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Karolinska Institutet, Stockholm, Sweden

LANGUAGE AS STRUCTURED SEQUENCES: A CAUSAL ROLE OF BROCA'S REGION IN SEQUENCE PROCESSING

Julia Uddén



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ABSTRACT

In this thesis I approach language as a neurobiological system. I defend a sequence processing perspective on language and on the function of Broca's region in the left inferior frontal gyrus (LIFG). This perspective provides a way to express common structural aspects of language, music and action, which all engage the LIFG. It also facilitates the comparison of human language and structured sequence processing in animals.

Research on infants, song-birds and non-human primates suggests an interesting role for non-adjacent dependencies in language acquisition and the evolution of language. In a series of experimental studies using a sequence processing paradigm called artificial grammar learning (AGL), we have investigated sequences with adjacent and non-adjacent dependencies. Our behavioral and transcranial magnetic stimulation (TMS) studies show that healthy subjects successfully discriminate between grammatical and non-grammatical sequences after having acquired aspects of a grammar with nested or crossed non-adjacent dependencies implicitly. There were no indications of separate acquisition/processing mechanisms for sequence processing of adjacent and non-adjacent dependencies, although acquisition of non-adjacent dependencies takes more time.

In addition, we studied the causal role of Broca's region in processing artificial syntax. Although syntactic processing has already been robustly correlated with activity in Broca's region, the causal role of Broca's region in syntactic processing, in particular syntactic comprehension has been unclear. Previous lesion studies have shown that a lesion in Broca's region is neither a necessary nor sufficient condition to induce e.g. syntactic deficits. Subsequent to transcranial magnetic stimulation of Broca's region, discrimination of grammatical sequences with non-adjacent dependencies from non-grammatical sequences was impaired, compared to when a language irrelevant control region (vertex) was stimulated. Two additional experiments show perturbation of discrimination performance for grammars with adjacent dependencies after stimulation of Broca's region. Together, these results support the view that Broca's region plays a causal role in implicit structured sequence processing.

LIST OF PUBLICATIONS

- I. **Uddén, J.**, Ingvar, M., Hagoort, P., & Petersson, K. M. (2011). Implicit acquisition of grammars with crossed and nested non-adjacent dependencies: investigation the push-down stack model. *Cognitive Science*. In press
- II. **Uddén, J.**, Ingvar, M., Hagoort, P., & Petersson, K. M. (2011). Implicit generalization in grammars with crossed non-adjacent dependencies. *submitted manuscript*
- III. **Uddén, J.**, Folia, V., Forkstam, C., Ingvar, M., Fernandez, G., Overeem, S., van Elswijk, G., Hagoort, P., & Petersson, K. M. (2008). The inferior frontal cortex in artificial syntax processing: An rTMS study. *Brain Research*, 1224, 69-78.
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ADDITIONAL PUBLICATIONS

- I. **Uddén, J.**, Araujo, S., Forkstam, C., Ingvar, M., Hagoort, P., & Petersson, K. M. (2009). A matter of time: Implicit acquisition of recursive sequence structures. *Proceedings of the Cognitive Science Society*, 2009, 2444-2449.
- II. **Uddén, J.**, Folia, V., & Petersson, K. M. (2010). Neuropharmacology of Implicit Learning. *Current Neuropharmacology*. 8, 367–381.
- III. Gisselgård, J., **Uddén, J.**, Ingvar, M., Petersson, K.M. (2006). Disruption of order information by irrelevant items: A serial recognition paradigm. *Acta Psychologica*. 124, 356-369
- IV. Folia, V., **Uddén, J.**, Forkstam, C., Ingvar, M., Hagoort, P., Petersson, K.M. (2008). Implicit learning and dyslexia. *Annals of the New York Academy of Sciences*. 1145, 132-50.
- V. Folia, V., **Uddén, J.**, Forkstam, C., Petersson, K.M. (2010). Artificial Language Learning in Adults and Children. *Language Learning*. 60 (S2), 188-220.

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LIST OF ABBREVIATIONS

AGL	Artificial grammar learning
AMPA	α -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid
BOLD	Blood-oxygen-level-dependent
DA	Dopamine
EEG	Electroencephalography
FMRI	Functional magnetic resonance imaging
IFG	Inferior frontal gyrus
IPL	Inferior parietal lobe
LIFG	Left inferior frontal gyrus
MTG	Middle temporal gyrus
MTL	Medial temporal lobe
rTMS	Repetitive transcranial magnetic stimulation
TMS	Transcranial magnetic stimulation
TDCS	Transcranial direct current stimulation
STG	Superior temporal gyrus
SRTT	Serial reaction time task

PREFACE

Good science starts with asking a good question. Let us start with a description of the question or problem I have been dealing with when writing this thesis. Spanning the fields of cognitive science, neuroscience and linguistics, this thesis presents a line of research where these fields are integrated into one topic, *the neurobiology of language*. I take a perspective on language as structured sequences, a perspective which emphasizes the common structural aspects of language, music and action. More specifically, I ask how structured sequence processing is instantiated in the brain. I focus on investigating the functional role of one node in the language network: Broca's region in the left inferior frontal gyrus (LIFG). Is activity in this region causally related to processing of structured sequences?

The large scale problem description which ultimately motivates the work in this thesis is however one described by David Marr (1982). Marr (1982) proposed a general framework for analyzing levels of explanation in cognitive sciences, including cognitive and computational neuroscience, by identifying three levels at which any cognitive machine carrying out information processing can be understood:

1. The **computational level** (problems that the cognitive system has to overcome).
2. The representation or **algorithmic level** (representations for input and output and algorithms for transformation between input and output, which may be used to achieve a solution).
3. The **implementation level** (how representations and algorithms are implemented on a hardware level, e.g. in spatiotemporal dynamics of neural activity and neural structure).

Understanding the brain as an information processing system entails sophisticated knowledge at all of these levels as well as knowledge about how the levels map to each other. Another way to describe the enterprise of cognitive neuroscience is that we want to constantly refine and update the cognitive interpretation of spatiotemporal brain dynamics. This interpretation can be understood as a neural code.

In neuroscientifically oriented research, some neural level phenomena might be linked to some (usually rough) computational level term, such as attention or working

memory. Spelling out the corresponding algorithms and computations in detail is usually not in focus. Sometimes, the investigation is on quite vague psychological concepts, without precise definitions. *Reasoning*, *consciousness* and *memory* are examples of concepts which are sometimes researched in an underspecified context. Such concepts may not unfold naturally at the algorithmic or neural levels. An example which is discussed throughout this thesis is the memory concept. Memory can be seen as another word for brain process extended in time. The memory concept might be too general to provide relevant perspectives on brain data. On the other hand, cognitive scientists are sometimes stuck in conceptual issues too far from being testable and thus warrant a meaningful discussion.

Much research has restricted itself to one level, e.g. the computational level in linguistics and the neural implementation level in neuroscience. The computational level is usually assessed using behavioral data. In classical linguistics, the data are the intuitions of the linguist and in psycholinguistics the data are the controlled experiments on a group of participants. Algorithmic level models will more often need data in the form of reading times, eye-tracking data or EEG-data to confirm its more specified hypotheses. Neuronal implementation is assessed across modern neuroimaging techniques, as well as genetic and molecular methods. The neural level can also be explored in the field of computational neuroscience. All these approaches are worth pursuing, but they are not multi-level approaches. The most common multilevel mapping approach in psycholinguistic research is to use neuroimaging methods to find out whether some concepts from linguistics and cognitive science have unique brain correlates, meaning that they are *natural kinds* (Barrett, 2009).

The approach of looking for natural kinds is good, but can be further improved by looking for natural kinds which are stable *traits*. Traits do not vary from measurement to measurement and day to day in a participant. They are good targets for the study of the genetic basis of cognition. Traits should be studied on the neural level. Such research is both interesting per se and interesting from a computational level, since the neural level can constrain the computational level. Marr's problem description thus makes it clear that the interdisciplinary scientist should master the foundations of the current state of human knowledge in all involved disciplines, paying attention to all facets of data, methods and theorizing.

The papers of this thesis are examples of the level mapping approach. I will (1) present sequence processing as a computational level problem, (2) discuss algorithmic solutions to this task, such as finite state grammars and the push-down stack model and

(3) discuss the gross anatomical implementation of sequence processing in the left inferior frontal gyrus. Future work will aim at the genetic and molecular level, hopefully by discovery of new genes and replication of candidate genes for language and sequence processing in human subjects. I also want to use the genetic handle to understand biological pathways for language and sequence processing at the micro- and mesoscopic brain level.

As can be seen in the contents, the first half of the thesis is an introduction (Part I), consisting of three chapters: one on language as a neurobiological system, one on implicit learning and one on the brain, Broca's region and transcranial magnetic stimulation. In Part I also sometimes discuss the empirical results of the thesis, related to specific topics raised in the introduction. A discussion of the empirical papers included in this thesis is provided in Part II where it is intertwined with a discussion of the so called sequence processing perspective in chapter 4 and 5, which are an extended, modified and adapted version of a recently submitted paper (Uddén & Bahlmann, 2012). In chapter 6 I discuss the role of memory in language and structured sequence processing. Conclusions are provided in chapter 7.

PART 1 – INTRODUCTION

1 LANGUAGE AS A NEUROBIOLOGICAL SYSTEM

Geoffrey Pullum and Barbara Scholz (2001) state three main computational level problems in linguistics: (1) the communication problem: how is it possible that we can communicate meaning so that the concept in the speaker brain is transferred to a similar concept in the listeners brain? (2) The parsing problem: how can *syntactic structures* be assigned to sentences, so that speech sounds are mapped to concepts correctly? (3) The acquisition problem: how can all of this be acquired? In this chapter, I examine this problem description from the perspective of the multilevel mapping project and I will introduce what I regard as the most important issues related to each of the problems. This analysis will also serve as an introduction to the topic of the empirical work in part II of this thesis. I will end this chapter with a slight modification of the problem description by Pullum and Scholz.

1.1 THE COMMUNICATION PROBLEM: A MARRIAN ANALYSIS

1.1.1 The computational level

When trying to understand a communicative message, encoded as a spoken sentence, the listener has to decode a stream of sounds. This sound stream is decoded using *phonological* structure, which is a description of regularities in the sounding aspect of speech. Different kinds of information are integrated to segment a chunk of sounds into words. For instance, the frequencies of syllables and smaller phonological elements called *phonemes* constitute *phonotactic* structure. Phonotactic structure occurs below word level. Information about e.g. the frequency of words will feed into the decoding process and this information may be seen as retrieved from a *mental lexicon* storing *lexical* structure, a construct created by Chomsky (1965). In this framework, a word is called a lexical item. The phonological encoding/decoding problem is one part of the communication problem. It can be seen as the first part of the processes of comprehending a sentence and the last part of the process of producing a sentence.

We now move on to the second problem in Pullum and Scholz's analysis. Historically, a lot of linguistic analysis has been devoted to a problem that I will analyze as a part of the communication problem: the parsing problem. Pullum and Scholz analyses it as one of the three central problems, at the same level as the communication problem. The syntactic domain of language makes a *parse* of a word

sequence by assigning a *syntactic* structure to it. The goal of the parse is to make the structure satisfy some grammatical rules as well as possible. Thus, let us look at the output from the segmentation process as a collection of words together with some information about the order they were heard. There are now three main parts of information for syntactic parsing, which I have ordered in a possible order of importance: (1) syntactic features of the words that are present (e.g. which word category they belong to), (2) *morphosyntactic structure* (e.g. inflections on verbs: help instead of helps) and (3) word order information (distinguish sentences like “A is above B” from “B is above A”). However, communicative exchanges also take place independent of the syntactic information in (1)-(3), an issue we will return to. This leads us to the third part of the communication problem.

The third part of the communication problem concerns the domain of meaning or conceptual structure, which is called *semantics*. Semantic or conceptual structure (henceforth called used interchangeably) contains the information connected to concepts, e.g. that a verb like “sleep” designates an action of a living organism. The sentence “Colorless green ideas sleep furiously” thus follows English syntax, but it violates the sentence level conceptual structure since ideas are not alive. Conceptual structure has its own rules and combinatorial principles. The combinatorial nature of conceptual structure can be seen in the sentence “Jill jumped until the alarm went off”¹. When encountering the word “jumped” (which designates a very short event) together with the word “until” (which establishes a temporal bound on an ongoing process), conceptual structure tells us that “jumped” has to be made an ongoing process (by repetition of the event). An algorithmic solution to the parsing problem that is connected to some semantic word-by-word look up table, but lacks accurate conceptual structure, might thus be as likely to interpret “jumped” in this sentence as describing one long jump. This example might seem quite exotic, but it suggests the existence of combinatorial conceptual structure, which underlines the possibility that conceptual structure is constantly used as a (sometimes redundant) source of information to parse a sentence correctly and that semantics thus partly may be formalized in a similar manner as syntax and phonology.

I will now describe *pragmatics* as the fourth part of the communication problem. While conceptual structure, describes the literal meaning of words or sentences,

¹ Example from Jackendoff, 2002.

pragmatic structure, describes the context specific meaning or speaker meaning of words or sentences. Pragmatic structure can for instance be indicated by so called *information structure*. Information structure denotes the structural relations between two elements: new (focused) and given (non-focused or background) information in a sentence. This kind of structure can be conveyed for instance through prosody or syntactic structure. Information structure determines the depth of semantic and syntactic processing. In everyday communication, shallow processing of sentences is a fact and because of our limited cognitive resources, we are often confined to "good enough" processing (Ferreira, Bailey, & Ferraro, 2002; Wang, 2011). A good enough analysis satisfies the comprehender but is not necessarily a full syntactic analysis of who did what to whom or a full conceptual analysis of the relations between the ingoing concepts. Evidence for good enough processing comes from the presence of illusory semantic or syntactic structure. An example of a semantic illusion is an anomalous sentences like "The authorities had to decide where to bury the survivors" (Barton & Sanford, 1993), where the semantic anomaly is often overlooked.

How sharp is the distinction between conceptual and pragmatic structure? Since conceptual structure has evolved to describe properties of the world, we can expect a considerable overlap between conceptual and pragmatic structure, as we have defined them. The distinction between syntax and semantics can be discussed with parallel reasoning. From one point of view, the purpose of syntax is to provide a rich enough (and probably not much more) structure to map a speaker intention, via pragmatic and conceptual structure onto linear sequences of language production actions, so called *surface forms* of written or spoken language. Conversely, syntax is used to parse surface forms all the way back to a decoded speaker intention.² Syntactic structure thus overlaps with conceptual structure. Since only the part of semantics which needs to be mapped to surface form needs to be encoded in syntactic structure, conceptual structure might be analyzed as richer than syntactic structure. Communication via conceptual structure will also take place without linearized surface forms. For instance, there are situations with lots of communicative exchange but where few surface forms are needed. If you meet a relative that you have not seen for a long while, the encounter itself is communicative. The manner of the initial greeting might communicate more

² Syntactic structure is to a large extent mapped to conceptual structure in an arbitrary manner. We can get an approximation of how arbitrary this mapping is by regarding the linguistic variation in syntactic structure across the world.

than the rest of the conversation. A view largely due to Jackendoff (2002) and Culicover & Jackendoff (2005) is that speech sounds often are used to disambiguate between several possible semantic and syntactic structures that could be intended in a larger pragmatic (communicative) context.

Having narrowed down the communication problem into these four parts of phonological, syntactic, semantic and pragmatic structure, we start to see how the communication problem might look like at the computational level. But, how far has the field come in mapping Marr's levels to each other? For instance, a relevant question is whether syntax/semantics/pragmatic structure should be distinguished at the lower levels: the procedural and neural level. If these structures are partly overlapping, would the brain not save energy by storing the overlapping part of these structures with one representation? As there has yet been little work on pragmatics on the procedural and neural level, the focus will be on phonology, syntax and semantics.

1.1.2 The algorithmic or procedural level

Jackendoff (2002) presents one of the few multilevel descriptions created within the linguistic tradition. His starting point is language divided into the domains of phonology, syntax and semantics and he then elaborates a procedural model of the interplay of these domains which could make sense from a neural point of view. Jackendoff's proposal is that neural processing in these domains is not serially ordered, neither during comprehension nor production. Instead, the three richly structured domains are to some extent working in parallel. In Jackendoff's so called parallel architecture, there is continuous communication between the domains (see **Figure 1.1**). For example, when determining word boundaries, phonological structure (e.g. in the form of likelihoods of syllables onsets and word on- and offsets) is used. This information will be connected to syntactic and semantic information about whether a possible segmentation can lead to a coherent syntactic and conceptual structure of the segmented words in a sentence.

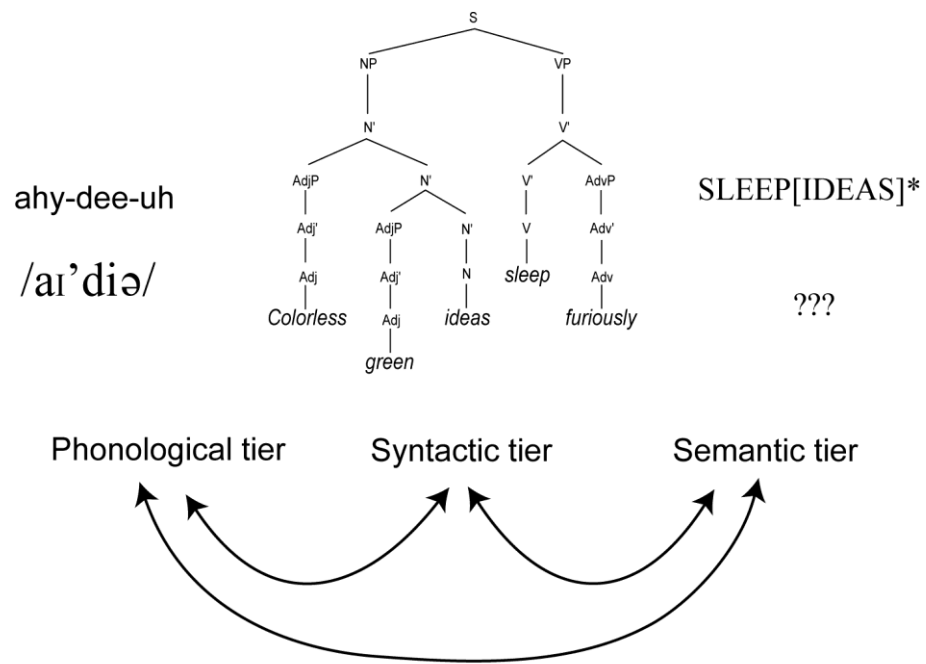


Figure 1.1. In the parallel architecture by Jackendoff (2002), the phonological, syntactic and semantic domains all have rich structure. The input to and output from parallel processing within these domains is received and fed out to the other domains via interface structures. When the sentence “Colorless green ideas sleep furiously” reaches the semantic domain, it will be hard to build a conceptual structure that is coherent with reality and this triggers a feed-back error signal to the other domains. This signal will increase the bias towards alternative syntactic and phonological decoding schemes.

In a development of the parallel architecture, Culicover & Jackendoff (2005) articulates that linguistic structure is instantiated in *constraints* that apply in parallel and incrementally, i.e. online as the sentence arrives, a development from earlier *derivational* models such as mainstream generative grammar (see section chapter 2).

1.1.3 The neural level

The *tripartite model*, divides linguistic processing into phonological, syntactic and semantic level processing. The model has been supported in a meta-analysis of neuroimaging data, where the mentioned domains can be separated on a gross-anatomical scale in the brain in the inferior frontal gyrus (Bookheimer, 2002). It is possible that a similar division is present in the posterior language areas (Shalom & Poeppel, 2008; Xiang, Fonteyjn, Norris, & Hagoort, 2010). In the inferior frontal gyrus, phonological, syntactic and semantic processing has been segregated (see **Figure 1.2**)

in the posterior–anterior direction (Bookheimer, 2002), with Brodmann (BA) 6/44 connected to phonology, BA 44/45 to syntax and BA 45/47 to semantics (see further nomenclature in chapter 3). For a further discussion of this division, see chapter 5, page 81.

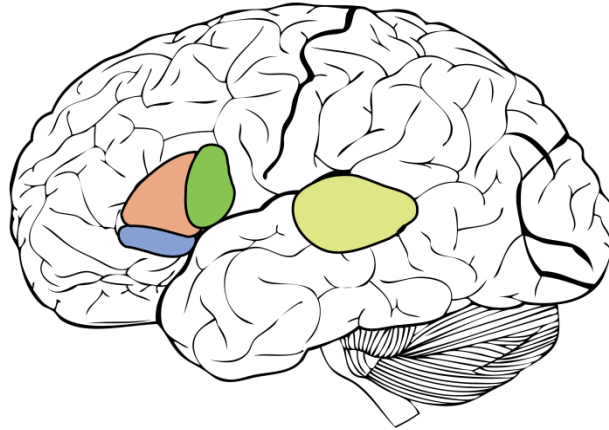


Figure 1.2. One of the strongest arguments for the division of the faculty of language into a phonological (green), syntactic (red) and semantic (blue) domain around Broca’s region in the inferior frontal gyrus, as well as a mental lexicon (yellow) around Wernicke’s region is that they can be functionally segregated on a gross anatomical level, using neuroimaging (Bookheimer, 2002, Snijders, 2009). The simplified image builds on much more complex underlying space of findings described in the present chapter as well as chapter 5-

The larger left-hemisphere language network and the MUC-model

The memory, unification and control framework (Hagoort, 2005) centers on generic computational operations, common to all domains. The memory component corresponds to long-term representations needed for language processing, e.g. lexical items stored in the mental lexicon. The unification component (Hagoort, 2005; Vosse & Kempen, 2000) entail clipping together words or small sentence fragments (treelets) that have been activated in the mental lexicon to larger fragments, a central combinatorial feature of language. For instance, during language comprehension, unification can start when the second word have been activated and is thus a slightly later process than the activation of the first word in a sentence. Similarly, the generic unification operation might be applied to processes at the level of unifying a word from syllables or phonemes. There are many variations on this binding theme in the literature. Processes similar to unification has also been called merge (Chomsky, 1995) or unify pieces (Jackendoff, 2002). The merge and unify pieces operations are seen as syntactic rules (in fact this is the only rule in these respective syntactic frameworks).

Syntactic rules describe how syntactic structures that denote the abstract or invariant structure of sentences can be generated. The perspective in these frameworks is thus that our knowledge about which sentences are grammatical or not is incorporated in the details of the computational operation that allows the stepwise generation of larger and larger syntactic structures from smaller pieces. Kempen's (2000) unification operation, on the other hand, is not necessarily specific to syntax, but can take place in parallel in the phonological, syntactic and semantic domains (Hagoort, 2005).

I would now like to elaborate on the memory and unification components, by a small discussion on the information flow between them. It is an open empirical question whether it is relevant to describe unification or binding in language as lexical items being *copied* from long-term memory storage into some kind of working memory work bench for merge or unify pieces (Jackendoff, 2002), or a unification space (Hagoort, 2005), where they are clipped together. *Prima facie*, strict copying of a neural representation or a neural process on the level of neural implementation (e.g. copying a set of connection weights from one part of the brain to another) is relatively unlikely, since it would be associated with an energy cost without clear advantages. A transformation of a neural representation or process from one type of code to another is more likely.

In a classical model of language in the brain which was built on evidence from aphasic patients, the left posterior superior temporal gyrus (STG)/posterior middle temporal gyrus (MTG), also called Wernicke's region (see **Figure 1.2**), was implicated in language comprehension specifically, while Broca's region was implicated in language production. This model is however largely obsolete (Bookheimer, 2002; Fedorenko & Kanwisher, 2009). The last decades of neuroimaging has provided a computationally more well-defined role of the left posterior superior temporal gyrus and sulcus as implicated in auditory speech processing or phonological processing (for a recent study with intracranial recordings and three reviews, see Chang et al., 2010; Hickok, 2009; Indefrey & Cutler, 2003; Scott & Johnsrude, 2003).

As we have already touched upon, it has been suggested that the mental lexicon (listing lexical items that may have phonological, syntactic and semantic features) is subserved by the left posterior superior and middle temporal gyrus (Hagoort, 2005). Support for this suggestion was provided in a recent study where ambiguous words were presented visually within word list or sentences. The left posterior MTG/STG was activated when comparing ambiguous words, which were hypothesized to invoke an

increased load on lexical retrieval processes compared to the unambiguous control words (Snijders et al., 2009). This study supports the conclusion that the left posterior MTG and surrounding cortices provide a neural substrate for retrieval from the mental lexicon. In a recent meta-analysis, a handful of studies on semantics using written material were collected and these studies consistently produces activation in the posterior STG (Vigneau et al., 2006). Altogether, there is abundant support for phonological processing in posterior STG and some support for a modality independent mental lexicon residing in this area. In another meta-analysis comparing processing of syntactically complex vs simple sentences, the posterior STG and MTG were reliably activated, supporting the role of posterior temporal cortex in storing syntactic features of lexical items (Indefrey, 2011). This account predicts that neuroimaging of reading and writing language would activate the posterior temporal cortex since these modes of language also use includes lexical retrieval. Indeed, in a review study of neuroimaging of written language, convergence of activations was mainly found in left fusiform gyrus, the angular gyrus in the parietal lobe and the middle or inferior posterior temporal cortices (Hillis & Rapp, 2003).

Information exchange is massive between the inferior frontal region and the superior temporal region, through pathways that are described in the beginning of chapter 3. Connections from the phonological, syntactic and semantic foci in the left inferior frontal region (as in the model of Bookheimer, 2002) are to some extent specifically connected to what could be a similar division between a phonological, syntactic and semantic lexical information, organized along a dorsal-ventral axis in the posterior temporal lobe (Xiang et al., 2010).

The most important additional areas in the natural language network are the bilateral basal ganglia (in particular striatum), the left inferior parietal lobule (IPL), also called Geschwind's territory, the anterior temporal lobe (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996), the bilateral superior and middle frontal gyrus on the lateral surface of the prefrontal cortex (Hagoort, 2005), as well as the right homologue areas of the described network (Menenti, 2010). For instance, in the already mentioned study comparing ambiguous and non-ambiguous words (Snijders et al., 2009) the right striatum showed a large effect of ambiguity. Striatum had been found in studies of syntax (Friederici & Kotz, 2003; Moro et al., 2001) and when using a speaker's spatiotemporal brain activity to model listeners' brain activity (Stephens, Silbert, & Hasson, 2010). Patients with damage to the basal ganglia show deviances in semantic

priming (Copland, 2003). The role of the basal ganglia in language processing is a good open question.

