Neural correlates of vocal learning in songbirds and humans

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Citation

Kant, A. M. van der. (2015, January 28). *Neural correlates of vocal learning in songbirds and humans*. Retrieved from https://hdl.handle.net/1887/31633

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Title: Neural correlates of vocal learning in songbirds and humans : cross-species fMRI studies into individual differences
Issue Date: 2015-01-28

Part II

Neural correlates of artificial grammar learning in human adults

In the first part of this thesis, the songbird model was employed in order to study the neural correlates of vocal learning in a species that shows some interesting behavioral similarities to humans with regard to the development of their species-specific vocalizations. The data collected in the songbird studies have shown that the brain selectively processes the song that is learned from the tutor early in life. Furthermore, these studies have shown that this selectivity develops and changes during the song learning process and that its strength is related to learning success.

In the remainder of this thesis, we will explore whether the neural correlates of human language learning share some of the characteristics found for birdsong learning. If the neural processes undelying birdsong learning and human language learning show similarities, this would strengthen the songbird model for vocal learning. For ethical reasons, humans cannot be isolated from speech input at any time during or after the sensitive period for language acquisition, which means that the full extent of their language knowledge cannot be controlled. Furthermore, human language is highly complex and learning it requires many levels of analysis. This means that "what is learned" is too extensive to study in a single experiment. However, studies of language deprived children have shown that the acquisition of syntactic structure is most impaired when humans start to learn language after the sensitive period for language acquistion.

Because the acquisition of syntactic structure is such a central part of human language learning, we employ an artificial grammar learning paradigm to simulate and study grammar learning in human adults. This study serves as a basis for further studies on artificial grammar learning, which will be focused on children and compare adult learners to children in order to measure the impact of the sensitive period on the neural correlates of human language acquisition. In the study described in Chapter 5 the learning process is studied on-line using auditory fMRI and related to learning outcomes. Furthermore, structural and functional connectivity related to artificial grammar learning are explored in Chapter 6.

CHAPTER 5

Neural correlates of individual differences in non-adjacent dependency learning in human adults

How does the brain reflect the learning of a new language? In previous studies, the effects of language learning on the state of the brain have been investigated, but mostly off-line (after learning). In the present study, individual differences in brain function were studied during auditory artificial grammar learning. The neural correlates of individual differences in adult language learning were investigated in a functional Magnetic Resonance Imaging (fMRI) study using an auditory artificial grammar learning paradigm. FMRI data from 20 adults were collected while they were presented with an artificial grammar containing non-adjacent dependencies and a control language lacking these dependencies. After exposure participants were tested on learning and generalization of the artificial grammar. Our data showed a correlation between the differential neural activation in response to the grammar containing non-adjacent dependencies in the Left Inferior Frontal Gyrus (LIFG) and the bilateral Superior Temporal Gyri and Insulae and the level at which individual subjects showed sensitivity to the non-adjacent dependencies. Furthermore, during the grammatical judgment task, LIFG showed a differential activation in response to correctly versus incorrectly judged violations. These results indicate that individual differences in learning success are reflected in neural activation that develops early in the learning process and is largely dependent on sensitivity to violations.

5.1 Introduction

Both during first and second language acquisition learners are confronted with speech streams from which they need to extract word boundaries and syntactic rules in order to acquire the grammar of the language. In order to complete this task, the human brain analyzes the input at several levels (Uddén & Bahlmann, 2012). In the present study, we will focus on the level of syntactic analysis and the process of syntactic rule learning. This process has been hypothesized to depend on statistical learning, which might be based on abstract algebraic rules (Marcus, Vijayan, Rao, & Vishton, 1999) or predictive dependencies between words or phrases (Saffran, 2001, 2002).

5.1.1 The role of non-adjacent dependency learning in language acquisition

Syntactic structures that underlie language are hierarchical and therefore they cannot be learned purely based on associations between adjacent elements (Chomsky, 1957). In order to acquire the syntax of a language, one also needs to acquire the dependencies between non-adjacent words and morphemes (non-adjacent dependencies) which are abundantly present in natural language and often mark syntactic relations such as number and tense agreement (e.g. in English: *The dogs* ***are*** *bark****ing*** and Dutch: *Wij* ***hebben*** *gisteren samen* ***gegeten*** *"Yesterday we* ***have*** *dine****d*** *together"*. Learning non-adjacent dependencies has proven to be a difficult task for adults (Bonatti, Pena, Nespor, & Mehler, 2005; Grama, Wijnen, & Kerkhoff, 2013; Newport & Aslin, 2004; Onnis, Monaghan, Richmond, & Chater, 2005; Peña, Bonatti, Nespor, & Mehler, 2002; Perruchet, Tyler, Galland, & Peereman, 2004; Van den Bos, Christiansen, & Misyak, 2012) as well as infants and children (Gómez, 2002; Gómez & Maye, 2005; Kerkhoff, De Bree, De Klerk, & Wijnen, 2013; Santelmann & Jusczyk, 1998; Van Heugten & Johnson, 2010). Both the linguistic level of analysis (Bonatti et al., 2005; Newport & Aslin, 2004) and the distance between the dependent elements (Grama et al., 2013) were shown to influence the degree to which participants are able to acquire the dependencies (for a review see Sandoval & Gómez, 2013). However, the nature of the computational mechanisms underlying the ability to acquire non-adjacent dependencies is still a topic of debate (Newport & Aslin, 2004; Peña et al., 2002; Perruchet et al., 2004; Van den Bos et al., 2012). In the present study, we ask which neural mechanisms underlie the acquisition of non-adjacent dependencies.

5.1.2 Artificial Grammar Learning in the brain

Behavioral studies have provided important insights with regard to the mechanisms involved in learning non-adjacent dependencies and the difficulties that learners face when acquiring these dependencies. A number of studies have used Artificial Grammar Learning (AGL) paradigms to uncover the neural underpinnings of non-adjacent dependency learning (e.g. De Vries, Petersson, Geukes, Zwitserlood, & Christiansen, 2012; Uddén, Ingvar, Hagoort, & Petersson, 2012). Implicit Artificial Grammar Learning (Reber, 1967) has been used in many studies addressing language development and second language learning because AGL paradigms allow researchers to control a higher number of variables compared to a natural language learning setting.

