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Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

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Abstract and Keywords

The artificial grammar learning (AGL) paradigm enables systematic investigation of the acquisition of linguistically relevant structures. It is a paradigm of interest for language processing research, interfacing with theoretical linguistics, and for comparative research on language acquisition and evolution. This chapter presents a key for understanding major variants of the paradigm. An unbiased summary of neuroimaging findings of AGL is presented, using meta-analytic methods, pointing to the crucial involvement of the bilateral frontal operculum and regions in the right lateral hemisphere. Against a background of robust posterior temporal cortex involvement in processing complex syntax, the evidence for involvement of the posterior temporal cortex in AGL is reviewed. Infant AGL studies testing for neural substrates are reviewed, covering the acquisition of adjacent and non-adjacent dependencies as well as algebraic rules. The language acquisition data suggest that comparisons of learnability of complex grammars performed with adults may now also be possible with children.

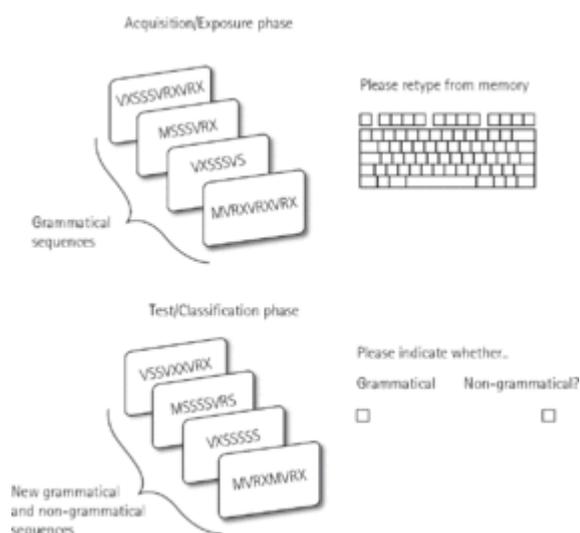
Keywords: artificial grammar learning (AGL), statistical learning, language acquisition, neuroimaging, meta-analysis

33.1 Introduction

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THE artificial grammar learning (AGL) paradigm enables systematic investigation of acquisition of linguistically relevant structures by exposing participants to examples. The AGL task was first used by Arthur Reber (1967). In AGL, participants acquire a formal grammar on which they are later tested, in a separate testing phase (see Fig. 33.1). In the first acquisition phase, participants are exposed to a sample of sequences generated from a formal grammar. In the standard format for adult human participants, they are informed (after exposure) that sequences were generated according to a complex system of rules and asked to classify novel items as grammatical or not. However, the procedure of testing will inevitably vary depending on the population studied.

There are two basic strengths of the AGL paradigm for use in the language sciences. First, it is used as a model system to study aspects of natural language processing; for example, syntactic or phonological processing, in isolation from semantic influence. Since an artificial language is novel to all participants, prior learning is controlled. AGL has been most widely used as a model system for syntax, but work related to phonology has also appeared (Tessier, 2007). The second strength is the possibility to study a wide range of populations using identical, or at least comparable, paradigms. Populations have ranged from prelinguistic infants to adults, as well as non-human primates and songbirds (a review on comparative animal studies using AGL is, however, outside the focus of this (p. 756) chapter). Comparisons allow contributions to research questions on language acquisition and evolution. These two strengths of the paradigm will be illustrated throughout this chapter, where we will review the state-of-the-art in AGL research, including research with infants, with a particular focus on neuroimaging work. A main limitation of the paradigm, namely the constraints on generalization to natural languages, will also be addressed, through clarifications of some of the main differences between AGL and natural language research.



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Fig. 33.1 The AGL paradigm was introduced by Reber (1967). Reber separated an acquisition phase, where the participant is exposed to grammatical sequences, from a test phase, where new grammatical and non-grammatical sequences were presented. The participants were asked to indicate whether each test sequence is grammatical or non-grammatical. This figure depicts the original paradigm used by Reber (1967), although the acquisition phase here is adapted for use with a modern keyboard instead of pen and paper. The elements in Reber's experiments (and many experiments since) are consonants only, rendering sequences superficially dissimilar to language stimuli, which naturally include vowels as well. The sequence processing and sequence learning mechanisms at work in AGL are however here explored as relevant for language learning and language processing, independent of the element a particular AGL paradigm uses.

(p. 757) 33.1.1 The AGL key

We will start by introducing a key for understanding variants of AGL experiments. The key is composed of five questions: Which elements? Which grammar? Which simpler features controlled for? Which violations? Which learning?

33.1.1.1 Which elements?

The most common type of presentation in AGL paradigms is visual stimulus presentation. However, auditory paradigms are also frequent, and, furthermore, there are some examples of tactile AGL paradigms (Conway & Christiansen, 2005). Visual, auditory, and tactile paradigms might all use the same grammar, but they differ in the perceptual features of the discrete *elements* that carry the grammar. In principle, the elements of an AGL study can be any stimuli, in any sensory modality, that can be recognized by the participants as a discrete element. The most commonly used elements are (1) spoken or written consonant-vowel (CV) syllables, (2) written consonants, and (3) pseudowords. More unusual elements that have been used include, for example, abstract visual shapes (Fiser & Aslin, 2002; Sturm, 2011) or symbols (Altmann, Dienes, & Goode, 1995), visual tiles (Stobbe, Westphal-Fitch, Aust, & Fitch, 2012), and written symbols from notational systems unknown to the participant (Mei et al., 2014).

While the choice of grammar is usually in focus in AGL studies, the choice of elements will also affect outcomes. For instance, a faster learning speed is expected when using elements known to the participants (e.g., example letters) compared to unknown elements (e.g., letters from other writing systems). We will come back to the influence of using visual versus auditory elements in the section on neuroimaging data, where it will become clear that the underlying neural architecture subserving AGL changes, depending on the sensory modality of the elements.

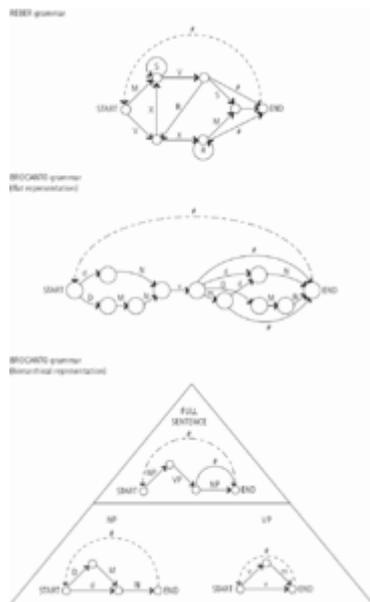
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33.1.1.2 Which grammar? Formal language theory and AGL

Informally, the *grammar* denotes the relation between the discrete elements in some sequences composed of those elements. A powerful illustration of a grammar is a transition graph (see Fig. 33.2—“REBER grammar”). To generate or parse a grammatical sequence such as “VXR,” we need to start from the start node, traverse the “V” arrow, followed by “X,” “R” and finally the start/end-of-string symbol, # and end up in the end node. The sequence “VRX” is an example of a non-grammatical sequence. This information is contained in the transition graph, because when the “V” arrow connected with the start node has been traversed, we end up in the lower left node where there is no arrow out that is labeled “R.” This results in a parsing failure. As soon as the arrows and nodes in this graph are changed, the graph corresponds to a different grammar. Features of the grammar used, such as its size and which class it belongs to, will be the most important factors determining learnability and generalization. In this section, we will introduce classes of grammars that might influence learnability in ways that are interesting for language sciences. Such grammar classes are the topic of study in the field of formal language theory.

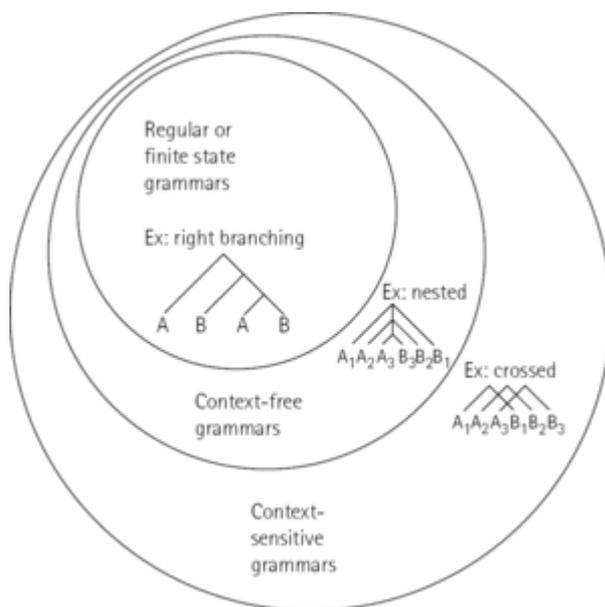
The branch of mathematics called formal language theory delineates important principles of sets of sequences (called sets of *strings*). Since the beginning of AGL research, formal (p. 758) (p. 759) language theory has been its theoretical basis. Formal language theory has been used in AGL research to test whether classes of formal grammars induced by the participant correspond to different levels of behavioral processing difficulties. Formal grammars stipulate a number of rules, for example written down as so-called *rewrite rules* between symbol sequences (see next paragraph). The rules can, however, also be written using other notations. The class of regular grammars for instance (see next paragraph), can alternatively be noted with regular expressions or transition graphs (which are diagrams of so-called finite state automata) as in the top two panels of Figure 33.2. Although transition graphs are commonly used in the empirical AGL literature, we now use rewrite rules, as they show the origin of the names of two more complex grammar classes relevant for AGL.

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Fig. 33.2 Exemplifies the class of finite state grammars (FSGs) with the transition graph representation of the REBER grammar. In addition, we illustrate (the two topmost layers) of BROCANTO with the same kind of “flat” FSG representation (see also Opitz, 2003). Here, we also illustrate BROCANTO using other (informal) representations to emphasize the hierarchical relation between its phrasal versus sentence layers (see lower panel).



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Fig. 33.3 The Chomsky hierarchy.

