

Language learning in the adult brain: A neuroanatomical meta-analysis of lexical and grammatical learning

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ABSTRACT

Language learning as an adult, though often difficult, is quite common. Nevertheless, the neural substrates of this process remain unclear, even though identifying them should clarify how language is learned and could lead to improved success at this endeavor. We addressed this gap by conducting multiple neuroanatomical meta-analyses to synthesize the functional neuroimaging literature of language learning. We focused on learning lexical and grammatical knowledge, two building blocks of language. Lexical and grammatical learning yielded overlapping activation in frontal (e.g., BA 44/45) and posterior parietal regions. Only lexical learning showed ventral occipito-temporal (ventral stream) activation, while only grammatical learning showed basal ganglia (anterior caudate/putamen) activation. To further elucidate the neurocognition of grammar learning, we also tested specific predictions of the declarative/procedural model of language. Consistent with the model, grammar learning predicted to rely especially on declarative memory (e.g., with explicit training) showed hippocampal involvement, while grammar learning predicted to rely particularly on procedural memory (e.g., with implicit training) showed anterior caudate/putamen involvement. Finally, given the prevalence of research on artificial grammars, we performed separate analyses of artificial grammar and non-artificial grammar (e.g., miniature language) paradigms. These yielded overlapping activation, especially in BA 44, underscoring the validity of artificial grammars as models for grammar learning in natural languages. In sum, the study elucidates the empirical and theoretical landscape of language learning and has applied implications.

1. Introduction

Barring developmental disorders or cases of extreme isolation and neglect, infants and children universally engage in language learning. While language learning is also a fairly common endeavor in adulthood, it is not quite as universal and generally not as successful as in childhood. Research elucidating the neurocognitive bases of adult language learning, that is, how language learning proceeds in the adult mind and brain, may shed light on the complexities of this process and may help scientists and practitioners guide learners aiming to acquire a new language.

There have been numerous empirical studies on adult-learned

language, using both behavioral and neural approaches. However, most of these have focused on the processing of already-learned languages rather than on learning *per se*, that is, how novel information about language is encoded and stored in the mind and brain (Abutalebi, 2008; Bailey et al., 1974; Bardovi-Harlig, 1992; Costa and Sebastián-Gallés, 2014; Gass and Selinker, 2001; Indefrey, 2006; Li et al., 2014; Li and Tokowicz, 2012; van Hell and Tokowicz, 2010). Furthermore, relatively little is known about how the neurocognition of language learning in adults differs for different aspects of language, most notably for the lexicon (i.e., words) and grammar (i.e., rule-governed combination), two critical building blocks of language (Bloomfield, 1933; Chomsky, 1965; Langacker, 1987; Pinker, 1994).

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The relative lack of research on language learning is partly due to the logistical difficulties involved in investigating this phenomenon; language is so complex that it generally takes years or decades to learn a new language. To address this problem, studies examining language learning have often relied on “model languages.” These include artificial linguistic stimuli and systems, such as lists of pseudowords or artificial grammars, and reduced natural language stimuli and systems, such as lists of foreign-language words and miniature languages (i.e., a small number of real words and sentences from an existing language). Unlike full natural languages, these systems or collections of stimuli are learnable in a short period of time and can be controlled regarding the amount, type, and timing of exposure provided to participants. In contrast, actual natural language exposure is difficult to control. For example, even students enrolled in the same German 101 class may differ as to how often they do homework or whether they listen to German songs outside of class. Moreover, model languages often target aspects of language in isolation, which decreases some of the inherent complexity of language while making it possible to answer questions about specific aspects of language learning that are more difficult to separate out in full natural languages. For example, pseudowords can be learned in the absence of grammar, whereas artificial grammars target grammar in the absence of lexical/semantic information.

Artificial grammars are of particular interest here because they are among the most widely studied model languages. Artificial grammars (Reber, 1967) typically consist of a sequence of items (e.g., letters, syllables) whose order is determined by rules. Moreover, as mentioned just above, artificial grammars do not contain any lexical/semantic information, allowing the study of grammar learning in isolation. Because artificial grammars have relatively simple structures and do not require participants to learn words and their meanings, they are typically learnable in a very short period of time (i.e., minutes; Robinson, 2010). Despite this simplicity, electrophysiological and functional neuroimaging studies have found overlap in the neural bases of artificial grammar and natural language syntactic processing, suggesting that artificial grammars may serve as useful models for understanding natural languages (Christiansen et al., 2010; Conway et al., 2007; Forkstam et al., 2006; Petersson et al., 2012; Silva et al., 2017). Other research has, however, highlighted crucial differences between some types of artificial grammars and natural languages (Fitch and Hauser, 2004; Friederici, 2004; Friederici et al., 2006). To date, the extent to which artificial grammar learning mirrors other forms of grammar learning in the mind and brain is still unclear, and elucidating this issue is likely to be of interest in the language and cognitive sciences.

1.1. Present study

Over the past two decades or so, an increasing number of functional neuroimaging studies have probed language learning in controlled learning paradigms, primarily with model languages. However, it has been difficult to synthesize these results, and thus to ascertain the pattern of brain activation found in adult language learning for lexical/semantics and grammar.

One approach that could substantially clarify the functional neuroanatomy of language learning is to conduct neuroanatomical meta-analyses of previous functional neuroimaging studies. A quantitative meta-analytical approach can rigorously synthesize the existing literature and reveal any consistent patterns of activation. Meta-analyses have substantial power because they examine a much larger number of participants than individual studies. Thus, meta-analysis results are likely more reliable and generalizable than single study findings. Additionally, they can be more objective than qualitative reviews.

In the present study, we attempted to elucidate the functional neuroanatomy of adult lexical and grammatical learning by conducting an Activation Likelihood Estimation (ALE) meta-analysis. ALE, the most widely used neuroanatomical meta-analytic technique, determines areas of significant spatial convergence based on peak activation coordinates

reported in previous studies (Eickhoff et al., 2009b; Laird et al., 2005; Turkeltaub et al., 2002; Turkeltaub et al., 2012).

We followed a rigorous approach to achieve our goal. We first identified papers that examined later/adult language learning (by individuals age 12 or older, with most studies probing learners 18 or older; Hartshorne et al., 2018) during controlled experimental paradigms, with a specific focus on either lexical or grammatical targets. Thus, studies examining language learning in younger individuals or adult learning of other aspects of language, such as phonology or pragmatics, while potentially interesting, were not included because they were beyond the scope of this study. We focused on studies that examined oral and/or written language, whether natural or artificial; thus, studies of sign language were excluded. We included only studies that probed language learning, almost all of which employed model languages. Thus, this paper excluded studies of second language (L2) processing that did not include a training component (for recent neuroanatomical meta-analyses of L2 processing, see Liu and Cao, 2016 and Tagarelli et al., in prep).

We ran three sets of analyses on these studies. First, we ran separate ALE analyses on lexical and grammatical learning, and on direct comparisons of these. Second, to further elucidate grammar learning, we tested specific predictions of a well-studied neurocognitive model regarding the functional neuroanatomy of grammar. That is, we tested the declarative/procedural model's predictions that grammar learning that occurs in particular conditions (with explicit training or knowledge, or with an emphasis on similarity or chunking) should depend especially on declarative memory, and thus on the medial temporal lobe, whereas in the absence of such conditions grammar learning should depend largely on procedural memory, and thus the basal ganglia (Ullman, 2004, 2015, 2016). Third, to specifically examine the functional neuroanatomy of the widely-used paradigm of artificial grammar learning, as compared to grammar learning with more naturalistic paradigms that include words with meanings, we ran ALE analyses on studies that trained participants on artificial grammars and those that trained participants on non-artificial grammars (specifically, artificial languages, miniature languages, and natural languages).

2. Methods

2.1. Search, screening, and selection of articles

Here we describe the search, screening, and selection of the articles included in the meta-analyses. This process is summarized in the PRISMA flowchart shown in Fig. 1.

2.1.1. Search

A systematic search for peer-reviewed articles in the MEDLINE and PsycINFO databases (using the PubMed and OVID search tools, respectively), together with a list of potentially relevant peer-reviewed articles known to the authors, yielded 5020 records as of January 28, 2015. The database searches were constructed to return records related to aspects of language AND learning or memory AND neuroimaging (specifically PET or fMRI), in humans. The exact search syntax used to query each database is shown in Table 1. In order to maximize the likelihood that all potentially relevant studies would be captured in our database search, our search terms were intentionally broad, particularly for the domain of language (in which terminology can vary substantially).

2.1.2. Screening

After removing duplicates from the initial set of 5020 records, 4566 records remained. Subsequently, a simultaneous title and abstract screening was performed to exclude any papers that were clearly unrelated to language learning and/or did not use PET or fMRI. A sufficiently broad database search typically yields records numbering in the thousands, and a title and/or abstract screening step is recommended to rapidly screen these records (Eden et al., 2011; Mateen et al., 2013). In order to minimize the likelihood of unwarranted rejections, we took a

conservative approach: if there was any indication that a paper could possibly be relevant to language learning, broadly defined, and might employ PET or fMRI, it was retained. For example, our search returned a paper that used fMRI to examine picture naming (de Zubicaray et al., 2014). Because picture naming is commonly used in language learning experiments, this paper was retained in the title/abstract screening step, though it was ultimately excluded in the final selection step because it did not in fact examine language learning. In contrast, the search also returned a paper that used electroencephalography rather than PET or fMRI to examine the learning of Kanji characters by native German speakers (Shinoda and Skrandies, 2013), and thus the paper was excluded during the screening step. During the screening step, we also excluded any papers that were not written in English. Overall, 251 papers survived screening, and were thus subjected to the final selection step.