Considering the divergence in terms of the effector muscles or sensory system used (visual, auditory, touch) across the modes of language expression, it should not come as a surprise that functional activation related to language can be found nearly anywhere in cortical and subcortical structures³. Speech has traditionally been the mode of language expression in focus in most linguistic models, although written language is also a frequent study object. Sign language attracts increasing attention during the last decade. It has been demonstrated that sign language is combinatorial (Senghas, Kita, & Özyurek, 2004), with temporal structure at many levels (Willems & Hagoort, 2007). Gestures accompanying speech show less combinatorial structure on their own, but they are integrated with spoken language in structured temporal sequences, a process which is subserved by the left inferior frontal gyrus (Willems & Hagoort, 2007). The sense of touch can be used to build up a receptive language, as in Braille reading. Extending this principle, I would suggest that odor sequences could build up a receptive language as well, as long as the temporal resolution needed can be achieved (this is partly a consequence of the sequence processing perspective, see chapter 4).

The language network from the perspective of processing and memory at different temporal scales

An alternative way of framing the division between memory and unification is that it is a division in terms of processing at different temporal scales. Ultimately, *processing* and *memory* are *two sides of the same coin of complex brain dynamics*, but it makes more sense to talk about *memory at a slow temporal scale* and *processing at a fast temporal scale*. Thus, the temporal lobe might implement solutions to the communication problem at a slower temporal scale (by forming stable representations), while the frontal cortices solve the problem at a faster temporal scale (e.g. by unification implemented in short term plastic changes forming representations at a shorter temporal scale, as a result of the influence from activated representations living at longer temporal scales in temporal cortex). See chapter 5 for a further discussion on the language network from the perspective of different temporal scales.

³ Possible cortical exceptions are the dorsal parietal areas, located beneath the vertex, used as a language irrelevant control area in Study IV.

I would now like to come back to our main issue: to revisit how the computational level problems of linguistics have been chosen. We have not yet discussed the third computational problem described by Pullum and Scholz: the problem of language acquisition.

1.2 THE ACQUISITION PROBLEM

A detailed explanation of how language is acquired, also in terms of neural responses, will involve determining to what extent language is acquired by general purpose learning mechanisms equally adapted to acquire information from different cognitive domains or is acquired by learning mechanisms specialized for language. If learning mechanisms are specialized or constrained in a way that is particularly fruitful for acquiring languages, the structure of language can be said to be partly known *a priori*, to be innate, instantiated in prior structure or biologically determined⁴. If there is prior structure, there might be a common component to all human languages, a set of *universal features* that arise from common biological constraints. This hypothesis was made famous by Chomsky.

Chomsky argued from the *poverty of the stimulus* for the existence of universal grammar, which I would like to present as follows. Say that we 1) have a good sense of some general purpose learning mechanisms a child brings to the language learning tasks and 2) how the primary linguistic data that the child is exposed to looks like. Then, we can determine whether these learning mechanisms, when exposed to the particular primary linguistic data, will produce an output similar to the output that a child actually gives at a certain age. If the actual output is more complex than what can be predicted by general purpose learning mechanisms under exposure to a certain set of stimuli, we need to postulate that there is some form of language specific prior knowledge, e.g. language specific constraints on the learning mechanisms. Chomsky's belief is that there must be language specific prior structure, primarily constraints on language specific learning mechanisms. The lack of empirical data on the innateness issue has however made some conclude that there is no reason to have an opinion in the innateness debate in its current state (Smolensky & Legendre, 2006).

⁴ These terms are used vaguely in this passage but will be further specified in the section on prior structure

The term prior structure is an alternative to other terms such as innate knowledge. Innateness is a complex concept which some have argued should be dropped for more specific concepts (Griffiths, 2002). For example, innateness can mean genetically inherited knowledge, biologically determined knowledge or *a priori* knowledge, as pointed out by Scholz and Pullum (2002). In this context, biologically determined knowledge can be exemplified by the knowledge of grammatical structure in one's native language. The knowledge of e.g. Swedish grammar in particular, is however not biologically determined. Biologically determined knowledge is the kind of knowledge that evolves under normal environmental conditions. In this example, genetically inherited knowledge would be the learning mechanisms present to acquire the knowledge of a grammar. A priori knowledge is knowledge that is independent of specific environmental states or some particular acquisition event. Although gene-regulatory networks determine which part of the genetically inherited knowledge that will be manifested, genetically inherited knowledge only constitutes a part of a prior knowledge. Prior knowledge could also be instantiated in epigenetic structure such as methylation patterns of DNA, existing prior to acquisition (see **Figure 1.3**). Further distinctions were made by Elman et al. (1997). In this paper, he defines representational nativism and chronotopic nativism. Representational nativism is when cortical representations are established prior to experience. Chronotopic nativism is when the timing of maturation is determined prior to experience.

The questions on what parts of linguistic behavior is explained by (possibly language specific) genetic structure and what is dependent on environmental factors, e.g. as in biologically determined knowledge, are both important. As outlined in Petersson and Hagoort (2011), language specific constraints may operate at many levels of the organism and its development. Constraints may for instance apply as initial conditions on the language system, as the limits of the possible states that the language system can take or as limits of the learning/developmental dynamics that update the states. Study II in this thesis studies the limits of sequence acquisition mechanisms that we argue are relevant for language acquisition.

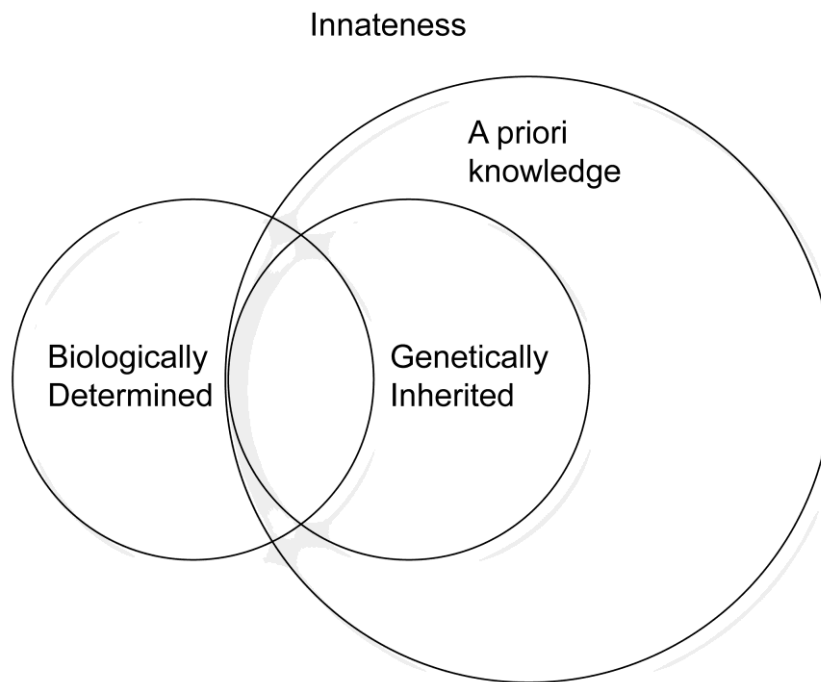


Figure 1.3 The innateness term can be further specified as biologically determined knowledge, genetically inherited knowledge and a priori knowledge. Genetically inherited knowledge is a subset of a priori knowledge, which contains all knowledge present prior to the exposure to the so called primary linguistic evidence. Biologically determined knowledge does not need to be existent a priori, since this kind of knowledge can be dependent on environmental conditions. Biologically determined knowledge is the knowledge that develops under *normal environmental conditions*, such as a fair amount of language exposure. However, biologically determined knowledge does not depend on the details of the content of the primary linguistic evidence.

Since brains are highly similar across the world (at least from the evolutionary perspective) a first step towards finding the content of prior structure is to find out what is common across languages. As already mentioned, linguistic features present in all languages are called linguistic universals and their presence is an oft debated issue (Evans & Levinson, 2009). If nothing is common, at least tendencies where many languages exhibit some feature are worth noting. Such features are called relative universals. A good metaphor to indicate the importance of relative universals is that the prior structure might provide a toolbox for languages, where only some tools are used (Pinker & Jackendoff, 2009).

A complementary approach is to define what is not present in any human language. The idea here is that language acquisition will only work on some of all conceivable languages, particularly if language acquisition is restricted by linguistically

specific prior structure. This could be tested by creating artificial languages and testing acquisition on these languages (this is done in Study II in this thesis).

Pullum and Scholz (2002) rightly point out that the poverty of stimulus argument needs empirical assessment. However, they also demonstrate how hard it is to actually show that there is a gap between the primary linguistic evidence that the child receives and the linguistic knowledge acquired. If the stimulus is not actually poor, there is little need of specialized acquisition mechanism for language, universal principles, even relative universals should not be expected. In this case, language does not require much cultural evolution to fit our acquisition mechanisms.

To list the main contributors to language acquisition and evolution: biologically determined knowledge, prior structure as well as general purpose learning acquisition mechanisms and genetic as well as epigenetic factors. All of them will have a role, but what we want to determine is the mechanisms of their relative contribution. Genetic factors have however been argued to be unlikely to ease the language acquisition problem, since there has been no time for adaption of the genome during the short time span that languages have existed (Christiansen & Chater, 2008).

1.3 LANGUAGE EVOLUTION

The language evolution problem is in some respects similar to the acquisition problem. If we know something about the communication problem, we know less about the acquisition problem and we know even less about the evolution of language, whether it is in historic time or on the time scale of the evolution of the human species. The lack of knowledge is partly due to the limitations of relevant test beds of the evolution of language. However, today e.g. genetic methods can provide information on the *prehistoric evolution* of language and computational methods on how languages are related (Dunn, Greenhill, Levinson, & Gray, 2011) provide important new windows to questions of the *historical evolution* of language. It is thus time to put the problem of language evolution on par with the other problems. The field of prehistoric evolution of language can be further divided into (1) the evolution of language in a broad sense (linguistic behavior shared with animal communication systems) and (2) the evolution of language in a narrow sense (the part of linguistic behavior which is uniquely human).

The foundations of the evolution of language as a neurobiological system is probably neuronal recycling, for instance recycling of visual areas specialized for recognizing angles reused for processing of written language (Dehaene, 2005). Genes are turned on and off due to complex gene-gene and gene-environmental interactions. The cultural invention of writing might thus be an environmental stimulus that changed protein expression and thus the structure of the visual cortex without genetic mutations.

One of the core questions in the field of language evolution is whether there was one or a series of mutations that was necessary to develop language in a narrow sense. In addition, if mutations in the human lineage was necessary, to what extent did these genetic changes induce linguistic behavior only, or also other perhaps uniquely human traits such as complex social behavior, theory of other minds, music, dexterity, the use of tools, etc (see **Figure 1.4**). Another central question in the field of language evolution in the narrow sense is to determine the relative contribution of different sources of evolutionary pressure that made language in a narrow sense evolve.

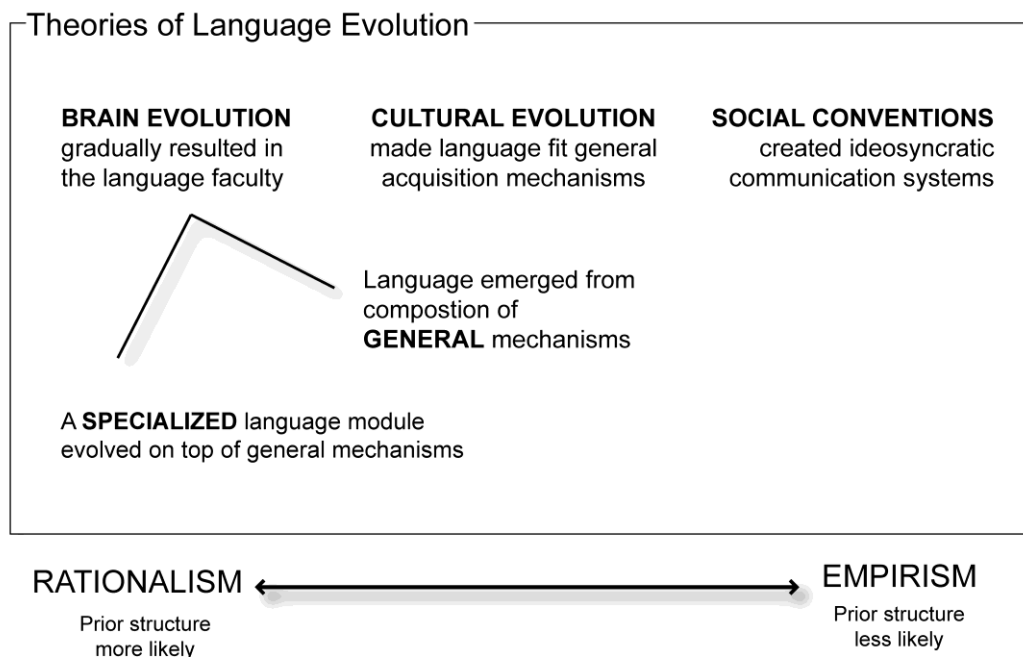


Figure 1.4 Different theories of language evolution can be understood as connected to a position in the classical philosophical debate of empiricism vs rationalism. If language evolution is a result of (from a neurobiological perspective) idiosyncratic events that established social conventions and our brains are have powerful general purpose learning mechanisms, this means that there is less need for presence of language specific prior structure. If learning mechanisms were more restricted, language evolution could rather be described as a process of cultural evolution where language was adapted to the prior structure in the brain (Christiansen & Chater, 2008). Alternatively, language evolution could be a consequence of

some minimal additional brain evolution. This addition could be linguistically specific or also used for other cognitive tasks.

For instance, language might have evolved for internal thought, for communicative purposes or for both. I will now discuss this question in the light of the empirical results of Study II. Historic language evolution (which is sometimes called *language change*) has at least two distinguishable components: (1) the creation of new structures and (2) selection for when and how to use which of these new as well as the old structures. In Study II in this thesis, we show that participants exposed to artificial syntax can implicitly generalize beyond their experience with particular examples sequences from the artificial grammar. In this context, I would like to note that this can be seen as an empirical demonstration of a mechanism for the first of the mentioned components of language evolution: creation of new structures. We show evidence for generalization of preference judgments as well judgments of grammaticality. These judgments rely on brain representations. There is no reason to believe that these representations would not be reachable for use in language production and thus communication, if we would allow them to grow strong enough, e.g. by extended exposure. This process might gain speed under evolutionary pressure for evolvement of internal thought and communication.

This mechanism is internal to the language user and might be enough to explain most of the component of creation of new linguistic structures, while the second component of selection among new and old linguistic structures takes place both internally and in a communicative context. The factors that contribute to the second factor could be described at the cognitive level or the level of brain implementation, such as the view that language is adapted to the brain (Christiansen & Chater, 2008) and at the level of communicative needs specified by social or environmental conditions.

Conclusion Chapter 1

The division of the communication problem as separate from the acquisition problem is adequate but the parsing problem should not be analyzed as on the same level as the other problems. I would like to add language evolution as a problem on par with the language acquisition problem and the communication problem.

2 IMPLICIT LEARNING OF LANGUAGE

2.1 IMPLICIT LEARNING: A MARRIAN ANALYSIS

2.1.1 The computational level

In this chapter, I introduce implicit learning. I also describe the current role of implicit learning within a larger context of cognitive neuroscience. This analysis arrives at a slight redefinition of implicit learning and implicit *knowledge*.

The acquisition of complex knowledge structures without deliberate explicit strategies and supervised teaching has been investigated under the umbrella term of implicit learning. Alternative labels that are sometimes used interchangeably are statistical learning and sequence learning. In order to situate implicit learning in the context of the learning literature and the long term memory literature, we need to know that implicit learning constitutes a branch of the non-declarative memory tree (see **Figure 2.1**). The division between declarative and non-declarative memory has been the most important division of long term memory in the literature (Squire & Zola, 1996). Non-declarative memory is a collective term for all processes which are not declarative and thus non-declarative memory is quite heterogeneous. Skill learning, habit learning and procedural learning are related forms of non-declarative learning, sometimes considered together as one and sometimes separately (Seger, 1994; Yin & Knowlton, 2006). Repetition priming (also called implicit memory) is a possible mechanism for implicit as well as other forms of learning (Bock & Griffin, 2000).

In general terms, implicit learning is “the process whereby a complex, rule-governed knowledge base is acquired, largely without any requirements of awareness of either the process or the product of acquisition” (Reber, Walkenfeld, & Hernstadt, 1991). More precisely, implicit learning has been defined as learning with the following four characteristics: (1) no or limited explicit access to the knowledge acquired and how it is put to use; (2) the acquired knowledge is more complex than simple associations (such as simple stimulus-response associations) or exemplar specific frequency-counts; (3) it is an incidental consequence of information processing and not a result of explicit hypothesis testing and (4) it does not rely on declarative memory mechanisms, such as the medial temporal lobe memory system (Forkstam & Petersson, 2005a; Seger, 1994). Implicit learning is often investigated with stimuli such as patterns or structured sequences. Artificial grammar learning is such a sequence processing task

which can be adapted to the implicit learning criteria and we will describe this task in depth in the later part of this chapter.

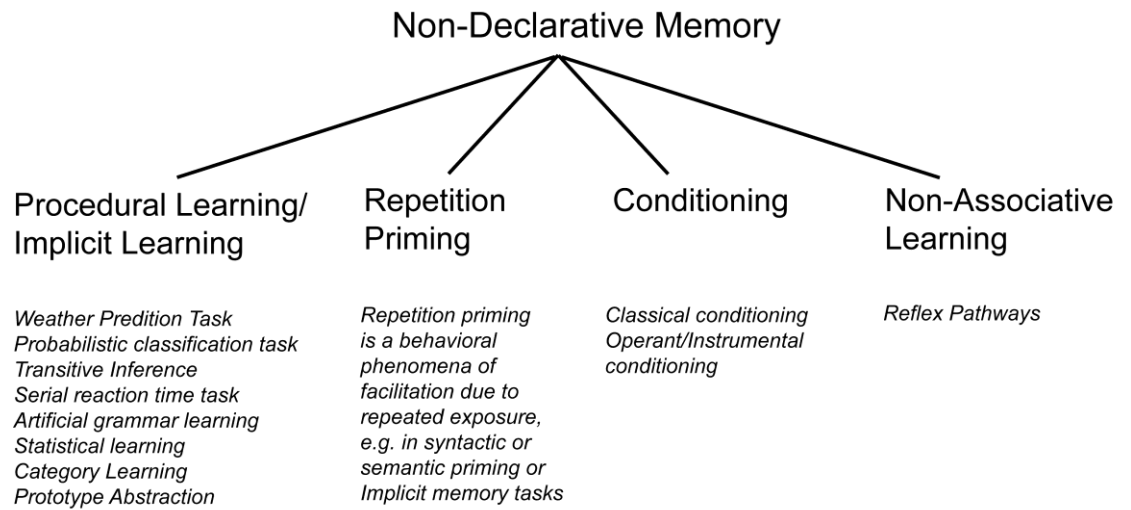


Figure 2.1. Divisions of non-declarative memory with examples or example tasks.

Accessibility, complexity and incidentalness

I will now review the criteria of implicit learning in order to arrive on the way I would like to use the implicit learning term and the implicit knowledge term. The first three criteria for implicit learning: accessibility, complexity and incidentalness; are straightforward, computational level constraints. The fourth criterion for implicit learning is that the implicit learning system is segregated from the declarative memory system in the medial temporal lobe. This is a criterion at the neural level. Intact implicit learning in amnesic patients (Knowlton & Squire, 1996) and other evidence for this segregation should however perhaps be regarded as support for the relevance of the computational level construct of implicit learning, rather than a criterion itself.

The access criterion describes a subjective state of the learner with respect to the content that is being acquired. This state can for instance be objectively measured through verbal report. The subjective state of access corresponds to the neural representations of the accessed content being activated in such a way that access is reached. We can call such activation access-activation. Implicit learning is when neural representation are formed or changed without the access-activation of those representations.

*Complexity*⁵ can be seen as an abstract feature of the stimuli or the knowledge base itself. I would like to remove this criterion for implicit learning, since it is not a feature of the acquisition process, but of the stimuli. The complexity criterion is however tightly linked to the access criterion since complex knowledge is hard to make accessible in a concise yet precise way, e.g. in verbal report. Some minimal frequency and duration of exposure is needed for any learning to take place, independent of the complexity of the stimuli. Above this point, the more frequent and durable exposure, the more likely it is that access to knowledge about the stimuli will develop. By extended exposure to complex stimuli, the time window for studying implicit learning, e.g. with neuroimaging techniques, can thus be maximized (see **Figure 2.2**).

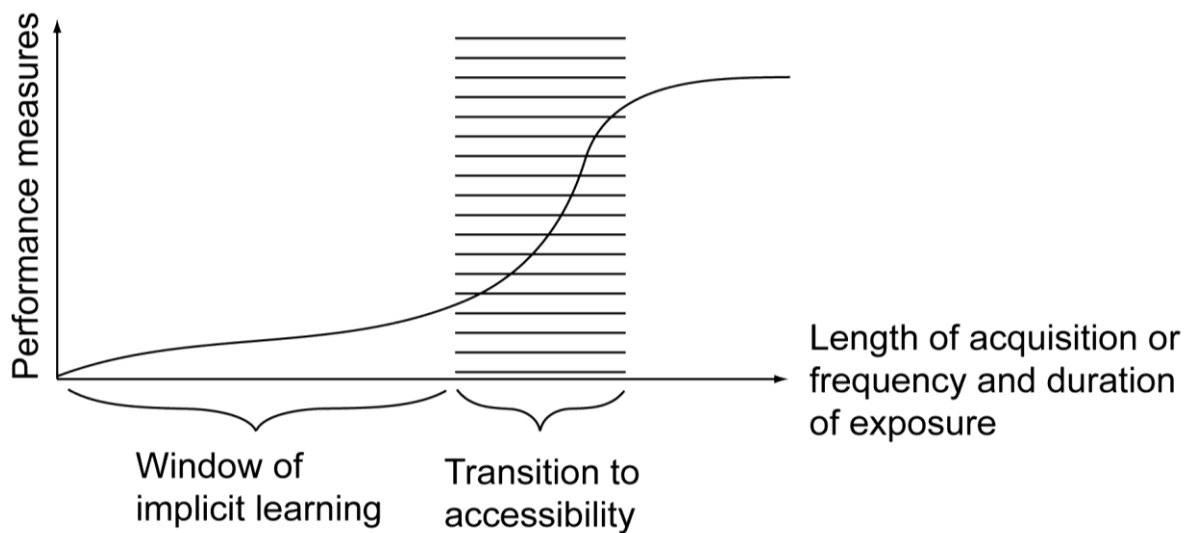


Figure 2.2 When studying implicit learning process, it is useful to maximize the window before the content of acquisition might become accessed. The more frequent and durable exposure, the more likely it is that access to knowledge about the stimuli will develop. When using **complex** stimuli, this process is slower. In this figure, the transition to access is described in a non-linear learning process. This is a speculation on what effect a transition to accessibility of the knowledge might have on performance measures. A gradual development of performance, rather than sharp transitions, was found in the empirical part of this thesis (see Study I and II).

The criterion of *incidentalness* is about the way the knowledge was acquired. The original suggestion to include incidentalness as a third criterion for implicit learning is due to Seger (1994). In her opinion, the implicit learning concept should embrace situations where the subject has noticed aspects of the knowledge to be learned, but in

⁵ Complexity is used vaguely in this context. I note that there is a whole branch of mathematics dealing with different descriptions of complexity (see the section on complexity in this chapter).

the absence of hypothesis testing. Crucially, she suggests a difference between the mechanisms underlying implicit learning and those underlying hypothesis testing or *explicit* hypothesis testing, where the hypothesis is stated before the test. Incidental learning is when learning is a bottom-up consequence of the information processing on the stimuli, changing the way the stimuli is processed. Note that incidentalness does not mean absence of access to the acquisition process. Absence of access to the acquisition process implies absence of explicit hypothesis testing, but the converse is not true. Thus the criterion of absence of explicit hypothesis testing is a weaker criterion and this is the intended incidentalness criterion by Seger (1994).

I would like to redefine implicit learning as the combination of two features: (1) incidental learning, meaning the absence of explicit hypothesis testing during acquisition and (2) learning without access to the content that is learned. Implicit *knowledge* can mean two things: (1) knowledge which is a result of implicit learning or (2) knowledge which is inaccessible. When using this term, it is thus important to specify in which sense it is used. For instance, explicitly learned knowledge (such as taught association pairs e.g. the capital of a nation) can become inaccessible when it is forgotten, but the knowledge might still be present to some extent since it has left a trace in the neural circuitry. I would like to use implicit knowledge as in (1): implicit knowledge is knowledge which is a result of implicit learning. We have now specified implicit learning. Explicit learning is then the complement of implicit learning, e.g. learning in the presence of access using explicit hypothesis testing.

2.1.2 The neural level

The fronto-striatal network

There is good evidence that the frontal cortex and the basal ganglia (fronto-striatal circuits) are involved in implicit learning in humans (just as in natural language, see chapter 1). This has been characterized in patient (lesion) studies (for reviews see e.g. Forkstam & Petersson, 2005a; Seger, 1994) and functional neuroimaging studies in healthy volunteers (Forkstam, Hagoort, Fernandez, Ingvar, & Petersson, 2006; Lieberman, Chang, Chiao, Bookheimer, & Knowlton, 2004; Rose, Haider, Weiller, & Buchel, 2002). Likewise, there is empirical research showing that the lateral prefrontal cortex is involved (Forkstam, Hagoort, Fernandez et al., 2006; Petersson, Forkstam, & Ingvar, 2004; Seger, 1994).