Reprinted from *Brain and Language*, 120 (2), Karl-Magnus Petersson, Vasiliki Folia, and Peter Hagoort, What artificial grammar learning reveals about the neurobiology of syntax, pp. 83–95, doi.org/10.1016/

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Formal grammars
generate *string sets* that
are grammatical. These

string sets are the formal languages. If a sequence does not belong to this string set, it is non-grammatical. Formal grammars are finite definitions of possibly infinite formal languages. 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 Fig. 33.3)¹. In one version, this hierarchy consists of regular (finite state), context-free, context-sensitive, and general phrase-structure (p. 760) grammars. The relation between classes of rules, classes of grammars, and classes of languages is subtle, since a language can be generated by many different grammars. However, if all grammars G generating the language L contain a context-free rule, for example, then L can be said to be context-free. Informally, regular 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). The non-regular context-free case allows the right-hand side to involve terminal symbols around the sentence symbol in addition, 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 $a_1 a_n S b_1 b_n \rightarrow a_1 a^n a_{n+2} S b_1 b^n b_{n+2}$ (cf., Davis, Sigal, & Weyuker, 1994). However, this latter class of grammars overshoots the machinery needed to formalize the structure of natural language. A class of grammars more closely on par with the needs for parsing natural languages is, for example, described by so-called *multiple* context-free grammars (accessibly handled in Clark, 2014, who also discusses the more well-known alternative formalism of mildly context-sensitive grammars), an issue we will return to in this chapter.

Although AGL research inhabits a unique niche in language research, one must remember its limitations. For generalization to natural language to be valid, it is crucial to determine which of the many differences (e.g., between the rules of artificial grammars and natural grammars) are surface differences and which are deeper, so that they actually limit generalizations. One such potential difference is the absence of hierarchical rules in many artificial grammars (see section 33.1). An additional and related difference is that most AGL experiments do not introduce syntactic word categories upon which natural grammar rules can be applied. Here, validation of results from AGL in natural language paradigms, as well as “hybrid” languages is a good way forward. Some AGL paradigms include grammars like BROCANTO (see Fig. 33.2), where the language is more closely modeled on a natural language. BROCANTO is a small language that has words belonging to particular word categories such as nouns, verbs, adjectives, adverbs, and determiners. The nouns refer to objects in a board game, and the verbs refer to particular actions in the game (e.g., push), and so forth. The language is learned via a game in which participants learn the semantic content of the words. Moreover, BROCANTO has grammatical rules mimicking rules of a natural language in the sense that participants are able to build phrases according to separate phrase finite-state

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grammars (FSGs) for the noun phrase and verb phrase (see Fig. 33.2, lower panel). These are then combined according to a sentence-level FSG. On the other side of the spectrum of artificial grammar learning stimuli, there are simplistic triplet stimuli, for example ABB or AAB patterns. Results obtained with such stimuli are harder to assess in relation to natural language, but are more useful for comparative studies on non-human or infant cognition.

33.1.1.3 Which simpler features are controlled for?

AGL paradigms enable sophisticated control of the computational properties of sequential stimuli as well as the simpler features such as letter positions, chunk frequency, repetition patterns, and so forth. To start with, it has been shown that start and terminal positions in a sequence have a salient role, and subjects are more attentive to regularities at these positions (Endress, Nespors, & Mehler, 2009). One possibility is to minimize the role of terminal positions by using stable prefixes and suffixes and by experimental manipulations in the middle part of sequences (Uddén, Ingvar, Hagoort, & Petersson, 2012). The second robust finding is that subjects are highly sensitive to chunks of two or three adjacent letters (p. 761) (so-called bi- and trigrams) that are frequent in the exposure sequences. The sensitivity to these chunks can be viewed as an initial shallow processing of the grammar. 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, Elwér, Ingvar, & Petersson, 2008). From one point of view, it is likely that participants become sensitive to n-grams with larger and larger n, with continued exposure. When n is large enough, the whole grammar will be contained in such chunks. However, this gives a highly inflexible representation of the grammar, so it is clear that this does not explain all learning that takes place in an AGL experiment. In particular, for grammars that use multiple non-adjacent dependencies (languages where elements far apart predict each other), pure n-gram representations will be an inflexible processing path. A common way of segregating at least some aspects of pattern- or similarity-based learning from learning the full grammar is to control for the presence of bi- and trigrams, for example in order to match their frequency over grammar and non-grammatical sequences. The procedure when controlling for short n-grams using a measure called associative chunk strength (ACS) has been described previously (Meulemans & Van der Linden, 1997).

Other “similarity-based” or “pattern-based” accounts are also present (Kinder & Lotz, 2009). An influential study (Brooks & Vokey, 1991) presented a *repetition structure account* of AGL, suggesting that the repetitions of elements (globally in the sequence) create a pattern that is learned and used as a template during the test phase. Repetition patterns can be represented in different ways. As two examples, the sequence “ABCDEA” has the repetition pattern “x - - - x” and the sequence “ABBCAC” has the repetition pattern “122313.” The presence of repetitions of the same elements across a sequence has been shown to explain so-called *transfer effects*, where successful classification is achieved, although the test phase is implemented on a different set of elements, for

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example from a different modality (Gómez, Gerken, & Schvaneveldt, 2000; Tunney & Altmann, 1999). If repetition structure is controlled for when designing the stimulus material (e.g., simply by not letting any element repeat in any sequence), it is a sign of quality. A final pattern similarity that can be controlled is the similarity of the whole test strings compared to whole acquisition strings, for example as tested with the so-called “edit distance.” Similarity-based accounts of AGL can be contrasted with rule-based accounts (Hauser, Hofmann, & Opitz, 2012), and these forms of learning are then thought to operate in parallel during a standard AGL experiment (Opitz & Hofmann, 2015). To conclude, we consider ACS to be the most important pattern to control for. More generally, any pattern that is salient to an observer of the complete stimulus set should be removed or controlled for. While pattern learning is a real issue, it is perhaps too much to expect all patterns to be controlled for in the same experiment. Thus, one good approach is, for example, to minimize the effect of terminal positions, manipulate ACS, and to get some kind of handle on the amount of pattern/similarity-based learning and how it might interact with the experimental manipulations in focus.

33.1.1.4 Which violations?

The most common way of probing grammatical knowledge is to create sequences that violate the grammar. The participant’s task is then to segregate grammatical sequences from the ungrammatical sequences that include violations. Depending on how violations are constructed, different aspects of the grammar can be probed. Different violations can lead (p. 762) to large differences in the learning outcome (de Vries, Monaghan, Knecht, & Zwitserlood, 2008). The underlying neurobiology might also change (Opitz & Friederici, 2007). A related issue is the inclusion of proper tests for generalization, not only to new grammatical sequences that look similar, but also to new kinds of sequences (e.g., longer sequences). Although such tests help clarify which aspects of the grammar participants actually acquired, they have rarely been applied.

These aspects are important to consider when comparing AGL to other statistical learning (SL) tasks. At least for the SL studies we review in this chapter (note that this might not apply to SL tasks more generally), the main differences between AGL and SL experiments are that (1) SL regularities are not necessarily explicitly stated as following a grammar (although a formal analysis would probably often lead to the answer that they do). High transition probability is, for example, a more common way of expressing the form of regularities in SL experiments. It is more often the case that there is no generalization test at all, not even to new examples with the same transition probabilities. (2) AGL experiments often use two basic conditions: correct versus violation sequences (in all the violation sequences, large parts still follow the grammar), where SL tasks, in the context of this chapter, use correct versus random sequences (random sequences have no regularities whatsoever). In the wider SL literature, it is common to contrast higher transition probabilities with lower transition probabilities. Generally, as well as for this chapter, AGL paradigms are more homogenous than SL paradigms, and AGL can also be considered a part of a wider range of statistical learning (SL) tasks. Statistical learning is a term that can refer to the learning processes that take place during AGL

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paradigms, but others use this in a narrower, or wider sense. Due to this situation, it is crucial that the intended meaning of *statistical learning* is specified in the local context where it is used.

33.1.1.5 Which learning (implicit/explicit)?

When Reber (1967) introduced the AGL paradigm, the focus was the use of the paradigm for research on implicit learning. Today, there is more variation in the purpose of using the paradigm, and thus there are also varied methods that might ensure the grammar is implicitly learned, or not. Generally, it is important to keep the distinction between implicit versus explicit learning processes in mind because the processes are potentially segregated, for instance on a neurobiological level (Yang & Li, 2012, see discussion next), and this distinction also accounts for some differences in how infants acquire their L1 (implicitly) and how adults *study* languages (explicit learning). Note, however, that explicit learning is the exception and implicit learning the rule; hence, implicit learning processes will form the bulk of what is learned also during adult language learning. One of the clearer definitions of implicit learning is that by Seger (1994), reviewed in Uddén et al. (2010). In her view, implicit learning has four characteristics: (1) no or limited explicit access to the knowledge acquired and how it is put to use; (2) the acquired knowledge does not consist of simple association, but is more complex; (3) it is an incidental consequence of information processing and not explicit hypothesis testing; and (4) it does not rely on declarative memory mechanisms for learning—far from all AGL studies which describe learning processes that have all of these characteristics. This results in a literature with mixed learning styles (i.e., different proportions of implicit and explicit learning). The present situation for AGL (and SL) is that the same stimuli can be learned implicitly, explicitly, or with a mixture of these learning styles. This is a rare situation (p. 763) for cognitive neuroscience, and there is now an empirical literature focusing on this aspect in particular (Gheysen, Van Opstal, Roggeman, Van Waelvelde, & Fias, 2010; Wierzchon, Asanowicz, Paulewicz, & Cleeremans, 2012).

Studies emphasizing fully implicit learning processes are rare, and most study designs allow for explicit processes to influence results. Ways of assessing subjective conscious access are evolving fast, and with updated paradigms it has become clear that there is a fair amount of conscious access during standard AGL experiments (Wierzchon et al., 2012). In this study (as in the standard case), participants were engaged in a short-term memory task using an acquisition sample of sequences generated from a formal grammar. Subjects were later informed that the sequences were generated according to a complex system of rules and asked to classify novel items as grammatical or not. Subsequent ratings on five different scales, including confidence ratings, “feeling of warmth,” and a rule awareness scale, suggest that increased conscious access is related to increased performance under these standard conditions. Similar findings are present with a common SL task (Batterink, Reber, Neville, & Paller, 2015). In future studies, where learning style (implicit or explicit) is of crucial importance for the interpretation of the

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results, a combination of rating scales should be used to assess conscious access during AGL paradigms.

