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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, focusing 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-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 gyrus, and superior frontal and middle frontal 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

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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

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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 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).

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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 Szafarski, 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 signif-
cantly differ in their fluid intelligence scores (see Chapter 1), the pre-
sent 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 particu-
lar, they argue that “the attentional system acts as a filter to any in-
coming stimulation, influencing perception, and therefore may affect
learning” (p. 2). Such influence of attentional processes is also well doc-
dumented 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 atten-
tional 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 abili-
ties 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 microstruc-
tural 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 foun-
dations 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 limi-
tations. First, even though we combined several different methodologi-
cal 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.