Imaging studies of AGL repeatedly find activations in the basal ganglia, in particular the striatum (Forkstam, Hagoort, Fernandez et al., 2006; Petersson, Folia, & Hagoort, 2010). Implicit motor learning and procedural learning, for instance as indexed by the serial reaction time task (SRTT) are processed in the basal ganglia (for a review, see Forkstam & Petersson, 2005a). Another aspect of the link between the basal ganglia and implicit learning comes from neuropharmacological findings. Dopamine and serotonin are two neurotransmitter systems that have been found related to implicit learning. They originate in midbrain nuclei and project directly to the striatum. The neurotransmitter systems (noradrenaline, acetylcholine) that do not project directly to the striatum have a weaker relation to implicit learning empirically. As we have concluded in a recent review paper (Uddén, Folia, & Petersson, 2010), the strongest evidence for a causal role of a neuropharmacological system in implicit learning is dopamine levels in the dorsal striatum, which has been specifically studied in rats and Parkinson patients. In sum, these neuropharmacological studies of implicit learning support the view that the striatum is involved in implicit learning (just as in natural language, see chapter 1).

Two memory systems

Implicit learning does not rely on declarative memory mechanisms (i.e., the medial temporal lobe, MTL, memory system), as evidenced by preserved implicit learning in amnesic patients (Ferreira, Bock, Wilson, & Cohen, 2008; Knowlton & Squire, 1996; Seger, 1994). There is little evidence that the MTL is engaged by implicit learning tasks (Forkstam, Hagoort, Fernandez et al., 2006; Seger, 1994). In a recent study (Petersson et al., 2010) the MTL was deactivated during an AGL paradigm. This is consistent with the view that implicit processing does not rely on declarative memory mechanisms that engage the MTL memory system. I will now critically examine this view of two distinct memory systems.

In the memory and learning literature, just as in the field of neurobiology of language, it is important to find precise computational level definitions and map them onto the neural level (see the preface). On first approximation, hippocampus and the surrounding perirhinal, parahippocampal and entorhinal cortex are structures subserving the function of forming and consolidating long term memory representations which are reorganized to all over the cortex for long term storage. There is now a considerable debate on functional specialization of these four structures within

the medial temporal lobe. For instance, familiarity based item-memory (independent of context) is thought to be subserved by perirhinal cortex while episodic memory with a spatial and temporal extent is subserved by an MTL-network including hippocampus (for a review see Graham, Barense, & Lee, 2010). The perirhinal cortex may also be seen as an extension of the ventral visual stream for object identification and the perceptive and memory aspects of processing in this area might not be easily separated (O'Neil, Cate, & Kohler, 2009). This is along the lines of the principle of colocalization of memory and processing (Hebb, 1949; Petersson, 2005a). The modular view of MTL subserving formation and consolidation of declarative long-term memory independent of the content of the memory may not stand.

This has consequences for implicit learning. For instance, if the perirhinal cortex can be seen as yet a more abstracted layer in the processing hierarchy of the ventral visual stream, the representations in this part of cortex should also be able to be formed with implicit learning processes. Thus, the declarative MTL memory system and the fronto-striatal implicit/procedural/skill/habit learning system might not stand as two memory systems encoding any type of information, but rather as two higher order information processing systems, specialized in information from certain domains. Along these lines of reasoning, the fronto-striatal system might reduce to processing sequence information, in particular originating from the motor and language domains (for an exception, word learning seems to be dependent on MTL, Graham et al., 2010).

Access at the neural level – interface with neurobiology of access consciousness

If we take an evolutionary perspective, having access to knowledge using explicit hypothesis testing might be late developments and rare throughout the animal kingdom. The evolution of explicit learning might be a consequence of qualitatively different brain mechanisms or alternatively there could be a qualitative or quantitative difference in how the brain mechanisms for implicit learning are used. We have reviewed possible gross anatomical differences in which functional networks are recruited for implicit and explicit learning. These results come from the learning or memory literature. The neurobiology of access-activation has however also been studied in the consciousness literature. The part of this quite problematic literature which I have been able to identify as showing some promise is the literature on verbal

access, or Ned Block's (1997) term *access consciousness*, where neuroimaging techniques have been successfully used.

In the neurobiology of consciousness literature, access has been studied mainly in early sensory domains. In this line of research, the term *perceived stimulus strength* is used. An increased perceived stimulus strength means that the stimulus has a higher probability of reaching access, e.g. access to the verbal system. The perceived stimulus strength is seen as amplified e.g. by transmission through a global workspace consisting of a number of cortical areas across the brain (Dehaene, Kerszberg, & Changeux, 1998) or through long or short range recurrent neural connections (Lamme, 2006). I have named the neural process subserving access *access-activation*, defined as any kind of cortical activation corresponding to some accessed content, irrespective of whether the content is in the sensory domain or e.g. the language domain. When testing the relevance of the implicit learning concept at the neural level, the global workspace model or other suggestions of the neural correlates of access consciousness are relevant to study. These suggestions have not yet been studied in the context of implicit learning⁶.

Measurements of access

Measurements of the access criterion at a behavioral level could also be developed in the implicit learning literature if methods are translated from consciousness research. Generally, measurement through verbal report or forced choice tests are used to determine access consciousness and of these two, forced choice tests are more sensitive. For instance, crucial aspects of the stimuli might be accessed e.g. for explicit hypothesis testing, but may still not be easy to put into words. Moreover, the verbal response takes long to generate and the access might partly be lost along the way. Forced choice test are therefore better for determining e.g. whether a stimulus was accessible. However, it should be noted that a successful strategy in the forced choice test is to use the implicit knowledge to respond. In a sense, access might thus be successfully bypassed during accurate performance in this test. Depending on what questions are in focus, it can be important to measure access with multiple measures in order to characterize more nuances of how implicit some acquisition process are, or

⁶ Conversely, neural segregation of the implicit and explicit learning systems is relevant for the neurobiological study of access, since access is a crucial part of what distinguishes explicit from implicit learning.

how implicit some knowledge is at the end stage of implicit acquisition. In the empirical part of this thesis, we use forced choice tests as well as questionnaires based on verbal report.

Access can also be investigated through the objective and subjective threshold criteria for awareness (Dienes, 2012; Dienes & Longuet-Higgins, 2004; Kuhn & Dienes, 2005, 2006). In objective measurements, such as classification judgments, a criterion for unconscious knowledge can be that indirect tests of knowledge (such as the preference test) lead to greater discrimination ability than more direct tests (such as the grammaticality test). From my point of view, this is a highly conservative criterion which can work as a proof of existence of unconscious knowledge for skeptics and for specific questions where the degree of implicitness needs to be assessed. An alternative criterion of access which might be less conservative is when above chance performance on a direct test is orthogonal to confidence ratings. Since these ratings are subjective measures, this criterion is called the subjective criterion of access. I think that these two kinds of measurements: (1) direct to indirect test ratio and (2) correlation between confidence and performance, have their strengths as continuous measures enabling nuanced measurement of degree of access of knowledge. It is not clear whether access should be construed as being "on or off".

A promising way forward in the measurements of access is to use more sophisticated biological markers of the knowledge e.g. eye-tracking, galvanic skin response and pupil diameter. Advances in the fields of neurobiology of consciousness and measurements of access must be monitored within the implicit learning field since these fields are in fact entangled through the crucial implicit learning criterion of access.

2.2 IMPLICIT LEARNING AS A TRAIT

An approach to scrutinize implicit learning from a neurobiological perspective, complementary to the theorizing in the previous sections, is to try to understand whether implicit learning is a stable trait. If implicit learning corresponds to a certain set of brain mechanisms, there should be at least some stability in this mechanism and the behavior connected to it, in a participant. Implicit learning research would also be reinforced if implicit learning is a trait which is sufficiently independent from other traits of higher cognition. This can for instance be assessed by correlating individual variation in implicit learning with individual variation in other higher order cognitive

tasks and constructs. Examples of such tasks or constructs are intelligence⁷ and general working memory (c.f. chapter 6), which are quite poorly understood conceptually but empirically established. In a recent study, there was a lack of correlation between implicit classification in AGL and verbal working memory measures such as the reading span tasks (Robinson, 2010).

In a study by Gebauer & McIntosh (2007) 600 German students were assessed in three different implicit learning tasks: a processing control task, an AGL task (see next section) task and the SRTT, under explicit and implicit instructions (thus varying incidentalness). This study is unique because of the large number of subjects studied. Individual variation in the processing control task was not correlated with either SRTT or AGL under implicit or explicit conditions. While intelligence is correlated with AGL under explicit instructions, no correlation is present between intelligence and implicit AGL performance. These results were similar for the SRTT, while processing control was generally correlating with intelligence. Kaufman (2010), again found no correlation between individual differences in performance on a probabilistic SRTT and multiple intelligence measures. No correlation was found with working memory measures and explicit associative learning. However, individual differences in this task were related to verbal analogical reasoning and second language learning. All together, these findings are along the lines of interpreting AGL and SRTT under implicit instructions as sharing an implicit learning component which is interesting as a trait different from e.g. intelligence. In another large-scale study of 109 undergraduates, AGL was found unrelated to cognitive abilities in math, English, reading and science as measured with ACT, which a standardized test widely used in the US school system (Pretz, Totz, & Kaufman, 2010).

Three findings by Gebauer & McIntosh (2007) make it more questionable whether an implicit learning component is a stable trait underlying both AGL and SRTT. (1) Performance on AGL and SRTT was not correlated under implicit instructions, but only under explicit instructions. The opposite would be predicted if implicit learning was a stable trait underlying both AGL and SRTT. (2) AGL

⁷ Jensen (1981) proposed a system for which aspects of a learning task will make it dependent on intelligence. The absence of these features can thus be seen as suggestions for implicit learning features that can be relevant if we want to study implicit learning as a trait separate from intelligence. On top of the criteria we have discussed, Jensen's criteria include absence of meaning (implicit learning is not a consequence of comprehension) and the isolation of the knowledge base (transfer from earlier experience should not be possible, since this will be sensitive to intelligence, according to Jensen).

performance was found to be better after implicit compared to explicit instructions. Performance in the SRTT was however better under explicit instructions. Thus, given the particular implementation of these tasks used in the study, there seems to be a crucial difference in how these tasks relate to the criterion of incidental learning. AGL seems to be a better model for incidental implicit learning compared to the SRTT, since performance in this task is enhanced under explicit instructions. This establishes an ecological advantage of an incidental implicit learning system in relation to tasks such as AGL. The SRTT most often involves a motor learning component, which is an important difference to AGL.

As we have seen, Squire defines declarative memory as different from non-declarative memory, pointing to different forms of non-declarative memory as more inhomogeneous than different forms of declarative memory. Similarly, it might be better to talk about non-explicit learning rather than implicit learning. Of the three tasks measured in this study, AGL seems to provide the most interesting implicit learning task from a neurobiological point of view. This might indeed be due to relative absence of meaning of AGL and SRTT task compared to the processing control task and the higher degree of isolation of the knowledge base in AGL compared to SRTT and the processing control task, along Jensen's suggestion (see the footnote on the previous page). Other potential explanations is the presence of non-adjacent items, which is a more common feature of AGL and the degree of generalization from an acquisition set to a test set needed in the tasks. AGL includes generalization, while this is rarely performed with the SRTT. (3) The test-retest reliability for AGL in Gebauer (2007) was significant, but low (personal communication). Preliminary analysis of the behavioral data presented in this thesis however suggest that there is an increased reliability in AGL paradigms which span multiple days, compared to the single day study of Gebauer (2007). Processing of adjacent dependencies such as associative chunk strength is a better predictor of AGL performance in the first days of the task (Forkstam, Elwér, Ingvar, & Petersson, 2008).

Implicit learning and natural language

We have seen that although there is some evidence that implicit learning, in particular AGL, is a stable trait, evidence is still largely lacking. If implicit learning is a stable trait, the link between this trait and natural language processing traits also needs to be established. There has been several suggestions on what aspect of natural language performance would be most related to implicit learning abilities (Wells, Christiansen,

Race, Acheson, & MacDonald, 2009). Among the suggestions are: discovery of phonological and distributional cues to lexical categories, acquisition of gender-like morphological systems, segmentation into syntactic phrases, relative clause comprehension and long-distance relationships between words. None of them have been sufficiently tested to draw conclusions. The evidence for shared neural mechanisms, e.g. as evidenced by individual differences in implicit learning predicting individual differences in natural language processing, is yet scarce. Implicit learning as measured with the SRTT was correlated with proficiency in second language learning, in two different groups of second language learners (Kaufman, 2010). It has been shown that individual differences in processing of non-adjacent dependencies in natural language is correlated with individual differences in implicit learning in the SRTT, where the sequences were generated from an artificial grammar (Misyak, Christiansen, & Tomblin). Conway et al. (2010) found correlations in individual differences between two different implicit learning tasks (a visual implicit learning task and an auditory AGL task) and a sentence processing task where the task was to predict the final word. This effect was not mediated by individual differences in working memory (as measured with the digit span task), cognitive control (as measured with the Stroop task) or non-verbal intelligence. Moreover, individual differences in the location of regional functional activity during a natural language task, which varied from the anterior to the posterior portion of the left inferior frontal gyrus, overlapped with individual differences in the location of functional activity during sequence processing (Petersson et al., 2010). Individual differences in semantic and phonological processing and sequence learning have not yet proven to be correlated and this is an area for future research.

2.3 ARTIFICIAL GRAMMAR LEARNING

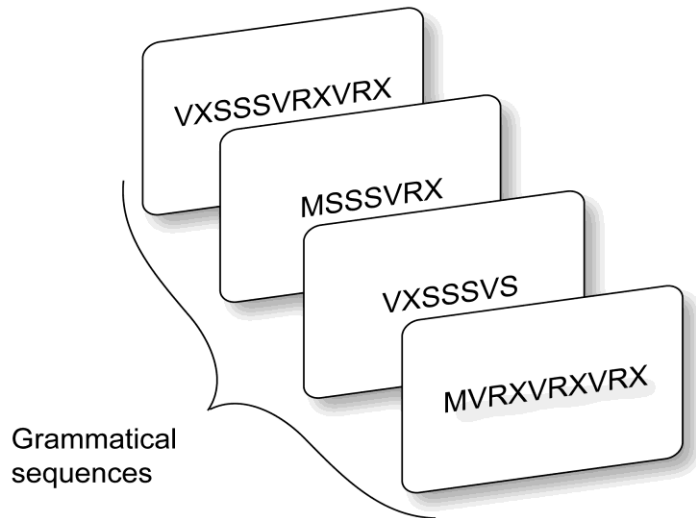
The AGL paradigm allows the systematic investigation of the implicit acquisition of new linguistic structures from positive examples. The AGL task was based on an idea by Miller and Chomsky (1958) and first used by Arthur Reber (1967). It is used throughout the empirical part of this thesis. In AGL, one separates the acquisition and testing phase (see **Figure 2.3**). In the acquisition phase, participants are typically engaged in a short-term memory task using an acquisition sample of sequences generated from a formal grammar. In the standard version, subjects are informed after acquisition that the sequences were generated according to a complex system of rules and asked to classify novel items as grammatical or not (i.e., grammaticality status),

typically with the instruction to base their classification decisions on their immediate intuitive impression (i.e., guessing based on "gut feeling").

The AGL paradigm has two basic assets as a model for language: (1) the possibility to study a wide range of populations. These can be adults or children from different language groups. Moreover, pre-linguistic infants, primates and song birds are important populations to measure when studying language acquisition and evolution. Sequence learning mechanisms are important during language acquisition. AGL opens up the possibility to study the evolution of the sequence learning aspect of language acquisition by the study of non-human (e.g. primate or avian) sequence processing. By using comparable behavioral paradigms as well as sequences in humans and animals, we can determine in what respects non-human sequence processing differ from human sequence processing at a computational, algorithmic and neural level. Such differences can be a result of random evolutionary events but they may also constitute a step in the evolution of language and language acquisition and are thus targets for further research. (2) The AGL paradigm can also be used to study syntactic or phonological processing in isolation from semantic influence and controlling for prior learning. Syntax has been the natural language domain for which AGL experiments has been used as a model system, but work related to phonology has also appeared (Tessier, 2007).

From the perspective of research on language acquisition, AGL is one of few language acquisition paradigms for adult subjects. Using adult subjects when studying language acquisition has inevitable drawbacks. From a neurobiological point of view, we cannot ensure that we are studying the same mechanisms in adults as those in play when children learn language. Moreover, there is contamination from the explicit learning system which is highly evolved in schooled adults. The methodological developments of AGL that I now will describe are centered on minimizing contamination from explicit learning, e.g. avoiding the use of trivial strategies that the child is unlikely to use during language acquisition.

Acquisition/Exposure phase



Test phase

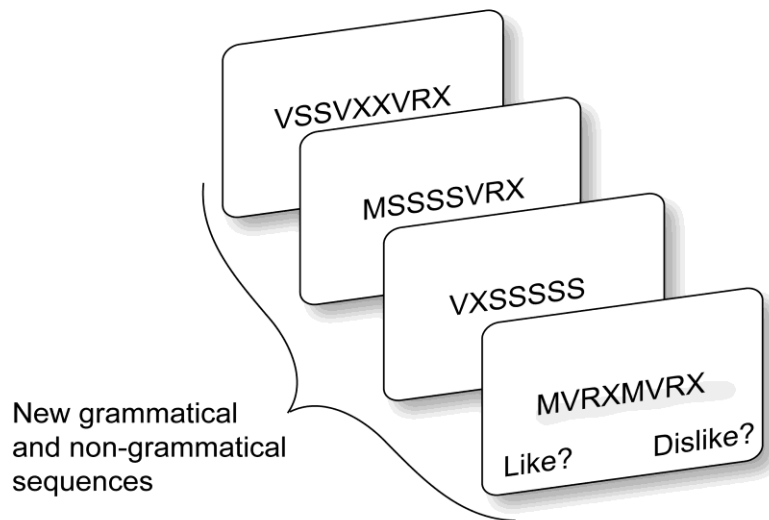


Figure 2.3. The AGL paradigm with preference instruction.

Methodological developments

In the empirical work of this thesis, we made use of three methodological developments of the AGL paradigm: (1) during the acquisition phase, we used enough time (five days in Study I, nine days in Study II and seven days in Study III-IV) for abstraction and consolidation processes to take place; (2) during the classification phase, the non-grammatical sequences are constructed so that explicit strategies, for

example counting, are unhelpful; and (3) the critical measure for showing successful implicit learning is the participants' relative *preference* for grammatical and relative aversion of non-grammatical sequences. Participants only need to indicate whether they like or dislike a sequence and therefore there is no need to inform them about the presence of a complex generative rule system before classification. Moreover, from the subject's point of view, there is no such thing as a correct or incorrect response and the motivation to use explicit (problem solving) strategies is thus minimized. The fact that preferences develop as an effect of exposure has been investigated under the name of the structural mere exposure effect (Manza & Bornstein, 1995; Zajonc, 1968). In the standard version of AGL, subjects are informed about the presence of a grammar, but not the actual rules, in the end-stage of acquisition.

A computational explanation of preference

Why are grammatical sequences preferred? This section will make the first step to apply a statistical physics principle called the free-energy principle by Karl Friston (2009) to answer this question. It is beyond the scope of this thesis to introduce the full terminology, but here it suffices to reiterate Friston's note that living biological organisms can be reasonably described by two features. (1) They are open non-equilibrium systems, meaning that they exchange energy with an environmental system. (2) They can interact with the environment e.g. by moving. The organism resists disorganization by trying to maintain some fixed number of states, keep in these states with high probability and minimize the probability of being in other states. This can be translated to the situation of artificial grammar learning, where brain states are visited as a consequence of the stimuli. The same tendency to resist disorganization can explain why the organism prefer stimuli where the visited states are few and visited with high probability, compared to stimuli where a larger set of states are visited with lower probability.

Consider the finite state grammar that we use to generate the stimuli as an approximate description of brain states visited when encountering the stimuli (see **Figure 2.4**). It is possible to incorporate all possible non-grammatical sequences that we use in our experiments with a finite state grammar, but if this grammar was implemented, it would mean that many states are visited with lower probability. Thus, the assumption that organisms' actions are made to resist disorganization through maintaining a situation where few states are visited with high probability implies that

the system *prefers* grammatical stimuli over non-grammatical stimuli, although the subjects have no access to the principles generating the stimuli. This can also explain why subjects might be able to respond according to a systematic preference also without access to their gut-feeling or emotion. We are currently investigating the empirical question whether there is an emotional component in preference judgments in AGL and whether such a potential emotional component causally affects preference judgments. This theory can be seen as a theory of at least one basic component of aesthetic preference, more generally. Note that e.g. structural aspects of music, dance and possible visual art could be described by similar representations.

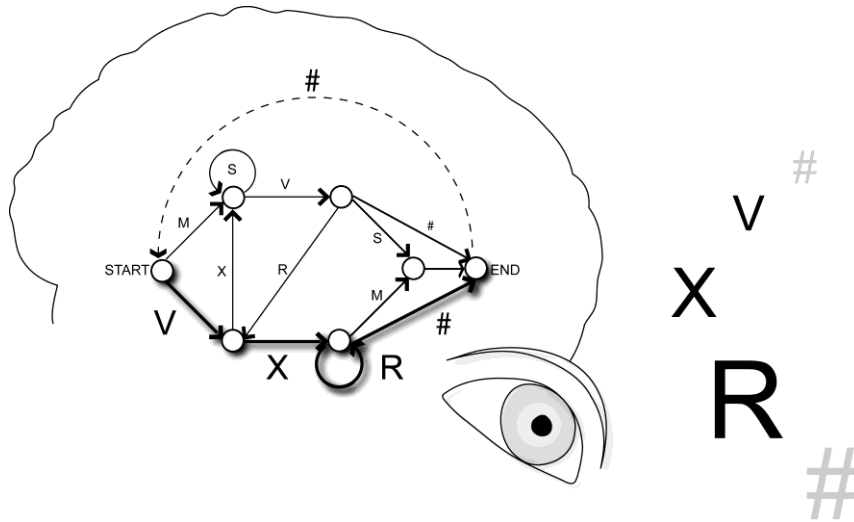


Figure 2.4. The classical Reber grammar is here represented by a transition graph. After the acquisition phase, the information contained in the transition graph is represented in the brain. In this section, we will study the example of what happens when a subject sees the short grammatical sequence VXR, which is preceded and followed by the start/end of string symbol, #. The sequence VRX is an example of a non-grammatical sequence. This information is contained in the transition graph, since when V has been parsed; we end up in the lower left node where there is no arrow out labeled “R”. This results in a parsing failure. Note that the sequences used in Study I-IV were longer.

Parameters of AGL

Visual stimulus presentation is the most commonly used in AGL, and it is also used throughout the studies of this thesis. Auditory paradigms, typically using consonant-vowel (CV) syllables, are however also frequent and there are also some examples of

tactile AGL paradigms (Conway & Christiansen, 2005). The presentation of the sequences is necessarily letter-by-letter in these two modalities, while in visual paradigms one can choose between whole sequence presentation and sequential presentation. In this thesis, whole sequence presentation is used. An important reason for this is to look at the classification decision as having two inherent aspects: accuracy and speed. In whole string presentation experiments, response times are calculated from the onset of the string. In sequential presentation, a fixed presentation window is used for all letters, which results in less variation in measured response times compared to whole sequence presentation, when participants reads each letter in their own pace. Thus, we can expect that the response time measure is less sensitive in the context of sequential presentation compared to whole sequence presentation. Sequential presentation might on the other hand be seen as more ecologically valid, since speech – the primary linguistic data in language acquisition – is sequentially presented. From this point of view, whole sequence presentation can be seen as more ecologically valid when investigating written language acquisition. In any case, results have been similar across studies using paradigms that differ in this respect (see Study III and Folia et al., 2008; Forkstam, Hagoort, Fernandez et al., 2006).

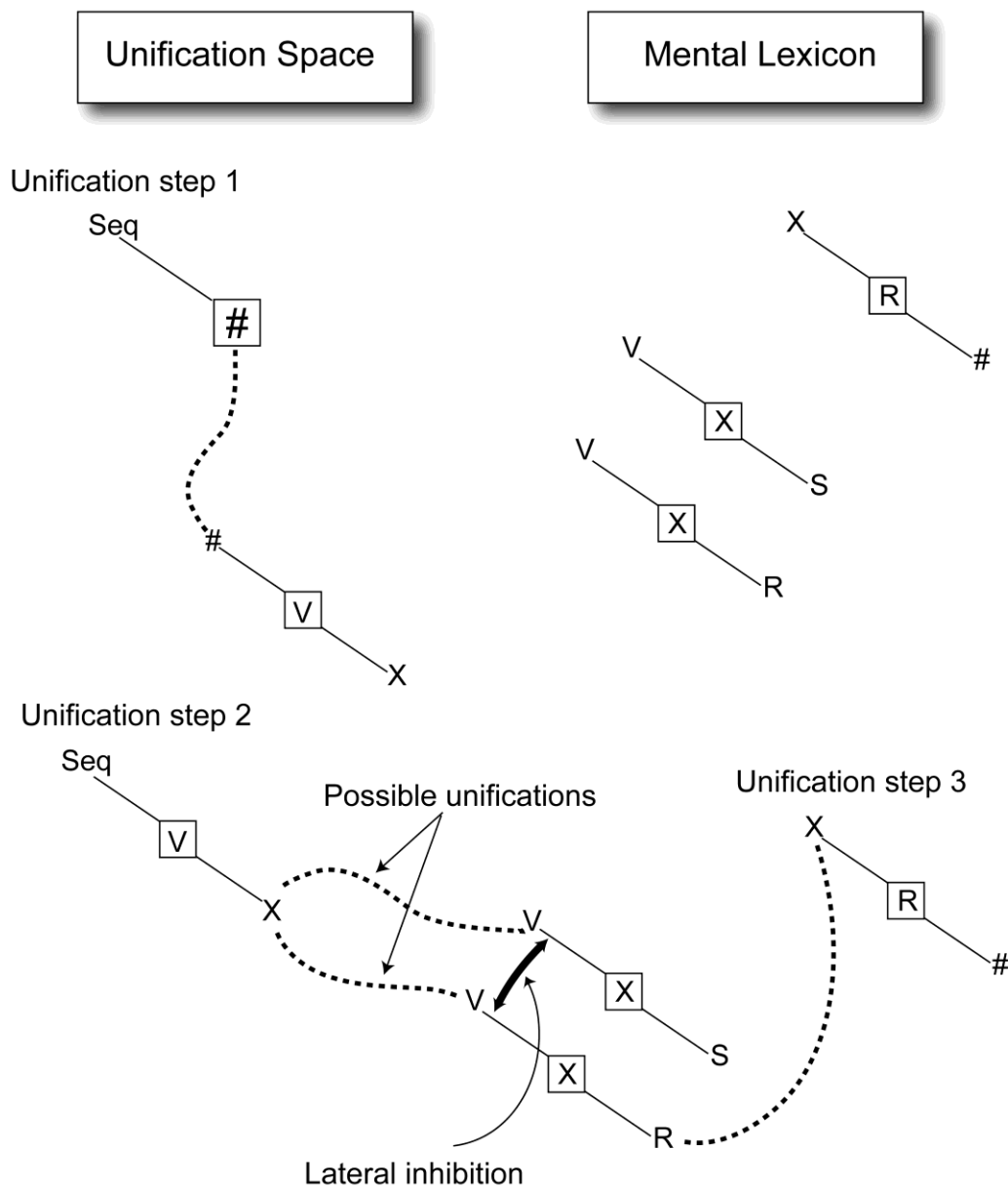


Figure 2.5. An example of how the sequence VXR, following some grammar, would be *unified*. Fragments of the Reber grammar, called syntactic frames have been stored in the mental lexicon during acquisition. Here we have only drawn frames with adjacent dependencies, but larger frames could also represent the so-called non-adjacent dependencies which are studied in this thesis. When there are many possible unification options, such as VXS and VXR in the figure, the frames which could be unified inhibit each other. For instance, a higher frequency of VXR vs VXS during exposure might solve this conflict in favor of unifying VXR.

