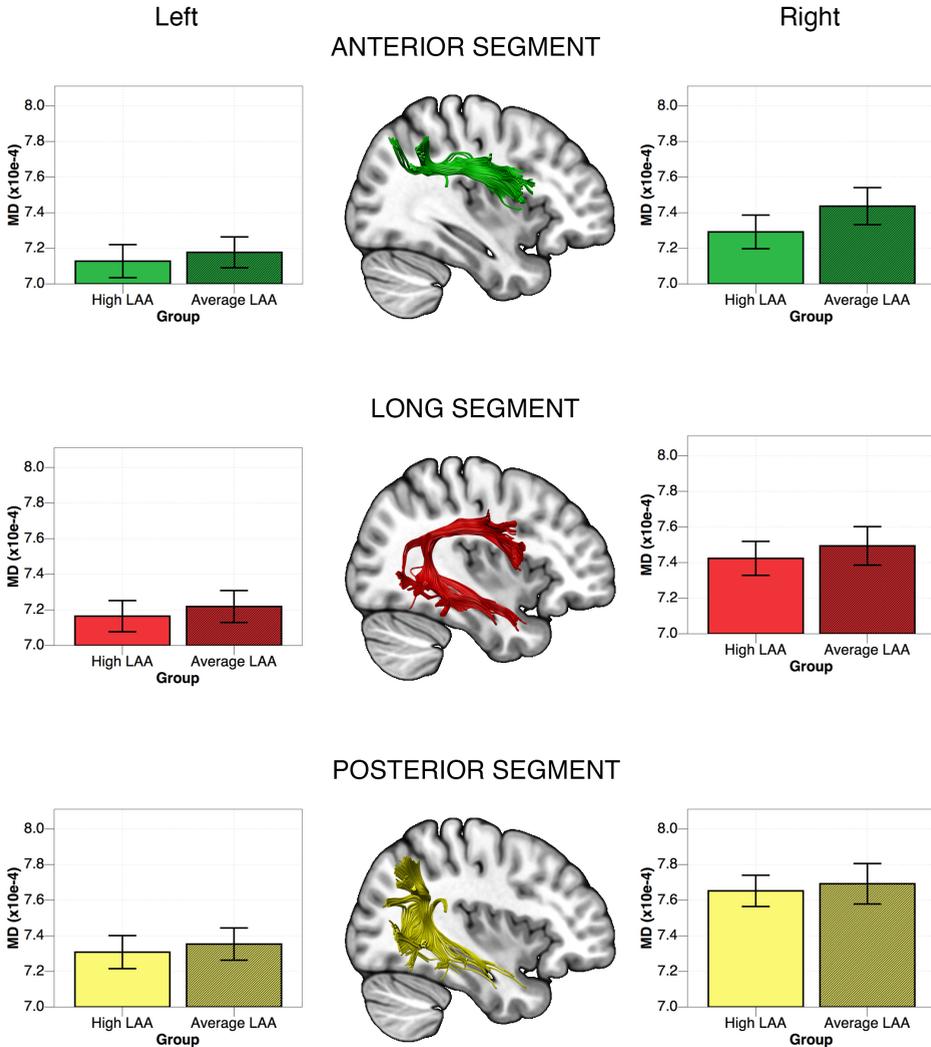


Figure 6.1 MD of the six dissected tracts for the High and Average LAA groups. According to the LDA, values of the right anterior segment predicted group membership the strongest, followed by values of the left long segment and the left anterior segment. The error bars represent 95% Confidence Intervals.

The contribution of the microstructural architecture of the left long segment of the AF to participants' classification can be traced back to its proposed involvement in syntactic analysis (Catani & Bambini, 2014), and the evidence for its relation to language learning abilities in other domains (López-Barroso et al., 2013; Vaquero et al., 2016). The functional role of the fronto-parietal white matter connections has been proposed to be coupled with attentional processes (de Diego-Balaguer, Martinez-Alvarez, & Pons, 2016) thanks to which visual and auditory percepts turn into relevant information (Catani & Bambini, 2014). Jung and Haier (2007) postulated interactions between frontal and parietal association cortices to underpin individual differences in reasoning abilities. This notion seems to be in line with the suggestion of Skehan (1998) about a relationship between language learning abilities and intelligence, which is particularly strong for the analytical abilities (cf. Biedroń & Pawlak, 2016; S. Li, 2016). From an evolutionary point of view, Schoenemann, Sheehan and Glotzer (2005) underscored the importance of white matter connections between the prefrontal cortex and posterior regions for the development of higher cognition, in particular language skills. This view seems to be in line with language acquisition experiments, in which fronto-parietal activity patterns and interactions are a well-established finding. Aside from our previous studies mentioned above, they were previously described by Tettamanti et al. (2002) who reported bilateral dorso- and ventrolateral prefrontal, and parietal cortical activations to acquisition of natural language syntax; Fletcher, Büchel, Josephs, Friston and Dolan (1999) noted a bilateral fronto-parietal network in an artificial grammar learning paradigm. Recently, Goranskaya, Kreitewolf, Mueller, Friederici and Hartwigsen (2016) pointed to the fronto-parietal network as one orchestrating successful artificial grammar learning.

Our results are furthermore in line with findings concerning right-hemispheric white matter pathways predicting Mandarin learning success (Qi, Han, Garel, San Chen, & Gabrieli, 2015). The structures established as underlying individual differences in L2 attainment were partly overlapping with the ones found in the present study, i.e. the right fronto-parietal connection. Qi et al. (2015) offered an interpretation of white matter connectivity in the right hemisphere underlying successful L2 learning as being driven by its involvement in prosodic processing and L2 learning in general. However, as Qi et al. investigated language learning success, it might be that their findings could at least in part be related to superior language analytical abilities of the learners, as is the case for the present data. In a similar vein, right-hemispheric white matter integrity of the lower parietal regions has been shown to be im-

portant for pitch related novel grammar learning (Loui et al., 2011) and suggested to be a marker of neurobiological differences in learning abilities.