Although AGL cannot represent the full complexity of learning a natural language, it is the paradigm of choice when studying neural correlates of syntactic development, because syntactic processing of previously learned artificial grammars has demonstrated a considerable overlap in neural activation with natural language processing in the posterior part of the left inferior frontal gyrus (BA 44/45), including Broca's area (Petersson, Folia, & Hagoort, 2012; Petersson & Hagoort, 2012). Previous AGL studies addressing non-adjacent dependency learning have mostly used complex artificial languages which participants learned over a longer period of time based on visually presented stimuli and have measured brain activation after the learning process was completed. This approach allows for consolidation, which has proved to be important in syntactic development (Nieuwenhuis, Folia, Forkstam, Jensen, & Petersson, 2013), but does not reveal how the brain reflects learning from mere exposure in real time. Although listening to a speech stream requires more sequential processing compared to visual presentation, the neural correlates of artificial grammar learning during auditory exposure to a speech stream have hardly been studied. In the present study, we use functional MRI in a highly controlled auditory artificial grammar learning paradigm to bridge this gap and to address on-line learning of non-adjacent dependencies.

The present experiment does not require participants to learn a complex artificial grammar with an extended vocabulary. However, computing transitional probabilities between adjacent elements is not sufficient for the acquisition of non-adjacent dependencies, which is expected to require complex unification operations at the phrasal level. Therefore, we hypothesize that acquiring non-adjacent dependencies from auditory exposure activates brain regions which are known to be involved in structural computations (for a review see Petersson & Hagoort, 2012). Based on an extensive body of research investigating the neural mechanisms underlying syntactic processing and artificial grammar learning (e.g. Bahlmann, Schubotz, & Friederici, 2008; Opitz & Friederici, 2003; Petersson et al., 2012; Uddén & Bahlmann, 2012; Uddén et al., 2008), we expect the Left Inferior Frontal Gyrus (LIFG) to be involved both during the exposure phase where the artificial grammar is processed for the first time and during grammatical judgment. In addition, we expect activation of the Superior Temporal Gyri (STG) during mere auditory exposure, as bilateral STG is hypothesized to be involved in speech perception (Hickok & Poeppel, 2000). Prolonged auditory exposure is expected to induce changes in activation over time in both of these structures due to habituation in the auditory cortex and an increase in recognition of non-adjacent dependencies in LIFG.

5.1.3 Individual differences in brain and behavior

Earlier studies addressing neural correlates of second language acquisition (Tettamanti et al., 2002; Veroude, Norris, Shumskaya, Gullberg, & Indefrey, 2010) as well as birdsong learning (Bolhuis et al. (2000); Van der Kant et al. (2013), see also Chapter 3 of this thesis), have uncovered a relation between neural activation in response to the processing of vocalizations and individual differences in learning success. Based on these previous results, we will address the relation between individual differences in learning capacities and neural activation during learning through mere auditory exposure. Individual differences in learning ability are expected to correlate with neural activation especially in LIFG.

Working memory capacity has been suggested to influence syntactic learning both on the behavioral (Baddeley, 2003; Ellis, 1996) and on the neural level (e.g. Santi & Grodzinsky, 2007), and is thus expected to play a role in the detection and acquisition of non-adjacent dependencies. Furthermore, previous studies (Birdsong & Molis, 2001; Johnson & Newport, 1989) demonstrated age effects on adult second language acquisition, suggesting that age might play a role in the ability of participants in the present study to acquire non-adjacent dependencies. Potential correlations between learning outcome and neural activity might thus be influenced by individual variation in working memory capacity and age, which will be considered as factors in the present study.

5.2 Methods

5.2.1 Ethical statement

All participants gave written informed consent prior to inclusion in this study and were financially compensated for their participation. In accordance with Leiden University Medical Center (LUMC) policy all anatomical scans were reviewed by a radiologist. This screening yielded no anomalous findings. All experimental procedures were conducted under approval of the Medical Ethical Committee of the Leiden University Medical Centre, The Netherlands (CME no. NL42690.058.12).

5.2.2 Participants

Twenty healthy adult volunteers (12 males, mean age 28, range 18-43) were included in the present study. All participants were right-handed and reported normal hearing and normal or corrected-to-normal vision. They re-

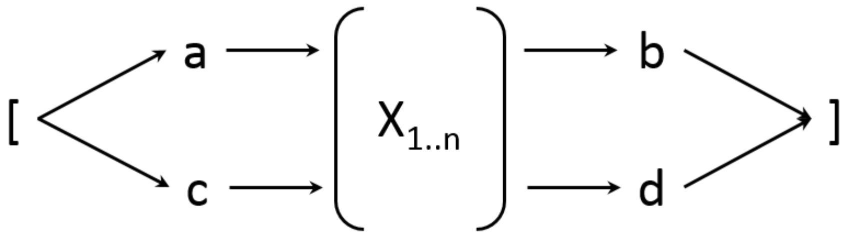

Figure 5.1: Artificial grammar containing non-adjacent dependencies Every X can occur in the middle position, but a is necessarily followed by b and c is necessarily followed by d. In the control condition, this dependency is absent.

ported no history of speech- or language disorders, other cognitive impairments or neurological damage. All participants were native Dutch speakers who used Dutch as their main language in daily communication and grew up in a monolingual Dutch environment.

5.2.3 Materials

For the present study, we employed an artificial grammar learning (AGL) paradigm where participants were first exposed to a learning set of the grammar described below and consequently tested on learning and generalization of the grammatical rules with a grammatical judgment task. The Artificial Grammar Learning paradigm enables us to study language learning in a more controlled way compared to natural language learning.