There are several methods of minimizing explicit processes during the acquisition phase. As already mentioned, participants are typically engaged in a short-term memory task using an acquisition sample of sequences generated from the grammar. This means that acquisition is relatively masked, for example compared to acquisition with an explicit instruction to figure out rules behind the sequences. Another way is to use a more complex grammar, acquired during a longer learning period. Avoiding explicit recognition of patterns by minimizing them in the stimulus set (see section on controlling for patterns) is another way. In the test phase, a critical measure for showing successful implicit learning is the participants' relative *preference* for grammatical and relative aversion of non-grammatical sequences. In this supposedly more implicit version of testing for sensitivity to the grammar, 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 participants' point of view, there are no correct or incorrect responses, 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 as the so-called "structural mere-exposure effect" (Manza & Bornstein, 1995; Zajonc, 1968). Using so-called *indirect measures*, for example, reaction times may also be a more sensitive method of tapping into implicit structural knowledge, when compared to the accuracy in judgment tasks (Batterink et al., 2015). Through the acquisition and testing phases, naturally the use of explicit feedback on performance should also be avoided if the goal is to minimize explicit learning.

We think it is crucial to put the discussion on the influence of learning style into proportion. It cannot be excluded that learning style has an influence on the underlying recruited neurobiology. At the same time, sensory neuroscience (i.e., neuroscience of visual perception, and so on) shows that the brain organizes according to features of stimuli. For instance, consider encountering a new creature for the first time. This will affect sensory pathways in a complex manner. Crucially however, we expect that the corresponding sensory regions will process the stimuli irrespective of whether the participant is explicitly informed about the existence of this creature (or even its parts or distinguishing features), or just encounters (p. 764) exemplars with familiarization as an incidental consequence (i.e., implicit learning). There might be slight variations, but the basic theme of brain organization is, in this case, according to stimulus features. While sequential structure might be considered an abstract stimulus feature, this remains to be demonstrated. We are not aware of any neuroimaging data in AGL literature that directly test this issue, for processing of structured sequences in AGL.

What about the distinction between declarative/explicit and non-declarative/procedural learning (Squire & Zola, 1996), which is clearly thought to segregate into the medial temporal lobe and the striatum, respectively? This distinction largely builds on reasoning from data across studies that use stimuli from different perceptual modalities, or alternatively, motor sequence learning. Although related proposals, linking hippocampal

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activation to spatial stimulus features, have appeared (O'Keefe, 1999), it is still too often overlooked that it is stimulus features that drive the distribution of activity across the medial temporal lobe and striatum. Experiments testing the same kind of regularities across perceptual and motor sequence learning modalities are needed. One study has yielded a more complicated pattern of activation across these regions for perceptual versus motor sequence learning (Gheysen et al., 2010), which cannot be accounted for by the more simple classical theory (Squire & Zola, 1996). In any case, current literature on neuroimaging studies of AGL, under fairly explicit learning conditions, may still contribute to answering a range of questions.

33.1.2 AGL performance as a trait

Traits do not vary from measurement to measurement and day to day in a participant, although some traits can change across the lifespan. If learning ability in AGL is a stable trait, it is possible that there is a link between this trait and some natural language processing trait. There have been several suggestions on which aspect of natural language performance would be most closely 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 processing of long-distance relationships between words. None of these have been sufficiently tested to draw conclusions. It has been shown that individual differences in the processing of non-adjacent dependencies in natural language are correlated with individual differences in an implicit learning task on sequences generated from an artificial grammar (Misyak, Christiansen, & Tomblin, 2009). 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. 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 (Pettersson, Folia, & Hagoort, 2012). From these correlations, it is clear that some relationships between individual differences in implicit learning and natural language processing do exist and that they, to some extent, may represent the same trait (i.e., overlapping traits). We are not aware of any studies on whether individual differences in (p. 765) phonological processing and AGL are correlated. This is an area for future research. For a wider discussion on SL as a trait, see Siegelman and Frost (2015).

We have already started the discussion on the relation between (adult) AGL and natural language processing, but how is this relevant to language learning? One point of view is that learning (particularly implicit learning), is a consequence of processing (e.g., through priming, see Chang, Dell, Bock, & Griffin, 2000), so in that sense, adult AGL might at least be relevant to understanding adult language learning (both implicit aspects of L2 learning and L1 adaptations). Implicit AGL paradigms are generally of higher relevance for L1 language acquisition. However, the underlying neurobiology develops/matures remarkably and changes in AGL performance are expected as a consequence of growing up. This limits the relevance of adult AGL experiments for L1 language learning.

33.2 Meta-analyzing neuroimaging of AGL

While AGL studies are used to answer a wide range of questions in adult psycholinguistic literature, it is important to understand their contribution to the literature on neuroimaging. This chapter will mostly cover studies using functional magnetic resonance imaging (fMRI), although event-related brain potential (ERP) studies and functional near-infrared spectroscopy (fNIRS) studies on infants will be covered in section 33.4 (there are yet no magnetoencephalography [MEG] studies that we are aware of).

Currently, fMRI literature on AGL spans at least 15 original studies on distinct samples (Bahlmann, Schubotz, & Friederici, 2008; Fletcher, Buchel, Josephs, Friston, & Dolan, 1999; Folia, Forkstam, Ingvar, Hagoort, & Petersson, 2011; Forkstam, Hagoort, Fernández, Ingvar, & Petersson, 2006; Friederici, Bahlmann, Heim, Schubotz, & Anwender, 2006; Hauser et al., 2012; Kepinska, de Rover, Caspers, & Schiller, 2016; Lieberman, Chang, Chiao, Bookheimer, & Knowlton, 2004; Opitz & Friederici, 2003, 2004, 2007; Petersson, Forkstam, & Ingvar, 2004; Seger, Prabhakaran, Poldrack, & Gabrieli, 2000; Skosnik et al., 2002; Strange, Henson, Friston, & Dolan, 2001; Wilson et al., 2015). A qualitative survey of this literature reveals that the left inferior frontal gyrus (LIFG), and left frontal operculum (FOP, sometimes with right homologue areas), sensory regions, striatum, the inferior frontal sulcus (IFS), the parietal cortex, and sometimes left posterior superior temporal cortex are often reported as active in AGL studies. Previous reviews have focused on LIFG contributions (Uddén & Bahlmann, 2012), and further on we will discuss contributions from other regions of noticeable interest from a natural language perspective. We will, however, start to describe the involved neural circuitry in AGL from a relatively unbiased position: by means of meta-analysis.

The above-mentioned literature is beginning to approach the volume where a systematic quantitative meta-analysis is possible. The strength of this approach is that it gives a summary of a few regions that are robustly activated by a task or *contrast* while avoiding selective biases (due to previous knowledge) that can arise during the process of interpreting, summarizing, and reviewing results. In an fMRI-context, the term *contrast* is used to refer to probing of the data of one condition relative to another condition (i.e., a comparison between two conditions). We will use the contrast comparing activity for non-grammatical sequences, over and above activity for grammatical sequences. For readers unfamiliar (p. 766) with terms like peaks, clusters, contrast, and multiple comparison correction in an fMRI-context, we refer to textbooks covering the basics of the method (e.g., Huettel, Song, & McCarthy, 2004).

We have used the GingerALE method in a first attempt. In order to simplify the description of this method, let us first consider its two main steps: (1) activity brain maps from different studies are overlaid on top of each other to determine coactivation, and (2) the joint activity is statistically tested (with permutation methods). In other words, by forming the union across statistical landscapes from each study, centered at the reported peak coordinates (spread determined by the number of subjects), the activation likelihood

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estimation (ALE) method determines the overall likelihood of activation of clusters in a union map by a permutation test (Eickhoff et al., 2009). The ingoing fMRI coordinates are, however, crucially dependent not only on the variations of paradigms (as described in the AGL key) but also on the contrasts used when probing activity. Thus, we included peak activations from one contrast (with corresponding limits on variations in the paradigm) in the meta-analysis. This is the contrast comparing activity for non-grammatical > grammatical sequences (NG > G) during the classification phase of grammaticality judgments. We considered AGL studies and studies where the task was framed as SL, but where stimuli involved a learning phase with exposure to structured sequences, as in AGL. Many studies (in particular SL studies) were excluded due to a lack of the NG > G contrast (Karuza et al., 2013; Opitz & Friederici, 2003, 2004; Weber, Christiansen, Petersson, Indefrey, & Hagoort, 2016; Yang & Li, 2012). To streamline the parameters of the ingoing studies further, we excluded peaks reported with behavioral performance included in the model (Kepinska et al., 2016) and the peaks reported when including measures from a receiver operating characteristic (ROC) analysis in the model (Hauser et al., 2012). Seven studies remained (Bahlmann, Schubotz, & Friederici, 2008; Folia, Forkstam, Ingvar, Hagoort, & Petersson, 2011; Forkstam, Hagoort, Fernández, Ingvar, & Petersson, 2006; Friederici, Bahlmann, Heim, Schubotz, & Anwender, 2006; Opitz & Friederici, 2007; Petersson, Forkstam, & Ingvar, 2004; Wilson et al., 2015). If a study used a 2×2 design and two levels of NG > G were reported, we inserted peaks from both levels. In multiday learning studies, we entered the last reported measurement (or alternatively the last day with subtracted NG > G contrasts at baseline, if not, the “last day only” was reported). In the case of one entered study, the overlap of session with grammaticality and preference instructions was used (Folia et al., 2011).