2.1.3. Selection of articles, and inclusion criteria

The final selection of studies was based on a full text evaluation of all 251 papers. This final step led to the exclusion of 205 additional papers, leaving 46 for inclusion in the meta-analyses, all of which met all of the following inclusion criteria. (1) They were empirical studies that were published or had been accepted for publication in peer-reviewed journals; conference presentations, master's theses, and doctoral dissertations were not included. (2) They examined brain activation using fMRI or PET (FDG-PET or O¹⁵-PET); studies using other neuroimaging techniques, such as SPECT, NIRS, or MEG, were not included. (3) Functional scanning covered the whole cerebrum (not necessarily the cerebellum, since many studies do not provide full coverage of this structure). (4) Activation foci resulted from whole-brain analyses (rather than region-of-interest analyses). (5) Activation foci were reported within the Talairach (Talairach and Tournoux, 1988) or Montreal Neurological Institute (MNI; Collins et al., 1994; Evans et al., 1993) standard stereotactic coordinate systems. Note that criteria (3)–(5) are required for whole brain ALE meta-analyses (Turkeltaub et al., 2002). (6) At least one subject group had no known neurological, neuropsychiatric, or neurodevelopmental disorders, with no participants younger than 12 years old; thus, papers examining individuals with disorders might not be excluded if they also examined healthy adult controls, though only the latter group would be included in the meta-analyses. (7) Language was presented aurally or in written form

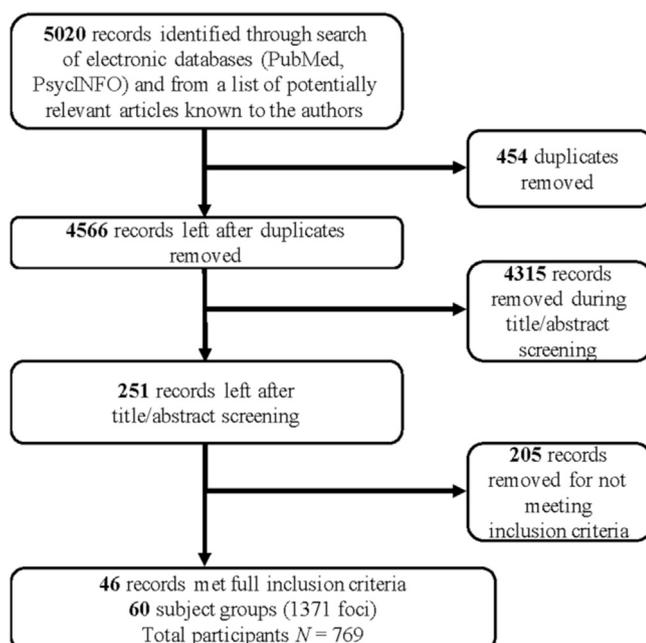


Fig. 1. PRISMA flowchart showing the process employed to identify the articles included in the meta-analyses.

Table 1

Search syntax used to query the MEDLINE and PsycINFO databases.

	Search Syntax
MEDLINE (PubMed search)	(language OR linguistics OR speech OR speech perception OR manual communication OR vocabulary OR semantics OR phonetics OR terminology as topic OR neurolinguistic programming OR verbal behavior) AND (learning OR memory) AND (persons OR humans) AND (neuroimaging OR Magnetic Resonance Imaging OR Positron-Emission Tomography)
PsycINFO (OVID search)	(exp Language/or language.mp. OR exp Linguistics/or exp Cognitive Linguistics/or linguistic*.mp. OR exp Semantics/or semantic*.mp. OR exp Oral Communication/or speech.mp. OR exp Vocabulary/or vocabulary.mp. OR word segmentation.mp. OR exp Language Development/or language development.mp. OR exp Word Recognition/or word recognition.mp. OR exp Speech Perception/or speech perception.mp. OR exp Phonetics/or phonetics.mp. OR exp Words) AND (learning.mp. or exp Learning/OR memory.mp. or exp Memory/) <i>Note that the search was limited to (peer reviewed journal AND human AND English language AND methodology = "0100 brain imaging")</i>

Note. All PubMed search terms (e.g., 'language') were specified as MeSH Terms, that is, as Medical Subject Headings, which are provided by the National Library of Medicine. In OVID, "exp" preceding a Keyword refers to 'explode' (found under the Search Tools option), which specifies the inclusion of all subheadings for that Keyword. The MEDLINE database only contains peer-reviewed articles, and the search was limited to peer-reviewed articles in PsycINFO.

(data from sign language were not included). (8) The reported neural activation was related to language learning, in particular to learning lexical or grammatical knowledge, as described in the following paragraph.

Specifically, language learning-related activation was defined as significant fMRI or PET signal increases measured in a controlled language training (learning) study, either during an actual training task (e.g., during exposure to word-picture pairs or to grammatical strings of an artificial grammar) or during a test on material trained during the study (e.g., during picture naming, grammaticality judgment, or passive viewing of trained stimuli). Lexical learning studies were defined as studies that examined the learning of word forms, with or without associated meanings. These included studies examining the learning of either pseudowords (made-up words) or words in a second language. Grammar learning studies were defined as studies that examined the learning of rule-governed sequential combination in inflectional morphology, morphosyntax, or syntax (Ullman, 2004, 2015, 2016). These included studies of artificial grammars (e.g., Bahlmann et al., 2008), artificial languages (e.g., Morgan-Short et al., 2015), miniature languages (e.g., Musso et al., 2003), and concentrated training paradigms in natural language (e.g., Sakai et al., 2004).

We excluded papers that only examined the learning of idiosyncratic information below the word level, such as phonemes (Golestani and Zatorre, 2004), letters (Hashimoto and Sakai, 2004), and pitch (Wong et al., 2007). We also excluded papers examining speech segmentation (our search yielded four such papers that also met our other criteria e.g., Karuza et al., 2013). Since learning in this paradigm may involve both the acquisition of lexical-like information (i.e., extracting specific phonological sequences from a speech stream) and the statistical learning of regularities in language (Karuza et al., 2013; Ullman, 2016), such studies could therefore not be clearly categorized as lexical or grammatical learning.

The 205 excluded papers included, among others: review papers that did not include original (empirical) research (criterion 1 above; e.g., Friederici, 2004); papers that did not use appropriate methodology, analyses, or reporting to be included in an ALE analysis (criteria 2–5; e.g.,

Ghazi Saidi et al., 2013); papers that examined only subject groups with children under 12 or individuals with disorders (criterion 6; e.g., Friedrich and Friederici, 2011); papers that examined sign language (criterion 7; e.g., McCullough et al., 2005); and papers that did not examine the functional neuroanatomy of lexical or grammatical learning (criterion 8; e.g., de Zubicaray et al., 2014; Scott-Van Zeeland et al., 2010; Stewart et al., 2003). Note that many excluded papers, including some listed above, failed multiple inclusion criteria (e.g., Friedrich and Friederici, 2011, tested word learning in infants using ERPs, and thus did not meet criteria 2–6). The first or second author carefully scanned each paper until it was determined that at least one inclusion criterion was not met (205 records), or that all eight inclusion criteria were met. In cases of uncertainty, the first and second authors conferred with each other and the last author to determine whether the inclusion criteria were met or not. Ultimately, 46 papers were identified as meeting all study inclusion criteria, with 100% agreement between the first, second, and last authors. These papers yielded 60 subject groups, 1371 foci, and 769 participants that were included in our ALE analyses; see Fig. 1.

2.2. Contrasts of interest

The primary goal of these meta-analyses was to examine the neural correlates of lexical and grammatical learning. To that end, we included all relevant contrasts that subtracted activation during baseline conditions from activation during lexical or grammatical learning conditions (we did not include the reverse contrasts, e.g., baseline > lexical learning, since such ‘deactivation’ is often not reported, and can be difficult to interpret). As stated above, the relevant contrasts could target activation during a training phase or during a test that followed a training phase. Baseline conditions primarily included sensorimotor control tasks or non-task conditions (e.g., rest). Contrasts targeting activation during a pretest – that is, before participants had begun the process of learning – were not included in our analyses, as they did not represent learning-related activation; however, contrasts that used pretest conditions as a baseline could be included (e.g., posttest > pretest).

Any *learning-related* contrast reported to change as a function of time or performance (e.g., accuracy) was also included. For example, a contrast of grammar learning > baseline for which activation increased linearly from the first through the last block of training was included (Fletcher et al., 1999). Such contrasts can identify areas of the brain that are more activated in later than earlier phases of learning. Similarly, a contrast of lexical learning > baseline that showed greater activation in the first day of training compared to a subsequent day was also included (Takashima et al., 2014). Such contrasts can identify areas of the brain that are more activated in earlier than later phases of learning. Crucially, both such types of contrast were included as they both represent activation related to learning.

We did not include any contrasts that were not specifically related to lexical or grammatical learning. Thus, we did not include contrasts that compared item types (e.g., cognates vs. noncognates, or ungrammatical vs. grammatical strings) or training conditions (e.g., word training focusing on words’ phonological forms vs. training focusing on both their forms and their meanings). This is because we were interested in general lexical or grammatical learning-related processes, and such contrasts address more specific item- or training-based questions, and are therefore likely to yield activation related to those specific questions rather than to learning more generally. Since the ability of ALE meta-analysis to reveal converging neural activation across studies is related to the proportion of studies that show activation in a given neural region (Eickhoff et al., 2016), including such contrasts could decrease the likelihood of identifying significant ALE results related to general processes underlying lexical or grammatical learning.