Participants were auditorily presented with phrases from an artificial grammar containing non-adjacent dependencies (NAD) and from a control language which had the same syllable structure and phonology, but lacked these dependencies. Stimuli were adapted from earlier behavioral studies on non-adjacent dependency learning by Dutch-speaking adults and children (Grama et al., 2013; Kerkhoff et al., 2013) and infant learners of English (Gómez, 2002) and were compatible with Dutch phonotactic constraints. Both the NAD and the control language consisted of strings of three pseudo-words. In the NAD language, a dependency exists between the first and last pseudo-word in each string, taking the form of aXb and cXd phrases (Figure 5.1). In the control language, there was no dependency between the first and last pseudo-word, resulting in strings where any of the a, b, c, and d-elements could occur both in the initial and in the final position and could be combined with any other of the a, b, c, and d-elements, maintaining the syllable structure of the strings. To allow for assessment of learning of the NAD language, ungrammatical stimuli containing a violation of the dependency were constructed. In these stimuli, the dependency between the first and last syllable was switched, resulting in aXd and cXb phrases.

Two sets of monosyllabic a, b, c and d-elements were used, where for each

	NAD stimuli	**Control stimuli**	**Ungrammatical stimuli**
Group 1	mo noeba zop tep noeba ra mo wadim zop tep wadim ra	poe noeba jik si noeba poe jik wadim si lut wadim jik	mo noeba ra tep noeba zop mo wadim ra tep wadim zop
Group 2	poe noeba jik lut noeba si poe wadim jik lut wadim si	mo noeba zop ra noeba zop zop wadim tep tep wadim ra	poe noeba si lut noeba jik poe wadim si lut wadim jik

Table 5.1: Examples of NAD and control stimuli for auditory presentation For illustration purposes, only a subset of the X elements occurring in the full stimulus set is used. The two groups only differentiate in the stimuli they hear and are not analyzed separately. NAD: artificial grammar containing non-adjacent dependencies, Control: artificial grammar lacking non-adjacent dependencies.

participant one set was assigned to each language (NAD or Control) to correct for any effects of acoustic differences between the sets. A set of in total 119 bisyllabic X-elements was constructed and combined with the a, b, c and d-elements to construct the full set of stimuli. A latin-square design was employed to counterbalance assignment of the stimuli to participants. Stimuli containing each of the sets of abcd-elements were either assigned to the NAD or to the control language for each participant. Moreover, X-elements were assigned to either the exposure or the test phase for each participant. A number of examples of stimuli from the two languages and of violations are given in Table 5.1.

According to earlier findings (Kerkhoff, personal communication; Peña et al. (2002)), rule learning only occurred the pseudo-words within a phrase were separated by short pauses. Therefore, we inserted 250 ms pauses between the pseudo-words in each stimulus. All pseudo-words were pronounced in carrier sentences by a Dutch-speaking male adult and recorded using Adobe Audition (Adobe Systems, San Jose, California) and a Sennheiser directional microphone (Sennheiser electronic, Wedemark, Germany). They were then isolated from the speech stream and concatenated into the final stimuli using Praat software (Boersma, 2002), version 5.3.41, freely available from http://www.praat.org/. The final stimulus inventory contained 476 NAD stimuli, 476 control stimuli and 476 ungrammatical stimuli. Although more combinations were possible for the control condition, a subset was selected for the stimulus inventory that balanced frequency and position between a, b, c and d-elements.

5.2.4 Experimental paradigm

In this two-phase fMRI experiment, participants learned an artificial grammar containing non-adjacent dependencies from mere auditory exposure. During an initial exposure phase, participants listened to the artificial grammar (NAD) and the control language, which were presented through pneumatic headphones, which were part of the scanner intercom system (Philips Healthcare, Best, The Netherlands). In a grammatical judgment task, which followed the exposure phase, participants listened to items that either followed or violated the artificial grammar they had been exposed to. Participants were then asked to judge the grammaticality of these items, thus testing learning and generalization of the artificial grammar. Stimulus presentation was controlled and responses were recorded using E-prime (Psychology Software Tools, Sharpsburg, Pennsylvania).

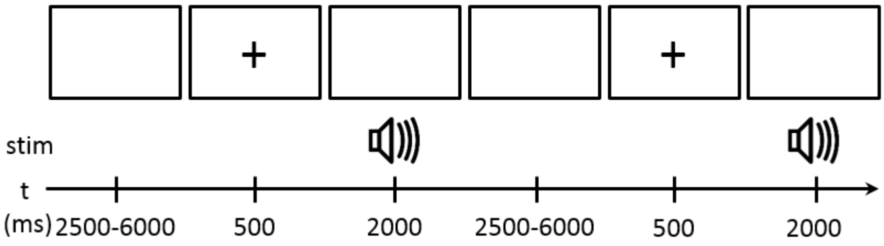

Figure 5.2: Experimental paradigm for the exposure phase Auditory stimuli ('stim') are played through headphones during presentation of a black screen for 2 s.

During the exposure phase, participants listened to the two artificial grammars (NAD and control) which were auditorily presented to them. Participants were presented with a total of 100 stimuli during two blocks of approximately six minutes, with a self-paced pause between the blocks. A different subset from the inventory of NAD stimuli was presented to each participant and stimuli were not repeated. Stimulus presentation followed an event-related paradigm with a stimulus duration of 2,000 ms and a variable inter-stimulus interval of 2,500-6,000 ms and presentation of each stimulus was preceded by a fixation cross presented on the screen for 500 ms. Behavioral pilots showed that random presentation of items from the two languages did not result in any learning (above-chance performance on grammaticality judgments). Therefore, stimuli from the NAD and control languages were alternated in groups of six stimuli, within which selection of items from the language was pseudo-random in the sense that stimuli could not be presented more than once per participant. During both blocks of the exposure phase a GE-EPI time-series was acquired.