When thresholding the meta-analysis of the NG > G contrast at an FDR-corrected level of 0.05 (assumed correlations in data: independence or positive dependence) or alternatively correcting at the cluster level (using a cluster-forming threshold of $p > 0.001$) with permutation testing, six clusters were significant: the left and right frontal operculum, the left and right IFG, and the left and right middle frontal gyrus (MFG). When correcting for multiple comparisons with FDR, without any assumptions on the correlations in the data, only the bilateral frontal operculum (extending into the inferior frontal gyrus on the left), were significant. These results emphasize the relatively larger contributions from the right hemisphere seen in AGL, compared for example to complex syntax in natural language experiments, which are largely left-lateralized (Hagoort & Indefrey, 2014). These results also emphasize the contributions from the frontal operculum. A majority of adult AGL studies use visual presentation, and the literature thus has to be carefully taken into consideration as being biased toward finding the activations related to visual processing. Only one study that went into the meta-analysis of NG > G contrast was an auditory study (p. 767) (Wilson et al., 2015). Interestingly, however, both the human and macaque data from this study point to the conclusion that the most robust region is the same region as in our meta-analysis: the frontal operculum (bilaterally). Right hemisphere contributions were also generally highlighted both by the meta-analysis, in right FOP, right IFG, and right MFG, as well as in the human data in

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Wilson et al. (2015), in right FOP, the right posterior parietal cortex (BA39), the right middle temporal gyrus, the right frontal pole, and the right lateral occipital gyrus. The bilateral FOP (often together with the neighboring anterior insula) has been implicated in cognitive (e.g., control, attention, awareness, decision-making) and perceptual (e.g., taste) processes. The FOP in particular has been established as a causal node affecting cognitive control processes (Higo, Mars, Boorman, Buch, & Rushworth, 2011). These authors assign a “*dual role [. . .] in using arbitrary rules to guide response selection [. . .] and in retrieving information from posterior regions to do so.*” Under this view of the FOP, activity seen in this region in the NG > G contrast of AGL studies could be interpreted as a consequence of domain-general cognitive control processes involving the application of rules (although rules should not be thought of as in opposition to, e.g., pattern learning, in this context, see section 33.1.1.3). The anterior insula, the ventromedial prefrontal cortex, and the FOP together form the so-called *salience network* (Craig, 2009). This network is activated, possibly linking with the sympathetic part of the autonomous nerve system, when a stimulus is particularly relevant for the participant, whether in a cognitive or emotional task, or when threatened, for example by uncertainty or pain (Seeley et al., 2007). A possible interpretation of the current FOP results in the NG > G contrast is that the non-grammatical sequences are more salient, perhaps even mildly threatening to participants (remember that they are also dispreferred in preference tests).

In summary, a relatively unbiased review of the neural circuitry involved in detecting violations (compared to correct sequences) in AGL experiments reveals a network markedly different from the regions most robustly involved in processing related aspects of natural language processing, for example natural language syntax (e.g., LIFG and left posterior superior/middle temporal gyrus). LIFG remains a region of overlap of artificial and natural syntactic processing. The robust activation of the nearby FOP region (bilaterally) is notable as a homologue pair of structures that are less often implicated in natural syntactic processing. However, the adjacent anterior insula, clearly left-lateralized, has repeatedly been implicated as one of the most reoccurring sites to display lesions in aphasia patients with both production and comprehension deficits (Bates et al., 2003; Dronkers, 1996). We will return to the left posterior superior/middle temporal gyrus in section 33.3.

33.3 AGL in relation to natural language

We have written on the properties of grammars of AGL and natural languages. Although artificial grammars are much smaller toy models of the grammars of natural languages, artificial grammars with the same formal properties as natural grammars can be studied to mitigate other methodological issues of natural language research (such as the influence of semantic processing).

(p. 768) 33.3.1 Syntax and phonology

We have already mentioned that syntax and phonology (more precisely phonotactics) are the two aspects of natural languages that have been studied with AGL. Recently, it has been noted that hierarchy, a hallmark of syntactic structure, is not present in phonotactic patterns (Berwick & Chomsky, 2016; Heinz & Idsardi, 2011). Finite state grammars (see section on formal grammar theory and AGL) suffice to describe phonotactically legal sequences of speech sounds. If this holds, it will be crucial to select the right kind of grammar when using AGL for studying natural language syntax and/or phonology. Whether (or how) these grammar aspects map onto differences in neurobiology would become an important future question.

Berwick and Chomsky (2016) review a way of defining more precisely what hierarchy in natural language syntax corresponds to in terms of formal grammar theory. They take the starting point of the internal merge operation as the core of human syntax. The internal merge operation corresponds to formal grammars of a class called multiple context-free grammars, which augments context-free grammars in one respect. Non-terminals (on both the left and the right hand side) can now include an extra *internal* variable (the same variable, e.g., *x* on the left and right). This variable can take on different words or word sequences. Application of this rule, when including the internal variable, corresponds to copying performed by internal merge (this is somewhat informally stated in Berwick & Chomsky, 2016). We also refer the interested reader to two of the more accessible, precise sources of the formal treatment of hierarchy in the context of multiple context-free grammars, that we are aware of (Clark, 2014; Stabler, 2011). Other less subtle, but laudably clearly stated definitions of hierarchical structure appear in Fitch (2014), where any structure whose graph takes the form of a rooted tree is hierarchical (where a rooted tree is an acyclic, fully connected graph with a designated root node). It is beyond the context of this AGL chapter to determine the most useful approach to hierarchical structure (when describing natural languages in formal language theory or more generally). Nonetheless, we note that this is a fundamental theoretical issue, where integration across disciplines would be fruitful.

33.3.2 AGL, hierarchically structured sequences, and the left dorsal language system

An alternative approach when reviewing neuroimaging literature on AGL is to consider the left dorsal language pathway. Not only is this particularly relevant for considering the relevance of AGL for models of natural language processing (Bornkessel-Schlesewsky & Schlewsky, 2013; Bornkessel-Schlesewsky, Schlewsky, Small, & Rauschecker, 2015), but it is also important for understanding the AGL literature. In the view of Bornkessel-Schlewsky and coauthors, the dorsal pathway subserves sequence processing in general. It has previously been noted (Friederici & Singer, 2015) that one needs to be careful when discussing the function of a pathway, in particular when there is a lack of

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research on connectivity. There are no connectivity studies that we are aware of that would give direct support for the involvement of the dorsal pathway as such in AGL (or other sequence processing paradigms without semantics). Another point to make when discussing the model by Bornkessel-Schlesewsky and coauthors (also pointed out by Berwick & Chomsky, (p. 769) 2016) is that hierarchical sequence structure is not treated separately in this model. Whether the dorsal pathway (as a whole) is involved in sequence processing without discrimination of different structures or whether it is more involved in hierarchical compared to non-hierarchical sequences (Friederici, 2012) has still not been directly tested. The developmental perspective might become particularly important, as exemplified by one study on natural language syntax performance that explained behavioral variation as a function of development of the dorsal (white matter) pathway as a whole (Skeide, Brauer, & Friederici, 2016). It is beyond the scope of the chapter to fully review this line of research, but we nevertheless would like to point it out as promising.

33.3.3 Temporal lobe contributions to AGL versus complex syntax

The LIFG, together with the left posterior superior/middle temporal gyri, are the two most robustly activated regions across different contrasts of syntactic complexity, and their role has been clarified in recent models of the neurobiology of language (Friederici, 2012; Hagoort & Indefrey, 2014). For a more general introductory text on the involvement of these regions in language processing, see Kemmerer (2014). As these regions are also the “end stations” of the dorsal language pathway, we will now discuss evidence on the involvement of the left superior/middle posterior temporal lobe in AGL. We will use the abbreviation LPUTG (left posterior superior/middle, i.e., upper, temporal gyri) to refer to this anatomical location, which also includes the posterior part of the intervening left superior temporal sulcus. When reviewing the literature that include contrasts where non-grammatical items are compared with grammatical items, a notable difference, probably related to grammar type, emerges. In our meta-analysis, as well as in many studies using finite state grammars, not a single peak is located in LPUTG (Folia et al., 2011; Forkstam et al., 2006; Petersson et al., 2004). One possibility is that this is related to the absence of semantics in AGL. A related observation is the absence of temporal lobe contributions in the inflectional morphology only condition, in Goucha and Friederici (2015). However, in one study using PSG (Friederici et al., 2006) and in a final study where PSG and FSG were studied together in the NG > G contrast (Bahlmann et al., 2008), this region was more active for NG than G, suggesting that semantics should not be the determining factor for what causes posterior temporal lobe activation in the context of (complex) syntax. In two studies using versions of the BROCANTO grammar (Kepinska, de Rover, Caspers, & Schiller, 2016; Opitz & Friederici, 2007), which includes semantics, there were peaks in LPUTG for NG > G, consistent with this interpretation. Another study using BROCANTO reported null results in the NG > G contrast (Hauser et al., 2012). We are not aware of any other studies on BROCANTO, PSG, or FSG grammars that report the standard NG > G contrast. In two other studies using non-modified

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BROCANTO (Opitz & Friederici, 2003, 2004), there were, however, *learning-related* (i.e., this did not come from the NG > G contrast but might reflect the same underlying process) effects along the left anterior and posterior temporal lobe (including LPUTG).

In an auditory study using finite state grammars, LPUTG was also activated in human participants in the NG > G contrast (Wilson et al., 2015). In an auditory SL study, there was activation in the LPUTG in a contrast of *randomized* syllable sequence > *regular* auditory (p. 770) syllable sequence (McNealy, Mazziotta, & Dapretto, 2006). In this study, during the course of exposure, there was an increase in the regular condition in the LSTG. This finding was independently replicated (Cunillera et al., 2009), as an interaction in LSTG, between the first and second blocks in the random versus rest contrast. These results of AGL and SL tasks might be a consequence of the brain processing auditory features of the elements in auditory cortex near LPUTG. For instance, the activation might be a “downstream” effect, during the absence of successful prediction (in the case of NG and random sequences), observed as increased BOLD in corresponding sensory regions. Alternatively, without reference to predictive processes, computation of sequence regularities as such might be partly subserved by sensory cortices. These suggested interpretations warrant a follow-up review of visual AGL and SL studies. Is it the case that NG > G and random > structured contrasts (or other “structure-contrasts”) do not engage LPUTG in visual experiments with simple regularities? Are visual areas instead active in corresponding contrasts? Indeed, two visual AGL and SL studies show bilateral or left visual ventral stream (VVS) activation, extending into the inferior temporal lobe, in structure-contrasts (Petersson et al., 2012; Turk-Browne, Scholl, Chun, & Johnson, 2009) without showing activation in LPUTG. One additional visual study did not report LPUTG, but is ambiguous with respect to a left VVS activation (Forkstam et al., 2006). There was no activity in VVS for an NG > G contrast, while a region in left VVS is reported as significant in results reporting the same contrast (shown in Figure 4B in the study). An additional visual study showed activity restricted to LIFG in an NG > G contrast (Petersson, Forkstam, & Ingvar, 2004). Are visual areas active in structure-contrasts of the auditory studies we have reviewed? Of the three studies we’ve just considered here, two do not show any VVS activity (Cunillera et al., 2009; McNealy et al., 2006), and one study showed right lateralized VVS activity in an NG > G contrast.