The inclusion and exclusion of contrasts was designed to maximize the proportion of studies probing either lexical or grammatical learning. As such, the ALE analyses are likely to reveal converging activation related to general lexical or grammatical learning-related processes,

rather than activation specific to particular learning-related contrasts. For example, because posttest > pretest contrasts make up only a fraction of the contrasts going into our analyses (see below), our analyses are not likely to identify regions that are specifically activated during later stages of lexical or grammatical learning.

2.3. Contrast categorization for the primary and exploratory analyses

For our primary set of ALE analyses, which examined the neural bases of lexical and grammatical learning, all contrasts were categorized as targeting either lexical learning (30 papers, 37 subject groups, 1267 foci, 578 participants) or grammar learning (20 papers, 25 subject groups, 512 foci, 336 participants); see Table 2 and Fig. 2.

We also conducted two additional sets of ALE analyses to further examine specific questions regarding grammar learning (see section 1.1). We consider these to be exploratory analyses because they are underpowered given current ALE recommendations that analyses include a minimum of 17 subject groups (Eickhoff et al., 2016). However, all of these analyses include at least 5 subject groups (indeed, 8 or more), which provides ALE with sufficient sensitivity to detect the true effect if all groups activate a given target location (Eickhoff et al., 2016). Still, we emphasize that these smaller underpowered analyses should be interpreted cautiously.

First, we conducted hypothesis-driven analyses to examine how the neural bases of grammar learning may differ depending on whether declarative memory is expected to be engaged (Ullman, 2001, 2005, 2015). Contrasts examining grammar learning under conditions that are hypothesized by the declarative/procedural model to lead to a heavy dependence on declarative memory were classified as “Declarative Grammar Learning” contrasts (Ullman, 2004, 2015, 2016). Specifically, grammar learning contrasts were coded as Declarative Grammar Learning if they met any of the following criteria (Ullman, 2004, 2005, 2015, 2016): (1) explicit training (e.g., explanation of grammatical rules) was provided to participants (e.g., Musso et al., 2003); (2) the participants showed evidence of having explicit knowledge of the grammatical rules during or after training (e.g., Fletcher et al., 1999); or (3) the experimental paradigm was designed (as specified in the paper) to emphasize similarity (e.g., Opitz and Friederici, 2004) or chunking (e.g., Forkstam et al., 2006; Lieberman et al., 2004) in learning or test rather than emphasizing combinatorial rules. Contrasts meeting these criteria came from 10 papers (11 subject groups, 96 foci, 134 participants). Grammar learning contrasts that did not meet any of these criteria were classified as “non-Declarative Grammar Learning.” These constituted contrasts from 14 papers (15 subject groups, 285 foci, 195 participants); see Table 2.

Second, we aimed to examine the neural bases of artificial grammar learning. We therefore separated grammar learning contrasts into those investigating artificial grammar learning (12 papers, 15 subject groups, 270 foci, 199 participants) and those investigating grammar learning using a different linguistic target, specifically an artificial language, a miniature language, or a natural language (6 papers, 8 subject groups, 139 foci, 88 participants).

2.4. Subject and task characteristics that were coded

For each subject group, we coded several characteristics of the participants, including the number of participants, the number of female participants, age (mean or closest available estimate, usually median or range), and handedness. These data were not always reported, but based on values that were reported, 50.6% of the participants in the studies contributing to this meta-analysis were female and the mean age of participants was 23.3 years old (SD = 5.2 years old). Participants ranged in age from 12 to 68 years old, with the vast majority of studies reporting mean ages between 20 and 25 years old, and none surpassing a mean of 36 years old. Only two studies included participants under 18 years old (Sakai et al., 2004; Stein et al., 2009). Aside from Sandak et al. (2004),

Table 2

Papers and subject groups included in the meta-analyses, together with relevant study characteristics.

Paper	Subject Group ID	N(f)	No. of Foci	Language Domain	DGL/nonDGL	Linguistic Target	Training Task(s)	Task(s) in Scanner
Bahlmann et al. (2008)	1	14(7)	29	Grammar	nonDGL	Artificial grammar	View grammatical strings while searching for rules, & GJT w/feedback	Same as learning
Bradley et al. (2013)	2a	20(8)	13	Lexicon		Word	Study word list for ~2 h at own pace until 90% on vocabulary test	Animacy judgment
Breitenstein et al. (2005)	2b	20(13)	5	Lexicon		Word	Picture matching: pseudowords presented with correct or incorrect image in a 10:1 ratio	Same as learning
Cao et al. (2013)	3	14(6)	23	Lexicon		Word	Presented with L2 character, pinyin, pronunciation, and L1 translation, write either character or pinyin 3× for each word; 5 ~1-hr sessions on separate days	Passive viewing of words
Clark and Wagner (2003)	4	17(7)	12	Lexicon		Word	Indicate # of syllables in visually presented words	Same as learning
Davis et al. (2009)	5	20(11)	38	Lexicon		Word	Auditory presentation of pseudowords while monitoring for a target phoneme	Same as learning
Deng et al. (2008)	6	16(nr)	42	Lexicon		Word	Paired associates: L1 auditory w/L2 written character; quiz w/feedback; over 2 weeks	Matching: auditory L1/ written L2 translation
Deng et al. (2011)	7	12(10)	9	Lexicon		Word	Paired associates: L2 auditory w/L2 written character, L1 translation given; quiz w/feedback; over 2 weeks	Matching: auditory L2 word/written character
Finn et al. (2013)	8	12(7)	32	Lexicon		Word	Exposed to sentences matched with descriptive scenes and asked to repeat; over 3 days	GJT
Fisher et al. (2012)	9a	10(5)	42	Grammar	nonDGL	Artificial language	1-back task on letter strings	Same as learning
Fletcher et al. (1999)	9b	10(5)	39	Grammar	DGL: Explicit knowledge, and surface similarity between training and testing sets	Artificial grammar	GJT w/feedback	Same as learning
	9 ab	20(10)	4					
	10	12(6)	35	Lexicon		Word		
Forkstam et al. (2006)	11	7(3)	26	Grammar	DGL: Explicit knowledge, and surface similarity between training and testing sets	Artificial grammar	View letter string and immediately type it, no feedback	GJT
	12	12(8)	46	Grammar	Both (24 foci) nonDGL (17 foci) DGL (5 foci): high chunk strength	Artificial grammar		
Jeong et al. (2010)	13	31(10)	20	Lexicon		Word	View video clips with L2 words in context or with translation	Matching: word/video
Krönke et al. (2013)	14	11(7)	2	Lexicon		Word	Paired associates: pseudowords (heard) and L1 German nouns (written), some accompanied by gestures	Passive viewing of pseudowords
Lieberman et al. (2004)	15	9(5)	11	Grammar	nonDGL (1 focus) DGL (10 foci): high chunk strength	Artificial grammar	View letter string and reproduce, up to 3 chances to get it right	GJT
Liu et al. (2007)	16a	7(7)	16	Lexicon		Word	Chinese characters presented with pronunciation, meaning, or both	Passive viewing of characters
	16b	8(8)	16					
	16c	8(8)	17					
	16abc	23(23)	34					
Majerus et al. (2005)	17	12(0)	9	Lexicon		Word	Hear and repeat nonwords	Same as learning
Makita et al. (2013)	18	14(nr)	8	Lexicon		Word	Paired associates: written word and picture; phonological rehearsal	Same as learning
Mestres-Misse et al. (2008)	19	12(6)	21	Lexicon		Word	Reading pseudowords in contextual or ambiguous L1 sentences	Same as learning
Mestres-Misse et al. (2009)	20	15(9)	33	Lexicon		Word	Reading pseudowords in contextual L1 sentences	Same as learning
Mestres-Misse et al. (2010)	21	21(11)	31	Lexicon		Word	Reading pseudowords in contextual L1 sentences	Same as learning
Morgan-Short et al. (2015)	22	13(6)	14	Grammar	nonDGL	Artificial language	Exposure to artificial language through computer game	GJT
Musso et al. (2003)	23a	8(4)	3	Grammar	DGL: Explicit training	Miniature language	Rule training interspersed with GJT with feedback	GJT
	23b	8(4)	2	Grammar		Artificial language		
Newman-Norlund et al. (2006)	24	8(4)	13	Grammar	nonDGL	Artificial language	Forced choice picture matching to auditory sentence; additional practice and instruction	Same as learning
Opitz and Friederici (2003)	25	14(7)	10	Grammar	nonDGL	Artificial grammar	View grammatical strings while searching for rules, & GJT w/feedback	Same as learning
Opitz and Friederici (2004)	26	21(9)	2	Grammar	nonDGL (1 focus) DGL (1 focus): Surface similarity between training and testing sets	Artificial grammar	View grammatical strings while searching for rules, & GJT w/feedback	Same as learning
Opitz et al. (2014)	27a	16(nr)	3	Lexicon		Word		

(continued on next page)

Table 2 (continued)