6.5 Conclusion

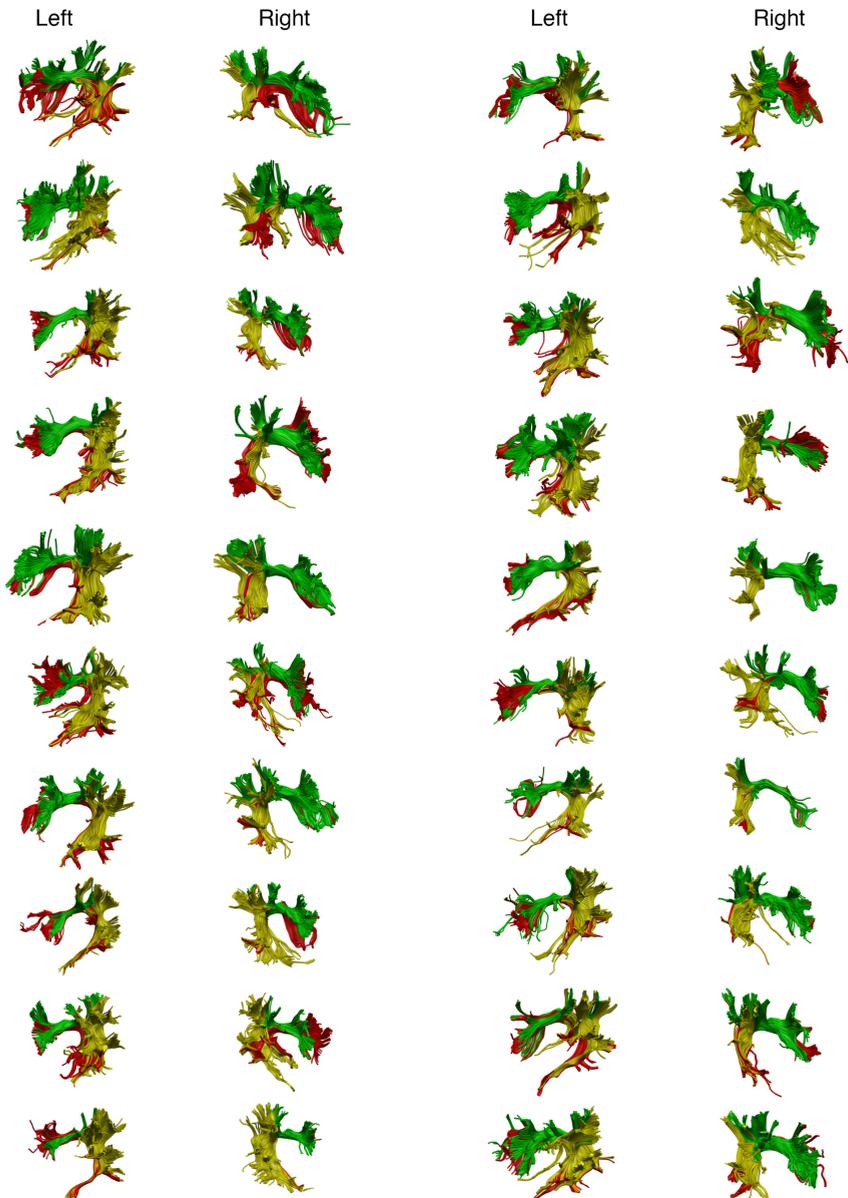
The present results provide insights into the brain's structural underpinnings of inter-individual differences in the ability to discern and learn novel morphosyntactic rules. Two groups of participants highly differing in such language analytical abilities appear to be best discriminated on the basis of the microstructural properties of their right fronto-parietal language pathways, i.e. the anterior indirect segment of the arcuate fasciculus. The results underscore the role of the right white matter fronto-parietal connectivity for superior language learning abilities, hint at the importance of attentional processes and reasoning abilities for successful L2 acquisition, and support previous findings concerning right-hemispheric involvement in language learning.

6.6 Acknowledgements

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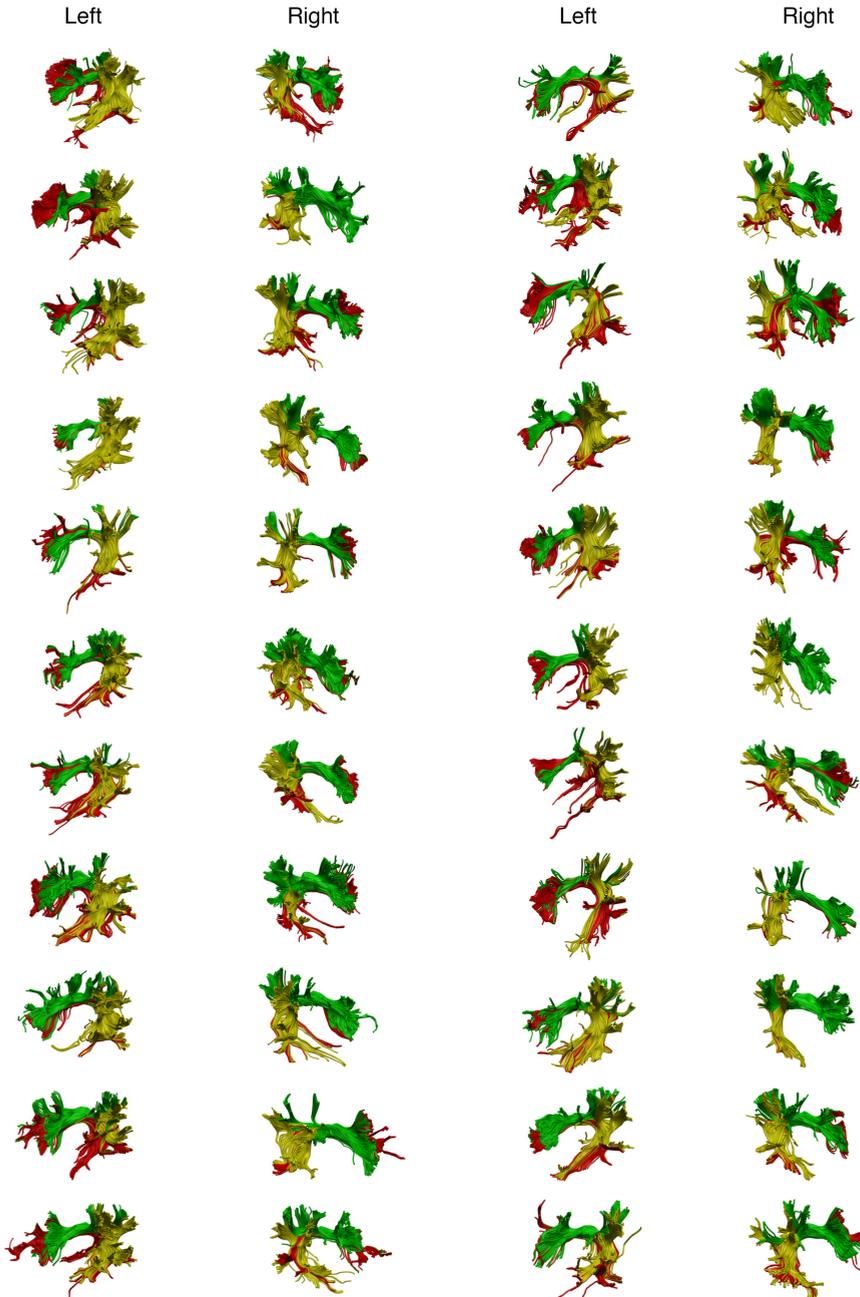
6.7 Supplementary material

AVERAGE LAA



Supplementary Figure 6.1 Individual dissections of the bilateral AF from Average LAA participants.

HIGH LAA



Supplementary Figure 6.2 Individual dissections of the bilateral AF from High LAA participants.

Chapter 7

General discussion

7.1 Summary of findings

The main aim of this thesis is to advance the understanding of neural mechanisms and brain structures underlying individual differences in L2 grammar acquisition, focussing on language learning aptitude, viz. language analytical abilities (LAA). As a preparatory phase for the study, a language aptitude test was administered to a large group of participants with the aim of recruiting two groups of learners (with high and average LAA) for the subsequent neuroimaging and electrophysiological experiments. Four functional and one structural neuroimaging experiments were performed with the overarching aim of gaining insight into “how the talented brain acquires language in comparison with the normal brain” (Ioup, Boustagui, El Tigi, & Moselle, 1994, p. 93; as cited by Abrahamsson & Hyltenstam, 2008).

The functional investigations reported in the present thesis, all employed an *artificial grammar learning* (AGL) task in which participants learned a novel grammar simultaneously to neuroimaging or electrophysiological data being recorded. The grammar was presented to the participants over the course of several learning and test phases. During learning, correct grammatical sentences were shown one by one on the screen and participants were asked to extract the underlying rules. The test phases consisted of both grammatical and ungrammatical items and participants’ task was to assess the grammaticality of the sentences. The grammaticality judgements served as an indication of the learning progress and showed that in both the MRI and the EEG experiments, the scores increased over the course of the task, and that the highly skilled learners performed better than the average ones.