Note that this observation of modality dependence would be trivial if the contrast we discussed was grammaticality judgment versus rest. Crucially, we observe this division into auditory and visual areas when contrasting two conditions of the same (visual or auditory) elements. In these contrasts, it is only the amount of structure (i.e., regularity in the sequences) which is different across conditions and it is thus not expected that these structure-contrasts would activate visual versus auditory areas in visual versus auditory experiments, respectively, under the assumption of domain-general structure sequence operations. In this context, it is also relevant to note that there is limited so-called transfer (from some acquisition elements to a new set of elements in the test phase) in AGL (Tunney & Altmann, 1999), as recently reviewed (Frost, Armstrong, Siegelman, & Christiansen, 2015)². Taken together, these findings point to non-shared neural substrates across modalities. This is in contrast to complex syntactic processing in

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natural language, which seems to be largely supramodal (Constable et al., 2004). Three possible factors explaining these differences are: (1) differences in what kind of regularities govern sequences (e.g., hierarchical); (2) semantics; and/or (3) the time needed for stabilizing neural representation of regularities, and during which maturational period they are acquired. In summary, the use of an auditory grammar might be a parallel reason (alongside the grammatical type described here) (p. 771) why peaks in LPUTG are observed in an AGL paradigm. See also Figure 33.3, the Chomsky hierarchy.

Altogether, this suggests that parts of the LPUTG are sometimes activated in AGL tasks and may thus play a role in processing, perhaps particularly complex syntax, also in the absence of semantic content. However, too few studies exist to draw conclusions on exactly which conditions lead to activation in the left posterior middle/superior temporal lobe (LPUTG) in AGL experiments. One interesting possibility is that the LPUTG, and LIFG (as end-stations of the left dorsal pathway), together form a network subserving sequence processing of hierarchically structured (in the sense we have attempted to formally describe already) sequences. This overall processing network might consist of distinguishable spatio-temporal processing aspects related to, for example, online memory versus syntactic operations such as internal merge. AGL paradigms will continue to shed light on these and related issues. A concrete suggestion for a tractable hypothesis to test in future research is that the degree of activation may interact with modality (possibly more likely to be active for auditory than visual AGL) and grammar type (so far, more for nested hierarchical grammars as well as the BROCANTO grammar, compared to studies on regular grammars). We also note that a review of the (inferior) parietal cortex in AGL studies would be valuable, as this region is also an end-station of the indirect segments of the dorsal pathway and often recruited during sentence processing.

33.4 AGL research in infancy

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In aiming to unravel first language acquisition, AGL studies have addressed how infants extract structural units and sequence regularities from speech input, and how they form generalizations and syntactic category knowledge (see Gómez & Gerken, 2000). Comprehensive behavioral research has revealed infants' impressive decoding of adjacent and non-adjacent relations of speech input elements as well as their realization in abstract speech patterns, so-called algebraic rules. We will briefly sketch the two associated lines of behavioral research and illustrate how neuroimaging research substantially contributes to delineating the developmental timeline of infants' structure processing abilities.

A first line of behavioral AGL research emerged from the landmark study by Saffran et al. (1996), showing that eight-month-old infants utilize transitional probabilities of syllables for defining word boundaries in continuous speech. Follow-up studies demonstrated that infants employ statistical speech properties in word segmentation (Marchetto & Bonatti, 2015; Saffran, 2001; Shukla et al., 2011), discovering non-adjacent structure regularities (Gómez & Maye, 2005; Marchetto & Bonatti, 2015), acquiring lexical-semantic categories (Lany, 2014; Lany & Saffran, 2010), and establishing grammatical categories (Höhle et al., 2004; Shi et al., 2006). A second line of behavioral AGL research is based on the seminal study by Marcus et al. (1999), reporting seven-month-old infants' ability to detect abstract speech patterns, as defined by repetitions and alternations of speech elements (see also Gómez & Gerken, 1999). This structure sensitivity might initially be perceptually driven by the detection of immediate repetitions (see Endress, Nespor, & Mehler, 2009). However, successful generalization of these patterns attests infants' abstract representations (Marcus et al., 1999). Follow-up studies showed that six- to seven-month-olds learn these so-called (p. 772) algebraic rules preferably from speech input, compared to other auditory and visual input, suggesting infants' pattern sensitivity to be speech-specific at this age (Marcus et al., 2007; Rabagliati et al., 2012).

During the last decade, a growing number of neuroimaging studies have significantly complemented the insights on language acquisition gained from behavioral AGL studies. Importantly, behavior-independent neuroimaging methods can capture the earliest instances of infants' structure sensitivity and, moreover, specify the underlying brain mechanisms. In the following, we will present ERP and fNIRS evidence sketching infants' advancing processing abilities, from adjacent dependencies, to repetition-based abstract speech patterns (algebraic rules), to computationally more demanding non-adjacent dependencies.

33.4.1 Processing of adjacent dependencies

Behavioral research has shown that statistical computations of adjacent input elements are among infants' earliest speech decoding abilities, functional during the second half of infants' first year (Saffran, 2001; Saffran et al., 1996). Extending this evidence, ERP studies indicate the presence of statistical mechanisms for neighboring input elements already at birth (Kudo et al., 2011; Teinonen et al., 2009). For example, Teinonen et al.

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(2009) presented newborns with a stream of syllable triplets (e.g., *ea-ke-sa*) that had high within-triplet, but low between-triplet transitional probabilities. Infants' ERPs revealed more negative responses to the first than to the other triplet syllables, suggesting that infants processed the statistically defined word onset syllable differently to the other syllables. The authors concluded that newborns readily segment words from the input by computing transitional probabilities of adjacent elements. In a recent fNIRS study, Ferry et al. (2016) demonstrated that newborns process adjacent dependencies in even longer stimulus sequences, but only in the presence of supporting perceptual cues. Specifically, results showed that after being familiarized with six-syllable sequences (e.g., *si-me-bu-ta-le-fo*) infants detected a sequence-internal switch of syllables (e.g., *si-me-ta-bu-le-fo*) if the two middle syllables were separated by a short pause and thus acoustically marked. Together, these findings highlight newborns' impressive decoding abilities for directly neighboring input elements and the crucial role of facilitating statistical and acoustic input cues (see Endress, Nespor, & Mehler, 2009).

33.4.2 Sensitivity to algebraic rules

In analyzing speech input, infants are not only challenged to process adjacent dependencies of elements, but also to recognize their underlying patterns. Behaviorally, it has been shown that seven-month-olds derive generalizations from stimuli containing the same repetition-based adjacent relations (Marcus et al., 1999). Using fNIRS, Gervain et al. (2008) followed up on this evidence and tested newborns with syllable triplets of repetition-based ABB structures (e.g., *mu-ba-ba*) or random ABC structures (e.g., *mu-ba-ge*). The authors found enhanced hemodynamic responses in temporal and left frontal regions for ABB versus ABC sequences, with increasing responses over time. These results suggest that newborns readily differentiate repetition-based and random structures, preferentially processing immediate (p. 773) repetitions in cortical areas specific to speech processing (see also Gervain et al., 2012). The fact that infants showed this differentiation across different syllable sequences indicates that even newborns are able to form some pattern abstraction. Interestingly, the enhancement for repetition-based patterns was only observed for adjacent ABB repetitions, but not non-adjacent ABA repetitions. This difference points to newborns' processing limitations, such that they successfully extract adjacent dependencies, but not yet computationally more demanding non-adjacent dependencies.

A process highly related to the detection of repetition-based abstract patterns is the detection of sequence changes; when expectations built from stimulus repetitions are violated by the occurrence of new stimuli. Basirat et al. (2014) evaluated three-month-olds' ERP mismatch responses to local sequence changes (e.g., rare vowel *a* after frequent vowel *i*) and global sequence changes (e.g., rare sequence *a-a-a* after frequent sequence *a-a-a-i*). Interestingly, infants showed a mismatch response to local stimulus changes that was modulated by global sequence changes. Specifically, changes in global context resulted in enhanced mismatch responses and were, in addition, followed by a

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late negative slow wave, most likely indicating stimulus integration. These results imply that infants at three months are not only sensitive to immediate changes in auditory sequences, but also to more global sequence patterns.

Following the findings of repetition-based pattern processing in newborns (Gervain et al., 2008), Wagner et al. (2011) examined the developmental trajectory of this ability. Interestingly, fNIRS results of seven-month-olds resembled the outcome in newborns, such that their hemodynamic responses were stronger for repetition-based ABB structures than random ABC structures. In contrast, nine-month-old infants showed the reverse pattern with enhanced responses to ABC over ABB structures. Based on these findings, the authors discuss a potential developmental change in the processing of abstract patterns, such that infants initially favor stimulus salience (i.e., repetition), but are later drawn to novelty (i.e., stimulus variability).