Paper	Subject Group ID	N(f)	No. of Foci	Language Domain	DGL/nonDGL	Linguistic Target	Training Task(s)	Task(s) in Scanner
	27abc	48(26)	6				Pairing of L1 and L2 translations (orthography and phonology), including review with feedback	Matching: L1/L2 translations
Paulesu et al. (2009)	28a	6(0)	1	Lexicon		Word	Passive listening to list of nonwords	Same as learning
	28b	6(0)	1				Passive listening to list of nonword + real word pairs	Same as learning
	28 ab	12(0)	20				Passive listening to list of nonwords or to nonword + real word pairs	Same as learning
Petersson et al. (2004)	29	12(3)	24	Grammar	nonDGL	Artificial grammar	Read and reproduce (type) consonant strings	GJT
Raboyeau et al. (2004)	30	10(2)	44	Lexicon		Word	Name objects in L2 with help of phonological and grapheme cues	Picture naming (overt)
Raboyeau et al. (2010)	31	10(5)	51	Lexicon		Word	Name objects in L2 with help of phonological and grapheme cues	Picture naming (overt)
Rauschecker et al. (2008)	32	14(6)	21	Lexicon		Word	Listening to and covertly repeating pseudowords	Same as learning
Sakai et al. (2004)	33	14(8)	10	Grammar (5 foci) Lexicon (5 foci)	DGL: Explicit training	Natural language	Matching L2 verbs to past-tense forms using BINGO-style game	Forced-choice correct past-tense form of verb
Sandak et al. (2004)	34	20(9)	161	Lexicon		Word	Make orthographic, phonological, or semantic judgment on each exposure to a pseudoword	Overt reading
Seger et al. (2000)	35a	7(3)	21	Grammar	nonDGL	Artificial grammar	View grammatical strings and attempt to memorize	GJT
	35b	7(1)	6	Grammar	DGL: Surface similarity between training and testing sets			Recognition test
Skosnik et al. (2002)	36a	12(6)	6	Grammar	nonDGL	Artificial grammar	View letter string and reproduce, up to 3 chances to get it right	GJT
	36b	11(5)	2	Grammar	DGL: Surface similarity between training and testing sets			Recognition test
Stein et al. (2009)	37	10(6)	50	Lexicon		Word	3-week intensive language course	Know/don't know meaning
Takashima et al. (2014)	38	23(21)	89	Lexicon		Word	Phoneme monitoring tasks of pseudowords with and without paired objects	Recognition test
Taylor et al. (2014)	39	19(13)	45	Lexicon		Word	Word sound/grapheme pairing or sound/object pairing	Same as learning
Tettamanti et al. (2002)	40a	7(nr)	3	Grammar	nonDGL	Artificial grammar	Passive reading of grammatical sentences	GJT
	40 ab	14(7)	35	Grammar				Same as learning
Thiel et al. (2003)	41	16(7)	5	Grammar	nonDGL	Artificial grammar	View pseudofont string, visually rehearse, then forced-choice of matching string presented on subsequent screen	GJT
Tuomiranta et al. (2014)	42	7(7)	9	Lexicon		Word	View pseudoword/picture pair and try to learn association	Same as learning
van den Broek et al. (2013)	43	22(22)	19	Lexicon		Word	Various L2 word-L1 translation association tasks View L2-L1 word pair and indicate whether they knew the translation	View word L2-L1 word pair or L2 word alone and indicate whether they knew the translation
Xue et al. (2006)	44	12(6)	25	Lexicon		Word	Exposure through visual form matching; viewing characters while listening, imitating, and comparing self production to native speaker; and various character-picture association tasks	Passive viewing of characters; Visual form matching, naming, and semantic judgment
Yang and Li (2012)	45a	20(11)	19	Grammar	DGL: Explicit training	Artificial grammar	View string, reproduce, view string again. (Before training, participants told that there is an underlying rule system.)	GJT
	45b	23(10)	21	Grammar	nonDGL		View string, reproduce, view string again. (Participants not told about underlying rule system before training.)	
Yusa et al. (2011)	46a	17(nr)	17	Grammar	DGL: Explicit training	Natural language	Intensive EFL classroom training on word-order rule	GJT

Note. Subject Group IDs with multiple letters represent combinations of two or more subject groups (e.g., 9 ab includes subjects from 9a and 9b). In some cases individual subject groups in these combined groups were not reported or did not meet the criteria for separate inclusion in our meta-analyses, and thus are not included in the table. For example, Opitz et al. (2014) reported relevant analyses for the combination of three groups (27abc) as well as for only one of these groups on their own (27a). f: females; nr: not reported; DGL: declarative grammar learning; nonDGL: non-declarative grammar learning; L1: first language; L2: second language; GJT: grammaticality judgment task; EFL: English as foreign language.

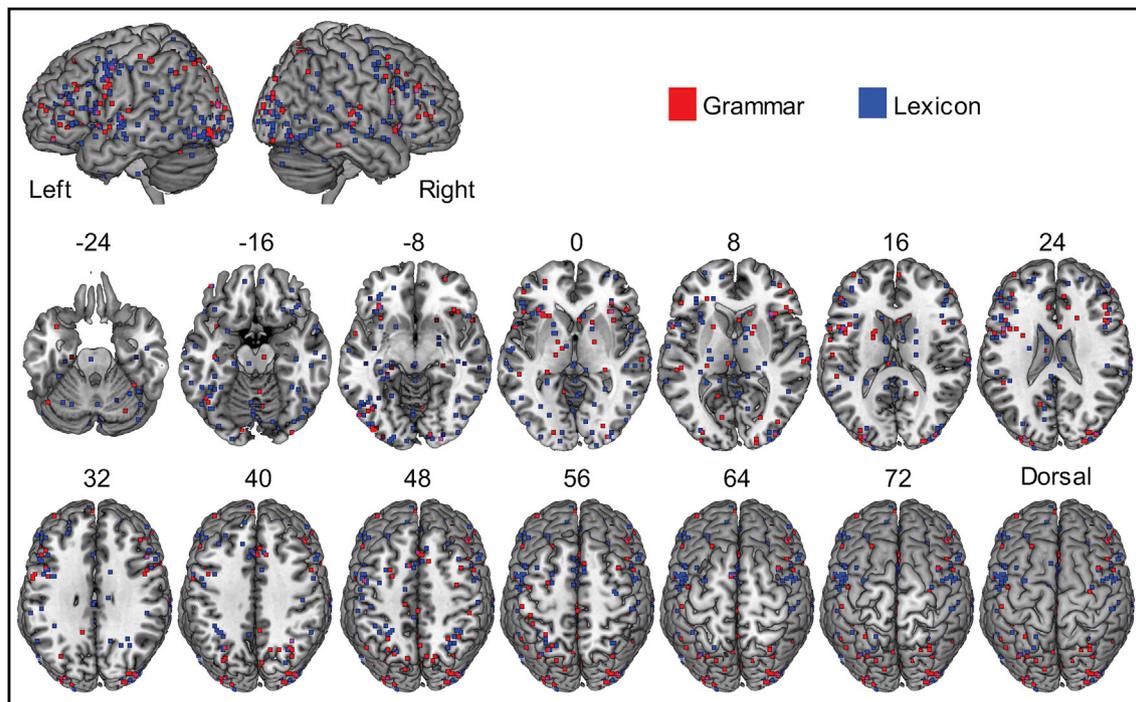


Fig. 2. Distribution of foci for the lexical and grammatical ALE analyses.

which did not report handedness, every study reported that all participants were right handed.

At the contrast level, we coded several task-related properties; see Table 2. First, because particular linguistic targets might be learned through different neurocognitive processes, we coded for the specific target of the training (i.e., word, artificial grammar, artificial language, miniature language, or natural language). This coding was used to categorize contrasts for the exploratory artificial grammar analyses. Second, we coded information about what the training tasks entailed (e.g., viewing sentences along with descriptive scenes, hearing a novel word while viewing an L1 translation). Third, we coded for which task(s) were performed in the scanner; these could be the training task, a test (e.g., grammaticality judgment), both, or a different task (e.g., passive viewing of words). Fourth, we coded grammar studies for aspects of the training paradigm or stimuli hypothesized to lead to learning in declarative memory (see section 2.3).

While some of the variables listed above were not of primary interest for our analyses, we have included them in Table 2 for completeness and transparency, as they are potentially relevant for language learning. Throughout this paper, Tables and Figures report a numerical identifier for each study and an alphabetical identifier for each group within multigroup studies (e.g., Bradley et al., 2013, tested two groups, which are identified as 2a and 2b). See Table 2 for each subject group's alphanumeric identifier.

2.5. ALE analysis procedure

All analyses were conducted using GingerALE 2.3.6 (Eickhoff et al., 2012; Eickhoff et al., 2009b; Turkeltaub et al., 2012). The ALE algorithm tests against the null hypothesis that activation foci in the dataset are distributed uniformly across the brain, and thus tests for regions with an above-chance likelihood of activity across experiments (Eickhoff et al., 2012; Laird et al., 2005). We used the non-additive algorithm described in Turkeltaub et al. (2012), which pools the foci by subject group (rather than by experiment), and thus prevents subject groups with multiple experiments or tasks in a given ALE meta-analysis from influencing ALE values more than others. In some studies, the same subjects were allotted

to multiple subject groups for different analyses. To maintain independence across subject groups, two subject groups that contained overlapping participants were only entered as separate groups if more than 50% of the participants in one group were not part of the other group. For example, Opitz et al. (2014) trained three groups of participants on Chinese vocabulary. The groups all had the same lexical training, but differed in the type of intervening working memory training they received. The paper reported language-learning related activation for all three groups combined together ($N = 48$; 30b), as well as for one of the individual groups ($n = 16$; 30a). These were entered as two distinct subject groups because only one-third of the participants in Group 30b were also in Group 30a.

Input to the meta-analyses consisted of X, Y, Z stereotaxic coordinates for all activation peaks (reported in the study as significant, i.e., $p < 0.05$) for the contrasts of interest. Because all of the foci must be in the same coordinate space, foci that were reported in Talairach space were transformed to MNI (Montreal Neurological Institute; Collins et al., 1994; Evans et al., 1993) coordinates using the Lancaster transform (tal2icbm; Lancaster et al., 2007), via the “Convert Foci” tool in GingerALE.