Artificial grammar learning enables sophisticated control of the computational properties of sequential stimuli. For instance, it has been shown that start and terminal positions in a sequence have an outstanding role and subjects are more attentive to regularities at these positions (Endress, Nesp r, & Mehler, 2009). In this thesis, we have minimized the role of terminal position by using stable pre- and suffixes and by making experimental manipulation in the middle part of sequences, where processing might be more implicit. The second robust finding is that subjects are highly sensitive to chunks of two or three adjacent letters (so called bi- and trigrams) which are frequent in the exposure sequences. The sensitivity to these chunks can be viewed as an initial shallow processing of the grammar. As already mentioned, it has been shown that bi- and trigram chunk strength predicts classification performance at the beginning of the acquisition phase, rather than at the end, where grammaticality status of the complete string is a better predictor (Forkstam et al., 2008). One way to explain the process of acquisition is that subjects grow sensitive to n-grams with larger and larger n. At a large enough n, the whole grammar will be contained in such chunks. This however gives a highly inflexible representation of the grammar, which argues against this form of representation. The grammars used in this thesis include multiple non-adjacent dependencies. Pure n-gram representations are particularly inflexible for processing these kinds of grammars. Study II argues against n-gram representations. The unification operation (see chapter 1 and **Figure 2.5**) is one possible computationally explicit account of how artificial grammars could be processed.

Although sequence learning as measured with AGL is a promising reduction of a vastly complex language problem, one must remember its limitations. Validation of results from AGL in natural language paradigms is important (see the section on implicit learning as a trait in this chapter) and will probably result in a better grasp on which aspects of natural language processing and acquisition are more closely modeled by AGL. Artificial language paradigms also include paradigms where the language is actually not artificial, but a natural language unknown to the subject. On the other side of the spectrum of artificial grammar learning stimuli, there are simplistic triplet stimuli, e.g. ABB or AAB patterns. Results obtained with such stimuli are harder to assess in relation to natural language because of their simple structure which might make explicit learning strategies successful. It is a sign of quality if the artificial grammar has rich structure probing some specific computationally explicit research question. One way to get inspiration for such questions is to look at the mathematical

discipline which investigates properties of abstract sequences, that is formal language theory. Since this is the basis of the empirical work in this thesis, I will introduce formal language theory in some detail in the next section.

2.4 FORMAL LANGUAGE THEORY AND AGL

As noted in the section on implicit learning as a trait, the link between implicit learning and natural language is most clearly shown for syntax. Artificial grammar learning has often been used as a test bed for syntactic theories. One issue in theoretical investigation of syntax is to determine how to describe the complexity of syntax formally and this issue is touched upon in the discussions of Study I and II. I will present some basic syntactic theory with broad brushstrokes here.

2.4.1 The generative grammar framework

Syntax is in fact one of the most developed of all cognitive domains with regard to the presence of computationally explicit models. Mainstream syntax has since Chomsky's early work (1965) oscillated between very complex and simpler descriptions. The maximum complexity can be found in the *Government and Binding* framework created by Chomsky in the 80's. This led to a paradigm shift with the goal to search for simplicity and along with this, the *minimalist program* was created. Disciples of Chomsky have been called generativist since they are working on generative (forward) models of grammar.

Generative grammars generate structural descriptions of sentences. A key to understanding the scope of the theory is that it is a theory at the computational level, stipulating linguistic *competence* and not *performance*, which is determined by a range of additional factors such as noise in the brain, as well as working memory limitations. Generative grammars are paradigmatic examples of *symbolic* models, stipulating a number of rules, e.g. rewrite rules between symbol sequences. There are however no directions for how these rules should be used for processing, e.g. the order in which these rules should be applied when parsing a sentence. Such a theory would rather be a performance theory at the algorithmic/representational level in Marr's sense.

The generative framework provides the basic idea that in order to flexibly recognize regularities in stimuli presented to a cognitive system, the cognitive system will have to be able to *generate* those regularities online. The ability of producing the

same regularities then comes for free. The introduction of the *grammar* as the generative device can thus be seen as a step towards making an explicit procedural model of how structural regularities are recognized and produced. Grammars can be translated to formally equivalent automata which provide further procedural details. Formal grammars generate *string sets* corresponding to sets of full sentences that are grammatical. If a sentence does not belong to this string set, it is non-grammatical. Chomsky proposed the term *acceptability* rather than *grammaticality* for models of performance, i.e. algorithmic level models. Further work on performance models will be useful when trying to find neural level implementations with increasing levels of detail. Three core developments have to be accounted for by performance models, as extensions of competence models. (1) A nuanced option between grammatical and non-grammatical, i.e. a theory of acceptability rather than grammaticality. As discussed by Pullum and Scholz (2001), speaker perceptions of the acceptability of sentences are of graded rather than an absolute character. This is consistent with brain dynamics almost exclusively being explained in graded signals, i.e. variables that can take a large number of discrete values (e.g. membrane potentials, numbers of receptors, concentrations of neurotransmitters, etc.). Binary variables such as action potentials are also present in the brain, but are rather exceptions. (2) The previous focus on complete sentences should be extended to include acceptability of fragments of sentences as well. (3) The brain seems to process language in an incremental manner (fragments are considered as they arrive). This has not been accounted for in the competence theory of main stream generative grammar, where the first step in the parsing process is to merge constituents that often come at the end of the sentence (i.e. the innermost constituents in a syntactic tree created by recursive application of merge).

There are suggestions of developments of the generative grammar framework which account for these phenomena. In a version of the stochastic grammar framework, probability assignments to all possible expressions over a vocabulary indicate well-formedness (Pullum, 2001). The probabilities can range from 0 to 1 on a fine grained but discrete scale and thus provide a graded signal. Language fragments thus have lower probabilities than full sentences, but their likelihood can still be different from zero and different language fragments could thus be compared as more or less well-formed. Stochastic grammars also allows for language change to be modeled as e.g. rising and diminishing probabilities of certain words or sentence fragments, or in the case of AGL: sequence fragments.

Optimality theory (OT) is a framework, originally developed for the phonological domain, where generative grammars are enhanced with an additional set of constraints, which makes it possible to explain graded grammaticality and which also provide a link to acquisition. A universal grammar (common to all languages) provides the set of constraints which evaluate the generated syntactical structures that are possible to assign to a sentence or language fragment. The structure with optimal fit to the constraints will be called grammatical. Many constraints apply to fragments of sentences and thus fragments can also be assigned a grammatical status within OT. The constraints are often in conflict with each other and the way this conflict is resolved is by ranking the importance of each constraint. The particular ranking order between the constraints is different for every language and from the point of view of OT, this is what makes syntax different from language to language. Acquisition of constraint ranks is a major part of language acquisition from the OT perspective (Tesar, Prince, & Grimshaw, 1999). The question whether OT can translate into a well-defined graded grammaticality concept is beyond this discussion, but indeed the concept of optimality is more graded than the dual distinction between grammatical and non-grammatical in standard generative theories.

Stochastic generative grammars or standard generative grammars combined with an OT set of constraints represent models which might be particularly interesting from the translational neuroscience perspective. Syntactic frameworks are however even more interesting if they also fulfill the requirement that parts of their dynamics can be simulated in neural networks, gradually introducing more and more neural realism. Indeed, stochastic grammars and optimality theory represent an attempt to bridge the gap between symbolic models and so called sub-symbolic models, which in some parts of the literature have become synonymous with connectionist models (see the section on computational models of AGL).

Formal Language Theory and the Chomsky Hierarchy

From the mathematical point of view, languages are not seen as neurobiological systems, but rather as abstract mathematical objects called *formal languages*. Formal language theory delineates important principles of sets of sequences or *strings*. These sets are the formal languages. The most important concepts from formal language theory will be introduced here and they are important for understanding the terminology and interpretations of Study I, II and IV.

The set of all strings ω over an alphabet Σ (of arbitrary surface symbols) is denoted Σ^* and any subset of this set is called a language, L . A language is thus a string set. When we want to ask whether a particular string ω is in L or when we want to generate a string that belongs to L , we need a parser or a generator, respectively. *Formal grammars* are language parsers and generators at the same time and they can also be seen as (finite) definitions of (possibly infinite) languages (in the sense of sequence sets). More precisely, formal grammars are algorithms with a set of instructions. These algorithms are typically non-deterministic since there is no specified order of how the instructions should be applied. Depending on the form of the rules, formal grammars can be classified into the complexity classes of the Chomsky hierarchy (see Definition 1). In one version, this hierarchy consists of regular (finite-state; T3), context-free (T2), context-sensitive (T1), and general phrase-structure grammars (Turing-Thue; T0).

Definition 1 A **grammar** or **context-sensitive grammar** is a quadruple $G = (V, \Sigma, R, S)$ where V is an alphabet, Σ is a set of terminal symbols, S is the start symbol which is a member of $(V - \Sigma)$, R is the set of rules, a finite subset of $(V^*(V - \Sigma)V^*) \times (V^*)$. If all the rules of G are of the form $(V - \Sigma) \times (V^*)$ the grammar is called a **context-free grammar**. If all the rules of G are of the form $(V - \Sigma) \rightarrow a$ or $(V - \Sigma) \rightarrow aV$ where $a \in \Sigma$ the grammar is called a **regular grammar**.

In Examples 1-2 (Pullum & Scholz, 2010), we see that the grammar G_{abc} can only make one string, abc . However, this language, consisting of the only string abc , can also be generated by the grammar G_{abc^*} . Thus, we cannot simply specify the complexity of a *language* (or a string set) by referring to whether can be generated by a grammar that includes more complex rules or not. There is confusion on this relationship in the literature and current discussion. One way to see the relation between formal grammars and languages is the following. If all grammars G generating the language L contain e.g. a context-free rule, then L can be said to be context-free. This is important in the context of the thesis since all string sets in psycholinguistic experiments are finite, which implies that they can be generated by regular grammars. In the context of finite string sets, regular grammars are enough to capture the competence in the most strict formal sense. It is however still formally well specified to talk about the classes of the Chomsky hierarchy for finite string sets. Such investigations are one step closer to the performance perspective.

Example 1 The context sensitive grammar G_{abc} consisting of:

$V = S, A, B, a, b, c$	
$\Sigma = a, b, c$	
$R = S \rightarrow AB$	"context free rule"
$B \rightarrow BB$	"context free rule"
$A \rightarrow a$	"regular rule"
$aB \rightarrow ab$	"context sensitive rule"
$abB \rightarrow abc$	"context sensitive rule"

Example 2 The regular grammar G_{abc}^*

$V = S, B, C, a, b, c$	
$\Sigma = a, b, c$	
$R = A \rightarrow aB$	"regular rule"
$B \rightarrow bC$	"regular rule"
$C \rightarrow c$	"regular rule"

Automata are abstract devices that compute functions of the input delivered on an input tape and can also work as language recognition devices or parsers and language generators. The finite state automaton (see Definition 2) generates the same class of languages as finite state (regular) grammars. A second more complex automaton is the push-down automaton (see Definition 3), which generates the same class of languages as the context-free grammars. In order to parse context-sensitive grammars in general, multiple stacks must be used. I will however not show that definition here since the basic memory architecture of the push-down stack is not changed.

Definition 2 A finite automaton, or finite state machine is a quintuple $M = (Q, \Sigma, q_I, q_H, f)$ Where Q is a finite set of states, Σ is a input alphabet, q_I and q_H are the initial and halting states, and f is a transition function $f : Q \times \Sigma \rightarrow Q$

Definition 3 A push-down automaton is a 6-tuple $M = (Q, \Sigma, \Gamma, q_I, q_H, f)$ Where Q is a finite set of states, Σ is a input alphabet, Γ is the stack alphabet, q_I and q_H are the initial and halting states, and f is a transition function $f : Q \times \Sigma \times \Gamma^* \rightarrow Q \times \Gamma^*$ (where both the range and domain are finite sets)

Formal language theory can be informative for research on the neurobiology of language if classes of formal grammars induced by the subject correspond to different levels of behavioral processing difficulties (see also the paragraph on complexity in the end of section 4.1.2). In order to determine which grammar individual subjects have

induced, we need to probe how subjects generalize from the acquisition string set to a (possibly quite different) test set, preferably on the basis of implicit generalization (see Study IV). Automata theory underlines that the manner in which memory resources are integrated into language processing might be important, for example since different memory architectures will typically result in different processing biases. This line of thinking started as early as in the 1960's with the Chomsky hierarchy (see **Figure 2.6**) for formal grammars, which shows that the grammars that were analyzed as more complex grammar require more powerful memory architectures. The formulation of the Chomsky hierarchy as classes of grammars is equivalent to the formulation in automata. It seems more relevant from a psycholinguistic perspective to consider the Chomsky hierarchy as a memory hierarchy. Taking the memory perspective of formal complexity of languages is one example of going in the direction of a performance/algorithmic level model. This is done in Study I. This is a departure from how formal complexity had been studied in the empirical part of the AGL literature so far.

The further study of complexity

The neurobiology of sequence processing in artificial and natural languages would be enriched by similar studies using other ways of inducing complexity, using a wide range of complexity measures. Complexity has been studied in mathematics and theoretical computer science (I have also used it more vaguely in the discussion of how to define implicit learning earlier in this chapter). For instance, using the *Kolmogorov complexity* measure, the complexity of a *string* is here defined as the length of the string when it is described in some universal description language. Another complexity measure is *computational complexity*. Here, *languages* are divided into complexity classes. If the time it takes to recognize whether a string belongs to the language scales with the length of the string in a polynomial time, the language belongs to the P-class. If it scales in non-polynomial time, it belongs to the NP-class. Yet another measure of the complexity of a language (or more generally a function) is circuit complexity. In *circuit complexity*, the complexity of a function is determined by the size of the circuit which implements that function⁸ (Savage, 1998). In the study of what complexity

⁸ Note that formal languages are functions, more specifically indicator functions, mapping a domain of strings to a range of e.g. 0 and 1. If a string is mapped to one, it belongs to the language, otherwise not.

measure best explains the acquisition success of sequence processing mechanisms, a goal is to get clues about mechanistic details.

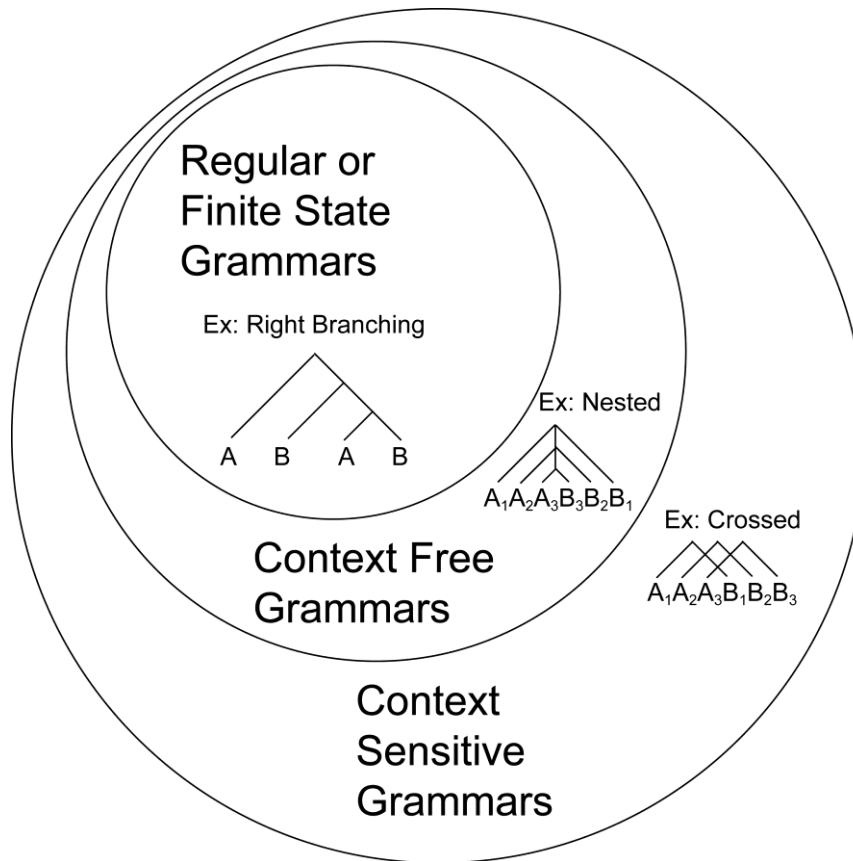


Figure 2.6. The Chomsky hierarchy. Informally, regular or right-linear phrase structure grammars are built from a collection of production rules of the form $S \rightarrow abS$ and $S \rightarrow ab$ (where lower case indicates terminal symbols and S a non-terminal sentence or start symbol). It is the inclusion of the start symbol on the right hand side of the first regular rule ($S \rightarrow abS$) that makes this grammar recursive (Soare, 1996). The non-regular context-free case allows the right hand side to involve terminal symbols around the sentence symbol additional as in $S \rightarrow aSb$ and $S \rightarrow ab$. In the non-regular context-sensitive case, the left hand side has a “context” as exemplified in $a_1a_2a_3b_1b_2b_3 \rightarrow a_1a_2a_3b_1b_2b_3$ (cf., Davis, Sigal, & Weyuker, 1994).

Recursion, infinitude and self-embedding

The presence of a rule with a non-terminal symbol, e.g. S in the rule $S \rightarrow abS$, appearing both on the right and the left hand side, makes a grammar recursive (Soare, 1996). Alternatively, there can be a recursive rule set, e.g. a pair $S \rightarrow abT$ and $T \rightarrow S$ which

would also make the grammar recursive. There has been much ado about recursive grammars in the literature, e.g. in the form of the so called *recursion-only hypothesis* for the faculty of language in a narrow sense. This hypothesis, stating that processing of structure determined by recursive grammars is a uniquely human skill, was outlined in a seminal paper by Hauser, Chomsky and Fitch (Hauser, 2002). This paper built on the empirical finding from one experiment where cotton top tamarinds could learn regular/finite-state grammars, but not the A^nB^n -grammar, which was analyzed as a context-free grammar. Since many regular grammars include recursive rules, a more precise term than the recursion term could have been chosen in this context. The terminology of regular grammars vs non-regular grammars (non-regular grammars include e.g. context-free and context-sensitive grammars) would have been preferable.

As Chomsky notes (Chomsky, 1965), neurobiological systems are finite and thus cannot process, produce, or parse arbitrarily long sequences. As any physical systems, neurobiological systems are noisy and thus work with finite precision (Petersson, 2005). The Chomsky hierarchy is thus clearly a competence theory including so much abstraction that one can question whether it is at all relevant for neurobiological language research. After all, we can only present bounded sentences or sequences in our experiments (Levelt, 1974; Petersson, 2005, 2008; Petersson, Folia, & Hagoort, 2010; Pullum & Scholz, 2009; Pullum & Scholz, 2010). The distinction between processing of adjacent vs non-adjacent dependencies is a partly analogue distinction to the distinction between regular vs non-regular grammars. The distinction between processing of adjacent vs non-adjacent dependencies abstracts away from a lot of detail which is good for some purposes. In a sense, it is the simplest possible way of classifying structure from a memory perspective.

The notion of recursion has also attracted a lot of attention in relation to the so called *infinitude claim*, which states that natural languages are infinitely large sets of expressions. This might build on a misunderstanding between competence and performance type theories (Lobina, 2011) that has delayed progress in the literature. The infinitude claim only makes sense when talking about languages as abstract entities, since any neurobiological system is finite thus cannot entail infinite languages. The fact that many formal grammars stipulate infinite languages was in the 1950's seen as a practical shortcut, as described Pullum (2010). In order to let the formal grammars stipulate finite languages, one would have to add rules with arbitrary upper bounds. Indeed, this seems artificial. As we have already stated however, for translation to the

neural implementation level via the algorithmic/representational level and performance theories, more relevant grammars are the finite-state grammars (Petersson, 2005b) and the equivalent strictly local SL_k grammars (for further suggestions, see Pullum & Scholz, 2001). I think that the study of how brain phenotypes of AGL change as a function of k would be worthwhile.

As pointed out by Pullum (2010), it is not that case that recursive rules necessarily generate infinite languages (see Example 1)⁹. Early on, Chomsky discusses another property close to the recursion property which perhaps captures many of the impressionistic intuitions that has caused the focus on recursion: the property of self-embedding (Chomsky, 1965). Self-embedding is defined as a relative clause embedded in a relative clause of the same type (e.g. a verb-phrase within a verb-phrase, as in “[called the man who wrote the book [you told me about] up]”). He assumes (based on native speaker intuitions) that self-embedding is harder than left or right branching nesting which can be easily solved by iteration, such as in “[John’s [father’s [mother’s cat]]]”. If this is true, this might constrain possible performance models or suggest that self-embedding is distinguished from left or right-branching on a brain implementation level. For Chomsky, if self-embedding is more unacceptable than other nested structures, this suggests a bottle-neck in how many parallel procedures working on a certain phrase-type there can be. In other words, if self-embedding is what makes some nested structures hard to parse, this would be explained if e.g. verb-phrases had one specialized parsing procedure with limited capacity and noun-phrases another. This is an example of a sequential dependency which could be studied both in AGL and in natural language. Since the structure of noun and verb-phrase in many cases is the same (Chomsky, 1970), there is however probably also one aspect of the parser which also treats them the same way.

2.5 COMPUTATIONAL MODELS OF ARTIFICIAL GRAMMAR LEARNING

Computational models come in different flavors (e.g. symbolic, connectionist, spiking neural networks, molecular, etc.) and might all serve their purposes, e.g. as proofs of principles, generating new ideas for higher level descriptions, detailed connected summaries of theories or as illustrations and metaphors aiding e.g. generation of

⁹ However, if there is no way to avoid a recursive rule in the generative grammar stipulating a language, I note that this language is infinite.

experimental predictions. *Connectionism* is a general level theory of cognition spanning the representational and neural implementation level, although language has been the main cognitive domain for discussing the theory. From the connectionist point of view, it is assumed that any cognitive process can be simulated within parallel, distributed, sub-symbolic neuronal networks and that these simulations might provide some additional understanding of the true underlying processes. The foundation of the connectionism school is to emphasize that general purpose learning algorithms are powerful. It has been demonstrated that connectionist simple recurrent networks (which include a hidden layer, providing an internal memory of so called context units) can learn regular grammars (Petersson, Grenholm, & Forkstam, 2005), also with non-adjacent dependencies (Christiansen & Chater, 1999; Tong, Bickett, Christiansen, & Cottrell, 2007). For connectionism style ideas, a good way forward is probably to gradually introduce increasing degrees of biological realism.

McClelland and Rumelhart's development of early connectionist models was motivated by their wish to get rid of explicit but inaccessible rules in language (Rumelhart & McClelland, 1986). They wanted to provide an alternative account where language knowledge is implicit. The notion of implicit and explicit in this context is not exactly the same as when talking about learning systems in the brain, but yet it is no coincidence that the same terms have been used in both contexts. For McClelland and Rumelhart, the statement that language knowledge is implicit knowledge means that there is an absence of rules, at all levels of the brain. In other words, the computation is fundamentally distributed and can only be approximated by a rule.

In Study I and II, we show that lawful classification behavior of sequential stimuli gradually builds up as a consequence of domain general sequence learning. This phase is probably characterized by the absence of rules or possibly the presence of fuzzy rules or incomplete rules. It is possible that if we gave subject enough time, or some particular clues as to how they could pack these rules in a more efficient way, symbolic rules could emerge on top of the implicit knowledge. The implicit knowledge might ultimately transcend into explicit knowledge. One point of view on the connectionist literature is thus that the connectionist models are more closely modeling an early learning phase of complex information (which is the characteristics of implicit learning). As a speculation, explicit knowledge could in this view consist of a particular kind of connectionist network closely approximating symbolic processing. An important open question is to what extent there are segregated neuronal populations

or networks of neuronal populations dealing with information processing that can be described with symbolic models.

Conclusion Chapter 2

I would like to redefine implicit learning as based on two criteria: absence of access to the knowledge acquired and absence of explicit hypothesis testing during acquisition. The complexity of the stimuli is rather a condition that increases the likelihood that the knowledge will be inaccessible. An important future topic in the implicit learning literature is to determine whether implicit learning is a stable trait. The methodological developments used in this thesis provide good conditions to test whether implicit learning is a trait. It is also important to determine which aspect of natural language processing, if any, are related to a potential implicit learning trait.

From the point of view of cognitive neuroscience, performance theories are more interesting than competence theories. Formal grammar theory can provide inspiration for computationally relevant distinctions for the further study of structured sequence processing.

3 BROCA'S REGION AND THE BRAIN

This chapter is a collection of issues that is dealt with in this thesis that are related to the level of brain implementation. I introduce some terminology of Broca's region as well as the transcranial magnetic stimulation method. This introduction is necessary to understand the empirical part of the thesis. I also suggest which methodological developments are necessary for replications of the experiments in the empirical part of the thesis. This discussion shows the methodological limitations of the experiments done.