Following the exposure phase, participants were asked to judge phrases from the NAD language and violations of the NAD language on their grammaticality in a test phase. A total of 66 stimuli were presented through headphones in two blocks of approximately five minutes with a pause between blocks. Participants were asked to indicate for each stimulus whether the phrase belonged to the language they had heard during the exposure phase. Participants were given a 3 s time window, which was indicated with a question mark on the screen, to respond with a button press of the right or left index finger. Stimuli were presented in an event-related paradigm using the same timing parameters as in the exposure phase. In the grammatical judgment task, stimulus presentation was randomized with no grouping of NAD or ungrammatical stimuli. Participants were never presented with the same NAD phrases in the exposure phase and test phase. To further assess generalization of the grammar, part of the stimuli in the test phase contained X-items that the participants had not heard in the exposure phase. Selection of the NAD phrases and X-items that were only presented in the test phase was counterbalanced between participants. During both blocks of the test phase, fMRI data were acquired.

In addition to the fMRI experiment, participants were tested on their working memory capacity using both a verbal and a non-verbal working memory task (WAIS-IV forward and backward digit span (Pearson, The Netherlands) and Exef mental counters (Department of Developmental Psychology, University of Amsterdam, The Netherlands)). All participants completed a questionnaire on their language background, followed by a questionnaire assessing the strategies participants had used and the regularities they had detected during the AGL task.

5.2.5 MRI data collection and analysis

All MRI data were acquired at the LUMC using a 3 Tesla Philips Achieva TX MRI system (Philips Healthcare, Best, The Netherlands) with a whole-head receiver coil. Participants were screened for counter-indications before entering the scanning room. In order to minimize movement and increase the comfort level of the participant, cushioning was placed around the head and ear plugs and headphones were provided for hearing protection.

Both during the exposure phase and the test phase, two fMRI time series of 130 T_2^*-weighted whole-brain single-shot GE-EPI volumes were acquired for each participant, including two dummy scans to allow the longitudinal magnetization to reach equilibrium (35 transverse slices, TR/TE: 2550/30 ms, flip angle: 80°, voxel size 2.75 mm^3, including a 10% inter-slice gap, field of view (FOV): 220 x 217.25 x 96.25 mm). The slightly longer TR and the smaller number of slices compared to the EPI sequence used for the resting state scans were selected in order to minimize the gradient noise level. To further reduce the noise level inside the scanner during presentation of the auditory stimuli, the gradient slew rate was increased using the Philips soft-tone parameter (factor 5), which has shown to reduce sound pressure levels with 12dB (Rondinoni, Amaro Jr, Cendes, Dos Santos, & Salmon, 2013).

Preprocessing of the functional data acquired during both the exposure phase and the grammatical judgment task was carried out using SPM8 (Wellcome Trust Centre for Neuroimaging, London, UK; http://www.fil.ion.ucl.ac.uk/spm/). To allow for accurate localization of the functional activations, the high-resolution T_1-weighted anatomical scan of each subject was segmented and registered to the Montreal Neurological Institute (MNI) T_1-template. Each fMRI time series was realigned to correct for head movement and it was confirmed that head movements did not exceed 5 mm in the x, y or z direction. Functional images were then co-registered to the high-resolution anatomical scan of the same participant and normalized to the MNI template using the parameters obtained from the registration of the high-resolution anatomical scan. Finally, the fMRI images were smoothed with an 8 mm full-width-at-half-maximum (FWHM) isotropic Gaussian kernel.

Statistical analyses of the fMRI data at the individual and group level were performed using the General Linear Model implemented in SPM8. Data were modeled as a series of events and convolved with a canonical hemodynamic response function (HRF) and low-pass filtered at 128 Hz. For both the exposure phase and the grammatical judgment task, the start of presentation of each auditory stimulus was modeled as an event of interest. Separate regressors were defined for NAD and control trials from each session in the exposure phase. For the grammatical judgment task, separate regressors were defined for correct and incorrect trials and NAD and ungrammatical trials, respectively, resulting in a total of four regressors. Regressors were entered into a group level random-effects analysis as separate contrast images for each individual. Statistical differences between stimulus-evoked BOLD signals were assessed using a one-way repeated measures ANOVA followed by post-hoc one-tailed t-tests. Regression analyses with behavioral results from the test phase and behavioral post-tests were also performed to assess potential brain-behavior correlations. For all group analyses p-values were corrected for multiple tests using the Family Wise Error method based on the Random Field Theory (Worsley et al., 1996) on the cluster level and a cluster threshold of five voxels was applied.

5.3 Results

5.3.1 Behavioral results

Data from the grammatical judgment task which was administered in the scanner after exposure showed that most participants had major difficulties learning the non-adjacent dependencies in the NAD grammar. Participants performed significantly above chance on the rejection of violations (one-tailed: T = 1.79, p = 0.045), while performance on accepting NAD phrases was below chance level (Table 5.2). A paired t-test showed that accuracy scores differed significantly between NAD phrases and violations (two-tailed: T = -3.1, p = 0.005). However, no significant difference was found between reaction times to NAD phrases and violations (paired t-test: T = -0.41, p = 0.69, see Table 5.2 for means).

	% Correct responses Mean (sd)	**Response time (ms)** Mean (sd)
NAD phrases	39 (18)	955 (310)
Violations	58 (19)	968 (337)
Total	48 (13)	961 (317)

Table 5.2: Behavioral performance on the grammatical judgment task Percentage of correct responses is given. For NAD stimuli, a response is correct when the participant accepts the phrase, while rejecting the phrase is the correct response for violations. 50% correct represents chance level.

5.3.2 Exposure phase

Unless stated otherwise, all fMRI results are FWE-corrected for multiple comparisons at the cluster level with corrected p-values below p = 0.05 considered significant. R^2-values are computed based on the highest T-value within the reported cluster from the SPM correlation map. MNI coördinates, Z-values and cluster extents for the results reported in this section can be found in Tables 5.3 and 5.4.