Foci in MNI space were then entered into GingerALE, which computes the ALE values for every voxel in the brain using an automatically determined full-width half-maximum (FWHM) value (Eickhoff et al., 2009b). The resulting ALE maps were thresholded using cluster-level family-wise error (cFWE) correction, with a cluster-level requirement of $p < 0.05$ and a voxel-level clustering threshold of $p < 0.01$. ALE maps generated by subtraction analyses (Eickhoff et al., 2011) were thresholded using uncorrected thresholds of $p < 0.01$ with a minimum cluster size of 200 mm^3 . For all analyses, significance levels were determined via nonparametric permutation testing using 10,000 random-label resamples (Acikalin et al., 2017; Eickhoff et al., 2012, 2016). It has been shown that, compared to other correction methods, the cFWE correction method that we used in our analyses is the most reliable approach for revealing true effects (neural activation) with high power while, at the same time, controlling for false positives (Eickhoff et al., 2016). Our primary ALE analyses included 25 or more subject groups, which is greater than the number recommended to provide sufficient power for detection of true effects when multiple groups activate a given target location (Eickhoff

et al., 2016). Any ALE analyses with fewer than 17 subject groups are considered exploratory.

We report all peaks and subpeaks (determined as local maxima separated by a minimum of 8 mm), as well as the subject groups that contributed coordinates to each (sub)peak. Contributing subject groups to each (sub)peak of a cluster were determined as those reporting coordinates no further from the (sub)peak than three standard deviations (SDs) of the spatial uncertainty distribution calculated in the ALE analysis (Eickhoff et al., 2009b; Turkeltaub et al., 2011). No (sub)peak had fewer than three contributing subject groups (see Table 3). Results were visualized using MRICron and overlaid on the Colin 27 brain template (Holmes et al., 1998). The identification of anatomical structures corresponding to (sub)peak locations (see Tables 3 and 4, and S1–S3) was aided by the Neuromorphometrics atlas (Neuromorphometrics, Inc., www.neuromorphometrics.com/) provided with SPM12 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, London, UK; www.fil.ion.ucl.ac.uk; Penny et al., 2007)), as well as the Anatomical Atlas Label (AAL) toolbox for SPM (Tzourio-Mazoyer et al., 2002).

2.6. Analyses

2.6.1. ALE analyses

We conducted two main ALE analyses. First, the “Lexicon” analysis included all eligible contrasts that subtracted activation during baseline conditions from activation during lexical learning conditions. Second, the “Grammar” analysis included all eligible contrasts that subtracted activation during baseline from activation during grammar learning. Additionally, we conducted subtraction and conjunction analyses to establish differences and overlap in activation between these two main analyses (Lexicon > Grammar, Grammar > Lexicon, Lexicon | Grammar).

Next, we conducted two sets of exploratory ALE analyses to examine artificial grammar learning and declarative grammar learning. For the artificial grammar learning analyses, we conducted an ALE analysis on all contrasts from the Grammar analysis that examined artificial grammar learning, as well as a second ALE analysis on all contrasts from the Grammar analysis that examined grammar learning with a linguistic target other than artificial grammar (see Table 2). Again, we conducted subtraction and conjunction analyses to establish differences and overlap in activation between these analyses (Artificial Grammar > non-Artificial Grammar, non-Artificial Grammar > Artificial Grammar, Artificial Grammar | non-Artificial Grammar). Similarly, for the declarative grammar learning analyses we conducted separate ALE analyses on Grammar contrasts categorized as declarative grammar learning and non-declarative grammar learning (see Table 2), as well as their subtractions and conjunction (Declarative Grammar Learning > non-Declarative Grammar Learning, non-Declarative Grammar Learning > Declarative Grammar Learning, Declarative Grammar Learning | non-Declarative Grammar Learning).

2.6.2. ROI cross-tabulation analyses

Additionally, because we were testing *a priori* hypotheses about medial temporal lobe (MTL) involvement in declarative grammar learning, and had concerns about the sensitivity of ALE to identify converging activation in the MTL (see just below), we also ran ROI-based cross-tabulation analyses. These analyses tested whether declarative grammar learning was more likely to activate the MTL than non-declarative grammar learning. We first calculated the number of subject groups that included declarative grammar learning or non-declarative grammar learning contrasts. The MTL ROI was created by combining bilateral hippocampal, entorhinal, and perirhinal ROIs from the Neuromorphometrics anatomical atlas in MNI space (Neuromorphometrics, Inc., <http://neuromorphometrics.com/>). We then created a 2 × 2 contingency table that identified the number of subject groups within each of the two types of grammar studies that either did or did not report any foci within the MTL ROI. Finally, to test the prediction

that MTL activation was more likely to occur in declarative than non-declarative grammar learning contrasts, we ran a one-tailed Fisher’s exact test to compare the proportions of study groups that showed MTL activation between each grammar type.

Such ROI-based activation frequency analyses provide some important benefits over traditional ALE analyses. First, they combine foci by theory-driven modular regions rather than simple Euclidian Gaussian distributions, thus reducing the risk of Type 2 (false negative) errors when testing *a priori* ROI-based hypotheses. Second, they require fewer statistical tests compared to voxelwise analyses, thereby reducing the risk of spurious Type I (false positive) errors. It should be noted, though, that like any ROI-based analysis, these benefits do come at the cost of spatial specificity. The MTL in particular is a good candidate for testing *a priori* hypotheses with increased sensitivity. Specifically, an underlying assumption of the ALE method null hypothesis is that activation foci are equally likely to be reported across each voxel in the brain. However, the MTL (and the hippocampus in particular) shows notoriously decreased BOLD-fMRI sensitivity (see Ekstrom, 2010, for a review). Furthermore, the hippocampus is a relatively long structure such that even if multiple studies do find activation within the MTL, if those foci of activation are not localized to a particular portion of the MTL (e.g., anterior hippocampus), they may not yield significant areas of convergence using the ALE method. These properties of the MTL and hippocampus, along with our specific predictions regarding this region of the brain for declarative and non-declarative grammar learning (Ullman, 2005, 2015, 2016), motivated our decision to run these more sensitive ROI analyses.

2.7. Data code and availability statement

The data supporting the findings of this study are available from the corresponding author (KT) on request.

3. Results

3.1. Main ALE analyses: Lexical and grammatical learning

Table 3 shows, for each ALE analysis (Lexicon, Grammar, and the conjunction of the two), the anatomical location, cluster size, MNI coordinates, ALE maximum, and the contributing studies, for each (sub)peak. Analogous results from the subtraction analyses are presented in Table 4. The related ALE maps are shown in Fig. 3a and b.

3.1.1. ALE analyses: Lexicon and Grammar

In the Lexicon ALE analysis, six areas showed significant convergence across subject groups (Table 3 and Fig. 3a): 1) left inferior frontal gyrus (IFG), pars opercularis, with subpeaks in the pars triangularis, anterior insula, and precentral gyrus; 2) left angular gyrus, with subpeaks in the superior parietal lobule; 3) left inferior temporal gyrus, with subpeaks in the fusiform gyrus and inferior occipital gyrus; 4) right anterior insula, with subpeaks in the pars triangularis, pars opercularis, and precentral gyrus; 5) right inferior occipital gyrus, with a subpeak in the inferior temporal gyrus; and 6) a midline cluster centered on the supplementary motor area (SMA), with subpeaks in the superior medial frontal gyrus, superior frontal gyrus, and middle frontal gyrus.

In the Grammar ALE analysis, six areas showed significant convergence across subject groups (Table 3 and Fig. 3a): 1) left anterior insula, with subpeaks in the pars triangularis, pars opercularis, Rolandic operculum, precentral gyrus, putamen, and caudate nucleus; 2) left superior parietal lobule, with subpeaks in the angular gyrus; 3) right anterior insula, with subpeaks in the pars triangularis, pars opercularis, and frontal operculum; 4) right precentral gyrus; 5) right angular gyrus, with subpeaks in the superior parietal lobule and precuneus; and 6) a midline cluster centered on the superior medial frontal gyrus, with a subpeak in the SMA.

The conjunction of the Lexicon and Grammar ALE analyses revealed five common areas of convergence between lexical and grammar

Table 3
Results from ALE analyses of lexical learning, grammatical learning, and their conjunction.