33.4.3 Processing of non-adjacent dependencies

In contrast to infants' early processing of adjacent relations and their generalization, the considerably more complex processing of non-adjacent relations has been suggested to arise between children's first and second year of life (Gómez & Maye, 2005; Marchetto & Bonatti, 2015). Neuroimaging studies extend this behavioral evidence, showing that infants master non-adjacent computations before reaching their first year. Mueller et al. (2012) observed that even at three months of age infants were able to detect non-adjacent rule violations in syllable triplets, as evidenced by infant mismatch responses in the ERP. In this oddball paradigm, two frequent syllable frames (i.e., *le . . . bu* and *fi . . . to*) served as standards that established the non-adjacent dependency rule. Infrequent deviants either violated the acoustic stimulus features of the third syllable (i.e., pitch deviants) or the rule features (i.e., rule deviants). Interestingly, infants' ability to process non-adjacent dependencies was associated with their auditory processing capacities, such that only those infants who showed a more mature mismatch ERP response to pitch violations also detected the rule violations. This association suggests that infants only begin to master non-adjacent dependency processing once their processing and memory capacities can (p. 774) sufficiently capture distant relations. Kabdebon et al. (2015) examined non-adjacent dependency processing in infants at an older age, in full-term and preterm eight-month-olds. The authors evaluated infants' ERP responses and EEG-phase-locking to three-syllabic test words that were consistent (e.g., *ku-na-bi*) with a non-adjacent rule introduced in a familiarization speech stream (i.e., *ku . . . bi*) as compared to test words that were inconsistent with this rule (e.g., *fi-bi-na*). Regarding ERPs, consistent test words evoked larger responses than inconsistent words during the second and third syllables, interpreted as a familiarity effect driven by rule prediction. In a later time window, however, inconsistent words evoked larger ERP responses than consistent words, interpreted as an attention allocation to unexpected events. Moreover, EEG-phase-locking results during test revealed higher beta band values during the first syllable of all words and higher alpha band values after the offset of inconsistent than consistent words. In the language domain, power changes in the beta band have been consistently found to reflect the degree of a word's contextual predictability (see Lewis et al., 2016) and here likely reflect infants' expectation of the putative word onset. In contrast, increased alpha power has been observed for increased working memory loads, specifically during adults' processing of long-distance dependencies in sentences (Meyer, Obleser, & Friederici, 2013), and may imply infants' prolonged attention orientation to the unexpected, inconsistent words with an attempt to correct. Importantly, there were no processing differences between full-term and preterm-infants, thus confirming the previous finding of non-adjacent dependency processing being functional early during infants' first months of life (Mueller et al., 2012).

Complementing this AGL research, Friederici et al. (2011) demonstrated infants' early processing of non-adjacent relations for natural language learning by utilizing a non-native language. In this ERP study, German four-month-olds were familiarized with Italian sentences containing two grammatical non-adjacent dependencies between a respective

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auxiliary and a verb's inflection, with 32 different verb stems being the variable middle element (e.g., *stacant-ando*; is singing; *puo cant-are*; can sing). Following the familiarization, infants were presented with new sentences that were either grammatical or contained a violation of the non-adjacent dependency, resulting in ungrammatical structures (e.g., *staarriv-are*, is arrive; *puo arriv-ando*; can singing). ERP responses in the first test phase revealed no processing differences between grammatical and ungrammatical structures, whereas in the last test phase there was a pronounced positivity in the ERP response to the dependency violations as compared to the grammatical structures. These results indicate that at four months of age, infants can acquire non-adjacent dependency rules in a natural language online, after only brief structure exposure.

Together, these studies demonstrate infants' impressive ways of extracting structural input features by means of statistical computations, abstract pattern recognition, and their generalization. To date, there is increasing evidence on the developmental timeline of these abilities, such that the ability to process adjacent structures is present at birth and advances toward non-adjacent structure processing during infants' first year of life. Thus, highly sensitive neuroimaging techniques have uncovered much earlier instances of structural learning than have been observed with behavioral techniques (Gómez & Maye, 2005; Marchetto & Bonatti, 2015). Differences in reported acquisition age, however, might not only reflect methodological differences, but also result from capturing different knowledge representations (for discussion, see Gómez, 2016). While current neuroimaging studies mostly focus on (p. 775) infants' fast encoding of structural patterns, future studies will have to evaluate the retention of learned patterns over time.

Despite current advances in studying infants' structural learning capacities, there is still a lack of developmental AGL studies on more complex grammatical relations typical for human language. Natural language involves not only adjacent and single non-adjacent dependencies, as described here, but also, for example, multiple embedded non-adjacent dependencies (Bever, 1974; Gibson, 1998). A first step into studying more complex structure processing is the behavioral study by Kovacs and Endress (2014), showing that seven-month-olds process embeddings in repetitive structures. The authors tested whether infants detect how word-level repetition patterns define higher-level sentence patterns. During familiarization, infants listened to three-syllable ABB words (e.g., *du-ba-ba*) or ABA words (e.g., *du-ba-du*), thus containing adjacent or non-adjacent repetitions. These words were organized in three-word ABB sentence structures, such that the two last words had the same repetitive structure (e.g., *du-ba-du lo-mo-mo za-vu-vu*). When tested with new instances of the known ABB sentence structure (e.g., *ti-pe-ti re-je-je fe-si-si*) and novel AAB sequences (e.g., *ti-pe-pe re-je-je fe-si-fe*), infants looked at the new sentence structure type longer. The fact that infants only detected the higher-level change in sentence structure, if words contained adjacent ABB repetitions, but not non-adjacent ABA repetitions, again points to infants' early processing advantage of adjacent over non-adjacent dependency relations. Nevertheless, these data reveal first evidence of infants' ability to process word-level structures embedded in higher-level structures during the first year of life. Following this work, there are now first ERP studies

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indicating that infants are not only able to process one level of embedding, but even multiple levels of embedding (Winkler et al., 2015, 2016). In these studies five-month-old infants were tested with seven-tone sequences that contained three non-adjacent dependencies, nested around a center marker tone. In an auditory oddball paradigm, frequent standard sequences established the multiple center-embedded structure, while infrequent deviant sequences contained violations of the two outer dependencies. Importantly, mismatch responses to these violations indicated infants' detection of the underlying structural rules. Thus, infants at this young age show impressive abilities in processing multiple nested dependencies, which even for adults are challenging to accomplish (de Vries et al., 2011; Karlsson, 2007).

Future neuroimaging research will have to specify the potentially different neural mechanisms underlying these complex processing abilities across development. Parallel to the literature showing infant learning of non-adjacent dependencies (even multiple non-adjacent dependencies), there is an ongoing line of work on adult learning of multiple non-adjacent dependencies (Ottl, Jager, & Kaup, 2015; Uddén et al., 2012). Follow-up experiments (e.g., using passive listening paradigms) in infants and adults exposed to nested, crossed, and other theoretically interesting structures would be a promising way forward for future integration of adult and developmental AGL literature.

33.5 Conclusion

We have created an AGL key that exposes the most relevant variations in the AGL paradigm, in the light of current open questions, for example with regard to its relevance for natural language processing and language learning. Currently, an outstanding tractable question in (p. 776) AGL research is whether it can be demonstrated that domain-general sequence processing mechanisms explain at least part of the performance observed in AGL studies. We speculate that complex grammars might trigger relatively more domain-general processes than less complex ones, but this remains to be validated in both psycholinguistic and neuroimaging experiments. The lack of conclusive evidence of such domain-general processes is salient, as the lesson from sensory neuroscience is that brain organization can largely be understood as based on stimulus features. The issue of domain-generality of sequence processing is of importance for understanding the limitations of generalizability of AGL results to research on natural syntax, since there is a literature showing that syntactic processing in natural language should be understood as largely supramodal. The issue of whether implicit versus explicit sequence learning might be subserved by different neurobiological mechanisms is also still open, and studies addressing this question in the future should take novel, more sensitive ways of probing for (conscious) access into account. This is important for clarifying the relevance of the AGL paradigm for language learning. Implicit AGL paradigms are generally of higher relevance for L1 language learning, but still, the underlying neurobiology develops/matures remarkably and changes in AGL performance

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are expected as a consequence of growing up. This naturally limits the relevance of adult AGL experiments for L1 language learning and comparative developmental studies are warranted. Our meta-analysis of fMRI-studies including the NG > G contrast highlights *similarities and differences* between robustly activated regions in AGL and natural language processing (in particular for complex syntax). While a lot has already been said about the LIFG in this context, we now extend this discussion to also include, for instance, the FOP and LPUTG. We have also identified a problem at the interface of AGL and natural language research, which is that the central term *hierarchy* is often used without references to which out of several existing definitions it refers to. Particularly in the context of a well-defined notion of hierarchy, AGL experiments on relative learning difficulties and neural implementation of hierarchical versus non-hierarchical grammars is of continuing importance. Given methodological advancements, these open questions are now also increasingly tractable in the developmental AGL literature.

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References

Altmann, G. T. M., Dienes, Z., & Goode, A. (1995). Modality independence of implicitly learned grammatical knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*, 899-912.

(p. 777) Bahlmann, J., Schubotz, R. I., & Friederici, A. D. (2008). Hierarchical artificial grammar processing engages Broca's area. *NeuroImage*, *42*, 525-34.

Basirat, A., Dehaene, S., & Dehaene-Lambertz, G. (2014). A hierarchy of cortical responses to sequence violations in three-month-old infants. *Cognition*, *132*(2), 137-50.

Bates, E., Wilson, S. M., Saygin, A. P., Dick, F., Sereno, M. I., Knight, R. T., & Dronkers, N. F. (2003). Voxel-based lesion-symptom mapping. *Nature Neuroscience*, *6*, 448-50.

Batterink, L. J., Reber, P. J., Neville, H. J., & Paller, K. A. (2015). Implicit and explicit contributions to statistical learning. *Journal of Memory and Language*, *83*, 62-78.

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

Berwick, R. C., & Chomsky, N. (2016). *Why Only Us: Language and Evolution*. The MIT Press, Cambridge, MA.

Bever, T. G. (1974). The ascent of the specious or there's a lot we don't know about mirrors. In: Cohen, D. (Ed.), *Explaining Linguistic Phenomena*. Hemisphere Publishing Corporation, New York, NY, pp. 173–200.

Bischoff-Grethe, A., Proper, S. M., Mao, H., Daniels, K. A., & Berns, G. S. (2000). Conscious and unconscious processing of nonverbal predictability in Wernicke's area. *The Journal of Neuroscience*, *20*, 1975–81.

Bornkessel-Schlesewsky, I., & Schlewsky, M. (2013). Reconciling time, space and function: A new dorsal-ventral stream model of sentence comprehension. *Brain and Language*, *125*, 60–76.

Bornkessel-Schlesewsky, I., Schlewsky, M., Small, S. L., & Rauschecker, J. P. (2015). Neurobiological roots of language in primate audition: common computational properties. *Trends in Cognitive Sciences*, *19*, 142–50.

Brooks, L. R., & Vokey, J. R. (1991). Abstract analogies and abstracted grammars—Comments on Reber (1989) and Mathews Et-Al (1989). *Journal of Experimental Psychology: General*, *120*, 316–23.

Chang, F., Dell, G. S., Bock, K., & Griffin, Z. M. (2000). Structural priming as implicit learning: A comparison of models of sentence production. *Journal of Psycholinguistic Research*, *29*, 217–29.