3.1 BRAIN LEVELS

From the point of view of descriptive neurobiology, the brain is an organ with structure at several levels. In the neurobiology of language research, as in other domains of cognitive neuroscience, the macroscopic level of the brain is in focus, since measurements are cost effective at this level. For example, specialized brain regions, white matter fiber tracts, resting state networks, ongoing oscillations, functional and effective connectivity or more generally, large scale neural networks with spatial and temporal properties, live at the macroscopic level. The classical example of the mesoscopic level is the level of a neural column (about 1 mm scale), localized in the secondary visual regions. This column could compute the recognition of a line with a certain angle, but ongoing oscillations, structured processing in the layers of cortex etc can also be assigned to this level. The mesoscopic level will be tractable by high resolution MRI in the coming decade. Neurotransmitters, membrane potentials, metabolic and signal transduction pathways, action potentials, refractory periods, spike-timing dependent plasticity, spines, glia and interneurons live at the microscopic level.

Brodmann areas still have a central role in cognitive neuroscience although spatially and temporally more complex aspects of neural networks at the macroscopic level are becoming more and more in focus. At the very least, BAs provide a grid of appropriate size for the spatial resolution of group level fMRI. The original purpose of Brodmann's division was to create a cytoarchitectonic map. Recently, it has been found that cytoarchitectonic division coincide with receptorarchitectonic and myeloarchitectonic divisions in Broca's region (Amunts et al., 2010; Amunts & von Cramon, 2006). But what functional significance do these divisions have?

The argument against strong functional significance of these divisions is that central properties of cortical circuits, such as asymmetrical connections between pyramidal cells in different layers, are similar across the brain. Other properties, such as pyramidal cell size and dendritic complexity change gradually in the anterior-posterior direction (Douglas & Martin, 2004). Along the lines of a general cortical architecture, patches of cortex can change its function, such as in congenitally blind where the occipital cortex has been demonstrated to be reorganized for tactile processes (Uhl, Franzen, Lindinger, Lang, & Deecke, 1991). These arguments are often combined with the suggestion that long-range connectivity is what determines the function of a particular patch of cortex and a brain wide network as a whole. But why were these areas wired together in the first place? What determines the function of a particular node in a brain wide network? Although anatomical micro and mesoscopic structure might not exclude the possibility of a certain area performing many different functions, there might be an ever so small bias to perform one function over the other, which after millions of iterations over the course of development will result in e.g. computationally specific representations in that area or patch of cortex.

The function of a particular node in a brain network can be reused for new purposes. This might be an important part of the evolution of higher cognitive process, a hypothesis called the neuronal recycling hypothesis and one example is how high-level vision is recycled during reading (Dehaene, 2005). One of the first patches which were functionally described was Broca's region, a part of the left lateral frontal lobe, centered on the third frontal convolution.

3.2 TAXONOMY OF BROCA'S REGION

Broca's region is named after the anatomist, anthropologist and surgeon Paul Broca, who related lesions in the region to problems with speech production. The condition of problems in speech production is called Broca's aphasia, although it is important to note that this condition does not always include lesions in Broca's region. The term Broca's region is not very rigorously used, as shown in a meta-analysis were 52% of the 542 examined articles talked about Broca's region without a definition or with a broad or misleading definitions (Lindenberg, Fangerau, & Seitz, 2007). The most common well-defined way to talk about Broca's region is that it designates left BA 44 and 45 (27% of the studies examined by Lindenberg et al., 2007, use this definition). The left inferior frontal gyrus, or third frontal convolution, refers to a slightly larger region, also including BA 47, dorsally limited by the inferior frontal sulcus. This gyrus

is divided into pars opercularis, pars triangularis and pars orbitalis (roughly corresponding to BA 44, 45 and 47, respectively) in a complementary system of nomenclature which follows the gyri and sulci rather than cytoarchitectonic differences (see **Figure 3.1**).

In this system, pars opercularis and pars triangularis are bisected by the ascending ramus of the Sylvian fissure. Pars triangularis is ventrally intersected with pars orbitalis along the horizontal ramus of the Sylvian fissure. There is, however, great inter-individual variability in the shape, length, continuity and number of these sulcal contours which gives rise to the great variability in size, surface area and volume of the pars opercularis and pars triangularis (Keller, Crow, Foundas, Amunts, & Roberts, 2009).

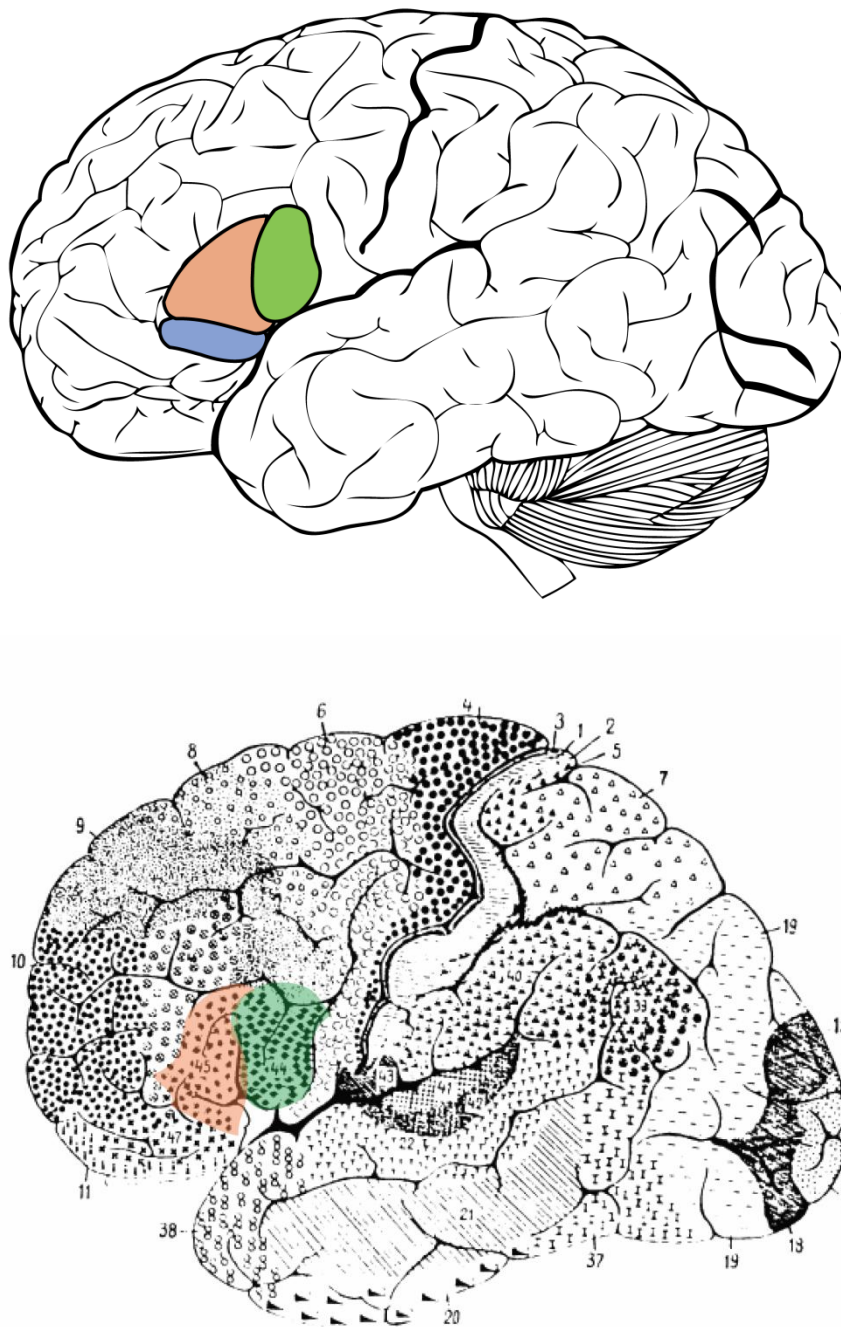


Figure 3.1. The two nomenclature systems of Broca's region. Above is the anatomically division into pars opercularis, pars triangularis and pars orbitalis. Below is the cytoarchitectonic division into BA 44, 45 and 47.

BA 44 and 45 both have six-layers of cortex. The cytoarchitectonic properties of these areas change in a stepwise manner in the posterior-anterior direction from BA 44 to 45. BA 44 is dysgranular, meaning that there is a tendency to a presence of the granular layer IV, while in BA 45 the granular layer IV is present (Keller, Crow, Foundas, Amunts, & Roberts, 2009; Sanides, 1964). It has been shown that the cellular morphology of areas 44 and 45 are more similar to each other than to other cytoarchitectonic regions of the brain, such as area 6 and visual areas V1 and V2 (Amunts & von Cramon, 2006). BA 47 is also more different to BA 44 and 45 than BA 44 is to BA 45. There is also the presence of large pyramidal cells in layers III and V in both areas 44 and 45 (Amunts et al., 2010; Amunts et al., 1999; Judas & Cepanec, 2007).

An important debate is whether Broca's region has a leftward asymmetry. In any case, this asymmetry is less pronounced than in the planum temporale. The white matter tracts reaching out from Broca's region constitute the dorsal pathway (arcuate fasciculus), which is a part of the superior longitudinal fasciculus. In addition, there is a ventral pathway consisting of the fasciculus uncinatus and connecting the middle and posterior portion of the superior temporal region with the inferior frontal gyrus and the insula and the extreme capsule, connecting the anterior temporal pole with the anterior and middle parts of the inferior frontal gyrus. There is evidence that these pathways are stronger in the language dominant hemisphere (Powell et al., 2006).

3.3 TRANSCRANIAL MAGNETIC STIMULATION

Like any other complex system, the brain can be studied through reverse engineering. By spatially and temporally focal perturbation of brain activity, we can refine our description of the functional role of a piece of cortex; determine how different regions interact and the timing of the interaction. Brain stimulation tools such as transcranial magnetic stimulation (TMS) and transcranial direct current stimulation (tDCS) are recently developed means to this end. Crucially, brain stimulation tools can establish causal relations between a part of cortex and a task measuring some computational level construct.

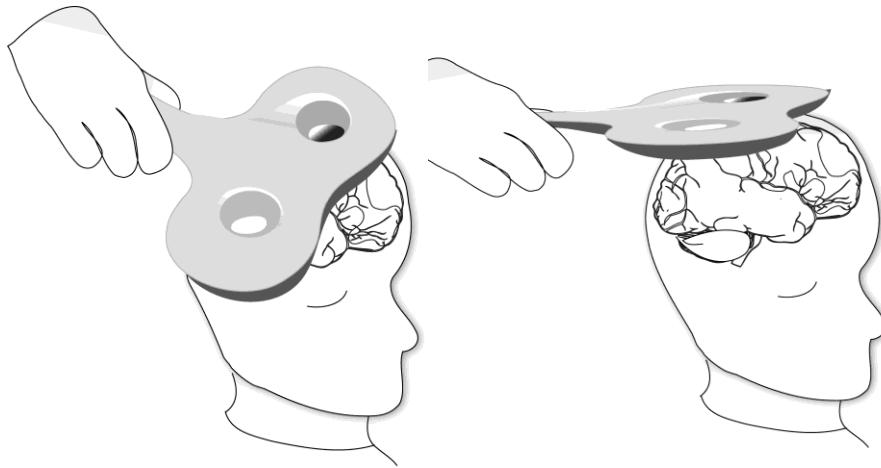


Figure 3.2. Transcranial magnetic stimulation as we applied it to the left inferior frontal gyrus and the vertex control region.

TMS as applied in this thesis (see **Figure 3.2**) partly suffers from the same critique as FMRI/PET group-level based approaches. As Federenko & Kanwisher (2009) point out in relation to activation studies, intersubject anatomical variability may result in insensitivity to detect a brain area with a particular function. Stimulation applied to a group level activation target suffers from the same source of insensitivity. This is probably the main factor reducing sensitivity in Study III and IV. We have tried to minimize this by taking into account the large macro level subject specific anatomy, i.e. the overall size and shape of the brain, as measured with a structural MRI scan. The overall size and shape of the brain is then transformed into a standard brain size and shape. This procedure is called normalization¹⁰. When determining our target region for stimulation in a specific subject, we inverted the transformation matrix from the normalization of that particular subject's structural scan and apply the inverted matrix to our predefined target (BA 44/45) in a standard brain.

On one hand, as with all problems of sensitivity, the problem of intersubject anatomical and functional anatomical variability is mainly an argument against interpretation of negative results. On the other hand, the alternative approach of localizing the target with single subject functional activations would probably be fruitful when trying to replicate the findings in this thesis; since it is expected to increase significance and effect sizes. Functional localization can be done either with a

¹⁰ Gyrus and sulcal patterns are also part of macro level anatomy, but as of today there are no normalization procedures on this level.

localization task or with the task tested in relation to TMS. The downside of the functional localization approach is that is slightly more circular. If a TMS effect is found, it is harder to make the generalization this effect to an exact spatial location over subjects, since the exact target location actually might have varied quite a bit. The functional localization approach is thus based on the assumption that the division into functional brain regions is stable over subjects although their exact location might vary (e.g. on the order of a cm). The combination of studies across these two approaches could yield the desirable combination of robust effects and the possibility to ascribe a causal relation between activity in a fairly specified spatial location and a computational level concept.

Distal effects

Studies monitoring the effects of TMS with fMRI and ERP patterns have observed changes in other regions than the stimulated area (Hilgetag, Theoret, & Pascual-Leone, 2001; Taylor, Nobre, & Rushworth, 2007). Moreover, results from a combined TMS and fMRI study (Sack et al., 2007) suggest that distal fMRI changes are secondary to primary task related changes induced by TMS at the target site. No distal effects were observed in the absence of target site activity before TMS. This was demonstrated both with a control task not engaging the target site and the contra lateral homotopic control region not causally related to the task. Altogether, this suggests that the default interpretation of a causal relation between target and task in case of an observed performance change after TMS is valid (Sack et al., 2007). It is plausible that distal effect are a mainly a result of TMS modulating activity indirectly through functionally connected brain network, rather than as consequences of its direct influence on activity at the target site. Based on the finding that the caudate nucleus is sensitive to grammaticality (Forkstam, Hagoort, Fernández, Ingvar, & Petersson, 2006), together with the result that rTMS (albeit at 10 Hz) to the left prefrontal cortex can trigger dopamine release in the caudate nucleus (Strafella, Paus, Barrett, & Dagher, 2001), it is possible that distal effects of our stimulation could be present in the basal ganglia. This hypothesis could be tested by combining offline TMS with fMRI.

Finally, I would like to clarify what is meant with a causal relation between a part of cortex and a task (in our case artificial grammar classification) measuring some computational level construct (in our case sequence processing). A brain region plays a causal role in a task if the region is a *non-redundant part of a sufficient network of regions* that together subserve the task (Mackie, 1965). Thus, by showing a causal role

of Broca's region in sequence processing, we can show that Broca's region is non-redundant part in one network solution which is sufficient to solve the task. Since the TMS effect is found across participants, we can also conclude that the sequence processing network where Broca's area is a node is used in a major part of our subjects. We can however *not* show that activity in Broca's region is *necessary* for sequence processing, since there might be other brain networks that are sufficient to subserve the task. The causal role of brain regions as determined from intervention by brain stimulation techniques thus investigate brain networks during normal conditions and the value of these measurements are based on stability of the brain networks recruited by a task over subjects.

Conclusion Chapter 3

Although long-range connectivity in a brain network partly determines the function of a particular patch of cortex and the brain wide network as a whole, there might be an ever so small bias to perform one function in a particular patch of cortex, e.g. because of its cytoarchitectonic structure. This might, after millions of iterations over the course of development, result in functionally specific brain regions.

Further studies on the TMS over Broca's region should complement the anatomical localization approach used in the thesis, e.g. by using a functional localization approach. Distal effect in our paradigm could be expected, for instance in the basal ganglia. There effects are not necessarily a direct consequence of the stimulation of Broca's region, but can also be a consequence of the brain adapting to the perturbation by TMS, e.g. as compensatory activity to restore performance specifically when Broca's region is used.

PART 2 – REVIEW AND DISCUSSION OF THE EMPIRICAL WORK

Chapter 4 and 5 are modified pieces from Uddén, J., & Bahlmann, J. A rostro-caudal gradient of structured sequence processing in the left inferior frontal gyrus (submitted manuscript).

The contribution of this thesis is the combination of (1) the reanalysis of the structured sequence processing perspective on Broca's region in the left inferior frontal gyrus (LIFG) and (2) the empirical work which supports and extends the scope of this perspective to implicit processing of non-adjacent dependencies, crucially by showing that Broca's region plays a causal role in structured sequence processing. This perspective provides a way to express common structural aspects of language, music and action, which all engage the LIFG and it facilitates the comparison of human language and structured sequence processing behavior in animals.

In the last decade, a growing number of papers, including Study III and IV, has combined the AGL paradigm with neuroimaging methods to study sequence processing, pattern perception and/or rule learning (Bahlmann, Schubotz, & Friederici, 2008; Bahlmann, Schubotz, Mueller, Koester, & Friederici, 2009; de Vries, Barth, Knecht, Zwitserlood, & Floeel, 2010; Dominey, Hoen, Blanc, & Lelekov-Boissard, 2003; Folia, Forkstam, Ingvar, Hagoort, & Petersson, 2011; Folia, Uddén, De Vries, Forkstam, & Petersson, 2011; Forkstam, Hagoort, Fernandez et al., 2006; Friederici, Bahlmann, Heim, Schubotz, & Anwender, 2006; Friederici, Steinhauer, & Pfeifer, 2002; Petersson et al., 2010; Petersson et al., 2004; Uddén et al., 2008). No consensus on what results mean for the functional role of the LIFG, which is consistently linked to processing of artificial grammars across experiments, has been reached within this literature. In addition, a broader take on how the results should be integrated from a general cognitive neuroscience perspective is missing.

The purpose of Chapter 4 is to describe the so called structured sequence processing perspective, which provides a framework in which a range of AGL experiments can be integrated. I review the empirical work in the thesis and the literature on LIFG activation across different cognitive tasks involving processing of sequentially structured stimuli, including sequence processing per se (as in AGL), but

also language, music and the action domain. I then underline the potential of the structured sequence processing perspective on LIFG function.

The purpose of chapter 5 is to apply the structured sequence processing perspective to an open question somewhere in between the sequence and language processing literature on LIFG function and the cognitive control literature on lateral prefrontal cortex (PFC) function. This application is fairly independent from the empirical thesis work, although the ideas of chapter 5 grew out of the thesis work, in collaboration with Jörg Bahlmann.

It is an ongoing project in cognitive neuroscience to describe the functional organization of the lateral PFC in higher order cognitive tasks, such as goal directed behavior and language processing. One recent summarizing finding on lateral PFC function is a rostro-caudal axis in terms of abstraction or cognitive control demands (Badre & D'Esposito, 2009; Botvinick, 2008; Fuster, 1997; Koechlin & Hyafil, 2007). I use the structured sequence processing perspective to critically examine and integrate the functional segregation of phonology, syntax and semantics across a rostro-caudal axis in the LIFG, with a general rostro-caudal axis in the lateral PFC. I focus on structural sequence processing in the domains of language, action and music in the context of on the LIFG, which spans BA 44, 45 and 47, in the ventro- lateral PFC.

4 THE STRUCTURED SEQUENCE PROCESSING PERSPECTIVE

I will start with a theoretical motivation of the sequence processing perspective. The structured sequence processing perspective is an attempt at understanding LIFG function in general. The problem of describing language as a neurobiological system is addressed in parallel. Chances are that LIFG function will be easier to describe in general mathematical language, since such a formulation facilitates the articulation of, and emphasis of, common aspects across traditional cognitive domains, such as language, actions and music (2010; Folia, Uddén et al., 2011; Friederici, Bahlmann et al., 2006; Petersson, 2008).

The central empirical observation in favor of the sequence processing perspective is that when studying language processing, divided into phonological, syntactic and semantic aspects, all of these robustly activates the LIFG (Bookheimer, 2002; Indefrey, 2011; Lindenberg et al., 2007; Poldrack et al., 1999; Vigneau et al., 2006). The same is true for music (Gaser & Schlaug, 2003; Janata & Grafton, 2003; Maess, Koelsch, Gunter, & Friederici, 2001; Patel, 2003; Patel, Iversen, Wassenaar, & Hagoort, 2008) and action processing (Hamzei et al., 2003; Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2005). These results can be partly explained by common sequence processing mechanisms in the LIFG, used across the domains of language, music and action. In LIFG, language might thus be processed as sequences of phonemes, syllables, words and sentences, music as rhythmic sequences or tonal sequences of motifs and melodic passages and grasping movements or finger movements as sequences of actions. The domain of action is relatively underexplored from the sequence processing perspective. Sign language and sequences of dance movements (Opacic, Stevens, & Tillmann, 2009) should be explored with neuroimaging from this perspective.

What is a structured sequence? A sequence is an ordered combination of elements. Sequential encoding is necessary for stimuli presented in the temporal domain, such as speech, music or sequential movement patterns, such as in gestures or dance. Examples of stimuli that are probably encoded in other knowledge structures are visual patterns or scenes, which have complex spatial frequencies, or stimuli which are non-ordered combinations: e.g. combinations of tastes and smells in a dish, social

networks or conceptual networks or other networks (for suggestions of alternative knowledge structures see Tenenbaum, Kemp, Griffiths, & Goodman, 2011).

The sequence perspective on LIFG function can be illustrated in the language domain. The phonological and syntactic domains as well as at least parts of the semantic domains are examples of knowledge acquired and processed with sequence processing mechanisms, operating on linguistic elements. Written and spoken language, as well as phonology, syntax and semantics thus have a common knowledge structure in the form of sequences with adjacent and non-adjacent dependencies¹¹. Syntactic structure can be seen as sequences of words (Christiansen et al., 2010; Christiansen & MacDonald, 2009; Folia, Forkstam et al., 2011; Folia, Uddén et al., 2011; Friederici, Bahlmann et al., 2006; Misyak, Christiansen, & Tomblin, 2009; Petersson et al., 2010), morphosyntactic structure as sequences of word fragments and phonological structure as sequences of phonemes, onsets and codas, etc (for recent sequence processing perspectives on phonological structure, see (Bonatti, Pena, Nespor, & Mehler, 2005; Cristià, Seidl, & Gerken, 2011; Heinz & Idsardi, 2011). Recent modeling work on reading time measurements from a large text corpus suggest that sequence models are better at explaining reading times than e.g. hierarchical phrase structure grammars (Frank & Bod, 2011).

As expected from the sequence processing perspective on the LIFG, converging evidence suggest that the LIFG (BA 47/45/44) - as part of the perisylvian language network - is engaged e.g. in semantic, syntactic and phonological processing in natural language (Bookheimer, 2002; Indefrey, 2011; Lindenberg et al., 2007; Vigneau et al., 2006). These activations in LIFG can thus be seen as resulting from operations on (1) sequences of words or lexical items to produce full sentences. I will call this operation sentence level processing, as opposed to (2) word level processing, which involves operations on sublexical items to produce words, i.e. creating words from syllables or phonemes. I will now elaborate on the functional neuroimaging evidence in favor the sequence processing perspective on LIFG function¹² by looking at evidence from the thesis and from domains other than natural language.

¹¹ It has however been argued that phonological sequential structure is less complex, e.g. perhaps involving less non-adjacent dependencies, compared to syntactic sequence structure (Heinz & Idsardi, 2011).

¹² The proposed structured sequence processing machinery includes (but is not limited to) the LIFG. I am not focusing on the similarities and differences between left and right hemispheric contributions.

4.1 OVERVIEW AND DISCUSSION OF THE EMPIRICAL STUDIES

A critical test of the sequence processing perspective on LIFG function is whether the LIFG is involved in processing recently learned or acquired sequences, independent of the kind of elements the sequences are built from. These questions have been explored using the AGL paradigm (Forkstam & Petersson, 2005b; Stadler & Frensch, 1998) as well as in the music and action domains. The contribution of the empirical studies in this thesis is best understood in this context.

As described in chapter 2, the AGL paradigm consists of an acquisition phase and a test phase. In the acquisition phase of AGL, subjects are exposed to sequences generated from a complex rule system. The acquisition phase can be conducted to promote implicit or explicit learning processes, which is the first design choice we made. The rule system consists of a formal grammar that generates a set of rule-following, patterned or *grammatical* sequences. Subjects are informed, after acquisition, that the sequences were generated according to complex rules and asked to classify novel items as grammatical or not. The pattern consists of dependencies between adjacent or non-adjacent items and this is the second design choice explored. These two design choices place the main contribution the first two empirical studies in this thesis, which are behavioural studies, in the wider context of the AGL field.

4.1.1 Study I & II: Implicit acquisition of adjacent and non-adjacent dependencies

In Study I, we investigated implicit learning of multiple non-adjacent dependencies. We tested whether robust performance levels, similar to those observed with adjacent dependencies, could be reached. It has already been shown that non-adjacent dependencies can be processed explicitly.

Although more exposure and/or time for consolidation and abstraction are needed in the acquisition of non-adjacent dependencies compared to adjacent dependencies, we could demonstrate sufficient performance levels after nine days of acquisition. The results do not suggest separate mechanisms for the acquisition of adjacent and non-adjacent dependencies. We also wanted to compare acquisition of two different organizations of multiple non-adjacent dependencies: so called nested or crossed structures, in order to assess predictions from the so called push-down stack model as

well as natural language results (Bach, Brown, & Marslen-Wilson, 1986). This part of Study I is discussed in chapter 6.

We tested two different organizations of the multiple non-adjacent dependencies, into crossed or nested structures (see **Figure 4.1**). This was important to demonstrate the robustness of the acquisition effect. Since we tested crossed and nested structures in two different groups and then crossed structures in an additional group of participants, Study I includes replications in three independent subject populations with three slightly different grammars, all including multiple non-adjacent dependencies. Robust implicit learning of multiple non-adjacent dependencies is thus a replicable finding independent of particular stimulus set, subject population, and the organization of the dependencies into crossed or nested structures.

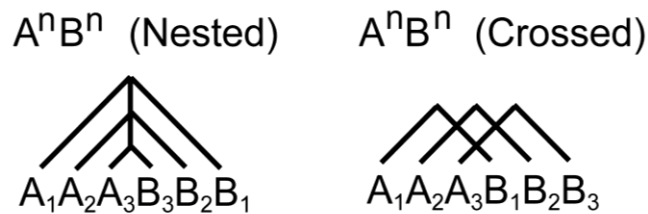


Figure 4.1. $A^n B^n$ grammar with two different kinds of organizations of the multiple non-adjacent dependencies. The dependencies are indicated by the drawn lined above the elements.