Anatomical Location	Cluster Size (mm ³)	MNI Coordinates of Local Maxima			ALE Max.	Groups Containing Foci within 3SD of Peak	# of Contributing Groups
		x	y	z			
Lexicon							
<i>Left Hemisphere</i>							
IFG, pars opercularis (BA 44)	22024	-46	6	28	0.045	2a, 4, 5, 6, 13, 16b, 16c, 20, 21, 31, 37, 38, 39, 44	14
IFG, pars triangularis (BA 45)		-46	28	20	0.036	2a, 2b, 5, 10, 16a, 16c, 16d, 21, 31, 37, 38, 39	12
		-50	16	30	0.024	5, 13, 16b, 16c, 16d, 20, 21, 31, 33, 37, 38, 39, 44	13
Anterior insula (BA 13)		-32	24	2	0.032	4, 6, 10, 13, 16a, 16b, 16c, 16d, 19, 20, 33, 37, 39, 44	14
		-32	16	8	0.025	4, 10, 13, 16a, 16b, 16c, 16d, 20, 30, 31, 37, 39	12
Precentral gyrus (BA 4)		-52	2	46	0.039	5, 6, 10, 16b, 16d, 19, 21, 30, 32, 37, 39, 42, 44	13
Angular gyrus (BA 39)	9240	-34	-52	42	0.041	2a, 2b, 4, 5, 8, 16a, 16b, 16c, 16d, 20, 21, 28a, 31, 37, 38, 39, 42	17
		-30	-64	40	0.025	2a, 2b, 5, 16a, 31, 33, 37, 38	8
Superior parietal lobule (BA 7)		-32	-60	54	0.025	5, 7, 16a, 16b, 16c, 16d, 30, 31, 42	9
		-24	-66	50	0.021	5, 7, 16a, 16b, 16c, 30, 31, 38, 39	9
Inferior temporal gyrus (BA 37)	7848	-48	-60	-10	0.034	4, 6, 7, 16c, 16d, 21, 27a, 27b, 31, 37, 38, 39, 42	13
Fusiform gyrus (BA 37)		-40	-54	-18	0.025	3, 7, 8, 10, 16b, 18, 20, 27a, 37, 38, 39, 42	12
Inferior occipital gyrus (BA 19)		-42	-78	-10	0.027	10, 16a, 16b, 16c, 16d, 19, 37, 39, 42	9
<i>Midline</i>							
Supplementary motor area (BA 6)	12008	-6	12	50	0.045	2a, 4, 5, 8, 10, 13, 16a, 16b, 16c, 16d, 21, 28a, 30, 31, 37, 38, 39	17
		-4	6	60	0.034	4, 5, 8, 16a, 16b, 20, 21, 28a, 31, 32, 37, 39	12
		4	16	48	0.026	5, 8, 13, 16a, 16b, 16c, 16d, 20, 30, 31, 32, 37, 38, 39	14
Superior medial frontal gyrus (BA 6)		-4	22	40	0.032	3, 10, 13, 16a, 16c, 16d, 31, 37, 38, 44	10
Superior frontal gyrus (BA 6)		-22	2	52	0.023	4, 5, 31, 34, 37, 38, 39	7
Middle frontal gyrus (BA 6)		-30	-2	62	0.019	4, 5, 16d, 31, 38, 39	6
<i>Right Hemisphere</i>							
Anterior insula (BA 13)	7680	32	22	0	0.033	2a, 4, 8, 13, 16a, 16b, 16c, 16d, 19, 21, 28a, 37	12
IFG, pars triangularis (BA 45)		46	26	20	0.028	3, 5, 8, 13, 16a, 16c, 16d, 20, 30, 38, 44	11
IFG, pars opercularis (BA 44)		56	18	32	0.018	5, 13, 16a, 16b, 16d, 38, 44	7
		50	14	20	0.016	3, 5, 8, 16b, 16c, 16d, 20, 30, 44	9
Precentral gyrus (BA 6)		44	4	28	0.019	5, 8, 16b, 16c, 16d	5
Inferior occipital gyrus (BA 37)	3408	48	-68	-14	0.029	4, 7, 8, 10, 16a, 16b, 16d, 18, 27a, 39	10
Inferior temporal gyrus (BA 37)		52	-64	-12	0.028	8, 10, 16b, 16d, 18, 27a, 38, 39	8
Grammar							
<i>Left Hemisphere</i>							
Anterior insula (BA 13)	19216	-32	22	-2	0.037	1, 9a, 9b, 11, 12, 35a, 36b, 40a, 45a, 45b	10
IFG, pars triangularis (BA 45)		-50	32	8	0.009	9a, 23a, 23b, 35a, 40a	5
		-44	28	4	0.010	9a, 23a, 23b, 35a, 40a	5
		-48	24	28	0.019	9a, 9b, 11, 12, 22, 29, 33, 45a, 46	9
IFG, pars opercularis (BA 44)		-46	16	24	0.021	9a, 9b, 11, 12, 22, 25, 29, 35a, 40a, 46	10
Rolandic operculum (BA 44)		-48	6	14	0.027	1, 9a, 12, 24, 25, 26, 29, 35a, 40a	9
Precentral gyrus (BA 6)		-46	2	32	0.017	9a, 9b, 11, 12, 29, 40a, 45a, 45b	8
		-58	2	30	0.013	9a, 9b, 12, 29	4
Putamen		-20	10	4	0.017	9, 15, 22	3
Caudate		-20	4	16	0.019	1, 9a, 9b, 15, 45b	5
Superior parietal lobule (BA 7)	5592	-26	-64	50	0.024	9a, 9b, 11, 12, 29, 40a, 45a, 45b	8
		-30	-54	58	0.013	9b, 11, 40a	3
Angular gyrus (BA 39)		-28	-72	38	0.010	9b, 29, 35a, 40a, 46	5
		-36	-72	50	0.010	9a, 9b, 36a, 45a	4
<i>Midline</i>							
Superior medial frontal gyrus (BA 6)	6760	2	26	38	0.021	11, 12, 29, 40a, 45a, 45b	6
		6	28	34	0.020	9a, 11, 12, 29, 36b, 40a, 45b	7
Supplementary motor area (BA 6)		2	20	50	0.019	9a, 9b, 11, 12, 29, 33, 40a, 45a, 45b	9
<i>Right Hemisphere</i>							
Anterior insula (BA 13)	5696	32	24	-2	0.024	1, 9a, 9b, 11, 12, 40a, 45b	7

(continued on next page)

Table 3 (continued)

Anatomical Location	Cluster Size (mm ³)	MNI Coordinates of Local Maxima			ALE Max.	Groups Containing Foci within 3SD of Peak	# of Contributing Groups
		x	y	z			
IFG, pars triangularis (BA 45)		52	38	6	0.010	11, 12, 35b, 40a	4
		48	26	6	0.013	9a, 9b, 12, 35a, 35b, 40a	6
IFG, pars opercularis (BA 44)		50	16	4	0.008	9a, 12, 15, 24, 35a, 35b	6
Frontal operculum (BA 13)		50	16	-6	0.012	9 15, 35a	3
Precentral gyrus (BA 6)	3952	48	8	28	0.025	9a, 11, 12, 23a, 24, 33, 40a, 46	8
Angular gyrus (BA 39)	7912	32	-64	40	0.018	9a, 11, 12, 25, 35a, 40a, 46	7
		44	-46	44	0.010	9b, 40a, 46	3
		36	-56	48	0.018	9a, 9b, 12, 35a, 40a, 45a, 46	7
Superior parietal lobule (BA 7)		30	-62	58	0.014	9a, 11, 12, 40a	4
Precuneus (BA 7)		12	-70	46	0.016	9a, 11, 40a, 45a, 46	5
Conjunction: Lexicon Grammar							
<i>Left Hemisphere</i>							
Anterior insula (BA 13)	10352	-32	24	0	0.030	LX: 1, 9a, 9b, 11, 12, 35a, 36b, 40a, 45a, 45b GR: 6, 10, 13, 16a, 16b, 16c, 16d, 19, 20, 33, 37, 39, 44	LX: 10 GR: 13
IFG, pars triangularis (BA 45)		-48	18	26	0.020	LX: 9a, 9b, 11, 12, 22, 29, 33, 40a, 46 GR: 2a, 5, 13, 16a, 16b, 16c, 16d, 20, 21, 31, 33, 37, 38, 39, 44	LX: 9 GR: 15
		-40	18	12	0.011	LX: 9a, 9b, 12, 22, 25, 35a, 40a, 46 GR: 4, 13, 16a, 16c, 16d, 20, 21, 30, 31, 37, 44	LX: 8 GR: 11
IFG, pars opercularis (BA 44)		-46	8	20	0.022	LX: 1, 9a, 11, 12, 22, 24, 25, 26, 29, 35a, 40a, 45b, 46 GR: 5, 6, 13, 16b, 16c, 20, 21, 30, 31, 32, 37, 38, 39, 44	LX: 13 GR: 14
Precentral gyrus (BA 6)		-46	2	32	0.017	LX: 9a, 9b, 11, 12, 29, 40a, 45a, 45b GR: 2a, 4, 5, 6, 13, 16b, 16c, 16d, 20, 21, 31, 37, 38, 39, 42	LX: 8 GR: 15
Superior parietal lobule (BA 7)	3344	-24	-66	50	0.021	LX: 9a, 9b, 11, 12, 29, 40a, 45a, 45b, 46 GR: 5, 7, 16a, 16b, 16c, 30, 31, 38, 39	LX: 9 GR: 9
		-28	-64	52	0.021	LX: 9a, 9b, 11, 12, 29, 40a, 45a, 45b GR: 5, 7, 16a, 16b, 16c, 16d, 30, 31, 38, 39	LX: 8 GR: 10
Angular gyrus (BA 39)		-28	-64	44	0.020	LX: 9a, 9b, 11, 12, 29, 40a, 45a, 45b, 46 GR: 2a, 2b, 5, 7, 16a, 16c, 16d, 31, 33, 37, 38, 39	LX: 9 GR: 12
<i>Midline</i>							
Supplementary motor area (BA 6)	2568	2	20	48	0.019	LX: 9a, 9b, 11, 12, 29, 33, 40a, 45a, 45b GR: 5, 13, 16a, 16c, 16d, 20, 30, 31, 34, 37, 38, 39, 44	LX: 9 GR: 13
Superior medial frontal gyrus (BA 6)		0	24	38	0.018	LX: 11, 12, 29, 40a, 45a, 45b GR: 10, 13, 16a, 16d, 20, 31, 37, 38, 44	LX: 6 GR: 9
<i>Right Hemisphere</i>							
Anterior insula (BA 13)	2344	32	24	-2	0.024	LX: 1, 9a, 9b, 11, 12, 40a, 45b GR: 4, 8, 13, 16a, 16b, 16c, 16d, 19, 21, 28a, 37	LX: 7 GR: 11
Precentral gyrus (BA 6)	1720	46	6	28	0.018	LX: 9a, 11, 12, 23a, 24, 33, 40a, 46 GR: 5, 8, 16a, 16b, 16c, 16d, 44	LX: 8 GR: 7
IFG, pars opercularis (BA 44)		50	20	28	0.015	LX: 11, 12, 23a, 24, 40a, 46 GR: 5, 8, 13, 16b, 16c, 16d, 20, 30, 38, 44	LX: 6 GR: 10
		48	14	22	0.015	LX: 9a, 11, 12, 23a, 24, 33, 40a, 46 GR: 3, 5, 8, 16b, 16c, 16d, 20, 30, 44	LX: 8 GR: 9

Note. BA: Brodmann's area; LX: Lexicon; GR: Grammar.