Chapter 2 and Chapter 3 both report on the functional MRI data collected during the learning phases of the AGL task, utilising different but complementary methodologies, and answering related but distinct research questions. Setting the scene for further investigations involving the between-group comparisons of highly and moderately skilled learners, the experiment reported in Chapter 2 investigated functional connectivity of crucial hubs in language processing and learning, namely the bilateral BA 44/45 and the hippocampi. We reported the connectivity patterns of the four regions of interest (ROIs) during the consecutive learning phases of the AGL task, their modulations over time, and by the behavioural performance. Previous studies (Opitz & Friederici, 2003) suggested interactions of the hippocampal system and the prefrontal cortex as the neural mechanism underlying novel grammar learning. On the neural level, such interactions can be directly explored

by investigating temporal correlations between the hemodynamic activity of different brain areas obtained with fMRI, e.g., by utilising psychophysiological interaction (PPI) analysis (Friston et al., 1997). Our results demonstrated parallel (but separate) contributions of the investigated regions, each with their own interactions, to the process of novel grammar acquisition. The functional connectivity pattern of Broca's area (left BA 44/45) pointed to the importance of coherent activity of left frontal areas around the core language processing region for successful grammar learning. Furthermore, the encoding of novel linguistic rules driven by the interplay of the visual (occipital lobe) and memory (hippocampus) hubs of the brain was found to be a strong predictor of successful grammar acquisition. Finally, we found increasing functional connectivity over time of both left and right BA 44/45 with the right posterior cingulate cortex and the right temporo-parietal areas. This finding pointed to the importance of multimodal and attentional processes supporting novel grammar acquisition. Moreover, it highlighted the right-hemispheric involvement in initial stages of L2 learning. These latter interactions were found to operate irrespective of the task performance, suggesting that they are an obligatory mechanism accompanying novel grammar learning.

The goal of the experiment reported in Chapter 3 was to establish whether the neural basis of AGL differs between populations of highly and moderately skilled learners. In this experiment, the scope of the analysis was not constrained to pre-defined regions of interest (as in the case of the Chapter 2 study), rather whole-brain functional connectivity during the process of new syntax acquisition in its initial phase was investigated. By means of an Independent Components Analysis, a data-driven approach to functional connectivity of the brain, the fMRI data collected during the learning phases of the AGL task were decomposed into maps representing separate cognitive processes. These included the default mode, task-positive, working memory, visual, cerebellar and emotional networks. Furthermore, we tested for differences within the components, representing the two levels of language analytical abilities (high and average). On the whole, highly skilled learners could be distinguished by stronger functional connectivity patterns than moderately skilled ones: the high analytical abilities were coupled with stronger contributions to the task-positive network from areas adjacent to bilateral Broca's region, stronger connectivity within the working memory network (from the right central opercular cortex), and within the emotional network (amygdala and mammillary body, both in the right hemisphere). When compared to the highly skilled learners, the average LAA participants displayed stronger engagement within the task-

positive network from areas adjacent to the right-hemisphere homologue of Broca's region and typical to lower level (visual) processing (right occipital fusiform gyrus), and increased connectivity within the default mode network (in the posterior cingulate gyrus, paracingulate anterior cingulate gyri, and in the right frontal pole and middle frontal gyrus).

In Chapter 4, we explored both differences in neural activity coupled with AGL between the highly and moderately skilled learners, and how the activity patterns change over the course of a task as a function of participants' behavioural performance on the task at hand. Data recorded during the AGL task's test phases were analysed. Overall, greater activity levels for ungrammatical than grammatical items were found for all participants. Furthermore, the highly skilled learners were found to engage more neural resources during the task, localised predominantly in the right hemisphere, i.e. in the right angular/supramarginal gyri and superior frontal and middle frontal gyri and in the posterior cingulate gyrus. The design of the experiment enabled a further investigation of the different ways the learning of a novel grammar proceeded over time, both behaviourally (by means of identifying participants' various learning curves), and on a neural level. We found that activity in the bilateral temporal and parietal regions increased over the course of the task and that the left parietal region displayed the biggest modulation of BOLD activity at the end of the task, especially among successful learners. The amount of activity in the left angular gyrus correlated with the behavioural performance, but only in the last AGL task phase. Additionally, we saw that a steep learning curve in the AGL task (starting out with low scores and quickly improving the performance) could be traced back to the modulation of BOLD activity in the left angular gyrus. Participants displaying such a pronounced difference in performance between the first and the last phase of the task, showed only one cluster of brain activation significantly greater in phase 3 than in phase 1 of the AGL task, localised in the left angular gyrus.

Electrophysiological data were collected in the experiment reported in Chapter 5. Here, we investigated whether learners with different degrees of LAA exhibit different oscillatory patterns during novel grammar learning. Two types of electrophysiological measurements were reported: spectral power variations and phase synchronisation (PS) values. The cortical connectivity patterns and profiles of spectral power modulations over time differentiated L2 learners with various levels of language analytical abilities. Over the course of the AGL task, the global PS values in the beta band frequency proved to significantly predict

behavioural performance as a function of language analytical abilities: the effect of global beta band phase synchronisation on task scores over time was larger for the participants with high analytical abilities. On a shorter time-scale, increasing proficiency on the AGL task appeared to be supported by stronger local synchronisation (in theta, alpha and gamma bands) within the right hemisphere regions. This effect differentiated the highly and moderately skilled learners: the highly skilled learners exhibited a larger increase of the local PS values from baseline than the moderately skilled ones. The difference was localised at the right frontal electrodes for theta band, and right centro-parietal electrodes for alpha and gamma bands. Finally, we observed that the highly skilled learners might have exerted less mental effort, or reduced attention for the task at hand once the learning was achieved (at a late stage of the task), as evidenced by a higher alpha band power.

In the last section of this thesis (Chapter 6), results of a structural imaging experiment employing deterministic tractography of the main language-related white matter pathways (the perisylvian language network, or the arcuate fasciculus) were reported. This experiment aimed at determining how the microstructure of the pathways could be related to one's language analytical abilities. Six tracts per participant were virtually dissected (left and right long direct segment, left and right indirect anterior segment and left and right indirect posterior segment) and measurements pertaining to their microstructural organisation were collected. The results pointed to mean diffusivity (MD) values of three tracts (right anterior, left long and left anterior segments) as best discriminating between the two groups, i.e. participants with high and average LAA. By far the highest coefficient was obtained for the MD values of the right anterior segment, pointing to the role of the right white matter fronto-parietal connectivity for superior language learning abilities. The results supported our findings concerning right-hemispheric involvement in language learning reported in the experiments investigating the functional underpinnings of successful L2 learning. Furthermore, they suggest the importance of attentional processes and reasoning abilities for successful L2 acquisition.

7.2 Integration of findings

Having combined different analytical approaches applied to the collected neuroimaging and electrophysiological data, the present thesis offers a multi-layered view on the initial stages of language learning on a neural level, together with an account of individual differences in L2 grammar acquisition. In what follows, a threefold answer will be given

to the question of what – from a neurobiological perspective – makes some learners more successful and efficient than others. In short, the present thesis shows (1) that they utilise more neural resources, which are organised in a more coherent and integrated way; (2) that these additional resources stem predominantly from right hemispheric involvement; and (3) are localised in the fronto-parietal system.

7.2.1 More (and better integrated) neural resources

The functional experiments reported in the present thesis, unanimously showed that during the initial stages of learning, higher levels of brain activity, and higher levels of their integration accompany successful learning of a novel grammar.