In Study II, we challenged the (implicit) acquisition mechanism by studying two levels of more advanced generalizations. At the first level, subjects had to generalize from the particular combinations of the non-adjacent dependencies they had seen during acquisition, to new combinations. At the second level, the subjects had to generalize to sequences including more non-adjacent dependencies than they had been exposed to. Both of kinds of generalizations control for the so-called repetition structure account of the successful classification. In this account, “FFDLLP” and “DDFPPL” can be represented as “112334”, where the later, abstract representation captures the structure of repetition of certain elements. The *repetition structure* is a term coined by Brooks and Vokey (1991). The repetition structure is however merely one of many plausible alternative forms that representations of non-adjacent dependencies might have. More generally, testing the degree of advanced generalizations possible after implicit acquisition demonstrates the power of the acquisition mechanisms we are studying while at the same time determining its limits.

In Study II, we demonstrated implicit generalization by sequence learning mechanisms exposed to complex sequences with multiple crossed non-adjacent dependencies. Generalization was present from sequences with three non-adjacent dependencies to new combinations of three crossed non-adjacent dependencies that were not presented in the acquisition material, and to four crossed non-adjacent dependencies. Individual differences in classification accuracy of short non-adjacent dependencies correlated with classification accuracy of long non-adjacent dependencies. High accuracy on short sequences did not translate into high accuracy on long sequences for any participant. Additional evidence for implicit generalization to longer non-adjacent dependencies came from the response time analysis.

These results extend our knowledge of the strength of implicit sequence learning mechanisms. It is to our knowledge the largest study in terms of the number of subjects, where a long exposure phase was combined with acquisition of complex stimuli and including tests of advanced generalizations. The results indicate that implicit generalization is gradual rather than instantaneous (see **Figure 4.2**). Interestingly, we show generalization to structures that are most likely not present in any human language (Karlsson, 2007). We cannot be sure that all possible human languages have been realized. However, if the language acquisition system would be highly specific and constrained, the likelihood of successful acquisition of structures beyond what is present in languages across the world is smaller. The fact that these structures are still acquired is thus evidence (albeit weak evidence) in favour of general purpose mechanisms and against the need for specific learning mechanisms.

Our results provide evidence against two kinds of representations that have been suggested for processing of non-adjacent dependencies in the literature: the repetition structures mentioned above, as well as context-sensitive grammars. If participants had instantiated a context-sensitive grammar, instantaneous generalization would have been more likely. We cannot exclude empirically that there is a context sensitive *competence* grammar at some level, but that performance factors, such as limited working memory capacity, explains the gradual/weak implicit generalization.

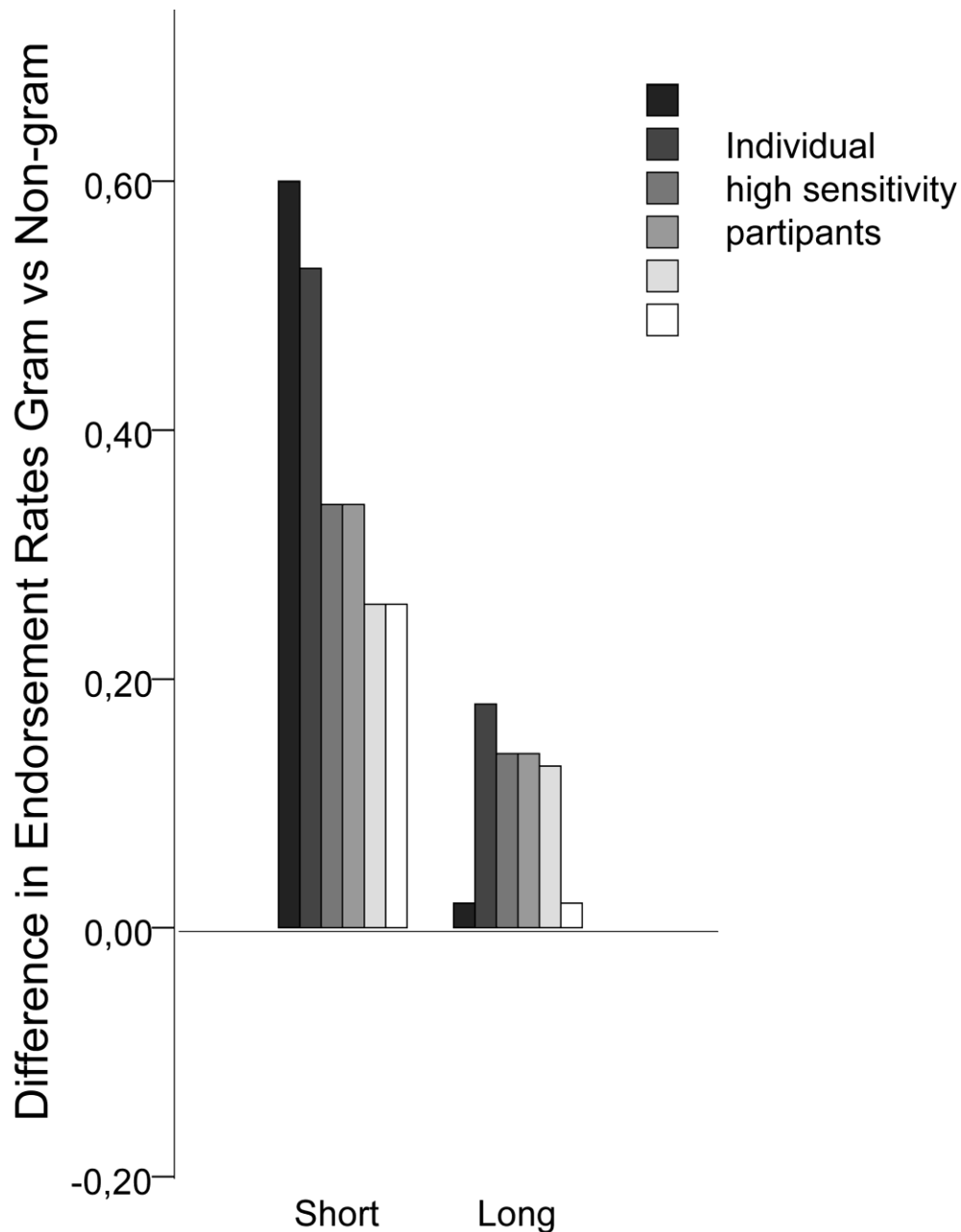


Figure 4.2 Additional data from Study II, not presented in the study. Classification performance in accuracy of G = Grammatical and NG = Non-grammatical sequences. Baseline= Baseline Preference, Pref = Day 9 Preference classification. Gram = Day 9 Grammaticality classification. On the y-axis we see the sensitivity to the grammaticality factor, measured as the difference in endorsement rates between grammatical and non-grammatical sequences. This is displayed for each subject that had sensitivity above 0.20 for short sequences in the grammaticality test. In none of these subjects did this translate to sensitivity above 0.20 for long sequences. Thus, implicit generalization is gradual rather than instantaneous.

4.1.2 Study III & IV: The causal role of Broca's region

Lesions of Broca's region are often found without persistent syntactic deficits (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 1994) in up to half of the cases (Dronkers, 2000). Thus, previous studies shows that lesions in Broca's region are neither necessary nor sufficient to produce e.g. syntactic deficits (Kaan & Swaab, 2002). In Study III and Study IV, we tested whether activity in Broca's region is causally related to the ability of subjects to discriminate between grammatical and non-grammatical sequences from an artificial grammar. Starting with Study III, we stimulated the LIFG and right inferior frontal gyrus (RIFG). In addition to the main question, we wanted to test whether there would be a stronger causal relation between the inferior frontal gyrus and outcome measures of AGL in the left compared to the right side.

We used a design comparing classification before and after transcranial magnetic stimulation (TMS) at the end state of acquisition of an artificial grammar with mainly adjacent dependencies. Classification accuracy improved after TMS to both the left and right inferior frontal region. This effect was significant when considering grammatical and non-grammatical sequences together and also significant for non-grammatical sequences analyzed separately. The effect was not significant when testing grammatical sequences separately. When analyzing response times, again non-grammatical sequences were more affected by TMS. This points to some consistency over which kind of processing was affected by the stimulation (i.e. both accuracy and speed of the processing of violations was affected).

There were significantly shorter response times after left-sided TMS and significantly longer response times after right-sided TMS for non-grammatical items. The items were driving a 3-way interaction between side, test and grammaticality. The interaction between grammaticality and test was significant after rTMS of the LIFG but not the RIFG. This suggests that the effect of TMS was regionally specific and more strongly related to LIFG processing of artificial syntactic violations. This was predicted by earlier FMRI results, where activations were strongest on the left side (Forkstam, Hagoort, Fernandez et al., 2006). These results provide evidence that the inferior frontal region is causally related to discrimination between grammatical and non-grammatical sequences and that this relation is stronger on the left side.

In Study IV, we wanted to investigate a potential causal relation between activity in Broca's region and discrimination of grammatical and non-grammatical sequences

with non-adjacent (crossed) dependencies. We also wanted to replicate the findings of Study III on adjacent dependencies using a modified stimulation protocol controlling for time and repetition effects (see **Figure 4.3**). In Study III, we compared classification behavior before and after stimulation. This comparison does not control for the effect of time and repetition. We could however indirectly argue against the presence of such effects in a control experiment without any TMS in between two classification sessions. In Study IV, we wanted to handle this issue by design.

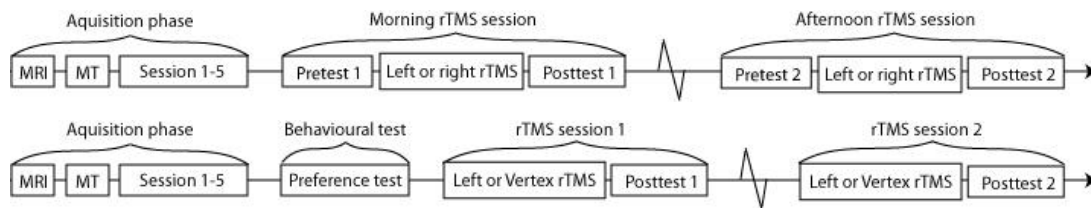


Figure 4.3 Comparison of the designs of Study III and IV. In Study III, we compared classification behavior before and after stimulation. In Study IV, we compared classification after stimulation of the left inferior frontal gyrus to classification after stimulation of a language irrelevant control region (vertex).

In a first experiment, we showed a decrease in classification performance of non-adjacent dependencies after stimulation of LIFG, but not after stimulation of a language irrelevant control region (vertex). In a second experiment, we used the same design but testing adjacent dependencies, as in Study III. The results show a decrease in sensitivity to the grammaticality factor in terms of response times, specifically after TMS to LIFG. We thus demonstrate a causal connection between Broca’s region and the processing of artificial grammars in general, independent of whether the dependencies are adjacent or non-adjacent. The effect cannot be attributed to non-specific effects of TMS.

Improvements and impairments

When looking at Study III and Study IV together, the first discrepancy is that Study III finds an improvement of classification performance after stimulation (compared to before) and Study IV finds an impairment after stimulation compared to when a language irrelevant control region had been stimulated. Although we did not have any hypothesis about the directionality of the effect in any of these experiments, a discussion of this is warranted. Improvements and impairments of language tasks are roughly equally common after TMS to the inferior frontal gyrus. Impairments are somewhat better understood theoretically and a bit more common after 1 Hz inhibiting TMS.

It is possible that Study IV would have shown an improvement if we had included a pretest (which was used in Study III), due to the following reason: It is known that the effects of TMS are state-dependent (Pasley, Allen, & Freeman, 2009; Silvanto & Muggleton, 2008). Recent findings show that the effect of TMS depends on the state of the stimulated neocortical region in general (i.e., the profile of neural activity preceding or during stimulation) and this principle was demonstrated by stimulation to Broca's region (Cattaneo, Devlin, Vecchi, & Silvanto, 2009). For example, experimentally induced cognitive activity prior to stimulation influences how different neural populations are affected by TMS, including the direction of effects (i.e., if an enhancement or impairment of performance is observed). In Study IV, brain adaptations that live on a relatively short time-scale were not present, unlike the situation in Study III. Altogether, this is a possible account of the difference in terms of the direction of the effect between Study III and IV.

The previous literature has reported both interference and facilitation effects on behavior after TMS. Several natural language studies have reported performance improvements after TMS to language relevant regions, including the left inferior frontal region (Andoh et al., 2006; Boroojerdi, Grafman, & Cohen, 2001; Harpaz, Levkovitz, & Lavidor, 2009; Joshi, 1990; Kirschen, Davis-Ratner, Jerde, Schraedley-Desmond, & Desmond, 2006; Martin et al., 2009; Mottaghy, Sparing, & Topper, 2006; Naeser et al., 2005; Pulvermüller, Hauk, Nikulin, & Ilmoniemi, 2005; Sakai, Noguchi, Takeuchi, & Watanabe, 2002; Stoeckel, Gough, Watkins, & Devlin, 2009; Töpper, Mottaghy, Brüggmann, Noth, & Huber, 1998). On the other hand, there are also many studies on natural language where TMS impaired performance, again, many of them with the left inferior frontal region as target (Aziz-Zadeh, Cattaneo, Rochat, & Rizzolatti, 2005; Devlin, Matthews, & Rushworth, 2003; Epstein et al., 1999; Flitman et al., 1998; Köhler, Paus, Buckner, & Milner, 2004; Manenti, Cappa, Rossini, & Miniussi, 2008; Pobric, Jefferies, & Lambon Ralph, 2007; Schuhmann, Schiller, Goebel, & Sack, 2009; Shapiro, Pascual-Leone, Mottaghy, Gangitano, & Caramazza, 2001; Verwey, Lammens, & Honk, 2002).

When the variability of TMS effects after stimulation of language related brain regions in ten studies was reviewed, three showed decreased response times and seven showed increased response times (Andoh & Martinot, 2008). Using transcranial direct current stimulation (tDCS), which is another imaging method which can provide evidence for causal brain function, but which has less spatial resolution compared to TMS, improvements in language related tasks after stimulation has been demonstrated

(de Vries, Barth, Knecht, Zwieterlood, & Floeel, in press; Sparing, Dafotakis, Meister, Thirugnanasambandam, & Fink, 2008). A majority of the low-frequency repetitive TMS studies on language produce interference effects (Cappelletti, Fregni, Shapiro, Pascual-Leone, & Caramazza, 2008; Knecht et al., 2002; Pobric et al., 2007; Robertson, Tormos, Maeda, & Pascual-Leone, 2001; Shapiro et al., 2001; Verwey et al., 2002) although some show enhancements (Andoh et al., 2006; Andoh et al., 2008; Martin et al., 2009; Naeser et al., 2005). These findings suggest that perturbations of a neural network with TMS or tDCS protocols do not necessarily lead to impaired performance. In this context, it has been suggested that facilitation effects, or behavioral improvements, are harder to interpret, since small currents introduced in neural tissue should be treated as noise and thus produce interference (Devlin & Watkins, 2007). However, theories of inter-hemispheric compensation provide one possible mechanism for enhanced performance after TMS (Andoh & Martinot, 2008; Sack, Camprodon, Pascual-Leone, & Goebel, 2005). I will now explain the mechanisms suggested. Brain stimulation may shift the balance of activity between the two hemispheres to improve performance, at least on a restricted set of tasks in a restricted time window. From the point of view of the complete system on longer time scales, this shift in balance might however not be beneficial. More generally, any multiple system model where the different systems compete to influence downstream processing, or where the systems inhibit each other, can explain enhancements in the same way. Taken together, the empirical literature suggests that the factors determining whether TMS will improve or degrade task performance are currently not well-understood.

Response times vs accuracy

In Study III, we find differences in classification behavioral both in terms of accuracy and response times. In Study IV, TMS affected accuracy of classification of non-adjacent dependencies and response times of classification of adjacent dependencies. I can only speculate on the reason for this difference. Memory requirements are clearly different in the two cases. Another part of the explanation for the absence of a perturbation effect on accuracy on adjacent dependencies might be the more robust classification accuracy for adjacent compared to non-adjacent dependencies during control stimulation, as indicated by stronger sensitivity to the grammar in terms of classification accuracy in adjacent compared to non-adjacent dependencies. We might be interfering with the processing of adjacent dependencies at a later stage of the acquisition process. This might translate into a slightly different neural processing

configuration, whether in terms of micro- or mesoscopic structure or in terms of connectivity, which is somehow more robust to changes in accuracy. On the other hand, we did see changes in accuracy of classification of adjacent dependencies in Study III. Thus, the complete pattern of results can only be explained by taking both the different protocol, (i.e. state dependent effects of TMS) and the performance differences in classification of adjacent and non-adjacent dependencies into account.

Discussion of the causal relation between Broca's region and the crossed dependencies

From the perspective of formal language theory (Davis, Sigal, & Weyuker, 1994), crossed dependencies are generated and parsed by context-sensitive grammars, constituting the most complex class of formal grammars relevant for natural language processing within the Chomsky hierarchy (Chomsky, 1956). However, it is uncontroversial that any physically realizable computational system is necessarily finite with respect to its memory organization and that it processes information with finite precision, e.g., due to presence of internal and external noise or architectural imprecision (Maass, Joshi, & Sontag, 2007; Minsky, 1967). This makes the Chomsky hierarchy less relevant for classical cognitive models and it makes the dynamical neurobiological analogue of the finite-state architecture relevant for non-classical computational models (Petersson, 2005a, 2005b, 2008; Petersson et al., 2010, in press). Thus, I do not interpret the results as supporting the presence of representations in Broca's region that correspond to context-sensitive grammars. However, Study II shows that there are representations in Broca's region that correspond to the crossed organization of non-adjacent dependencies. Study II in particular is informative for how such representations might look like since the representations must support the kind of generalizations that are observed.

In the context of neurobiological language research, the infinite memory aspect inherent in the Chomsky hierarchy makes it primarily relevant as a memory hierarchy, specifying the necessary memory resources needed for a given level of expressivity (Levelt, 1974; Petersson, 2005b; Petersson et al., 2010; Pullum & Scholz, 2009; Pullum & Scholz, 2010). Bounded versions of the different memory architectures entailed by the hierarchy might be relevant. For example, the push-down stack is a memory architecture corresponding to the class of context-free grammars, and it is conceivable that a bounded push-down stack is used in language processing, as suggested by for example by Levelt (1974) as one possibility. However, in principle it is possible to

extract structurally simpler grammars, such as finite-state grammars, from bounded context-sensitive dependencies. The finite-state grammars have an internal memory structure, but can also interface with a bounded external memory such as one or many bounded push-down stacks or a bounded register architecture (Savage, 1998). These different computational solutions might provide processing advantages in certain situations. Some evidence that subjects might use push-down stacks is provided in Study I, as discussed in chapter 6. Future research will have to investigate these and other memory architectures as well as their neural implementations.

The causal role of Broca's region: conclusions of Study III and IV

Syntax processing deficits can be found in the absence of lesions to Broca's region, and conversely, lesions of Broca's region are often found without persistent concordant syntactic deficits (Dronkers et al., 1994), sometimes in as much as 50% of the cases (Dronkers, 2000). Our results cast new light on these results. For instance, it is possible that these patients would have been impaired on artificial grammar learning, where they cannot rely on semantic information (for similar results in natural language processing in Broca's aphasia see Caramazza & Zurif, 1976), and where they have to process recently acquired structures. Indeed, there is evidence supporting impaired sequence processing after lesions to this region (Christiansen et al., 2010; Hoen et al., 2003; Pothos & Wood, 2009). Our demonstration of a causal connection between activity in Broca's region and grammaticality judgments in artificial syntax processing is important since grammaticality judgments are sometimes spared in Broca's aphasics that at the same time display impaired sentence processing (Linebarger, Schwartz, & Saffran, 1983). The fact that the results replicate over classification of sequences from fundamentally different grammars (i.e. with adjacent or non-adjacent dependencies) in Study I and II is important since they are potentially processed differently.

There is an ongoing debate on how much we can infer in terms of what kind of representations subjects might form as a result of exposure to sets of bounded sequences. We are cautious of interpreting exactly how subjects might process or represent our sequences. Different subjects probably differ in their representations, as indicated by different generalization abilities across subjects in Study II. We can however be sure that subjects processed non-adjacent dependencies in one way or the other, since the violations were specifically probing the knowledge of these dependencies. Our results show that TMS to Broca's region robustly manipulates

ongoing classification of bounded sequences, across structures which are fundamentally different and thus potentially processed differently¹³.

4.1.3 Implicit vs explicit AGL revisited

To summarize and further integrate this exposé of the studies in this thesis with the rest of the literature, let us take a step back to the distinction between implicit and explicit AGL. This is important since the explicit AGL is the more common way of performing AGL studies. Our methodological changes were aimed at minimizing contamination from explicit processes. I will now evaluate this aspect of the studies in relation to the AGL field as a whole.

Specific parameters of the AGL paradigm will result in implicit learning, relatively free from explicit problem solving strategies (for a further discussion of what implicit means in this context, see Forkstam & Petersson, 2005b). In implicit artificial grammar learning experiments, robust classification performance is accompanied by robust functional changes in language relevant brain regions, including the LIFG (Forkstam, Hagoort, Fernandez et al., 2006; Lieberman et al., 2004; Petersson et al., 2010; Petersson et al., 2004). In addition, this region plays a causal role in classification of artificial grammars at the end stage of implicit acquisition, as demonstrated in Study III-IV. Mid LIFG has been shown to be engaged during acquisition and processing of AGL also when explicit feedback was given (Bahlmann et al., 2008; Opitz & Friederici, 2004), for instance when most participants were able to explicitly state the nature of the center-embedded sequencing rule in a post-experimental questionnaire, outside the scanner (Bahlmann et al., 2008). This region also plays a causal role during the acquisition phase of AGL with feedback, as demonstrated using anodal transcranial direct current stimulation (de Vries et al., 2010). Explicit and implicit AGL must to some extent be different cognitive level processes and thus be different at some level of neural implementation. However, both processes operate on the same kind of stimuli. Study III-IV adds to the evidence of implicit AGL engaging the LIFG and in the literature, there is also evidence that explicit AGL engage LIFG. Thus, the bigger picture emerging is that the sequence structure of the stimuli is what drives the activation of common sequence processing mechanisms in the LIFG, rather than the manner these stimuli are processed (i.e. implicitly or explicitly).

¹³ If a sequence is structured rather than random, it implies that certain elements predict other elements. Whether those dependent elements are adjacent or non-adjacent is one of the most fundamental features of structure in sequences, at least from a memory perspective.

Since natural language acquisition starts already in the womb (Mampe, Friederici, Christophe, & Wermke, 2009) and is to a large extent unsupervised, the ecological validity of a sequence learning paradigm like AGL is increased in relation to natural language acquisition when contamination by problem solving strategies and access to the acquired knowledge is minimized. When investigating the organization of the LIFG using AGL, explicit AGL can work as a simplified paradigm for generating hypotheses that can be tested in a more ecologically valid implicit AGL paradigm.

4.1.4 Non-adjacent vs adjacent dependencies revisited

Besides the investigation into explicit vs implicit aspects of learning and processing of rule-based sequences, AGL paradigms have also been used to explore whether different types of sequential dependencies engage different brain regions. In neuroimaging studies of artificial grammars learning with grammars that only display adjacent dependencies, BA 44/45 is activated (Forkstam, Hagoort, Fernandez et al., 2006; Petersson et al., 2010). Study III and IV shows that there is a causal role of BA 44/45 in processing grammars displaying adjacent dependencies only.

A significantly increased hemodynamic response to non-adjacent dependencies in BA 44/45, when directly compared to adjacent dependencies, has been shown (e.g. Bahlmann et al., 2008). In the study of Bahlmann et al. (2008), some sequences followed the rule $(AB)^n$, where A and B belonged to two different categories of consonant-vowel syllables (n = number of elements in sequence, see Fig 4.1). In contrast, the rule A^nB^n generated multiple non-adjacent dependencies between category A and category B syllables. These dependencies were organized in a nested/center-embedded organization ($A1A2A3B3B2B1$, see Fig 4.1). Several precautions were taken in the experimental procedure to ensure that participants processed the A^nB^n rule and did not apply alternative strategies such as counting or other simple processing strategies (for details see Bahlmann et al, 2008).

The direct contrast between processing of multiple non-adjacent vs adjacent sequence processing produced activity in LIFG (BA 44). Moreover, BA 44 also showed increased hemodynamic response during the processing of a center-embedded compared to an adjacent dependencies in an AGL task using visuo-spatial stimuli (Bahlmann, Schubotz, Mueller, Koester, & Friederici, 2009). Study IV demonstrates a causal connection between activity in the LIFG and processing of multiple non-adjacent dependencies at the end stage of implicit acquisition. The multiple non-

adjacent dependencies were organized in a crossed manner (A1A2A3B1B2B3, see **Figure 4.1**).

Altogether, these findings support the conclusion that LIFG is a key region for structured sequence processing. The finding that some sequences engage neuronal populations within LIFG more than other sequential patterns should also be seen as evidence in favour of this position, rather than in favour of a specialization of LIFG for a particular sequence type. Mid LIFG is activated in fMRI studies where one kind of sentences or sequences is compared with another kind where some sequence aspect has been manipulated. This is the case both when comparing different kinds of grammatical sentences and sequences (Bahlmann et al., 2008; Bahlmann et al., 2009; Friederici, Fiebach, Schlesewsky, Bornkessel, & von Cramon, 2006; Makuuchi, Bahlmann, Anwender, & Friederici, 2009) and when comparing grammatical sequences against violation sequences, such as in Study III, IV and other studies (Forkstam, Hagoort, Fernandez et al., 2006; Petersson et al., 2010; Petersson et al., 2004). One invariant aspect involved in all of these comparisons is structured sequence processing. This also is consistent with other studies reporting activity in LIFG during processing of syntactically complex sentences as compared to syntactically less complex sentences in natural languages such as English (Meltzer, McArdle, Schafer, & Braun, 2010), French (Pallier, Devauchelle, & Dehaene, 2011), German (Fiebach, Schlesewsky, Lohmann, von Cramon, & Friederici, 2005), Hebrew (Ben-Shachar, Palti, & Grodzinsky, 2004) or Japanese (Sakai, 2005), for a review see (Indefrey, 2011).