F-tests on the group level did not reveal a main effect of session. With a threshold of $p < 0.001$, a small cluster in the left Insula showed a session*stimulus interaction, but this did not survive correction for multiple comparisons ($Fmax$ = 14.06, p-FWE = 0.999, p-uncorr < 0.001). Because no differences between sessions were found, we considered both sessions together in a paired t-test for stimulus effects. Both NAD minus Rest and control minus Rest showed activated clusters in bilateral STG (NAD > Rest: LSTG $p < 0.001$; RSTG $p < 0.001$; control-Rest: LSTG $p < 0.001$; RSTG $p < 0.001$) and IFG (NAD > Rest: LIFG $p < 0.001$; RIFG $p < 0.001$; Control > Rest: LIFG p = 0.002; RIFG $p < 0.001$). F-tests on the group level did not reveal a significant main effect of stimulus (NAD vs. control) for the exposure phase. Clusters shown in the right posterior and middle cingulate gyrus at a threshold of p <0.001 did not survive FWE-correction (Post. Cing.: p-FWE = 0.997, p-uncorr < 0.001; Mid. Cing.: p-FWE = 0.96, p-uncorr < 0.001). See Figure 5.3 for activated clusters and Table 5.3 for peak Z-values and cluster extents.

In line with previous fMRI results in humans (e.g. McNealy, Mazziotta, & Dapretto, 2006; Veroude et al., 2010) and songbirds (see chapter 3 and 4 and Van der Kant et al., 2013), we employed regression analysis to investigate individual differences in brain and behavior. Performance on rejection of violations was used as an indicator of sensitivity to the non-adjacent dependencies in the grammar, because participants scored below chance level on

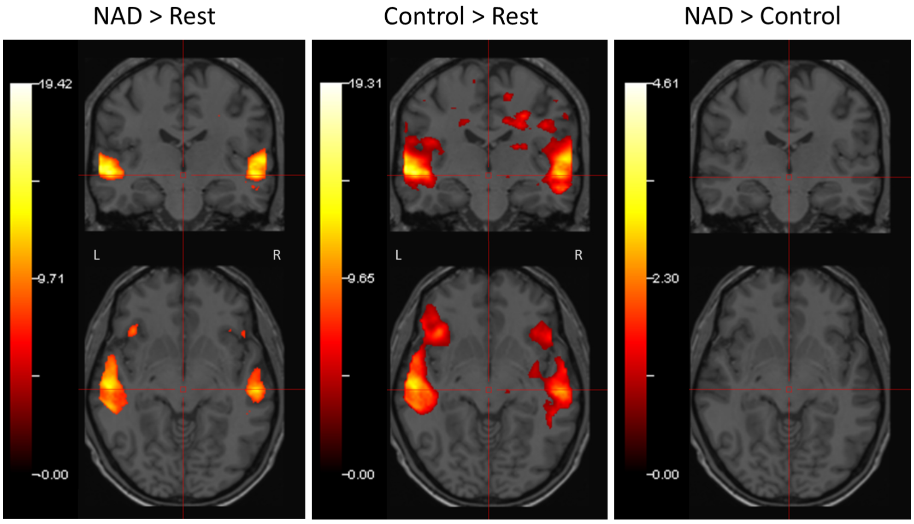

Figure 5.3: Brain activation during exposure to the NAD and Control languages, FWE corrected for the whole brain with a $p < 0.05$ 5-voxel threshold. Left: Activation in response to the language containing non-adjacent dependencies compared to Rest. Middle: Activation in response to the language without non-adjacent dependencies compared to Rest. Right: Differential activation induced by NAD compared to Control does not survive whole-brain FWE correction.

the acceptance of NAD phrases. Regression analyses showed a positive correlation between the success with which individual subjects were able to reject violations of the grammar (% correct) after exposure to the NAD and control grammars and neural activation in response to the NAD grammar compared to the control condition in the Left Inferior Frontal Gyrus (LIFG) (R^2max = 0.69, p = 0.004) and the bilateral Superior Temporal Gyri (STG) and Insulae (In) (Left: R^2max = 0.79, $p < 0.001$; Right: R^2max = 0.65, $p < 0.001$). A trend towards such a correlation was found in RIFG (R^2max = 0.7, p = 0.09). See Figure 5.4 for clusters and correlation plots and Table 5.4 for R^2, Z-values and cluster extents. Correlations with NAD minus Rest were neither significant in IFG (LIFG: R^2max = 0.73, p = 0.206; RIFG: R^2max = 0.48, p = 0.998) nor in STG (LSTG: no clusters, RSTG: R^2max = 0.53; p = 0.992) and In (L In: R^2max = 0.49, p = 0.771; R In: R^2max = 0.53, p = 0.121). No correlations with NAD $>$ Control were found for age or any of the behavioral variables digit span and mental counters.

5.3.3 fMRI results grammaticality judgment task

MNI coördinates, Z-values and cluster extents for the results reported in this section can be found in Table 5.5. Potential differences between the two sessions of the grammatical judgment task were first explored using a random-effects analysis. Because no significant effect of session (strongest cluster in