In Chapter 2, this was evidenced by the positive slope of the amount of functional connectivity modulated by behavioural performance and time during the task, and the overall stronger functional connectivity patterns of the highly skilled learners than the moderately skilled ones described in Chapter 3. Similarly, the results reported in Chapter 4 showed that not only did the highly skilled learners utilise more neural resources when learning the novel grammar, but also that high performance on the task at hand was reflected by the amount of brain activation levels. Finally, the electrophysiological data reported in Chapter 5 indicated that increasing proficiency on the AGL could be coupled with larger increases of local phase synchronisation values from baseline for the high than for the average LAA participants.

One theoretical implication which can be derived from the current findings concerns the neural efficiency hypothesis (see also Chapter 4 and Chapter 5). Understood as using fewer mental resources, in a more focused and goal-directed way, while dealing with demands of the task at hand (Neubauer & Fink, 2009), the neural efficiency hypothesis has been time and again employed in investigations into the nature of neural processing in gifted individuals (see Haier et al., 1988; Neubauer & Fink, 2009; Nussbaumer et al., 2015; Prat, 2011; Prat & Just, 2011; Prat, Long, et al., 2007; Reichle et al., 2000). On the basis of the neural efficiency framework, the higher performing learners in the present study should have exhibited less distributed activity networks, and should have been able to enhance connectivity in areas relevant for task solution (Neubauer & Fink, 2009). While the results of the present functional connectivity investigations corroborate these assumptions, the event-related fMRI experiment reported in Chapter 4 brings nuance to the hypothesis. In particular, the experiment showed that a demanding AGL task focussing on initial stages of learning, where differences in

performance between participants are significant, will not produce evidence in support of the neural efficiency hypothesis. Indeed, the results underscore the observation of Neubauer and Fink (2009) concerning difficult tasks in which more skilled individuals invest more cortical effort than individuals with lower abilities. Furthermore, as we observed in Chapter 5, such cortical effort is exerted by highly skilled individuals only up to a certain point, i.e., as long as necessary for the demands of a task. Once the learning is completed, areas not required for the problem at hand are disengaged and less mental effort is made, as evidenced by the increased alpha power once the learning was achieved (at a late stage of the task).

7.2.2 Right-hemispheric involvement in the initial L2 grammar learning

Lateralisation of the language function to the left cerebral hemisphere (Friederici, 2011; Gernsbacher & Kaschak, 2003) is an established finding dating back to initial descriptions of Paul Broca (1861). Our results indicate, however, that successful language learning is not constrained to contributions of the left hemisphere only. In Chapter 2, we observed that over the course of a language learning task, no matter the ultimate performance, both Broca's area (left BA 44/45), and its right-hemisphere homologue (right BA 44/45) increase their functional coupling with right-hemispheric regions. Engagement of the right hemisphere was further observed in the between-group comparisons in Chapter 3, Chapter 4, and Chapter 5, where we noted both increased functional connectivity contributions of right-hemisphere regions in case of the highly skilled learners (Chapter 3 and Chapter 5), and higher activity levels (Chapter 4). On top of that, the structural data point to right-hemispheric correlates of superior language abilities (Chapter 6).

Right-hemispheric contributions to L2 learning are in line with studies investigating bilingual laterality effects (see Qi et al., 2015 for an overview). Involvement of the right cerebral hemisphere regions have been shown for e.g., L2 speech perception (Archila-Suerte, Zevin, Ramos, & Hernandez, 2013) and visual word processing (Leonard et al., 2010). Also, structural data point to the importance of right-hemispheric white (García-Pentón et al., 2014; Hosoda, Tanaka, Nariai, Honda, & Hanakawa, 2013; Loui et al., 2011; Qi et al., 2015) and grey matter structures (Mårtensson et al., 2012) for L2 acquisition. Furthermore, the present findings challenge the notion that suppression of contralateral activity benefits language performance (Antonenko et al., 2012; Thiel et al., 2006). In our view, the right-hemispheric involvement

can be traced back to the difference between proficient language processing and language learning, on a par with bilateral language-related activity reported for child L1 processing. For example, Everts et al. (2009) showed that functional lateralisation strengthens during cognitive development and pointed to the dynamics of the process: emerging from an initially bilateral pattern, the cognitive functions in the language domain were shown to develop toward a specialised unilateral network. Similarly, increasing language lateralisation during childhood was reported by e.g., Holland et al. (2001), and Szaflarski, Holland, Schmithorst and Byars (2006), and Ressel et al. (2008). Our data seem to mirror the findings concerned with the development of L1 neural representation. In case of the development of neural representations for L2 (operationalised by the novel grammar learning paradigm), broader networks encompassing right-hemisphere regions have been shown to be beneficial for the learning process in its initial phase. Increasing left lateralisation (see Chapter 4) has also been reported, and argued to underlie proficient processing of the newly acquired rules. Combined with the research into L1 representation development, the presence of activity in the language-specialised left hemisphere might be seen as the “end stage” of the learning process. One question arising from this set of results is whether superior language learning abilities help adult L2 learners utilise similar learning mechanisms as used by child learners.

7.2.3 Fronto-parietal contributions to novel grammar learning

Our data offer converging evidence for the location of superior language learning abilities in the brain. The functional experiments (see in particular Chapter 4 and Chapter 5) have indicated frontal and parietal neural activity patterns of the right cerebral hemisphere as underlying high language analytical abilities. The structural data reported in Chapter 6 offer further support for this account, by pointing to the right fronto-parietal white matter connectivity as best discriminating between highly and moderately skilled learners. Together with other results (e.g., Prat et al., 2016), the present findings suggest that engagement of the right hemispheric frontal and parietal sites might lie at the centre of individual differences in L2 skills.

As postulated in Chapter 2 and Chapter 6, these results might also be seen in the context of the Parieto-Frontal Integration Theory of Intelligence (Jung & Haier, 2007), according to which the interactions between frontal and parietal cortices seem to underpin individual differences in reasoning abilities in humans. Considering clear links between language aptitude measures (in particular of LAA), and tests of reason-

ing abilities (S. Li, 2016), such an account is plausible. However, since the two groups of participants of the MRI experiments did not significantly differ in their fluid intelligence scores (see Chapter 1), the present results cannot be traced back to differences in reasoning abilities only. Another theoretically tenable interpretation situates the present findings in the context of attentional processes. De Diego-Balaguer et al. (2016) have recently proposed the attentional system to underlie the development of first language acquisition and pointed to the fronto-parietal system as one underlying attention related activity. In particular, they argue that “the attentional system acts as a filter to any incoming stimulation, influencing perception, and therefore may affect learning” (p. 2). Such influence of attentional processes is also well documented for second language acquisition (see Robinson, Mackey, Schmidt, & Gass, 2012 for an overview), and on the basis of the present data might be postulated to play an important role in differentiating between successful and less successful learners.

Whichever of the cognitive constructs – reasoning abilities, or attentional processes – might lie at the centre of high language learning skills, a clear pattern of results emerges from the experiments reported in the present thesis. Individual differences in language learning abilities are reflected in particular aspects of the structural and functional architecture of the brain: the engagement of additional neural resources in right frontal and parietal sites, together with favourable microstructural properties of the right fronto-parietal language pathway, both seem to enable more efficient L2 learning. As argued in Chapter 5, such identification of brain regions related to language learning success, opens possibilities for enhancing learners’ capabilities and offers foundations for probing the effects of non-invasive stimulation modulating neuronal activity patterns. Increasing evidence points to the possibility of non-invasive modulation of brain’s activity patterns by means of transcranial current brain stimulation (see e.g., Luft et al., 2014 for a review). The present thesis provides a suggestion for a possible target of such stimulation in the form of the right parietal and frontal regions, in particular in cases where the learning concerns novel grammatical rules.