Clark, A. (2014). Learnability and Language Acquisition, “An introduction to multiple context free grammars for linguists.” Available at: <http://www.cs.rhul.ac.uk/home/alexc/lot2012/>

Constable, R. T., Pugh, K. R., Berroya, E., Mencl, W. E., Westerveld, M., Ni, W. J., & Shankweiler, D. (2004). Sentence complexity and input modality effects in sentence comprehension: An fMRI study. *NeuroImage*, *22*, 11–21.

Conway, C. M., & Christiansen, M. H. (2005). Modality-constrained statistical learning of tactile, visual, and auditory sequences. *Journal of Experimental Psychology*, *31*, 24–39.

Conway, C. M., Bauernschmidt, A., Huang, S. S., & Pisoni, D. B. (2010). Implicit statistical learning in language processing: Word predictability is the key. *Cognition*, *114*, 356–71.

Craig, A. D. (2009). How do you feel—now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*, 59–70.

Cunillera, T., Camara, E., Toro, J. M., Marco-Pallares, J., Sebastián-Gallés, N., Ortiz, H., . . . & Rodríguez-Fornells, A. (2009). Time course and functional neuroanatomy of speech segmentation in adults. *NeuroImage*, *48*, 541–53.

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

de Vries, M. H., Monaghan, P., Knecht, S., & Zwitserlood, P. (2008). Syntactic structure and artificial grammar learning: The learnability of embedded hierarchical structures. *Cognition*, *107*, 763–74.

de Vries, M., Christiansen, M. H., Petersson, K. M. (2011). Learning recursion: Multiple nested and crossed dependencies. *Biolinguistics*, *5*, 10–35.

(p. 778) Davis, M., Sigal, R., & Weyuker, E. J. (1994). *Computability, Complexity, and Languages: Fundamentals of Theoretical Computer Science*. Newnes, Oxford/Boston.

Dronkers, N. F. (1996). A new brain region for coordinating speech articulation. *Nature*, *384*, 159–61.

Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Human Brain Mapping*, *30*(9), 2907–26.

Endress, A. D., Nespors, M., & Mehler, J. (2009). Perceptual and memory constraints on language acquisition. *Trends in Cognitive Science*, *13*, 348–53.

Ferry, A. L., Fló, A., Brusini, P., Cattarossi, L., Macagno, F., Nespors, M., & Mehler, J. (2016). On the edge of language acquisition: Inherent constraints on encoding multisyllabic sequences in the neonate brain. *Developmental Science*, *19*, 488–503.

Fiser, J., & Aslin, R. N. (2002). Statistical learning of higher-order temporal structure from visual shape sequences. *Journal of Experimental Psychology*, *28*, 458–467

Fitch, W. T. (2014). Toward a computational framework for cognitive biology: unifying approaches from cognitive neuroscience and comparative cognition. *Physics of Life Reviews*, *11*, 329–64.

Fletcher, P., Buchel, C., Josephs, O., Friston, K., & Dolan, R. (1999). Learning-related neuronal responses in prefrontal cortex studied with functional neuroimaging. *Cerebral Cortex*, *9*, 168–78.

Folia, V., Forkstam, C., Ingvar, M., Hagoort, P., & Petersson, K. M. (2011). Implicit artificial syntax processing: Genes, preference, and bounded recursion. *Biolinguistics*, *5*, 105–32.

Forkstam, C., Elwér, Å., Ingvar, M., & Petersson, K. M. (2008). Instruction effects in implicit artificial grammar learning: A preference for grammaticality. *Brain Research*, *1221*, 80–92.

Forkstam, C., Hagoort, P., Fernández, G., Ingvar, M., & Petersson, K. M. (2006). Neural correlates of artificial syntactic structure classification. *NeuroImage*, *32*, 956–67.

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

Friederici, A. D. (2012). The cortical language circuit: From auditory perception to sentence comprehension. *Trends in Cognitive Sciences*, 16, 262–8.

Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: Functional localization and structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 2458–63.

Friederici, A. D., Mueller, J. L., & Oberecker, R. (2011). Precursors to natural grammar learning: Preliminary evidence from 4-month-old infants. *PLoS One*, 6, e17920.

Friederici, A. D., & Singer, W. (2015). Grounding language processing on basic neurophysiological principles. *Trends in Cognitive Sciences*, 19(6), 329–38.

Frost, R., Armstrong, B. C., Siegelman, N., & Christiansen, M. H. (2015). Domain generality versus modality specificity: the paradox of statistical learning. *Trends in Cognitive Sciences*, 19, 117–25.

Gervain, J., Berent, I., & Werker, J. F. (2012). Binding at birth: The newborn brain detects identity relations and sequential position in speech. *Journal of Cognitive Neuroscience*, 24, 564–74.

Gervain, J., Macagno, F., Cogoi, S., Pena, M., & Mehler, J. (2008). The neonate brain detects speech structure. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 14222–7.

(p. 779) Gheysen, F., Van Opstal, F., Roggeman, C., Van Waelvelde, H., & Fias, W. (2010). Hippocampal contribution to early and later stages of implicit motor sequence learning. *Experimental Brain Research*, 202, 795–807.

Gibson, E. (1998). Linguistic complexity: Locality of syntactic dependencies. *Cognition*, 68, 1–76.

Gómez, R. L. (2016). Do infants retain the statistics of a statistical learning experience? Insights from a developmental cognitive neuroscience perspective. *Philosophical Transactions of the Royal Society B, Biological Sciences*, 372, 1711.

Gómez, R. L., & Gerken, L. (1999). Artificial grammar learning by 1-year-olds leads to specific and abstract knowledge. *Cognition*, 70(2), 109–35.

Gómez, R. L., & Gerken, L. (2000). Infant artificial language learning and language acquisition. *Trends in Cognitive Sciences*, 4, 178–86.

Gómez, R. L., & Maye, J. (2005). The developmental trajectory of nonadjacent dependency learning. *Infancy*, 7, 183–206.

Gómez, R. L., Gerken, L., & Schvaneveldt, R. W. (2000). The basis of transfer in artificial grammar learning. *Memory & Cognition*, 28, 253–63.

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

- Goucha, T., & Friederici, A. D. (2015). The language skeleton after dissecting meaning: A functional segregation within Broca's Area. *NeuroImage*, *114*, 294–302.
- Hagoort, P., & Indefrey, P. (2014). The neurobiology of language beyond single words. *Annual Review of Neuroscience*, *37*, 347–62.
- Hauser, M. F., Hofmann, J., & Opitz, B. (2012). Rule and similarity in grammar: their interplay and individual differences in the brain. *NeuroImage*, *60*, 2019–26.
- Heinz, J., & Idsardi, W. (2011). Sentence and word complexity. *Science*, *333*, 295–7.
- Higo, T., Mars, R. B., Boorman, E. D., Buch, E. R., & Rushworth, M. F. (2011). Distributed and causal influence of frontal operculum in task control. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 4230–5.
- Höhle, B. J., Weissenborn, J., Kiefer, D., Schulz, A., & Schmitz, M. (2004). Functional elements in infants' speech processing: The role of determiners in the syntactic categorization of lexical elements. *Infancy*, *5*, 341–53.
- Huettel, S. A., Song, A. W., & McCarthy, G. (2004). *Functional Magnetic Resonance Imaging*. Sinauer Associates, Sunderland, MA.
- Kabdebon, C., Pena, M., Buiatti, M., & Dehaene-Lambertz, G. (2015). Electrophysiological evidence of statistical learning of long-distance dependencies in 8-month-old preterm and full-term infants. *Brain and Language*, *148*, 25–36.
- Karlsson, F. (2007). Constraints on multiple center-embedding of clauses. *Journal of Linguistics*, *43*, 365–92.
- Karuza, E. A., Newport, E. L., Aslin, R. N., Starling, S. J., Tivarus, M. E., & Bavelier, D. (2013). The neural correlates of statistical learning in a word segmentation task: An fMRI study. *Brain and Language*, *127*, 46–54.
- Kemmerer, D. L. (2014). *Cognitive Neuroscience of Language*. Psychology Press, New York, NY.
- Kepinska, O., de Rover, M., Caspers, J., & Schiller, N. O. (2016). On neural correlates of individual differences in novel grammar learning: An fMRI study. *Neuropsychologia*, *98*, 156–68.
- Kinder, A., & Lotz, A. (2009). Connectionist models of artificial grammar learning: what type of knowledge is acquired? *Psychological Research*, *73*, 659–73.
- (p. 780) Kovacs, A. M., & Endress, A. D. (2014). Hierarchical processing in seven-month-old infants. *Infancy*, *19*, 409–25.

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

Kudo, N., Nonaka, Y., Mizuno, N., Mizuno, K., & Okanoya, K. (2011). On-line statistical segmentation of a non-speech auditory stream in neonates as demonstrated by event-related brain potentials. *Developmental Science*, *14*, 1100–6.

Lany, J. (2014). Judging words by their covers and the company they keep: Probabilistic cues support word learning. *Child Development*, *85*, 1727–39.

Lany, J., & Saffran, J. R. (2010). From statistics to meaning: infants' acquisition of lexical categories. *Psychological Science*, *21*, 284–91.

Lewis, A. G., Schoffelen, J.-M., Schriefers, H., & Bastiaansen, M. (2016). A predictive coding perspective on beta oscillations during sentence-level language comprehension. *Frontiers in Human Neuroscience*, *10*, 85.

Lieberman, M. D., Chang, G. Y., Chiao, J., Bookheimer, S. Y., & Knowlton, B. J. (2004). An event-related fMRI study of artificial grammar learning in a balanced chunk strength design. *Journal of Cognitive Neuroscience*, *16*, 427–38.

Manza, L., & Bornstein, R. F. (1995). Affective discrimination and the implicit learning process. *Consciousness and Cognition*, *4*, 399–409.

Marchetto, E., & Bonatti, L. L. (2015). Finding words and word structure in artificial speech: the development of infants' sensitivity to morphosyntactic regularities. *Journal of Child Language*, *42*, 873–902.

Marcus, G. F., Fernandes, K. J., & Johnson, S. P. (2007). Infant rule learning facilitated by speech. *Psychological Science*, *18*, 387–91.