Table 4
Results from ALE analyses of lexical learning versus grammatical learning (i.e., subtractions).

Location	Cluster Size (mm ³)	MNI Coordinates of Local Maxima			Z-Score	Groups Containing Foci within 3SD of Peak	# of Contributing Groups
		x	y	z			
Lexicon > Grammar							
<i>Left Hemisphere</i>							
Middle frontal gyrus (BA 6)	408	-40	2	52	2.664	LX: 5, 6, 16a, 16b, 20, 32, 37, 38, 39, 44 GR: 9	LX: 10 GR: 1
Precentral gyrus (BA 6)		-48	2	52	2.589	LX: 5, 6, 16a, 16b, 16d, 19, 21, 32, 37, 39, 42, 44 GR: 9a, 12, 22	LX: 12 GR: 3
Angular gyrus (BA 39)	832	-40	-54	42	3.161	LX: 2a, 2b, 4, 5, 8, 13, 16a, 16b, 16d, 20, 21, 28a, 31, 37, 38, 42 GR: 12, 29, 40a	LX: 16 GR: 3
Inferior temporal gyrus (BA 37)	448	-46	-56	-4	2.952	LX: 4, 6, 7, 16d, 21, 27a, 31, 37, 38, 39, 44 GR: none	LX: 11 GR: 0
Middle temporal gyrus (BA 21)		-50	-58	-2	2.947	LX: 4, 6, 7, 16d, 21, 31, 38, 39 GR: none	LX: 8 GR: 0
Fusiform gyrus (BA 37)	720	-30	-48	-16	3.580	LX: 3, 16b, 18, 20, 37, 39 GR: none	LX: 6 GR: 0
<i>Midline</i>							
Supplementary motor area (BA 6)	728	-4	12	54	2.892	LX: 2a, 4, 5, 8, 10, 13, 16a, 16b, 16c, 16d, 21, 28a, 30, 37, 39 GR: 9a, 9b, 12, 45b	LX: 15 GR: 4
		-10	4	50	2.395	LX: 2a, 4, 5, 6, 8, 10, 16a, 16b, 28a, 30, 31, 32, 37, 39 GR: 9b, 12	LX: 14 GR: 2
Middle cingulate gyrus (BA 32)		0	10	44	2.638	LX: 2a, 5, 8, 10, 16a, 16c, 16d, 30, 32, 37, 38, 39 GR: 9a, 12, 24	LX: 12 GR: 3
Grammar > Lexicon							
<i>Right Hemisphere</i>							
Anterior cingulate gyrus (BA 24)	632	12	24	26	3.200	GR: 9a, 11, 12, 23b, 29, 36b, 40a LX: none	GR: 7 LX: 0
Superior medial frontal gyrus (BA 6)		6	30	32	2.696	GR: 9a, 11, 12, 29, 40a, 45b LX: none	GR: 6 LX: 5
Cuneus (BA 19)	1904	10	-78	42	3.326	GR: 9a, 11, 45a, 46 LX: none	GR: 4 LX: 0
Superior parietal lobule (BA 7)		14	-64	50	2.932	GR: 11, 40a, 45a, 46 LX: none	GR: 4 LX: 0
		10	-64	48	2.906	GR: 9a, 11, 36a, 40a, 45a, 46 LX: none	GR: 6 LX: 0
		14	-70	50	2.908	GR: 9a, 11, 40a, 45a, 46 LX: none	GR: 5 LX: 0

Note. BA: Brodmann's area; LX: Lexicon; GR: Grammar.

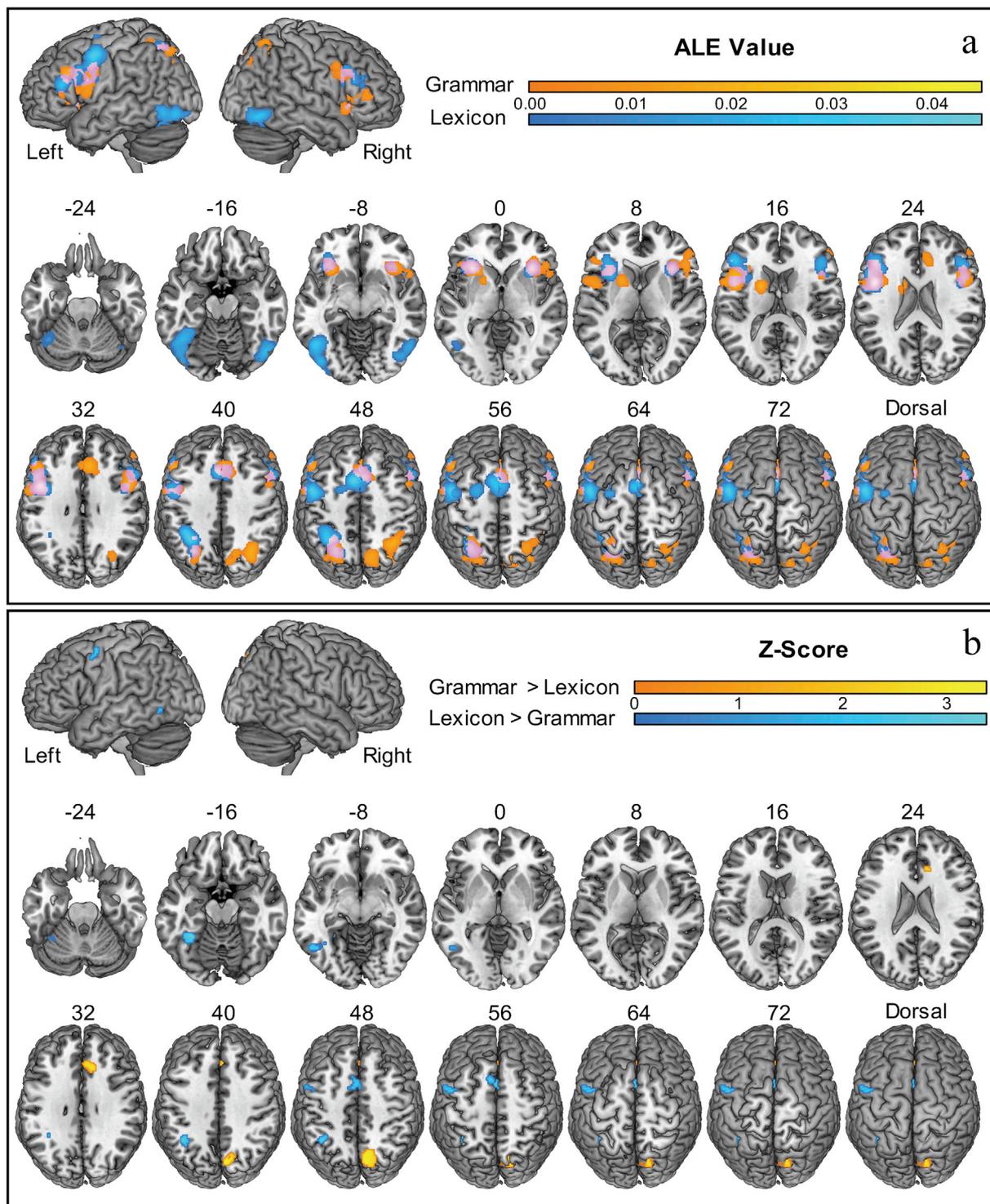


Fig. 3. ALE maps for (a) Grammatical learning, lexical learning, and the conjunction (pink) of grammatical and lexical learning; (b) Grammatical learning > lexical learning and lexical learning > grammatical learning. In this and all other similar figures, the values above each slice represent the location of the slice on the z-axis (e.g., $z = -24$, $z = -16$, etc.).

learning (Table 3 and Fig. 3a): 1) left anterior insula, with subpeaks in the pars triangularis, pars opercularis, and precentral gyrus; 2) left superior parietal lobule, with a subpeak in the angular gyrus; 3) right anterior insula; 4) right precentral gyrus, with subpeaks in the pars opercularis; and 6) a midline cluster centered on the SMA, with a subpeak in the superior medial frontal gyrus.