7.3 Limitations and future research

The experiments reported in this thesis are naturally not without limitations. First, even though we combined several different methodological approaches in order to arrive at a comprehensive view of the neural mechanisms and brain structures underlying individual differences in

L2 grammar acquisition, our scope can by no means be regarded as exhaustive. In particular, the structural underpinnings of high language skills were investigated in a constrained manner, exploring only a handful of white matter tracts. Even though the restriction was motivated by earlier studies (e.g., Catani et al., 2007, 2005), a broader range of enquiry into the structural connectivity could prove informative for our research questions. One avenue of investigations in this context can be derived from the results of the experiment reported in Chapter 2, which point to inter-hemispheric structural connectivity as a possible correlate of grammar learning. Furthermore, with respect to the structural neuroimaging data, morphometric measurements including grey matter volume, cortical thickness and surface area, all have great potential to further elucidate the structure-function relationship of the language learning brain.

Secondly, no causality can be inferred from the measures of the functional connectivity applied to the present data, due to their correlational nature. The directionality of the interactions between brain regions, although difficult to assess by means of standard neuroimaging techniques, can be addressed with effective connectivity analyses – a technique used to model the influence that regions exert over each other (Simons & Spiers, 2003). One possible question directly following from the results reported in Chapter 2, would concern the nature of the relationship between the parietal and prefrontal regions. Could their functional connectivity be a result of Broca's region influencing the activity of angular gyrus, or the other way around?

Thirdly, the data from the MRI experiments reported in the present thesis were all collected from one cohort of participants. Even though effort was made to keep the number of participants relatively high (at least 20 subjects per group), a replication of the present findings with a different cohort would render more robustness to our conclusions. On the other hand, it remains to be noted that the EEG data reported in Chapter 5, show a related pattern of results.

Finally, only one stage and one mode of learning were tested in the present thesis. Future studies should address L2 learning in more advanced stages, and by means of different paradigms (including the use of natural language input) in order to arrive at a more elaborate and nuanced answer to the question of how a talented brain acquires a second language.

7.4 Conclusion

The five experimental studies presented in this thesis contribute to a better understanding of neural underpinnings of novel grammar learning, and individual differences in second language learning and language learning aptitude. Specifically, the studies demonstrated that successful and efficient L2 learning is coupled with particular structural and functional features of the learners' brain encompassing the right frontal and parietal cortical sites, and connections between them.

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Appendix 1

Participants' instructions
explaining the procedure of the
LLAMA tests

Welkom bij het talenknobbelonderzoek!

Alvast heel erg bedankt voor je medewerking. Lees de volgende aanwijzingen zorgvuldig. Als je vragen hebt stel deze dan voordat je met de taakjes begint.

1. Log in met de volgende gegevens:

Username: [****]

Wachtwoord: [****]

2. Op de desktop krijg je 4 icoontjes te zien:



LLAMA-B



LLAMA_D



LLAMA_E



LLAMA_F

3. Doe de tests in deze volgorde en volg de bijgevoegde instructies.
LEES DE INSTRUCTIES GOED DOOR ALVORENS MET DE TAAK TE BEGINNEN!
4. Voor alle tests heb je koptelefoons nodig.
Voordat je met de taakjes begint check of het geluid hard genoeg is.
5. Als je klaar bent met de tests, vul de vragenlijst in.
Deze vind je ook op de desktop (LLAMA Survey Qualtrics Survey Software)
6. Als je klaar bent, verlaat de zaal zo stil mogelijk om andere participanten niet te storen. Graag krijgen we de instructies weer terug.
7. Bedankt voor je medewerking en succes!

1. LLAMA_B: A vocabulary learning task

In deze taak krijg je het volgende scherm te zien:

****LEES DE INSTRUCTIES GOED DOOR ALVORENS MET DE
TAAK TE BEGINNEN!****



1. Voer je naam en achternaam in in de velden gemarkeerd met ☞.
2. Start de test door te klikken op ▶.
3. Je hebt 2 minuten de tijd om de namen voor de 20 figuren te leren.
De naam van een figuur wordt getoond als je erop klikt.
Gebruik je tijd goed om zoveel mogelijk van de namen van de 20 figuren te onthouden. Maak GEEN notities.
4. De klok in het midden van het scherm laat je zien hoeveel tijd je nog hebt.
5. Als je tijd om is, zul je een pieptoon horen.
6. Je begint het volgende deel van de test door te klikken op ⇨.
7. Nu krijg je een woord te zien dat je aan de bijbehorende figuur moet koppelen.
Je doet dat door te klikken op de juiste figuur.
8. Je krijgt feedback in de vorm van een hoge pieptoon voor een goed antwoord en een lage toon als je een fout hebt gemaakt.
9. De taak is afgelopen als je een percentage ziet verschijnen.
10. Sluit het venster met de LLAMA_B taak en ga naar het volgende onderdeel (2. LLAMA_D).

2. LLAMA_D: A sound recognition task

In deze taak krijg je het volgende scherm te zien:

****LEES DE INSTRUCTIES GOED DOOR ALVORENS MET DE
TAAK TE BEGINNEN!****

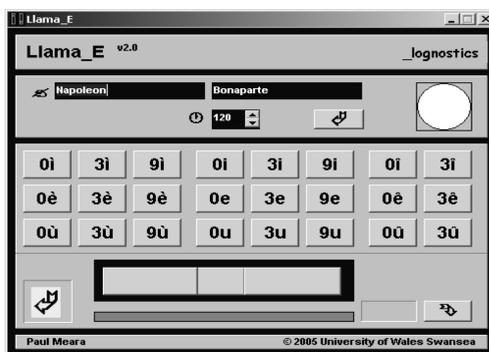


1. Voer je naam en achternaam in in de velden gemarkeerd met ☹.
2. Start de test door te klikken op ↩.
3. In het eerste deel van deze test ga je 10 woorden horen in een taal die je niet kent.
4. Luister goed naar die woorden.
5. Als het programma de 10 woorden heeft afgespeeld, zul je een pieptoon horen.
6. Je begint het volgende deel van de test door te klikken op ⇒.
7. Nu zul je naar de net gehoorde 10 woorden luisteren samen met nieuwe woorden.
Jouw taak is om te bepalen welke woorden je in het eerste deel van de test hebt gehoord en welke niet.
8. Klik op ☺ als je denkt dat je het woord al hebt gehoord.
9. Klik op ☹ als je denkt dat je het woord NIET hebt gehoord.
10. Om naar het volgende woord te luisteren klik op ⇒.
11. Je krijgt feedback in de vorm van een hoge pieptoon voor een goed antwoord en een lage toon als je een fout hebt gemaakt.
12. De taak is afgelopen als je een percentage ziet verschijnen.
13. Sluit het venster met de LLAMA_D taak en ga naar het volgende onderdeel (3. LLAMA_E)

3. LLAMA_E: A sound~symbol correspondence task

In deze taak krijg je het volgende scherm te zien:

****LEES DE INSTRUCTIES GOED DOOR ALVORENS MET DE
TAAK TE BEGINNEN!****



1. Voer je naam en achternaam in in de velden gemarkeerd met ☹.
2. Start de test door te klikken op ⏪.
3. In het eerste deel van deze test krijg je 22 lettergrepen te horen die gekoppeld zijn aan transcripties in een onbekend alfabet. Jouw taak is om de relatie tussen de klanken en letterreeksen te ontdekken.
4. Je doet dat door op de knopjes met letters klikken. Elk knopje speelt een kort geluid af. De tekst op het knopje informeert je hoe dit geluid in de taal wordt gespeld.
5. Je hebt 2 minuten de tijd om deze spellingregels te leren.
6. Je MAG notities maken.
7. De klok rechtsboven in het scherm laat je zien hoeveel tijd je nog hebt.
8. Als je tijd om is, zul je een pieptoon horen.
9. Je begint het volgende deel van de test door te klikken op ⇒.
10. Elke keer als je op ⇒ klikt zul je een woord horen en twee mogelijke spellingvarianten zien.
11. Klik op de spellingvariant die volgens jou correct is.
12. Je krijgt feedback in de vorm van een hoge pieptoon voor een goed antwoord en een lage toon als je een fout hebt gemaakt.
13. Om het volgende woord te horen klik op ⇒. In totaal zijn er 20 testwoorden.
14. De taak is afgelopen als je een percentage ziet verschijnen.
15. Sluit het venster met de LLAMA_E taak en ga naar het volgende onderdeel (4. LLAMA_F A grammatical inferencing task).