Marcus, G. F., Vijayan, S., Bandi Rao, S., & Vishton, P. M. (1999). Rule learning by seven-month-old infants. *Science*, *283*, 77–80.

McNealy, K., Mazziotta, J. C., & Dapretto, M. (2006). Cracking the language code: neural mechanisms underlying speech parsing. *The Journal of Neuroscience*, *26*, 7629–39.

Mei, L., Xue, G., Lu, Z. L., He, Q., Zhang, M., Wei, M., . . . & Dong, Q. (2014). Artificial language training reveals the neural substrates underlying addressed and assembled phonologies. *PloS One*, *9*, e93548.

Meulemans, T., & Van der Linden, M. (1997). Associative chunk strength in artificial grammar learning. *Journal of Experimental Psychology*, *23*, 1007–28.

Meyer, L., Obleser, J., & Friederici, A. D. (2013). Left parietal alpha enhancement during working memory-intensive sentence processing. *Cortex*, *49*, 711–21.

Misyak, J. B., Christiansen, M. H., & Tomblin, J. B. (2009). Statistical learning of nonadjacencies predicts on-line processing of long-distance dependencies in natural language. *Proceedings of the Cognitive Science Society, 2009*, 177–82.

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

Mueller, J. L., Friederici, A. D., & Männel, C. (2012). Auditory perception at the root of language learning. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 15953–8.

O'Keefe, J. (1999). Do hippocampal pyramidal cells signal non-spatial as well as spatial information? *Hippocampus*, *9*, 352–64.

Opitz, B., & Friederici, A. D. (2003). Interactions of the hippocampal system and the prefrontal cortex in learning language-like rules. *NeuroImage*, *19*, 1730–7.

Opitz, B., & Friederici, A. D. (2004). Brain correlates of language learning: The neuronal dissociation of rule-based versus similarity-based learning. *Journal of Neuroscience*, *24*, 8436–40.

(p. 781) Opitz, B., & Friederici, A. D. (2007). Neural basis of processing sequential and hierarchical syntactic structures. *Human Brain Mapping*, *28*, 585–92.

Opitz, B., & Hofmann, J. (2015). Concurrence of rule- and similarity-based mechanisms in artificial grammar learning. *Cognitive Psychology*, *77*, 77–99.

Ottl, B., Jager, G., & Kaup, B. (2015). Does formal complexity reflect cognitive complexity? Investigating aspects of the Chomsky Hierarchy in an artificial language learning study. *PloS One*, *10*, e0123059.

Petersson, K. M., Folia, V., & Hagoort, P. (2012). What artificial grammar learning reveals about the neurobiology of syntax. *Brain and Language*, *120*, 83–95.

Petersson, K. M., Forkstam, C., & Ingvar, M. (2004). Artificial syntactic violations activate Broca's region. *Cognitive Science*, *28*, 383–407.

Rabagliati, H., Senghas, A., Johnson, S. P., & Marcus, G. F. (2012). Infant rule learning: Advantage language or advantage speech? *Plos One*, *7*, e40517.

Reber, A. S. (1967). Implicit learning of artificial grammars. *Journal of Verbal Learning & Verbal Behavior*, *6*, 855–63.

Saffran, J. R. (2001). Words in a sea of sounds: the output of statistical learning. *Cognition*, *81*, 149–69.

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by eight-month-old infants. *Science*, *274*, 1926–8.

Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., . . . & Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *The Journal of Neuroscience*, *27*, 2349–2356

Seger, C. A. (1994). Implicit learning. *Psychological Bulletin*, *115*, 163–96.

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

Seger, C. A., Prabhakaran, V., Poldrack, R. A., & Gabrieli, J. D. E. (2000). Neural activity differs between explicit and implicit learning of artificial grammar strings: An fMRI study. *Psychobiology*, *28*, 283-92.

Shi, R., Cutler, A., Werker, J., & Cruickshank, M. (2006). Frequency and form as determinants of functor sensitivity in English-acquiring infants. *The Journal of the Acoustical Society of America*, *119*, EL61-7.

Shukla, M., White, K. S., & Aslin, R. N. (2011). Prosody guides the rapid mapping of auditory word forms onto visual objects in 6-mo-old infants. *Proceedings of the National Academy of Sciences*, *108*(15), 6038-43.

Siegelman, N., & Frost, R. (2015). Statistical learning as an individual ability: Theoretical perspectives and empirical evidence. *Journal of Memory and Language*, *81*, 105-20.

Skeide, M. A., Brauer, J., & Friederici, A. D. (2016). Brain functional and structural predictors of language performance. *Cerebral Cortex*, *26*, 2127-39.

Skosnik, P. D., Mirza, F., Gitelman, D. R., Parrish, T. B., Mesulam, M.-M., & Reber, P. J. (2002). Neural correlates of artificial grammar learning. *NeuroImage*, *17*, 1306-14.

Squire, L. R., & Zola, S. M. (1996). Structure and function of declarative and nondeclarative memory systems. *Proceedings of the National Academy of Sciences of the United States of America*, *93*, 13515-22.

Stabler, E. P. (2011). *Top-down recognizers for MCFGs and MGs*. Paper presented at the Proceedings of the 2nd workshop on cognitive modeling and computational linguistics. Available at: <http://linguistics.ucla.edu/people/stabler/Stabler11-CMCL.pdf>

Stobbe, N., Westphal-Fitch, G., Aust, U., & Fitch, W. T. (2012). Visual artificial grammar learning: comparative research on humans, kea (*Nestor notabilis*) and pigeons (*Columba* (p. 782) *livia*). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*, 1995-2006.

Strange, B. A., Henson, R. N., Friston, K. J., & Dolan, R. J. (2001). Anterior prefrontal cortex mediates rule learning in humans. *Cerebral Cortex*, *11*, 1040-6.

Sturm, J. (2011). *Domain-specificity in the Acquisition of Non-adjacent Dependencies*. Doctoral thesis, Northumbri.

Teinonen, T., Fellman, V., Näätänen, R., Alku, P., & Huotilainen, M. (2009). Statistical language learning in neonates revealed by event-related brain potentials. *BMC Neuroscience*, *10*, 21-8.

Tessier, A.-M. (2007). *Biases and Stages in Phonological Acquisition*. (PhD Dissertation), UMass Amherst, Amherst, MA.

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

Tunney, R. J., & Altmann, G. T. M. (1999). The transfer effect in artificial grammar learning: Reappraising the evidence on the transfer of sequential dependencies. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*, 1322–33.

Turk-Browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2009). Neural evidence of statistical learning: efficient detection of visual regularities without awareness. *Journal of Cognitive Neuroscience*, *21*, 1934–45.

Uddén, J. (2012). Language as structured sequences: a causal role for Broca's region in sequence processing (PhD thesis), Karolinska Institute, Stockholm. Available at: <http://hdl.handle.net/10616/40842>

Uddén, J., & Bahlmann, J. (2012). A rostro-caudal gradient of structured sequence processing in the left inferior frontal gyrus. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*, 2023–2032.

Uddén, J., Folia, V., & Petersson, K. M. (2010). Neuropharmacology of implicit learning. *Current Neuropharmacology*, *8*, 367–81.

Uddén, J., Ingvar, M., Hagoort, P., & Petersson, K. M. (2012). Implicit acquisition of grammars with crossed and nested non-adjacent dependencies: investigating the push-down stack model. *Cognitive Science*, *36*, 1078–1101.

Wagner, J. B., Fox, S. E., Tager-Flusberg, H., & Nelson, C. A. (2011). Neural processing of repetition and non-repetition grammars in 7- and 9-month-old infants. *Frontiers in Psychology*, *2*, 168.

Weber, K., Christiansen, M. H., Petersson, K. M., Indefrey, P., & Hagoort, P. (2016). fMRI syntactic and lexical repetition effects reveal the initial stages of learning a new language. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *36*, 6872–80.

Wells, J. B., Christiansen, M. H., Race, D. S., Acheson, D. J., & MacDonald, M. C. (2009). Experience and sentence processing: Statistical learning and relative clause comprehension. *Cognitive Psychology*, *58*, 250–71.

Wierzbichon, M., Asanowicz, D., Paulewicz, B., & Cleeremans, A. (2012). Subjective measures of consciousness in artificial grammar learning task. *Consciousness and Cognition*, *21*, 1141–53.

Wilson, B., Kikuchi, Y., Sun, L., Hunter, D., Dick, F., Smith, K., . . . & Petkov, C. I. (2015). Auditory sequence processing reveals evolutionarily conserved regions of frontal cortex in macaques and humans. *Nature Communications*, *6*, 8901.

Winkler, M., Männel, C., Friederici, A. D., & Mueller, J. L. (2015). Little grammar experts: 5-month-old infants' mismatch responses reveal the ability to process a triple center-

Artificial Grammar Learning and Its Neurobiology in Relation to Language Processing and Development

embedding. In: Error Signals from the Brain: 7th Mismatch Negativity Conference (p. 58). Leipzig: University of Leipzig. http://event.uni-leipzig.de/mmn2015/frontend/mmn2015_abstract_book_a4_double.pdf

(p. 783) Winkler, M., Mueller, J. L., Friederici, A. D., & Männel, C. (2016). Ontogenetic perspective on grammar learning: Infant's ability to process nested dependencies. In: MPI CBS, Research Report 2014–2016 (p. 81). Leipzig: MPI CBS. <http://www.cbs.mpg.de/174887/01-MPI-CBS-2014-2016.pdf>

Yang, J., & Li, P. (2012). Brain networks of explicit and implicit learning. *PloS One*, 7, e42993.

Zajonc, R. B. (1968). Attitudinal effects of mere exposure. *Journal of Personality and Social Psychology*, 9, 1–27.

Notes:

(¹) Figure 33.3 and the (informal) description of the Chomsky hierarchy was originally published in the PhD thesis, *Language as structured sequences: a causal role for Broca's region in sequence processing*, written by J. Uddén, 2012, and available at <http://hdl.handle.net/10616/40842>.

(²) However, we do not agree with how one of the included studies (Bischoff-Grethe, Proper, Mao, Daniels, & Berns, 2000) in this review was summarized (in our view this is the only visual study in which a structure-contrast supports domain-general structured sequence processing in LPUTG).

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