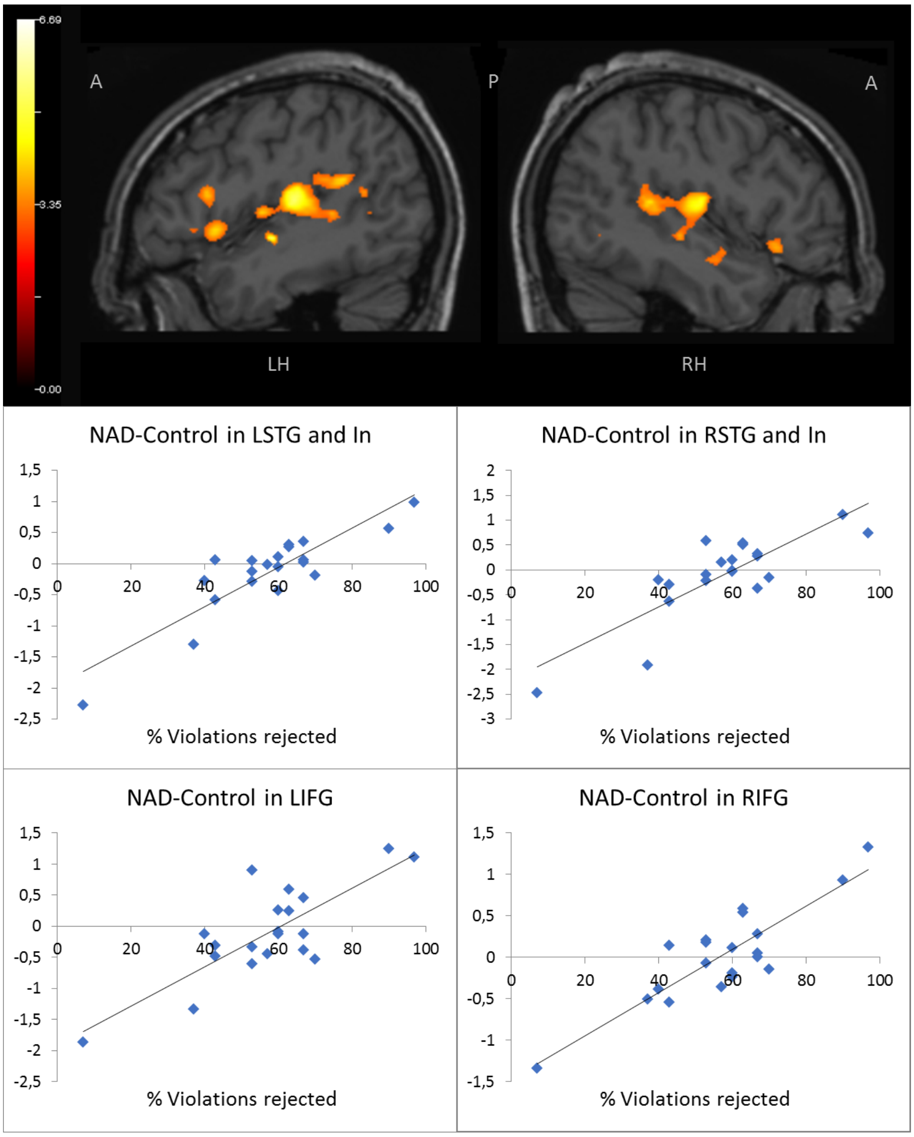

Figure 5.4: Correlation of NAD > Control activation with the percentage of correctly rejected violations in the grammatical judgment task. Top: Bilateral STG / Ins and LIFG show a correlation between the differential activation in response to NAD stimuli during the exposure phase and the number of correctly rejected violations. Bottom: Plots illustrating the correlation between the total NAD > Control activation within each cluster shown on the top and the performance on violation rejection in the grammatical judgment task. These plots are shown for illustration purposes and are not used as a source for the R^2-values reported in this section.

			MNI coördinates				
Contrast	**Brain region**	**L/R**	**x**	**y**	**z**	Z	**Vox.**
NAD	STG / In.	L	-54	-22	-4	6.96	1667
minus		R	66	-16	-2	7.52	2173
Rest	IFG	L	-44	24	-12	5.35	41
		R	40	26	-8	5.89	151
	Front. Par.	R	40	22	22	5.82	135
Control	STG / In.	L	-56	-22	-6	6.64	1442
minus		R	66	-16	-2	7.51	1986
Rest	IFG	L	-44	22	-12	5.10	7
		R	44	22	-18	5.64	141
	Ant. Cing.	R	24	24	20	5.53	28
	Post. Cing.	R	28	-30	34	6.17	54

Table 5.3: Brain activation during exposure to the NAD and Control languages. Cluster extents are based on the FWE-corrected T-map with a $p < 0.05$ 5-voxel threshold as shown in Figure 5.3. L/R = Left/Right hemisphere, Vox. = cluster extent in voxels, Z = Z-value of the peak voxel in the specified brain region, NAD = non-adjacent dependencies language, Control = language without non-adjacent dependencies, Stim = stimulus, Ant. / Post. Cing. = Anterior / Posterior Cingulate cortex, STG = Superior Temporal Gyrus, In. = Insula, IFG = Inferior Frontal Gyrus.

Right posterior Cingulate gyrus: $p = 0.324$) or session*stimulus interaction was present within the test phase, the two sessions were considered together in further analyses. One-sample t-tests for NAD phrases minus Rest and violations minus Rest showed significant activation for violations but not NAD phrases (violations Anterior Insula: peak-level $p = 0.001$; NAD: no clusters). F-tests for differences between NAD phrases and violations did not show significant activations, two clusters in the bilateral Middle Temporal Gyri did not survive correction for multiple comparisons (Left: p-FWE = 0.924, p-uncorr < 0.001; Right: p-FWE = 0.489, p-uncorr < 0.001). However, a trend towards a main effect of accuracy was shown in the Left inferior frontal gyrus (peak-level p = 0.066).