The relevance of the sequence processing perspective for LIFG function is also supported by impaired structured sequence learning, e.g. in agrammatic aphasics, predominantly with lesions in Broca's region (Christiansen et al., 2010; Hoen et al., 2003) Broca's aphasics (Hoen et al., 2003) and traumatic brain patients with prefrontal damage (Pothos & Wood, 2009). Moreover, the integrity of white matter fiber tracts in LIFG is associated with sequence processing performance (Floel, de Vries, Scholz, Breitenstein, & Johansen-Berg, 2009).

4.1.5 Integration with evidence from music and action

In summary, LIFG is engaged in processing structured sequences independent of how the dependencies were acquired (implicit vs explicit learning), largely independent of whether dependencies are adjacent or non-adjacent and independent of particular stimulus features of the elements (whether letters, syllables or abstract shapes are used).

This is consistent with involvement of the IFG in musical sequences and action sequences. Indeed, as predicted by the sequence processing account, LIFG is activated in musical sequence processing (Janata & Grafton, 2003; Maess et al., 2001; Patel, 2003). Moreover, musicians show increased grey matter density in LIFG compared to non-musicians (Gaser & Schlaug, 2003) and Broca's aphasics are impaired in processing musical sequences (Patel et al., 2008). Surrounding regions have also been activated in musical processing and artificial grammar learning alike, in particular the frontal operculum and the anterior insula (Engel & Keller, 2011; Forkstam, Hagoort, Fernandez et al., 2006; Mutschler et al., 2007; Petersson et al., 2010). Action sequences, action observation and action imitation activate posterior portions of the LIFG (Hamzei et al., 2003; Molnar-Szakacs et al., 2005; Seger & Cincotta, 2006)¹⁴. It is an open question whether LIFG is activated also by processing of sequences where the elements are not normally sequentially ordered, such as touch or odour sequences. In any case, neuroimaging of artificial grammar, music and action sequence processing suggests that the knowledge structure of structured sequences drive the activations observed in the LIFG in general. How does the structured sequence processing perspective on LIFG relate to other theories of LIFG function?

4.2 THEORIES OF LIFG FUNCTION

The function of Broca's region has been one of the most debated issues in cognitive neuroscience. Our results do not support a specific role of Broca's region in processing hierarchical¹⁵ sequences (Bahlmann et al., 2008; Bahlmann et al., 2009; Friederici, Bahlmann et al., 2006; Koechlin & Jubault, 2006; Makuuchi et al., 2009), nor a specific role in syntactic movement operations (Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Ben-Shachar et al., 2004; Santi & Grodzinsky, 2007a, 2007b) since Study I, II and IV show that Broca's region is involved in the processing of not only nested or hierarchical structures, but crossed non-adjacent dependencies and adjacent dependencies as well. Others suggestions are working memory, subvocalization or a cognitive control function of selection (c.f. **Figure 4.4**). These general suggestions are

¹⁴ The overlap and interaction between the action system and speech processing and language processing in general is a field of research of its own, often motivated by the so called the motor theory of speech comprehension.

¹⁵ In this context, I note that the term *hierarchical* is often used in the AGL literature to informally describe structures involving *multiple levels of nested structures*, exemplified by multiple embeddings.

hard to argue against empirically, since one would e.g. have to exclude the involvement of any kind of working memory process in the tasks involved. As discussed further in chapter 6, the fundamental reason for preferring the structured sequence processing account of LIFG function over the working memory account, the Thomson-Schill model of selection (Novick, Trueswell, & Thompson-Schill, 2005), etc., is that these suggestions are not as well defined computationally as structured sequence processing. Thus the structured sequence processing account is at the present state of the literature the most parsimonious explanation.

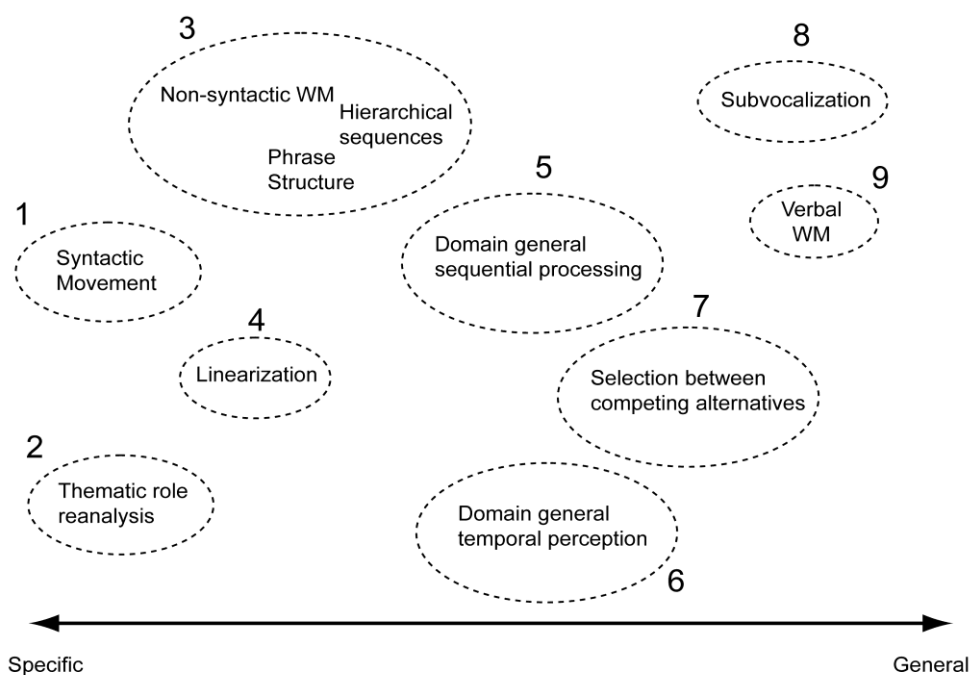


Figure 4.4. An overview of modern proposals of the function of Broca's region. The horizontal dimension divides these theories into more domain-general vs more language specific functions. The vertical dimension has no meaning. (1) (Ben-Shachar et al., 2003; Ben-Shachar et al., 2004; Santi & Grodzinsky, 2007a, 2007b) (2) (Caplan, Chen, & Waters, 2008; Caplan, Stanczak, & Waters, 2008) (3) (Bahlmann et al., 2008; Friederici, Bahlmann et al., 2006; Makuuchi et al., 2009) (4) (Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005) (5) (Christiansen et al., 2010; Petersson et al., 2010) (6) (Szelag & Pöppel, 2000) (7) (Novick et al., 2005) (8) (Dronkers, 2000) (9) (Kaan & Swaab, 2002; King & Just, 1991)

Conclusion Chapter 4

Implicit sequence learning mechanisms are more powerful than previously known. Implicit acquisition of non-adjacent dependencies is robust. There is no evidence that qualitatively different mechanisms subserve processing of adjacent and non-adjacent

processing. There is a causal role for Broca's region in processing implicit processing of structured sequences, independent of whether the structure is instantiated in adjacent or non-adjacent dependencies. There is evidence that LIFG has a stronger causal role in sequence processing than RIFG. LIFG is engaged in processing structured sequences independent of how the dependencies were acquired (implicit vs explicit learning), largely independent of whether dependencies are adjacent or non-adjacent and independent of particular stimulus features of the elements. The knowledge structure of structured sequences is the most likely explanation of what drives activation in LIFG.

5 ROSTRO-CAUDAL GRADIENTS IN LATERAL PREFRONTAL CORTEX

Recent models hypothesize a rostro-caudal (or anterior-posterior) gradient in lateral PFC as a function of abstraction during cognitive control processes (Badre & D'Esposito, 2009; Koechlin & Hyafil, 2007). The lateral PFC is engaged in cognitive control (Miller & Cohen, 2001), where cognitive control¹⁶ refers to the ability to flexibly adapt behaviour in order to achieve goals. Abstraction is a crucial prerequisite of cognitive control (Newell, 1994) and the ability to process abstract action goals is necessary to act flexibly in changing environments. Some goals require deeper abstraction than other goals. For example, the simple task of matching a certain object or stimulus with a particular response needs shallower abstraction than the integration of two different object-response matches.

When reading sentences out loud, a certain orthographic sign trigger the formation of a phoneme in the speech apparatus. This object-response mapping needs abstraction e.g. from the font of the sign. When integrating two such object-response mappings, the integration can be done by a mere summation of the abstractions made for the original object-response mappings. This corresponds to reading is often done during an early learning phase, when each phoneme is read out separately. The more advanced reader needs additional, deeper abstraction at the level of integration of the object-response mappings¹⁷. We cannot simply align separate sign-to-phoneme mappings since pronunciation changes dependent on the adjacent signs. There is need for brain representations at different levels of abstraction.

Experimentally, distinct brain activation in tasks that involve stimulus-response (S-R) mapping (less abstraction), task-switching (more abstraction), or relational integration (most abstraction) have been sought for. Interestingly, recent models summarizing the findings from the cognitive control literature suggest that lower levels of abstraction engage caudal (posterior) sub-regions and higher levels of abstraction are processes by rostral (anterior) sub-regions of the lateral PFC¹⁸. In particular, the dorsal

¹⁶ Including processes such as active maintenance, inhibition, task switching, decision making, conflict monitoring, error processing and interestingly from the sequential processing perspective, abstract rule processing

¹⁷ Thus, abstraction and integration are related concepts, but they are also different.

¹⁸ The spatial location of processing of action sequences to posterior LIFG, reviewed in the previous section, can thus be explained by less abstraction being present in these tasks.

premotor cortex was engaged during the lowest level of abstraction, posterior and mid parts of the inferior frontal sulcus were recruited at the middle level, and anterior inferior frontal sulcus and orbito-frontal gyrus were engaged during the highest level of abstraction (Badre, 2008; Badre & D'Esposito, 2009; Koechlin, Ody, & Kouneiher, 2003).

A computational explicit definition of abstraction

A more computationally explicit definition of the notion of abstraction was provided by Botvinick (Botvinick, 2008) who defined two features of abstraction: (1) temporal abstraction, referring to more abstract representations as able to span sequences of events at longer time scales and (2) state/policy abstraction, referring to the treatment of non-identical stimuli or situations as equivalent in a particular context. In Badre & D'Esposito's (2009) suggestion, abstraction is also (3) domain generality (flexibility with respect to which kind of representation that can be computed with a rule), and (4) relational integration, which means that increasing numbers of independent dimensions of stimuli are related to one another in a more abstract rule.¹⁹

Relation to the VLPFC

An intriguing question now arises: Is there a similar rostro-caudal gradient in ventro-lateral PFC (VLPFC), in particular LIFG, as in the rest of the lateral PFC? A recent recurrent neural network model focused on modelling hierarchically organized goal directed behaviour with tasks and subtasks, (Botvinick, 2007). It was shown that particular properties of connectivity within the network produced a temporal abstraction gradient so that subtask that could be accomplished on a shorter time scale were located at the base of the network and task that integrated these subtasks were located at the apex on the network.

If connectivity patterns are the sources of the rostro-caudal abstraction gradient in the PFC, there is no reason for an *a priori* belief that the LIFG would behave differently from the rest of the lateral PFC, since connectivity patterns are similar (Fuster, 1997). The literature we have cited on lateral PFC function indeed does not presume that LIFG would be different. This has however not been discussed within the

¹⁹ Note that the four different abstraction definitions are not necessarily independent but probably intertwined, e.g. temporal abstraction also implies relational integration (and vice versa), in many cases.

literature of LIFG function and the LIFG has not been extensively studied from this perspective. The purpose of the rest of this chapter is to explore the literature from this viewpoint, with a focus on a possible abstraction gradient from the sequence processing perspective, which emphasizes temporal abstraction. I will also briefly discuss the other three abstraction gradients mentioned in this section.

5.1 THE SEQUENCE PROCESSING PERSPECTIVE AND THE TEMPORAL ABSTRACTION GRADIENT

From the perspective of temporal abstraction, a more abstract sequential representation unites sequences of events over larger time scales. This computational notion applies to sequence processing of artificial grammars, natural language, as well as other cognitive domains with sequential structure. I propose and develop this new perspective here, although similar thoughts have been sketched before (Koechlin & Jubault, 2006). I will now review the evidence for a temporal abstraction gradient within the LIFG.

I will start from the observation which has named this thesis: it is possible to take a perspective on language as structured sequences of linguistic elements. Sentence level semantic structure, realized as sequences of phrases or words have dependencies at a similar or longer timescale compared to syntactic structure, which is mainly realized as sequences of words, and compared to morphosyntactic structure in particular, which is realized as sequences of syllables (e.g. inflectional patterns). Sequences realizing syntactic structure, in turn, have an inherently longer temporal scale than phonological structure, which consists of sequences of syllables and phonemes with dependencies between the sublexical items. The temporal abstraction gradient in the lateral PFC thus *predicts* a rostro-caudal gradient within LIFG, where semantic processing is located rostrally to syntactic processing, which in turn is located rostrally to phonological processing. This is the first simplified model that I will compare against the literature. A second, cruder model merely divides sentence level processing, where there are dependencies between words and phrases from word level processing, where there are dependencies between sublexical elements such as phonemes or syllables. The rostro-caudal division in this model is thus between sentence level processing in the rostral

part and word level or sublexical processing in the caudal part of LIFG (see **Figure 5.1**).²⁰

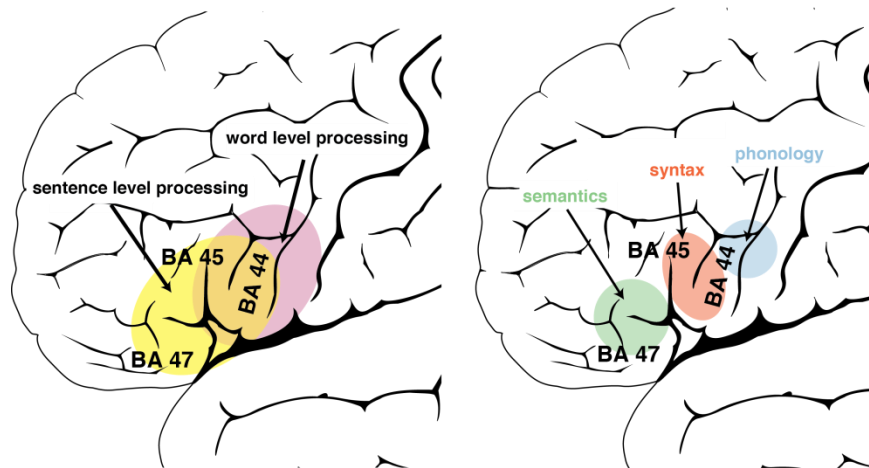


Figure 5.1. The LIFG is divided into pars opercularis, pars triangularis and pars orbitalis in the anatomical system of nomenclature, which follows the gyri and sulci. These areas roughly correspond to BA 44, 45 and 47, respectively, using cytoarchitectonic nomenclature. I illustrate two simplified models of the rostro-caudal temporal abstraction gradient. Left panel: Sub-regions in LIFG can be segregated between sentence level processing (processing of sequences of words) vs word level processing (processing of sequences of sublexical items e.g. syllables or phonemes). Right panel: A more fine-grained sub-division in LIFG between semantics, syntax and phonology is depicted.

Neuroimaging support for a rostro-caudal gradient in LIFG

As predicted from the hypothesis of a temporal abstraction gradient in LIFG; phonological, syntactic and semantic processing has been segregated in the rostral-caudal direction (Bookheimer, 2002). BA 47 has been linked to semantic processing, BA 45 in the middle to syntactic processing and the posterior BA 44 connected to phonological processing. The segregation of semantics and phonology was already found in a meta-analysis by Poldrack (1999). I will now discuss recent meta-analyses of this segregation.

²⁰ These models are highly simplified models, since this perspective can capture a continuity of longer and longer sequential dependencies between elements, which e.g. occupy longer and longer parts of the e.g. the speech stream.

The division between phonology, syntax and semantics has been reiterated by many review studies (Hagoort, 2005; Newell, 1994; Shalom & Poeppel, 2008). No large bodies of additional data are, however, systematically analyzed in these studies, when compared to the studies cited in Bookheimer et al (2002), who looked at 33 peak activations. A recent review study on syntactic processing reports reliable activity in BA 44 and/or 45 for various syntactic contrasts, while BA 47 is involved in sentence level processing, which might or might not be syntactic (Indefrey, 2011).

Two subsequent meta-analyses included a considerably extended body of data and the full segregation between phonology, syntax and semantics only partially replicated (Vigneau et al., 2006) or largely failed to replicate (Lindenberg et al., 2007). The results of Vigneau et al., (2006), who looked at 730 peak activations, do replicate a cluster of phonologically related activations in BA 44/6 and a cluster of semantic activations in BA 47, extending somewhat into the anterior part of BA 45. In the cluster analysis performed by these authors, no segregation of semantic and syntactic clusters was found. The anterior cluster rather reflected sentence processing in general.

Lindenberg et al., (2007) selected papers that included 311 peak activations produced from investigations on the function of Broca's area, irrespective of how Broca's area were defined, which makes the analysis biased toward the posterior parts of LIFG. They used two parallel cluster approaches: one anatomical approach blind to what kind of contrasts were used and one functional approach by dividing all contrasts into the most frequent categories (including semantics, syntax and phonology). No segregation between semantic, syntactic and phonological tasks could be found in this analysis. In the anatomical clustering approach, three clusters corresponding to 1) BA 45 2) BA 44 and 3) BA 44/6 were however found. This supports some kind of functional segregation within the LIFG, although perhaps not as closely coupled to phonology, syntax and semantics as previously believed. When looking at what tasks generated the contrast going into these clusters, the segregation account of e.g. Bookheimer (2002) were not supported, except in one respect: phonological clusters had a modest tendency to end up in the more posterior clusters. We note that the lack of replication of a functional segregation of semantics, syntax and phonology might explained by the limited search to posterior part of the LIFG rather than the whole LIFG in this study.

Using intracranial recordings, Sahin et al. (2009) found support for distinct spatio-temporal neural codes for lexical frequency of words within sentences,

morphological inflection of these words, and changing the phonological surface form of the words, in a production task. The best model of dipoles generating the three distinct spatio-temporal components assigned more posterior dipole to the sublexical phonological and morphological inflection component and more anterior locations to the lexical or sentence level component of lexical frequency of a word within a sentence (Sahin et al., 2009). Another sophisticated method to show functional segregation is to stimulate two brain regions with transcranial magnetic stimulation and show a double dissociation between two tasks and two brain regions. Such a dissociation was found between semantic and phonological processing and BA 47 and BA 44, respectively (Gough, Nobre, & Devlin, 2005).

Altogether, I conclude that the segregation of phonology, syntax and semantics in the inferior frontal gyrus is largely supported in large bodies of studies on blood flow (FMRI/PET) as well as when recent sophisticated neuroimaging and neurostimulation methods are used. The most clear result is that the anterior part of LIFG (BA 45/47) is more likely to be activated by sentence level processing and the posterior part (BA 44/6) is more likely to be activated by phonologically related tasks, e.g. at a sublexical or word processing level. Interestingly, in an FMRI-study directly probing sentence level processing, sentences activated the anterior LIFG (BA 45/47) more than unstructured word sequences, pointing to a role of anterior LIFG in sentence level processing (Snijders et al., 2009). A recent fMRI study on sentence processing gives further evidence for this suggestion (Pallier et al., 2011). These authors varied the number of constituents to be integrated in a sentence and found activity in mid (BA 44) and anterior (BA 45) parts of LIFG, also for so-called jabberwocky sentences. Interestingly, only the activation in anterior LIFG increased linearly as a function of constituent integration. This finding is consistent with the hypothesis that the more elements that need to be integrated in a sequence (and thus the more temporal abstraction needed) the more anterior the activation within LIFG. However, in Pallier (2011) the constituent size was parametrically varied between 1-6 and then jumped to 12 constituents. A paradigm where the parametric modulation of constituent size also covered larger sizes would provide a more direct test of the LIFG gradient we suggest, also ranging to BA 47.

In summary, there is evidence for a rostro-caudal temporal abstraction gradient when applying the sequence processing perspective to natural language. More abstract

sequential representations unite subsequences of events over larger time scales²¹. The more abstract the representations, the more rostral the spatial location of the neuronal populations that represent abstract sequential knowledge or, with other words, process more temporally abstract sequential structures.

5.2 A ROSTRO-CAUDAL ABSTRACTION GRADIENT IN LIFG

In this section I further explore whether the proposed rostro-caudal abstraction gradient in the lateral PFC applies to the LIFG as well and if this gradient is relevant for language processing, as an example of a sequential knowledge structure. To do so, I integrate the three additional abstraction features e.g. as proposed by Badre (2008): domain generality, relational integration, policy or state abstraction. My focus is on the language literature, due to the relative lack of papers on musical sequences, action sequences and abstract sequences such as AGL experiments.

I propose an integrated perspective where the rostral LIFG is involved in sentence level processing, integrating many facets of the speech stream with the goal of extracting e.g. the speaker meaning across longer time scales as well as by integrating formal semantics with world knowledge, gestures and pragmatic information (see **Figure 5.2**). In the mid LIFG and more caudally, syntactic and phonological structure, mainly realized as sequential dependencies at the level of phrases, words or sublexical fragments are processed. I will now review evidence for this proposal and the rostro-caudal abstraction gradient in the LIFG for each of the computational features of abstraction. In Uddén & Bahlman (Uddén & Bahlmann, 2012), we provide further evidence for this gradient across all four features is provided with focus on (1) cognitive control tasks that give rise to a gradient within LIFG and (2) evidence for the relevance of this gradient for language processing.

²¹ The important notion of time from the structured sequence processing perspective is logical time/sequence order (Petersson, 2008), or the relative time scales of slower and faster aspects of some sequential stimuli, rather than absolute or physical time.

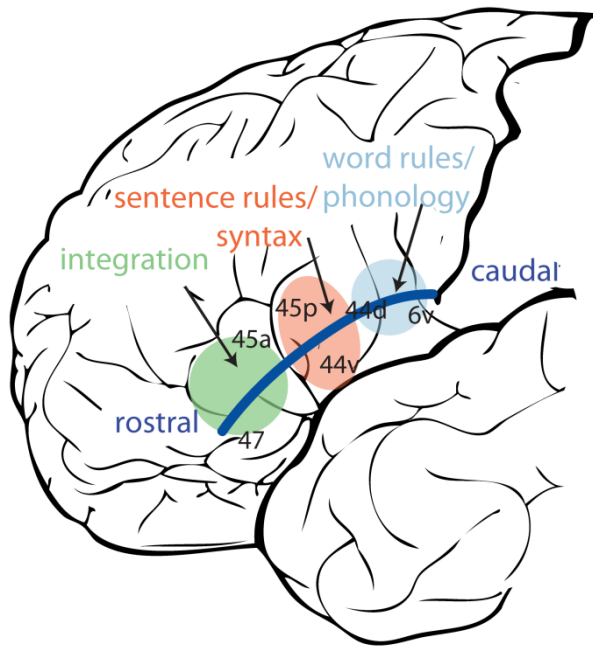


Figure 5.2, I propose a rostro-caudal abstraction gradient within the LIFG in terms of four parallel and intertwined abstraction features. The red lines in this figure correspond to BA 44 being sub-divided into a ventral and dorsal part (44v and 44d) and BA 45 comprised of an anterior and posterior part (45a and 45p), based on receptor-architectonic parcellations (Amunts, 2010). In this model, 44d and 6v are engaged in phonological processing (light blue), which instantiate sequential rules at the word level; 44v and 45p are engaged in processing e.g. syntactic rules at the word and sentence processing level and perhaps also semantic rules at the sentence level; and 45a and BA 47 are engaged in the integration of these processes as well as information from other domains (such as gesture information and word knowledge) with the primary goal of extracting the speaker meaning (light green), at the sentence processing level. The temporal abstraction gradient from **Figure 5.1** is thus here integrated with the three other abstraction gradients of domain generality, relational integration and policy or state abstraction.

Policy/state abstraction, domain generality, and relational integration

Policy or state abstraction refers to the generalization of specific sub-goals or task components to a given main goal or task set. Different ways of performing a subgoal can for instance be regarded as equivalent with respect to the main goal. At the level of the main goal, there is thus abstraction with respect to the subgoals. In the example of preparing breakfast, the main goal of ‘making coffee’ relies on abstractions of sub-goals like ‘opening the cupboard and grab the coffee box’. In sentence level processes operating on sequences of words, there are sub-policies of word level processes. Crucially, the sentence level process can treat non-identical words as identical. It might not matter for the sentence level process which noun should be integrated, but rather that it belongs to the noun class. This is a precise definition of policy abstraction. Thus,

we see how a rostro-caudal policy abstraction gradient also predicts e.g. the more rostral location of sentence level processing compared to word level processing.

Domain generality: From a broader perspective, several lines of research indicate that caudal lateral PFC regions are engaged in domain specific cognitive control processes, while rostral lateral PFC regions are domain general (Buckner, 2003; Gilbert et al., 2006; Sakai, 2008). A domain in this context is a domain of information. Pragmatic processing or sentence level processing can unite e.g. spoken words and gestures in parallel with the common goal of making sense of e.g. the meaning that a speaker is trying to convey. We can arrive at the same interpreted speaker meaning by using world knowledge in one context and conceptual or syntactic structure in another. There is thus invariance to which domain information comes from at the level of speaker meaning. Integration across multiple domains of information is not as prevalent at the word level. In this sense, sentence level processing is more domain general than word level processing. This predicts the location of sentence level and word level processing in LIFG along a rostro-caudal domain generality gradient. Neuroimaging evidence for this comes from the finding that integration of gestures into language is subserved by the anterior LIFG (Willems, Özyürek, & Hagoort, 2007). Moreover, in an fMRI study contrasting correct sentences vs sentences with semantic violations (The capital of Germany is *sour*) or world knowledge violations (The capital of Germany is *Stockholm*), the overlap of these two contrasts was found in the anterior LIFG (Hagoort, Hald, Bastiaansen, & Petersson, 2004). The same area was activated when the content of speech was incongruent with pragmatic information (voice characteristics), against pragmatically congruent sentences (Menenti, 2010; Tesink et al., 2009). Thus, although it remains to be tested whether processing of semantics, world knowledge and pragmatics only shows overlapping activations in BA 47, or whether they actually interact, the evidence up to the present day is consistent with the domain generality abstraction.