4. LLAMA_F: A grammatical inferencing task

In deze taak krijg je het volgende scherm te zien:

****LEES DE INSTRUCTIES GOED DOOR ALVORENS MET DE
TAAK TE BEGINNEN!****



1. Voer je naam en achternaam in in de velden gemarkeerd met .
2. Start de test door te klikken op .
3. In het eerste deel van deze test heb je 5 minuten om zoveel mogelijk te leren over de grammatica van een onbekende taal.
4. Je doet dat door te klikken op de kleine knopjes.
5. Elke keer als je op een knopje klikt krijg je een plaatje en een zin die dit plaatje beschrijft te zien.
6. Je MAG notities maken.
7. De klok rechtsboven in het scherm laat je zien hoeveel tijd je nog hebt.
8. Als je tijd om is, zul je een pieptoon horen.
9. Je begint het volgende deel van de test door te klikken op .
10. In het tweede deel zul je een plaatje zien en twee zinnen.
Een van de zinnen is grammaticaal correct.
11. Klik op de zin die volgens jou correct is.
12. Je krijgt feedback in de vorm van een hoge pieptoon voor een goed antwoord en een lage toon als je een fout hebt gemaakt.
13. Om de volgende zin te zien klik op .
14. De taak is afgelopen als je een percentage ziet verschijnen.
15. Sluit het venster met de LLAMA_F taak en vul de vragenlijst in.

Appendix 2

Participants' questionnaire

1. Vul uw gegevens in:
 Voornaam
 Achternaam
 Geboortedatum (DD.MM.YYYY)
 GeboorteplaatsBeroep of studierichting
2. Geslacht
 - Man
 - Vrouw
3. Hoe kunnen we u bereiken?
 Telefoonnummer
 E-mail
4. Wat is uw moedertaal?
 - Nederlands
 - Anders _____
5. Welke andere talen beheerst u?
 - 1.
 - 2.
 - 3.
 - 4.
 - 5.
6. Hoe goed beheerst u die talen? Geef voor elke taal aan hoe goed u die kunt begrijpen/spreken/lezen/schrijven: 4=moedertaalniveau, 3=zeer goed, 2=goed, 1=matig tot zwak, 0=niet
7. Vanaf welke leeftijd bent u voor de eerste keer begonnen met het leren van deze talen?
8. Speelt u een instrument en/of zingt u? U mag meer dan 1 antwoord geven.
 - Geen van beiden.
 - Ja, ik speel: _____
 - Ja, ik zing.
9. Als u zingt of een instrument bespeelt, hoeveel jaren doet u dit al?
10. Hoe actief zingt u of bespeelt u uw instrument? U mag meerder antwoorden geven.
 - Ik krijg les.
 - Ik heb vroeger in een orkest/ ensemble/ band gespeeld. (Vul het aantal jaren in.) _____
 - Ik zing in een koor/ band.
 - Ik heb vroeger in een koor of in een band gezongen. (Vul het aantal jaren in.) _____
 - Ik heb vroeger les gehad. (Vul het aantal jaren in.) _____
 - _____
 - Ik speel in een orkest/ ensemble/ band.
 - Niets van dit alles, ik speel/ zing alleen thuis voor mezelf.
11. Heeft u problemen met uw gehoor (gehad)?
 - Ja
 - Nee
12. Zo ja, beschrijf kort het probleem.

Appendix 2

13. Zou u aan onze vervolgstudie naar 'talenknobbel' willen meedoen? In die vervolgstudie onderzoeken wij het brein door middel van een MRI scanner of EEG. Het onderzoek duurt ongeveer 2 uur. De vergoeding voor de deelname aan het MRI of EEG onderzoek bedraagt 20 euro.
- Ja
 - Nee
14. Stottert u?
- Ja
 - Nee
15. Bent u ooit door een logopedist behandeld?
- Ja
 - Waarom? Wanneer?
 - Nee
16. Bent u ooit door een neuroloog behandeld?
- Ja
 - Waarom? Wanneer?
 - Nee
17. Heeft u wel eens een EEG ondergaan voor klinische doeleinden?
- Ja
 - Waarom? Wanneer?
 - Nee
18. Heeft u wel eens een een MR/CT scan ondergaan voor klinische doeleinden?
- Ja
 - Waarom? Wanneer?
 - Nee
19. Heeft u wel eens een zware hersenschudding gehad?
- Ja
 - Wanneer?
 - Nee
20. Heeft u last van migraine?
- Ja
 - Hoe vaak?
 - Nee
21. Bent u aan hoofd of hersenen geopereerd?
- Ja
 - Waarom?
 - Nee
22. Heeft u epilepsie?
- Ja
 - Nee
23. Heeft u last van hartritmestoornissen?
- Ja
 - Nee
24. Heeft u last van claustrofobie?
- Ja
 - Nee

Participants' questionnaire

25. Gebruikt u medicijnen?
- Ja
 - Welke?
 - Nee
26. Bevinden er zich in uw lichaam, behalve eventuele tandvullingen en kronen, metalen delen zoals:
- Beugels
 - Prothesen
 - Onverwijderbare piercings
 - Kunsthartklep
 - Metaalsplinters
 - Pacemaker
 - Insulinepomp
 - Andere: _____
27. Heeft u gehoorproblemen?
- Ja
 - Aan het linkeroor?
 - Aan het rechteroor?
 - Nee
28. Draagt u een gehoorapparaat?
- Ja
 - Nee
29. Heeft u problemen met zien?
- Ja
 - Hoeveel bedraagt de afwijking?
 - Nee
30. Heeft u als kind een bril gedragen?
- Ja
 - Nee
31. Heeft u contactlenzen?
- Ja
 - Nee
32. Is uw zicht met bril/lenzen goed?
- Ja
 - Nee
33. Heeft u leesproblemen?
- Ja
 - Nee
34. Heeft u dyslexie?
- Ja
 - Nee
35. Geef voor de onderstaande activiteiten aan of u ze bij voorkeur met de linker- of met de rechterhand verricht:

Appendix 2

| | Links | Rechts |
|--------------------------------|-------|--------|
| Schrijven | | |
| Tekenen en schilderen | | |
| Gooien van een bal | | |
| Knippen met een schaar | | |
| Eten met een lepel | | |
| Haar kammen | | |
| Tandenpoetsen | | |
| Een hamer gebruiken | | |
| Een tennisracket vasthouden | | |
| Een pagina omslaan | | |
| Een lucifer aansteken | | |
| Deksel van een pot verwijderen | | |

36. Beschouwt u zichzelf over het algemeen als links- of rechtshandig?
- linkshandig
 - rechtshandig
37. Heeft u ooit geneigdheid tot linkshandigheid gehad?
- Ja
 - Nee
38. Hebben opvoeders u ooit gedwongen om van hand te veranderen?
- Ja
 - Nee
39. Heeft u familieleden die linkshandig zijn?
- Ja
 - Welke?
 - Nee
40. Wilt u deelnemen aan andere onderzoeken van Leiden University Centre for Linguistics?
- Ja
 - Nee
41. Heeft u nog opmerkingen over ons onderzoek? Geeft u ze dan hier door.