To further investigate the origin of this trend a post-hoc t-tests was performed, showing a differential activation for Correct minus Incorrect responses in LIFG (peak-level $p = 0.033$). The difference in activation between correct and incorrect responses was significant in LIFG for violations of the NAD language ($p = 0.003$; temporal pole cluster did not reach significance: peak-level $p = 0.099$), but was absent for NAD phrases containing grammatical non-adjacent dependencies (no clusters). However, the stimulus*accuracy interaction in LIFG did not survive corrections (p-FWE = 0.73, p-uncorr < 0.001). It should be noted here that the only brain activity in response to the presentation of the stimulus and not to the response itself was measured and that no feedback on the response was given. Although participants did not learn the

			MNI coördinates				
L/R	**Voxels**	**Brain regions**	x	y	z	R^2	Z
L	2022	STG / Insula	-48	-22	12	0.79	4.71
		Angular Gyrus	-46	-44	20	0.59	3.93
		IFG	-44	22	-2	0.69	4.54
R	1150	STG / Insula	40	-14	10	0.65	4.67
		Angular Gyrus	58	-30	18	0.58	3.92
	128	IFG	42	26	-6	0.70	4.62

Table 5.4: Correlation between the success in rejecting violations and NAD $>$ Control differential activation during the exposure phase Cluster extents and R^2 values are based on the uncorrected T-map with a $p < 0.0001$ 5-voxel threshold as shown in Figure 5.4. L/R = Left/Right hemisphere, Voxels = cluster extent in voxels, STG = Superior Temporal Gyrus, IFG = Inferior Frontal Gyrus.

language in the behavioral sense, the brain was sensitive to violations.

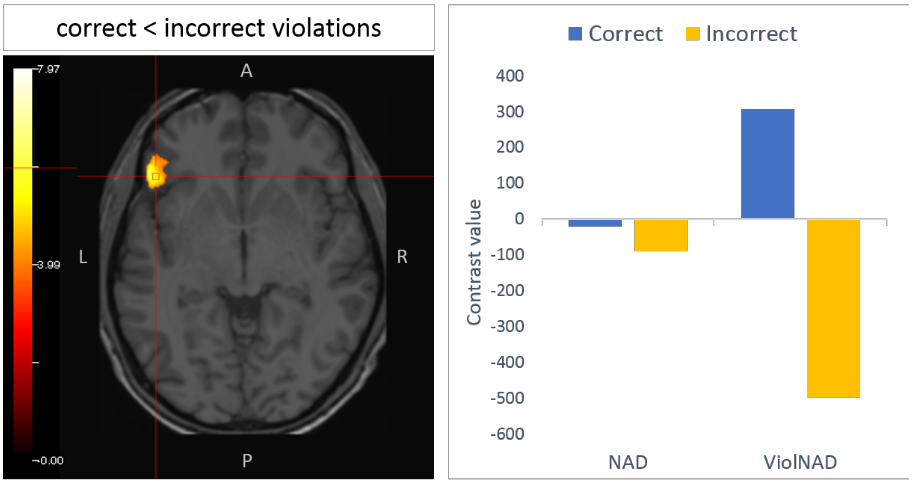

Figure 5.5: Activation and contrast values shown during the grammatical judgment task. Left: LIFG shows differential activation for (correctly) rejected compared to (incorrectly) accepted violations. Right: Contrast values for correct and incorrect trials per stimulus type.

5.4 Discussion

The present study aimed to unravel how the brain reflects online learning of an artificial grammar containing non-adjacent dependencies. The behavioral results showed that overall, participants scored significantly above chance

			MNI coördinates				
Contrast	**Brain region**	**L/R**	**x**	**y**	**z**	Z	**Vox.**
ME session	Post. Cing.	R	20	-38	32	4.13	16
viol. - Rest	Ant. Insula	L	-28	28	12	5.60	146
NAD vs viol.	Mid. Temp.	L	-48	-42	-8	3.66	34
		R	50	-30	-12	4.06	75
ME accuracy	IFG	L	-50	36	-12	4.66	93
Correct-Incorrect	IFG	L	-50	36	-12	4.80	133
Corr-Incorr viol.	IFG	L	-50	36	-12	5.92	308
	Temp. pole	L	-54	4	-26	4.53	86
Stim*Accuracy	IFG	L	-50	36	-12	3.87	40

Table 5.5: Brain activation during the grammatical judgment task Values are uncorrected with a $p < 0.001$ 5-voxel threshold. L/R = Left/Right hemisphere, Vox. = cluster extent in voxels, ME = main effect, viol. = violations, NAD = NAD phrases, Stim = stimulus, Post. Cing. = posterior cingulate cortex, Ant. = Anterior, Mid. = Middle, Temp = Temporal, IFG = Inferior Frontal Gyrus.

when rejecting violations but had difficulties judging phrases as grammatical that belonged to the grammar that they were previously exposed to. Because earlier behavioral pilots yielded higher grammatical judgment scores than the grammatical judgment task in the scanner, we can assume that despite our efforts to reduce scanner noise, learning the grammar was more challenging in the noisy scanner environment.

In the grammatical judgment task, we observed considerable individual differences both in the ability to accept grammatical NAD phrases and to reject violations. These individual differences were reflected in a correlation between the success with which participants rejected violations during the grammatical judgment task and the differential activation induced by the NAD language compared to the control language during the exposure phase in the bilateral STG and Insulae and the left Inferior frontal gyrus. Furthermore, during the grammatical judgment task, correct responses induced more activation in LIFG than incorrect responses for violations but not for NAD phrases.

5.4.1 Differential activation as a precursor for learning

The correlation between brain activation and learning success found in our data shows that the LIFG and the bilateral STG and Insulae are involved in implicit learning of non-adjacent dependencies through auditory exposure. Involvement of LIFG has been previously demonstrated in numerous artificial grammar learning studies (e.g. Folia & Petersson, 2014; Uddén & Bahlmann, 2012; Yang & Li, 2012), which among other also addressed hierarchical dependencies (Bahlmann et al., 2008). However, the role of (particularly the right) STG and Insula appears to be less prominent in most artificial grammar learning studies. This could either be a result of the modality of the present experiment, where all stimuli were presented auditorily, or of the fact that data were collected during as opposed to after exposure to the artificial grammar. Activation of the auditory cortex during the presentation of auditory stimuli is not surprising, but it should be noted that the bilateral STG is differentially activated by the NAD compared to the control language. Participants were given no clues that they were listening to two different languages and NAD and control stimuli were only distinguishable based on the higher auditory variation provided by the control language, which occurred because different combinations between first and last elements were possible. This variation could certainly be reflected in the differential activation induced by NAD compared to control stimuli. However, the amount of variation did not differ between participants while the differential activation showed considerable individual variation. Moreover, like in many AGL studies where fMRI data were acquired after learning, only LIFG activation was shown during the grammatical judgment task. Therefore, it is likely that both modality and data collection during learning play a role.