Relational integration: This type of cognitive abstraction has been experimentally tested using visuo-spatial intelligent tests (like Raven's Progressive matrices (Raven, 2000)) or analogy reasoning tests ('A lawyer is to a courtroom like a gladiator to an arena'). Bunge et al. (2005) showed that analogy reasoning in the language domain recruits anterior parts of LIFG (BA 47) and left fronto-polar Cortex (BA 10) in

comparison to a semantic retrieval task. This activation pattern is independent of various minor task manipulations (Wendelken, Nakhabenko, Donohue, Carter, & Bunge, 2007), such that relation completion (e.g. Painter is to brush as writer is to WHAT?) or relation comparison (e.g. Is painter to brush as writer to pen?), which engaged BA10/47 similarly.

Sentence level processing provides relational integration of word level or sublexical processing, as well as integration of gesture, i.e. a larger number of independent dimensions of the visual and auditory input from the speaker are related to one another. The relational integration abstraction gradient thus predicts the more rostral location of sentence level processing and the more caudal location of word level processing. From my perspective, relational integration, domain generality and state or policy abstraction are largely intertwined abstraction features and they might be hard to disentangle experimentally. If these three abstraction gradients can be reformulated in even more precise computational terms, we might find that there is no deep difference. As of today, however, they provide slightly different theoretical perspectives which all might prove useful.

In summary, I propose that structured sequence processing and language processing in the LIFG can be seen as following a rostro-caudal abstraction gradient, including the four computational notions suggested by Badre & D'Esposito (2009). I suggest that the rostro-caudal abstraction gradient in LIFG is a part of a general rostro-caudal abstraction gradient in the lateral PFC. Stimuli with a strong sequential component, such as language, music and action sequences are processed mainly in the LIFG, rather than the rest of the lateral PFC. I suggest that the structured sequence knowledge structure can be seen as driving activation in LIFG, although non-sequential components of stimuli with a strong sequential component might be processed in LIFG as well. I have mentioned empirical support for the structured sequence processing perspective across cognitive domains, while support for the rostro-caudal abstraction gradient in the LIFG mainly comes from the language domain and the cognitive control literature.

The rostro-caudal abstraction gradient hypothesis predicts similar results for all the sequential aspects of the domains of language, music, and action sequences as well as with abstract structured sequence processing paradigms such as artificial grammar learning. Thus, a possible future direction for this line of study is to integrate experimental paradigms from language research with paradigms from cognitive control

research in order to elucidate common neural substrates in lateral PFC, in particular the organization of the lateral PFC into a rostro-caudal gradient and perhaps a dorsal-ventral gradient as well. The AGL paradigm could be used to test the rostro-caudal abstraction gradient. For instance, in sequences spanning longer time scales, the temporal abstraction gradient predicts that longer sequential dependencies activate areas more rostrally than shorter sequential dependencies. The policy abstraction gradient predicts that if subparts of sequences have to be treated as identical, such processing will activate areas rostral to those activated when no such abstraction is needed. The domain generality gradient predicts that sequential processing that is invariant to the sequential domain, e.g. across sequential processing of visual and auditory input, will end up more rostral than sequential processing that does not generalize across the input domain. The relation integration gradient predicts that sequential dependencies where multiple parts of sequences have to first be locally processed and then integrated across a longer distances activate areas rostrally to sequences when no such relational integration is needed. These hypotheses about the functional architecture of lateral PFC remain critical objectives for future investigations.

Conclusion Chapter 5

Structured sequence processing and language processing in the LIFG can be seen as following a rostro-caudal abstraction gradient, including the four computational notions suggested by Badre & D'Esposito (2009). I suggest that the rostro-caudal abstraction gradient in LIFG is a part of a general rostro-caudal abstraction gradient in the lateral PFC. Stimuli with a strong sequential component, such as language, music and action sequences are processed mainly in the LIFG, rather than the rest of the lateral PFC. I suggest that the structured sequence knowledge structure can be seen as driving activation in LIFG, although non-sequential components of stimuli with a strong sequential component might be processed in LIFG as well. The AGL paradigm could be used to test the rostro-caudal abstraction gradient. For instance, in sequences spanning longer time scales, the temporal abstraction gradient predicts that longer sequential dependencies activate areas more rostrally than shorter sequential dependencies.

6 MEMORY IN STRUCTURED SEQUENCE PROCESSING

As discussed in the end of chapter 4, an alternative theory to the structure sequence processing account of LIFG function is that more general working memory or verbal working memory processes might explain the involvement of LIFG in language task and sequence processing. I will now discuss this suggestion to explain the problems with this view. I will also show how a more computationally precise memory concept – the push down stack memory architecture – can be empirically investigated in the context of sequence processing.

6.1 THE WORKING MEMORY CONCEPT

A concept as general as working memory, which has been studied for about half a century, is naturally multifaceted. Many divisions of working memory have appeared (spatial, verbal, phonological, conceptual, syntactic, non-syntactic, serial order working memory, etc). This speaks against a modular memory or working memory keeping information online independent of the content. In other words, the division of working memory into multiple subsystems, which has gradually been taking place in the literature, already suggests that the original concept might not be so useful. Furthermore, from an information processing perspective, working memory is the online maintenance of information, thus an aspect of all online processing. From an algorithmic point of view, a process and its online memory resources are intertwined. Memory is an integral part of processing, both a resource and a result, of each step at all levels of the process (Hebb, 1949; Petersson, 2005a; Petersson et al., 2010). We can think of the two concepts as separate at the computational and algorithmic level, but whether there is a separation at the neural level remains an open question. For instance, the principle of co-localization and integration of a process and its memory resources can be taken, e.g. at the level of macroscopic brain regions. A process is however not necessarily separable from its memory resources even at the molecular level.

A recent review of medial temporal lobe function presents a non-modular view of memory in which memory and perception depend upon the same anatomically distributed representations (Graham, Barense, & Lee, 2010). Although the authors note that this proposal is still controversial, many of the original studies in this review

represent a general tendency in the literature to move away from neural models of memory as a distinct, perhaps domain general function, separable from other perceptual and cognitive abilities. The kind of empirical results which suggests a to some extent modular view is e.g. transfer from working memory training of one working memory tasks to another working memory task, which has been demonstrated in some settings (Klingberg, 2010). Again, the crucial insight is that such training of memory can be viewed as training of a processing mechanism which instantiates neural processing at the time scales relevant for the tasks at hand. The cognitive neuroscience field should have the ambition to constantly transform more vague concepts of memory and working memory to more precise computational definitions of the object of study. One such definition could be “brain processes taking place at a temporal scale of seconds”, which is the approximate level of precision of the working memory concept in the literature that I will now review.

Three views on working memory in sentence level comprehension

I will now examine the literature on working memory and sentence level comprehension. This literature provides at least three separate views of the how this interaction should be construed. (1) The first theory holds that a domain general working memory capacity, corresponding to the central executive in Baddeley’s working memory model (Baddeley, 1986) limits syntactic parsing and sentence comprehension (Gordon, Hendrick, & Levine, 2002; Just & Carpenter, 1992; King & Just, 1991). The empirical support of this *single resource hypothesis* was reviewed by Caplan et al. (1999). However, the review shows that there are several studies showing dissociations between general working memory and syntactic processing and that the single resource hypothesis lacks empirical support. Instead, Caplan et al. (1999) argues that (2) domain specific syntactic working memory limits syntactic parsing.²²

The third view is largely based on connectionist models where (3) sentence level processing, e.g. syntactic computation, is a rather automatic result of activated traces of syntactic knowledge. The concept of working memory resources is either dropped or

²² However, this paper is mainly devoted to establish the dissociation of general working memory from syntactic processing and no elaborations on how syntactic working memory should be construed are made by these authors (Caplan & Waters, 1999, 2002).

explained away as activations of long-term representations in distributed neural networks (MacDonald & Christiansen, 2002).²³ This is the view which I hold.

A critical view on more recent developments of syntactic and non-syntactic memory

Other authors have developed these views. In Fiebach, Schlesewsky, & Friederici (2001), syntactic WM stores a partially parsed input sentence. Syntactic WM is thus distinguished from syntactic computation, which rather integrates new words into the structures built so far (Gibson, 1998). A working memory module for partially parsed syntactic structures could be (1) general (e.g. able to store all verbal material) or (2) specific to syntax (unable to store e.g. phonological information). Fiebach et al. (2001) and Gibson (1998) do not distinguish syntactic from general or verbal WM in the manner of Caplan (1999), but adopt the view of King and Just (1991), of a single resource.

There are several additional examples of similar divisions of verbal working memory, e.g. with a specialized limiting “workbench” for syntactic parsing and production of grammatical structures in Jackendoff (2002). Potter (1993) proposed a very short term memory for rapid parsing and comprehension, distinguished from general verbal working memory, which has a longer time range. She provides evidence that at presentation rates of e.g. 12 words per second, sentences can be parsed and understood. Recall of words lists of unrelated words at this presentation rate is however poor, supporting a simple dissociation between phonological WM and working memory for rapid parsing and comprehension. Lewis (1996) argues that there is a double dissociation, but fails to provide convincing evidence. The evidence he refers to is a trivial demonstration that we recall word lists in a phonological working memory task, where words were presented slowly (one word per second), while when the words are put in a highly complex centre-embedded sentence and read at normal conversation speed, the sentence is often misunderstood. A simpler explanation of the results of Potter is the third view, holding that performance in verbal working memory tasks, whether very short term or general, is subserved by parts of the neural infrastructure involved in parsing and comprehension.

²³ This view is also represented in a recent account of maintenance in verbal WM, which points out that serial order processes in language production are likely candidates for substrates for the ability to keep verbal information online (Acheson & MacDonald, 2009).

A variant on the views I have presented so far is the model where *non-syntactic working memory* is seen as *functionally segregated* (see definition in the following paragraph) from syntactic computation (Makuuchi et al., 2009). The study provides fMRI-data where the two processes activate different loci in Broca's region. The segregation hypothesis was most strongly formulated in Makuuchi et al. (2009), but this study also refers to earlier results of two other fMRI studies (interpreted as consistent) where similar contrasts were tested (Bahlmann et al., 2008; Friederici et al., 2006). However, it is important to keep in mind that these data concerns a rather restricted model system of the more general issues at hand. For example, the authors construe non-syntactic WM as the process of maintaining verbal information across time irrespective of which grammatical structure is kept online. However, even if similar fMRI-activations are produced by increased WM load in two grammatical structures, it is not enough to conclude that the activations correspond to a working memory component which is non-syntactic. The results might just be a consequence of sampling an insensitive part of the spectrum of different syntactical structures. The choice of the term non-syntactic WM is confusing since it is oblique to constructions of syntactic working memory in the literature (as described in the previous section, see **Figure 6.1**).

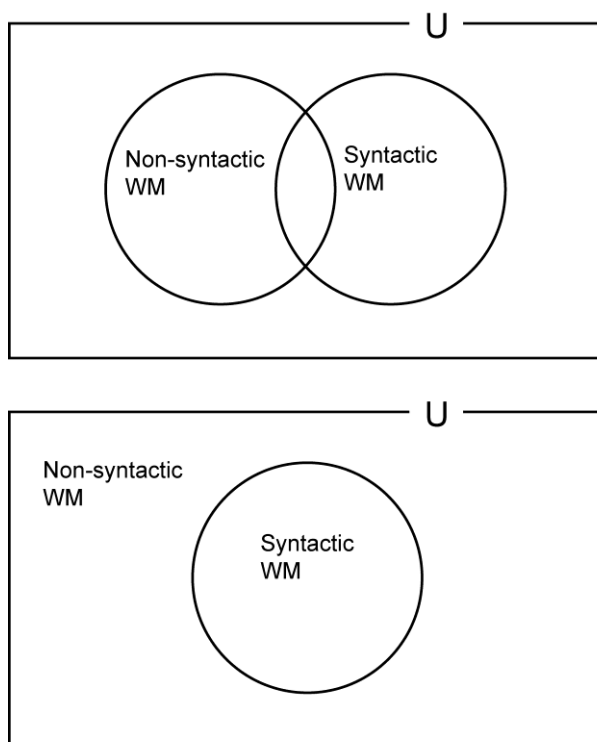


Figure 6.1. The upper Venn diagram represents the main constructions of syntactic and non-syntactic working memory components and their considerable overlap. This overlap contains memory components which are not unique for certain grammars, i.e. non-syntactic in the sense of Makuuchi et al., (2009), but

store representations of partially parsed sentences, i.e. syntactic in the sense of e.g. Fiebach et al., (2001). There is some convergence in the literature for the syntactic WM term, but little for the non-syntactic working memory construction of Makuuchi et al., (2009). As a consequence, the non-syntactic WM term should be reserved to talk about WM processes storing knowledge *other* than partially parsed syntactic structures. This would create the clearer terminological situation in the lower panel. U stands for the set of all WM processes.

Another concern when interpreting these three fMRI-studies is that it is possible that an apparent segregation of process and memory arise in neuroimaging paradigms. Contrast testing, for example, with two near equivalent contrasts can produce anatomically distinct activation clusters. This is because clusters will move around on the scale of localization precision in group studies (e.g., for fMRI ~10 mm). It is thus possible that findings interpreted as distinct ‘pure’ computation or ‘pure’ memory components (Bahlmann et al., 2008; Friederici et al., 2006; Makuuchi et al., 2009), are more apparent than real. This view is consistent with the absence of consistent localization of the two aspects of syntactic processing across these three studies (as pointed out in Petersson et al., 2010).

Evidence against functional segregation of working memory and syntax

A spelled out account of how the notion of *functional segregation* of two processes should be used in relation to neuroimaging data has been provided e.g. by Friston (1999), originally as a way to clarify Caplan et al.’s argument against the single resource pool hypothesis. In this view, failing to find an interaction between two processes allows asserting that functional segregation is a sufficient model for the observed findings. At the neural level, it is possible that a brain region subserve one or both of two functionally segregated processes, as long as no evidence for interaction in neural activity can be found between them. At the same time, other brain regions might show interactions in activity and thus subserve the functional integration of the two processes. In any case, when an interaction is found in behavioral measures or in neuroimaging data, a model of two completely functionally separated functions (such as general working memory and sentence comprehension/syntactic processing in Caplan’s 1999 model) is not enough to account for the data. Segregation of working memory and syntactic computation can thus be investigated with behavioral paradigms (see for instance Caplan & Waters, 1999; King & Just, 1991; Potter, 1993) and neuroimaging methods such as fMRI and measures of anatomical and effective

connectivity as in Makuuchi et al. (2009). In fact, neural integration of WM aspects of syntactic processing with the syntactic computation itself has been demonstrated with fMRI (Santi & Grodzinsky, 2007b). Two different grammatical constructions with varying length in non-adjacent dependencies, i.e. varying WM load were used in this study. For one of the grammars, there was a positive linear increase of the recruitment of BA 45 when WM load increased. In the other grammar type, there was a negative linear relationship between WM load and activity in BA 44. These results thus support the perspective of WM as intertwined with syntactic processing, perhaps even supported by the same neuronal population.

Working memory in sequence processing

In the AGL field, there have been a number of studies investigating the issue, also in the context of non-adjacent dependencies, where information has to be integrated across intervening material. For instance, non-adjacent dependency length has been varied, in the context of processing of multiple nested dependencies, with mixed results. Three studies have reported null findings with respect to length at the behavioural level, i.e. this factor did not produce any difference in classification behavior (Bahlmann et al., 2008; Bahlmann, Schubotz, Mueller, Koester, & Friederici, 2009; de Vries, Monaghan, Knecht, & Zwitserlood, 2008), perhaps due to too little variation in the length factor. This was the case for both main effects of length and interactions with grammaticality. When combined with fMRI, one study showed no activity as a result of increased length and no interactions between grammaticality and length (Bahlmann et al., 2009), probably also due to a lack of sensitivity. When contrasting the BOLD-response to six letter sequences with four letter sequences, Bahlmann et al. (2008) found activations in the bilateral anterior insula. Using a gross category violation that not only violate the dependency pattern between A's and B's (e.g., A₁A₂A₃**B₁B₃B₂**) but replaces B's for A's or vice versa (e.g., AAABBA) one study found an activation in Broca's region as well as the frontal operculum in response to increased sequence length (Friederici et al., 2006).

In a meta-analysis of 60 WM-studies, Broca's region was not found to be significantly specialized to keeping verbal rather than spatial or object information online, although there was a tendency in this direction (Wager et al., 2003). There was however a significant specialization to processing order information rather than mere storage of information independent of order. This is consistent with the conclusion of

this thesis work, where the function of Broca's region/LIFG, is described as sequence processing across language, music and action sequences with rich structure (Hagoort, 2005; Janata & Grafton, 2003; Maess et al., 2001; Patel, 2003; Patel et al., 2008; Tillmann et al., 2006; Willems & Hagoort, 2007).

I will now move on to show how a computationally sophisticated memory perspective can be applied to the domains of language and sequence processing, using the memory architectures defined in chapter 2 in an empirical investigation in the sequence processing context.

6.2 MEMORY ARCHITECTURES: THE PUSH-DOWN STACK AND THE RANDOM ACCESS MODEL

In Study I, we compared acquisition of two different organizations of multiple non-adjacent dependencies: so called nested or crossed structures. Nested or crossed (see chapter 4) non-adjacent dependencies are notoriously difficult to process in natural language (Bach, Brown, & Marslen-Wilson, 1986). Tree adjoining grammars (Joshi & Schabes, 1997) or the equivalent embedded push-down machines (Joshi, 1990) and other working memory models based on interference by similarity (Gordon, Hendrick, & Johnson, 2001; Lewis, 1996) are examples of natural language models accounting for the difficulty of processing these structures. Simple recurrent networks have also been used to show that crossed and nested dependencies are possibly processed without external memory architectures (Christiansen & MacDonald, 2009), such as stacks in Joshi's model. These models all predict increased processing cost as a function of increased length of the sequences with non-adjacent dependencies. This was one basic finding across all studies with non-adjacent dependencies (Study I, II and IV).

In Study I, we wanted to assess a prediction from the so called push-down stack model. Alternatively, a random-access model could be an algorithm solving the same computational problem. If an internal memory is implemented, this predicts that both structures are as easy, while the push-down stack (external memory) predicts that nested structures are easier. We found a larger acquisition effect for crossed compared to nested non-adjacent dependencies. In this respect, the results speak against the push-down stack memory model. However, the greater acquisition effect in the crossed group compared to the nested group can be explained by an initial sensitivity to the grammaticality factor in the nested group. The initial sensitivity was stronger in the second half of the baseline test, which point to early acquisition of sensitivity to at least

some aspects of the nested grammar. Thus, the apparent advantage of acquisition of crossed compared to nested grammars can be explained by crossed grammars having fewer aspects which are immediately acquired when subjects are exposed to a set of both grammatical and non-grammatical sequences. In this sense, there might be an, at least initial, acquisition advantage for nested compared to crossed structures. This supports the push-down stack model.

An alternative to the push-down stack model is that human online memory (working memory) is characterized by (weighted) random access (see **Figure 6.2**) in combination with certain forgetting characteristics (e.g., primacy/recency effects). The pattern of serial position curves in the memory literature suggest that there are strong primacy and recency effects (Glanzer & Cunitz, 1966). Based on serial position effects, it can be argued that noun-verb pairs in the middle of the nested or crossed sentence (i.e., A₂-B₂) should be more difficult to parse. However, our results from the crossed sequences showed that the first violation position was less salient than the middle one. The pattern of violation position results can be predicted by the push-down stack model, since the processing cost is higher at the first compared to the second and third position, as well as the absence of an effect of violation position for nested sequences. The analysis of violation positions thus provide some evidence for the use of the push-down stack for processing crossed grammars, and is consistent with its use in nested grammars. As a general caution, we note that it is possible that the results reported here might change if sequences were drawn from a significantly larger alphabet.

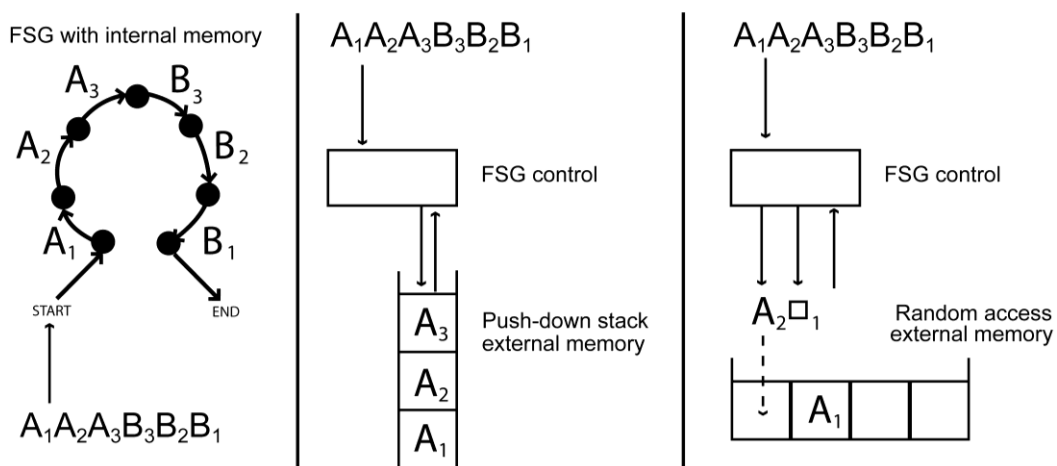


Figure 6.2. Three different memory architectures. In the external memory of a push-down stack, only the top element can be accessed. This creates predictions on processing biases. In the random access model, the finite state controller sends two inputs to the random access memory: the content to be stored as well

as the address of where it should be stored. Likewise, the address (denoted \square_1 in the figure) is needed when the content should be accessed.

It has been proposed that the underlying neurophysiology of memory might have stack-like properties (Siegelmann, 1999). The brain represents information in terms of dynamical variables, for example, a set of membrane potentials, which evolve over time and therefore can be viewed as a set of dynamic registers (i.e., information is represented in the decimal expansion of the membrane potentials). Recurrent neural processing in combination with multiplication/division of the membrane potentials by synaptic weights can be shown to implement memory representations with stack-like properties in artificial neural networks (see for example Siegelmann, 1999). Thus, it might be fruitful to specify possible neural mechanisms for multiplication and division, which represent each other's inverse transformations. Remember that the operation *pop* is the removal of the top element (in this case the top element is the first digit of the decimal expansion) from the stack and *push* is the storage of an element at the top of the stack. To implement *pop* we need (1) multiplication and (2) a specification how the popped element can be unmixed and separated from the rest of the decimal expansion. In recurrent neural networks models, the stack operations *push* & *pop* are implemented by division and multiplication with synaptic weights, respectively. Alternatively, multiplication/division and thus *pop*/*push*, can be implemented at the level of dendrites (Koch & Poggio, 1985), at the single neuron level, or in networks of neurons. An approximate multiplicative synaptic mechanism is exemplified by shunting inhibition (Koch, 1999). In networks of neurons, multiplication can be implemented in the linear excitatory and inhibitory connections between neurons which implement a logarithmic transfer function. If neuron A receives input x_1 and outputs $\log(x_1)$ and neuron B receives input x_2 and outputs $\log(x_2)$, then neuron C, receiving both of their outputs (again assuming linear summation) will receive the input $\log(x_1 x_2)$, by the logarithmic laws (Koch & Poggio, 1992). Together with our results, which lend some support for a memory model with stack-like properties, this sketch suggests that it is at least conceivable that on-line neural processing memory has stack-like neural memory properties. However, it is plausible that both memory architectures coexist. For instance, each biological entity that might implement a stack, e.g. each membrane potential, could be used as a register in a random access memory.

The results from Study I are also relevant in relation to the results of Bach et al (1986) who found a comprehension advantage for crossed compared to nested sentences when there were three non-adjacent dependencies. We replicated these results in a sequence processing paradigm, although our results suggest that nested sequences might have an advantage in the early phases of acquisition.

Conclusion Chapter 6

There is no reason to take any other perspective of working memory in sentence level processing and structured sequence processing than of intertwined memory and processing mechanisms, at least at a gross anatomical level. At a more fine grained level, it is plausible that many memory architectures coexist. One of them is the push-down stack model and we provide some empirical support for this model.

7 CONCLUSION

The conclusions of Study I and II, which investigate processing and generalization of multiple non-adjacent dependencies after implicit acquisition are:

- Implicit sequence learning mechanisms are more powerful than previously known.
- Implicit acquisition of non-adjacent dependencies is robust. Implicit sequence learning is a more ecologically valid model of natural language acquisition compared to explicit learning, since language acquisition to a large extent is unsupervised.
- There is no evidence that qualitatively different mechanisms subserve processing of adjacent and non-adjacent processing.

The conclusions of Study III and IV, which concerns the causal role of Broca's region, are:

- There is a causal role for Broca's region in processing implicit processing of structured sequences, independent of whether the structure is instantiated in adjacent or non-adjacent dependencies.
- There is evidence that LIFG has a stronger causal role in sequence processing than RIFG.
- Structured sequence processing is the most appropriate computational level concept describing the function of LIFG, not processing of hierarchical structure, syntactic movement or processing of multiple non-adjacent dependencies.

The conclusions from Chapter 4-5, which are on the structured sequence processing perspective is that the structure sequence processing perspective is preferably compared to other perspectives on LIFG function since:

- It integrates findings across the domains of language, music and action.

- The structure sequence processing perspective on LIFG function can be applied to integrate LIFG function with PFC-function, an area which need further empirical research. I have used it to formulate a rostro-caudal temporal abstraction gradient in the LIFG.

The conclusion from Chapter 6 is:

- It is plausible that many memory architectures coexist. One of them is the push-down stack model and we provide some evidence for this model.

The large scale project for cognitive neuroscience can be formulated as a level mapping project between Marr's three levels of analysis. The papers of this thesis are examples of the level mapping approach. I have presented sequence processing as a computational level problem, discussed algorithmic solutions to this task, such as finite state grammars and the push-down stack model (Study I and II) and discussed the gross anatomical implementation of sequence processing in the left inferior frontal gyrus (Study III-IV). Future work will aim at the genetic and molecular level, hopefully by discovery of new genes and replication of candidate genes for sequence processing in human subjects and by using these genes to understand biological pathways for sequence processing at the micro- and mesoscopic brain level.

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