Samenvatting in het Nederlands

Het doel van dit proefschrift is de kennis te bevorderen over de neurale mechanismen en hersenstructuren die de individuele verschillen in het verwerven van grammatica van een vreemde taal onderliggen. De focus ligt op de notie van ‘taalaanleg’, en in het bijzonder het taal-analytisch vermogen. Tijdens de voorbereidende fase voor de studie is een taalaanlegtest aangeboden aan een grote groep deelnemers met als doel twee groepen leerders (met een hoog en gemiddeld taal-analytisch vermogen) te werven voor de daaropvolgende neuro-imaging en elektrofysiologische experimenten. Vier functionele en één structurele neuro-imaging experimenten zijn uitgevoerd met het doel om inzicht in “hoe de getalenteerde hersenen een taal verwerft in vergelijking met de normale hersenen” (Ioup, Boustagui, El Tigi, & Moselle, 1994, p. 93; zoals geciteerd door Abrahamsson and Hyltenstam, 2008) te verkrijgen.

De functionele onderzoeken gerapporteerd in dit proefschrift, hebben gebruik gemaakt van een *artificiële grammatica leren* (AGL) taak waarin de deelnemers een nieuwe grammatica leren waarbij gelijktijdig neuro-imaging of elektrofysiologische data werden verzameld. De grammatica werd gepresenteerd aan de deelnemers in de loop van een aantal leer- en testfasen. Tijdens de leerfasen zijn de correcte grammaticale zinnen één voor één getoond op het scherm terwijl de deelnemers werden gevraagd om de onderliggende regels te ontdekken. De testfasen bestonden uit zowel grammaticale en ongrammaticaal items en de taak van de deelnemers is om de grammaticaliteit van de zinnen te beoordelen. De grammaticaliteitsoordelen dienden als een indicatie van de leeruitgang en toonden aan dat, in zowel de MRI en de EEG experimenten, de scores in de loop van de taak stegen, en dat de deelnemers met een hoge taalaanleg beter presteerden dan die met het gemiddelde taalaanleg.

Hoofdstuk 2 en Hoofdstuk 3 doen allebei verslag van de functionele MRI data opgenomen tijdens de leerfasen van de AGL taak. De twee hoofdstukken hebben gebruikgemaakt van verschillende maar complementaire methodologieën, en beantwoordden samenhangende maar verschillende onderzoeksvragen. Het experiment gerapporteerd in Hoofdstuk 2 kan als inleiding worden gezien op de daaropvolgende onderzoeken waar leerders met hoog en gemiddeld taal-analytisch vermogen met elkaar zijn vergeleken. Het in Hoofdstuk 2 gerapporteerde experiment onderzocht de functionele connectiviteit van vier cruciale hersengebieden die betrokken zijn bij taalverwerking en taalleren, namelijk de bilaterale BA 44/45 en de hippocampus. We rapporteren de connectiviteitspatronen van de vier regio's tijdens de opeenvolgende leerfasen van de AGL taak, hun modulaties door de tijd en de gedragsscores. Eerdere studies (Opitz & Friederici, 2003) stelden de interacties van het hippocampus-systeem en de prefrontale cortex voor als het neurale mechanisme dat het leren van een nieuwe grammatica onderligt. Met behulp van fMRI kunnen op het neurale niveau dergelijke interacties direct worden onderzocht door het onderzoeken van temporele correlaties tussen de hemodynamische activiteit van verschillende hersengebieden, bijvoorbeeld door gebruik te maken van psychofysiologische interactie analyse (Friston et al., 1997). Onze resultaten toonden parallelle (maar aparte) bijdragen van de onderzochte gebieden aan het proces van grammaticaverwerving. De functionele connectiviteitspatroon van het gebied van Broca (links BA 44/45) wijst op het belang van coherente activiteit in de linker prefrontale cortex rond die taalverwerkingsregio voor een succesvolle verwerving van een nieuwe grammatica. Bovendien hangt het verwerven van nieuwe grammaticaregels af van de samenwerking tussen de visuele (occipitale kwab) en de geheugengebieden van de hersenen (hippocampus). Die samenwerking bleek een sterke voorspeller te zijn van succesvolle grammaticaverwerving. Tenslotte vonden we dat de functionele connectiviteit van BA 44/45 (zowel links als rechts) met de rechter posterior cingulate cortex en de rechter temporo-pariëtale gebieden toenam in de tijd. Dit resultaat wijst op het belang van multimodale en aandachtsprocessen in het ondersteunen van het leren van een nieuwe grammatica. Bovendien benadrukt het de betrokkenheid van de rechterhersen helft bij de beginfase van de tweedetaalverwerving. Deze laatste interacties bleken onafhankelijk te opereren van de gedragsscores, wat erop wijst dat ze een verplicht mechanisme zijn bij het leren van een nieuwe grammatica.

Het doel van het in het Hoofdstuk 3 beschreven experiment was om te bepalen of de neurale basis van AGL verschilt tussen populaties van leerders met een hoge en met een gemiddelde taalaanleg. In dit experi-

ment werd de data analyse niet beperkt tot vooraf gedefinieerde regio's (zoals bij het experiment in Hoofdstuk 2). Echter, onderzocht werd nu de *whole-brain functional connectivity* (de functionele connectiviteit van de hersenen als geheel) tijdens de beginfase van nieuwe grammatica-verwerving. Door middel van een *Independent Components Analysis* (een data-driven benadering van de functionele connectiviteit van de hersenen) werden de fMRI data, verzameld tijdens de leerfasen van de AGL taak, gesplitst in activiteitsnetwerken die afzonderlijke cognitieve processen representeren. Deze omvatten het *default-mode* netwerk, het taak-positieve netwerk, werkgeheugen-netwerk, het visuele netwerk, het cerebellum-netwerk en het emotionele netwerk. Verder hebben we naar verschillen in de componenten gezocht, die de twee niveaus van het taalanalytisch vermogen (hoog en gemiddeld) representeerden. Vergeleken met deelnemers met een gemiddelde taalaanleg onderscheidde de deelnemers met een hoge aanleg zich in het algemeen door sterkere functionele connectiviteitspatronen. Het hoge taalanalytische vermogen is gekoppeld aan sterkere bijdragen aan het taak-positieve netwerk van regio's die aan de bilaterale gebied van Broca grenzen; sterkere connectiviteit in het werkgeheugen netwerk (van het rechter centrale operculaire cortex), en in het emotionele netwerk (van de amygdala en corpus mamillare, evenals in de rechter hemisfeer). In vergelijking met proefpersonen met een hoge taalaanleg, toonden de proefpersonen met een gemiddeld taalanalytisch vermogen een sterkere functionele connectiviteit binnen het *task-positieve* netwerk van gebieden grenzende aan de rechter hersenhelft homolog van het gebied van Broca, en van gebieden die typisch zijn voor lager niveau (visuele) informatieverwerking (rechter gyrus fusiformis). Verder toonden ze een verhoogde connectiviteit binnen het *default-mode* netwerk (in het achterste deel van de gyrus cinguli, gyrus paracingularis, het voorste deel van de gyrus cinguli, en in de rechter polus frontalis en de gyrus frontalis medius).