In addition to the involvement of LIFG, the Insulae and bilateral STG in artificial grammar learning, the correlation between behavioral learning measures and differential brain activation also indicates that individual differences in sensitivity to violations are already reflected in the brain during the learning process. Because the correlation with behavior in IFG, STG and In is only present for the differential (NAD > Control) activation, it is unlikely that these correlations are due to individual differences in auditory capacity or attention. Although attention and active processing has been suggested to play a large role in the ability to learn non-adjacent dependencies (Pacton & Perruchet, 2008), attentional factors cannot explain our results, because the NAD and control languages were not discernable during exposure and were thus unlikely to show differences in terms of attention. Because we were able to collect fMRI data online during learning and participants provided us with grammatical judgments after exposure, it is likely that the increased differential activation in more successful learners is a precursor rather than a result of learning. This interpretation is further supported by the fact that, although no significant difference between sessions was shown, most differential activity for the NAD compared to the control language in more successful learners was seen in the first session. Moreover, the individual differences in activation in an experiment where exposure times are short indicate that individual differences in language learning might result from differences in neural recruitment that develop early in the learning process.

The behavioral data also showed that after the limited amount of exposure to the NAD language, the learning process was not completed for most participants. The majority scored at or just above chance on the grammatical judgment task. Furthermore, in the post-test questionnaire administered after the grammatical judgment task, participants did not report any awareness of the non-adjacent dependencies present in the NAD grammar. It is therefore highly unlikely that the increased differential activation in participants with higher scores in the grammatical judgment task was due to the use of explicit learning strategies by more successful learners. In accordance with previous studies (McNealy et al., 2006; McNealy, Mazziotta, & Dapretto, 2010), these results show neural reflections of artificial grammar learning before learning can be reliably determined using behavioral methods. Similar correlations between learning success and neural activation or connectivity have been found in language learning studies (Veroude et al., 2010; White, Genesee, & Steinhauer, 2012) and in studies of birdsong learning (see Bolhuis et al. (2000); Van der Kant et al. (2013) and Chapter 4 of this thesis). These results suggest that increased neural activation during sensory stimulation might aid learning across modalities and species.

5.4.2 Sensitivity to the deviant as an early stage in learning

From the behavioral as well as the fMRI results from the grammatical judgment task it was apparent that violations of the NAD language served as a more salient stimulus compared to grammatical NAD phrases. In the grammatical judgment task, violations showed a higher response accuracy. Moreover, the differential activation in LIFG for correctly compared to incorrectly judged phrases was present for violations, but not for NAD stimuli. These results show that violations are processed differently from NAD phrases, however, because the segmental content of the languages is counterbalanced between participants, this difference in processing is purely a result of the knowledge about the NAD language obtained during the exposure phase. These findings are in accordance with earlier results which show that violations in a learned artificial grammar activate LIFG (Petersson, Forkstam, & Ingvar, 2004).

Both the stronger neural activation and the higher performance on the violations might result from the more general neural mechanism of deviance detection. Because participants have been exposed to 100 phrases containing the same non-adjacent dependencies, expectancies about similar stimuli have formed in the brain, which are strong enough to induce an error signal when violated. In contrast, the rules have not been learned to such an extent that a grammatical phrase can be reliably classified as such. The mechanism of deviance detection is used in non-linguistic (MMN), semantic (N400) as well as syntactic (P600) ERP studies to investigate the detection of violations. The amplitude of the P600 during grammatical judgment in second language acquisition has been shown to correlate with behavioral performance on the grammatical judgments (White et al., 2012), further illustrating the role of error signals in language learning. Deviance detection is also used in behavioral studies of infant language learning, where babies are expected to show more interest in new or deviant stimuli after exposure to a string of similar stimuli (several paradigms are discussed in Aslin & Fiser, 2005). This might suggest that the increased sensitivity to violations might be the result of a deviance detection mechanism, which aids language learners in very early stages of learning.

The differential activation in LIFG induced by correctly rejected compared to incorrectly accepted violations in the grammatical judgment task shows an increased sensitivity to ungrammatical compared to grammatical NAD phrases, for which no such difference was found. Correctly rejected violations induced activation of the LIFG and accepted violations induced de-activation of the same area, while listening to grammatical NAD phrases induced minor BOLD signal changes in LIFG. Although we should be cautious interpreting the de-activation of LIFG in response to violations that were consequently not rejected, the activation of LIFG in response to correctly rejected violations might represent the detection of a deviant dependency structure based on the knowledge of the NAD language that has been acquired during the exposure phase. This interpretation is in line with the finding of Hein et al. (2007) that in an audiovisual integration task incongruent stimuli activate IFG. The neural dissociation found between NAD and control stimuli in the exposure phase and the neural sensitivity to violations during the test phase without awareness of any differences suggests that these sensitivities developed based on statistical computations (Turk-Browne, Scholl, Chun, & Johnson, 2009).

5.4.3 Conclusions

The present study uncovered a number of interesting connections between brain and behavior during artificial grammar learning, which show how individual differences in artificial grammar learning and possibly natural language learning are reflected in the brain.

First, we showed that the extent to which participants were able to deduce non-adjacent dependencies from an artificial grammar correlated with the strength of activation in brain areas that are implicated in artificial grammar learning and natural language processing. This result suggests that neural activation in the language network during learning might predict artificial grammar learning and possibly also natural language learning outcomes.

Participants were found to be more sensitive to violations in the NAD language and showed a differential activation for rejected > accepted violations but not NAD phrases during the grammatical judgment task. Both these findings and the brain-behavior correlation were in absence of reliable behavioral learning. This suggests that the brain reflects early stages of learning, which might include the development of sensitivity to violations of regularities that are present in the input.