In Hoofdstuk 4, onderzochten we zowel de verschillen in neurale activiteit gekoppeld aan een AGL taak tussen leerders met een hoge en gemiddelde taalaanleg, als ook de manier waarop de activiteitspatronen veranderen in de loop van de taak en als functie van de prestatie van de deelnemers. De data verzameld tijdens de testfasen van de AGL taak zijn geanalyseerd. Voor alle deelnemers vonden wij meer activiteit gekoppeld aan ongrammaticale dan grammaticale zinnen van artificiële grammatica gebruikt in de taak. Bovendien vonden we dat de leerders met een hoge taalaanleg meer neurale structuren gebruiken tijdens de taak dan de leerders met gemiddelde taalaanleg. Die verhoogde hersenactiviteit wordt hoofdzakelijk gelokaliseerd in de rechter hersenhelft, dat wil zeggen in de rechter gyrus angularis/ supramarginalis, in de gy-

rus frontalis superior en de gyrus frontalis medius en in het achterste deel van de gyrus cinguli. Het design van het experiment maakte een nader onderzoek mogelijk van de verschillende manieren waarop het leren van een nieuwe grammatica in de tijd verloopt, zowel gedragsmatig (door middel van het identificeren van de diverse leerpatronen) als op neurale niveau. We vonden dat de activiteit in de bilaterale temporele en pariëtale regio's in de loop van de taak steeg en dat het linker pariëtale gebied de grootste modulatie van de BOLD activiteit toonde aan het einde van de taak, vooral bij succesvolle leerders. De hoeveelheid activiteit in de linker gyrus angularis correleerde met de gedragsprestatie, maar pas in de laatste fase van de AGL taak. Daarnaast zagen we dat een steile leercurve op de AGL taak (lage scores in het begin en een snelle verbetering van de prestaties) is gekoppeld aan de modulatie van de BOLD activiteit in de linker gyrus angularis. De deelnemers die een zodanig sterk verschil in hun scores boekten tussen de eerste en de laatste (i.e., derde) fase van de taak, vertoonden slechts één cluster van hersenactiviteit dat significant groter was in fase 3 dan in fase 1 van de AGL taak. Dit cluster was gelokaliseerd in de linker gyrus angularis.

Hoofdstuk 5 rapporteerde de verzamelde elektrofysiologische data? Hier hebben we onderzocht of leerders met verschillende niveaus van het taal-analytische vermogen verschillende patronen van EEG oscillaties vertonen gedurende het leren van een nieuwe grammatica. Twee typen elektrofysiologische metingen werden gerapporteerd: variaties in spectraal opzicht (*spectral power*) en fasesynchronisatie binnen frequentiebanden. De corticale connectiviteitspatronen en profielen van modulaties van *spectral power* in de tijd onderscheidden tweedetaalleerders met verschillende niveaus van taal analytisch vermogen. In de loop van de AGL taak bleken de globale fasesynchronisatie waarden in de bèta-band frequentie de gedragsprestaties significant te voorspellen als functie van het taal-analytische vermogen: het effect van de globale fasesynchronisatie in de bèta-band op de taak scores in de tijd was groter voor de deelnemers met een hoog taal-analytisch vermogen.

Op een kortere tijdschaal leek de toenemende vaardigheid op een AGL taak te worden ondersteund door sterkere lokale synchronisatie (in theta-, alfa- en gamma-banden) in gebieden in de rechter hersenhelft. Dit effect onderscheidde de leerders met een hoge taalaanleg van de leerders met gemiddelde taalaanleg: leerders met hoge aanleg vertoonden een grotere toename van de lokale fasesynchronisatie waarden ten opzichte van baseline dan de leerders met een gemiddelde aanleg. Het verschil was gelokaliseerd in de rechter frontale elektroden voor de theta-band en rechter centro-pariëtale elektroden voor alfa- en gamma-

banden. Ten slotte hebben we vastgesteld dat de participanten met een hoge taalaanleg minder mentale inspanning ondervonden (of verminderde aandacht voor de taak hadden) nadat het leren was voltooid (in een laat stadium van de taak), zoals bleek uit een hogere alfa band power.

In het laatste gedeelte van dit proefschrift (Hoofdstuk 6) rapporteerden we de resultaten van een experiment waar gebruik is gemaakt van deterministische tractografie van de belangrijkste taalgebonden witte stofbanen (het ‘*perisylvian* taalnetwerk’ of de *fasciculus arcuatus*). Dit experiment is gericht op het bepalen hoe de microstructuur van de banen kan worden gerelateerd aan iemands taal-analytisch vermogen. Zes banen per deelnemer zijn virtueel ontleed (het linker en rechter lange directe segment, linker en rechter voorste indirecte segment en linker en rechter achterste indirecte segment). Daarnaast zijn er metingen met betrekking tot hun microstructurele organisatie verzameld. De resultaten wezen op *mean diffusivity* (MD) waarden van drie banen (rechter voorste, linker lange en linker voorste segmenten) die het best de twee groepen (deelnemers met een hoge en gemiddelde taal-analytische vermogen) van elkaar onderscheidden. Verreweg de hoogste coëfficiënt is verkregen voor de MD-waarden van het rechter voorste segment. Dit resultaat wijst op de rol van de rechter fronto-pariëtale connectiviteit in witte stof voor superieur taalleervermogen en ondersteunt onze bevindingen met betrekking tot de betrokkenheid van de rechter hersenhelft bij het leren van talen, zoals gevonden in de experimenten die de functionele onderbouwing van de succesvolle L2 leren onder de loep namen. Bovendien suggereert het het belang van aandachtsprocessen en intelligentie voor een succesvolle T2-verwerving.

In dit proefschrift zijn er verschillende benaderingen toegepast op neuro-imaging en elektrofysiologische data, waardoor een meerlagig zicht op de beginfase van het leren van talen op neurale niveau biedt, alsmede een beschrijving van individuele verschillen in grammaticaverwerving. De vijf experimentele studies in dit proefschrift dragen zo bij aan een beter begrip van neurale onderbouwing van het leren van een nieuwe grammatica en individuele verschillen in tweedetaalverwerving en taalaanleg. De studies toonden aan dat succesvolle en efficiënte T2-leerders gebruik maken van meer neurale middelen, die in een meer coherente en geïntegreerde wijze worden georganiseerd. Deze extra middelen komen voornamelijk voort uit de rechter hemisfeer en zijn gelokaliseerd in het fronto-pariëtale systeem.

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Curriculum vitae

Olga Kepinska was born in Wrocław, Poland in 1986. After graduating from secondary school (XIV L.O. in Wrocław), she started her Bachelor's degree in Dutch Philology at Wrocław University. On the third year of the programme she spent a semester in the department of Dutch Studies at Leiden University. She came back to Leiden in September 2009 to pursue a Master's degree (completed *cum laude*) in Dutch Studies, which was made possible thanks to a grant from the HSP Huygens Scholarship Programme. In 2011, she completed a postgraduate study programme in English Translation at Wrocław University, Poland. In the academic year 2011-2012, she continued her education in Belgium, where she pursued a Master of Arts in Advanced Studies in Linguistics thanks to a specialisation scholarship from the Education and Training Department of the Flemish Government. She graduated (with the greatest distinction) from the Vrije Universiteit Brussel in September 2012. From September 2012 to April 2017 she was employed at the Leiden University Centre for Linguistics as a PhD candidate, followed by an appointment as a post-doctoral researcher.

This thesis aims at providing insights in the neural mechanisms and brain structures underlying individual differences in second language acquisition. It reports on a series of experiments investigating neural correlates of novel grammar learning and of the analytical component of language aptitude, using a variety of neuroimaging methods: functional magnetic resonance imaging, diffusion tensor imaging and electroencephalography.



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