3.1.2. Subtractions of ALE analyses: Lexicon > Grammar and Grammar > Lexicon

Results from the subtraction analyses are presented in Table 4 and Fig. 3b. Significantly greater likelihood of activation was found for lexical learning than grammar learning in five clusters: 1) left middle frontal gyrus, with a subpeak in precentral gyrus; 2) left angular gyrus; 3) left

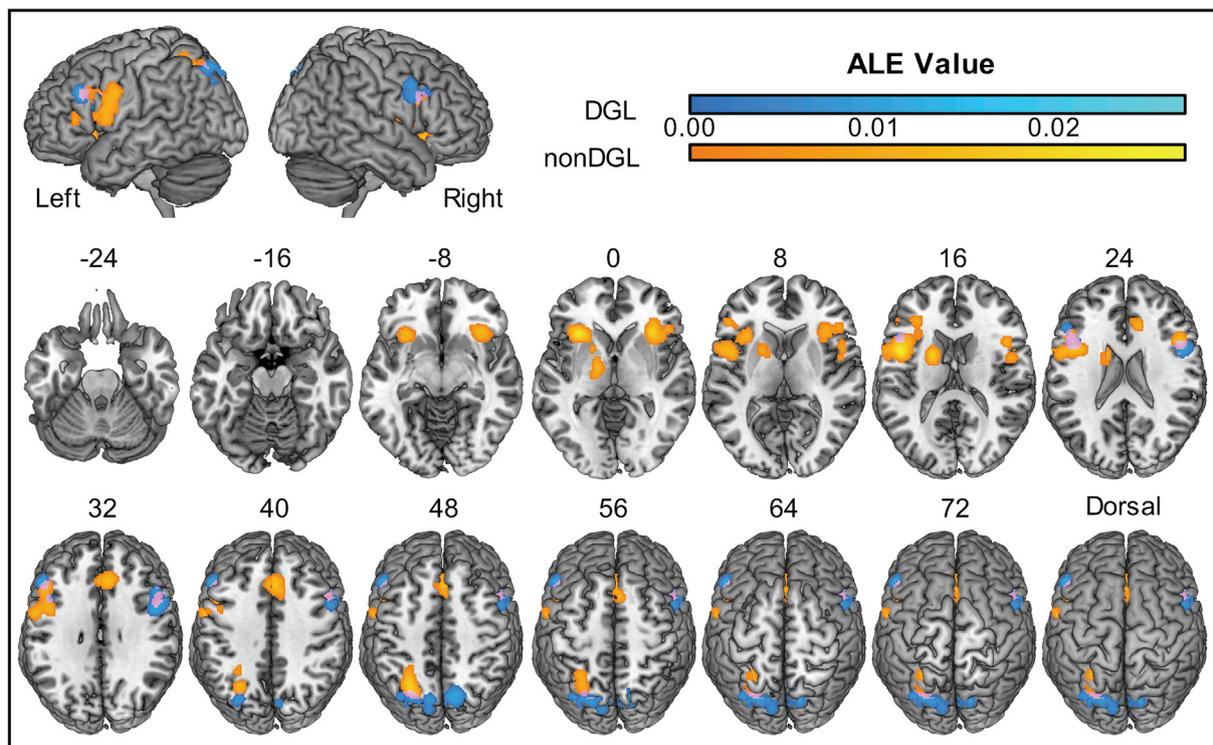


Fig. 4. ALE maps for Declarative Grammar Learning (DGL), non-Declarative Grammar Learning (nonDGL), and their conjunction (pink).

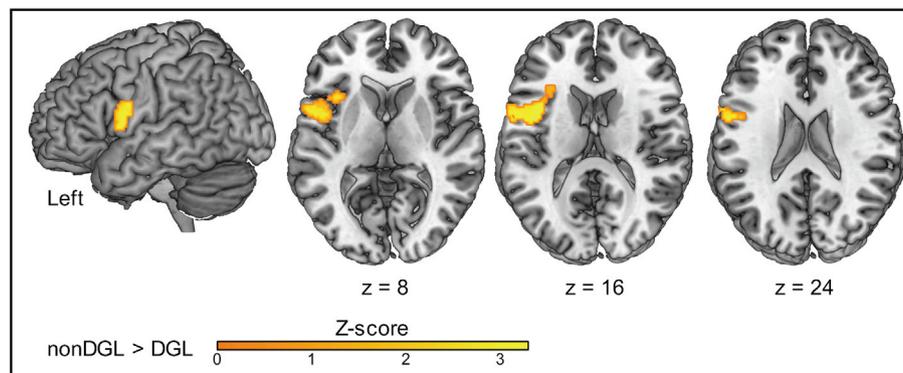


Fig. 5. ALE maps for non-Declarative Grammar Learning (nonDGL) > Declarative Grammar Learning (DGL). The reverse contrast did not reveal any significant ALE results.

inferior temporal gyrus, with a subpeak in the middle temporal gyrus; 4) left fusiform gyrus; and 5) a midline cluster centered on the SMA with a subpeak in the middle cingulate gyrus. For the Grammar > Lexicon subtraction, converging activation was found in two clusters: 1) right anterior cingulate gyrus, with a subpeak in the superior medial frontal gyrus; and 2) right cuneus, with subpeaks in the superior parietal lobule.

3.2. Exploratory analyses

3.2.1. Declarative grammar learning analyses

3.2.1.1. ALE analyses. See Figs. 4 and 5 and Tables S1 and S2. In the Declarative Grammar Learning ALE analysis, four areas showed significant convergence across subject groups: 1) left pars triangularis, with subpeaks in the pars opercularis; 2) left angular gyrus, with subpeaks in the superior parietal lobule; 3) right pars opercularis, with a subpeak in the precentral gyrus; and 4) right precuneus.

In the non-Declarative Grammar Learning ALE analysis, six areas

showed significant convergence across subject groups: 1) left rolandic operculum, with subpeaks in the pars triangularis, pars opercularis, anterior insula, precentral gyrus, and middle frontal gyrus; 2) left superior parietal lobule; 3) left caudate, with subpeaks in the putamen and thalamus; 4) right anterior insula, with a subpeak in the pars triangularis; 5) right pars triangularis, with subpeaks in the pars opercularis and rolandic operculum; and 6) a midline cluster in the superior medial frontal gyrus, with a subpeak in the SMA.

The conjunction analysis revealed three common areas of convergence between declarative and non-declarative grammar learning: 1) left pars opercularis, with a subpeak in pars triangularis; 2) left angular gyrus, with a subpeak in superior parietal lobule; and 3) right pars opercularis.

Results from the subtraction analyses are presented in Fig. 5 and Table S2. Significantly greater likelihood of activation was found for non-declarative grammar learning than declarative grammar learning in a single cluster in the left rolandic operculum, with subpeaks in pars triangularis, pars opercularis, and precentral gyrus. There reverse

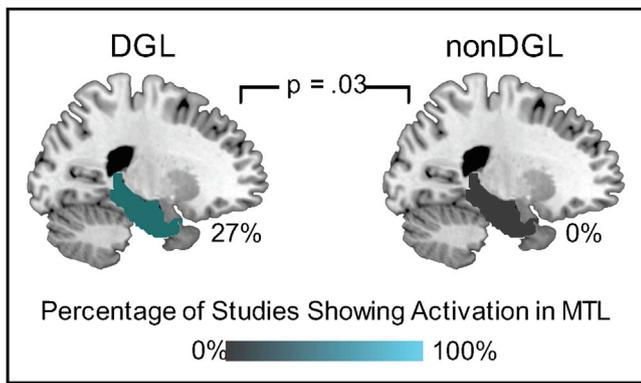


Fig. 6. Percentage of studies in Declarative Grammar Learning (DGL) and in non-Declarative Grammar Learning (nonDGL) that show MTL activation.

subtraction did not yield any significant results.

3.2.1.2. ROI cross-tabulation analyses. For Declarative Grammar Learning, activation was found in the MTL for three subject groups, while eight subject groups did not yield any MTL activation. For non-Declarative Grammar Learning, none of the 15 subject groups showed activation in the MTL. In other words, 27% of subject groups that learned grammar under conditions predicted to promote declarative learning showed activation in the MTL, whereas 0% of subject groups that learned grammar under conditions that were not expected to promote declarative learning showed activation in this ROI. This difference was statistically significant; see Fig. 6. Moreover, all foci in the MTL were in the hippocampus, revealing the importance of this specific MTL structure for Declarative Grammar Learning.

3.2.2. Artificial grammar learning ALE analyses

See Fig. 7 and Table S3. In the Artificial Grammar ALE analysis, six areas showed significant convergence across subject groups: 1) left

anterior insula; 2) left pars opercularis, with a subpeak in the precentral gyrus; 3) left superior parietal lobule; 4) left inferior occipital gyrus; 5) right anterior insula; and 6) a midline cluster centered on the superior medial frontal gyrus, with a subpeak in the SMA.

In the non-Artificial Grammar analysis, two areas showed significant convergence across subject groups: 1) left pars triangularis, with subpeaks in the pars opercularis; and 2) right precentral gyrus, with subpeaks in the pars triangularis and pars opercularis.

The conjunction analysis revealed one common area of convergence between artificial grammar and non-artificial grammar learning, in the left pars opercularis. Subtraction analyses between artificial grammar and non-artificial grammar studies did not reveal any significant ALE results in either direction.

4. Discussion

This study aimed to clarify the functional neuroanatomy of adult language learning, specifically for lexicon and grammar. Moreover, within grammar, we aimed to elucidate both declarative grammar learning, for which we had theoretically-motivated predictions, and artificial grammar learning, which is widely studied in the adult language learning literature. To achieve these goals, we conducted multiple ALE meta-analyses of previous functional neuroimaging studies of adult language learning, as well as an ROI cross-tabulation analysis to test our *a priori* predictions about the involvement of the MTL in declarative grammar learning. We employed stringent study selection criteria, focusing only on studies that examined lexical or grammatical learning in adults using controlled experimental training paradigms, most of which employed model languages. Crucially, for all papers included in our meta-analyses, participants were learning over the course of the experiment.

4.1. Summary of findings and interpretation

4.1.1. Lexicon and Grammar analyses

We first conducted separate ALE analyses on lexical and grammatical

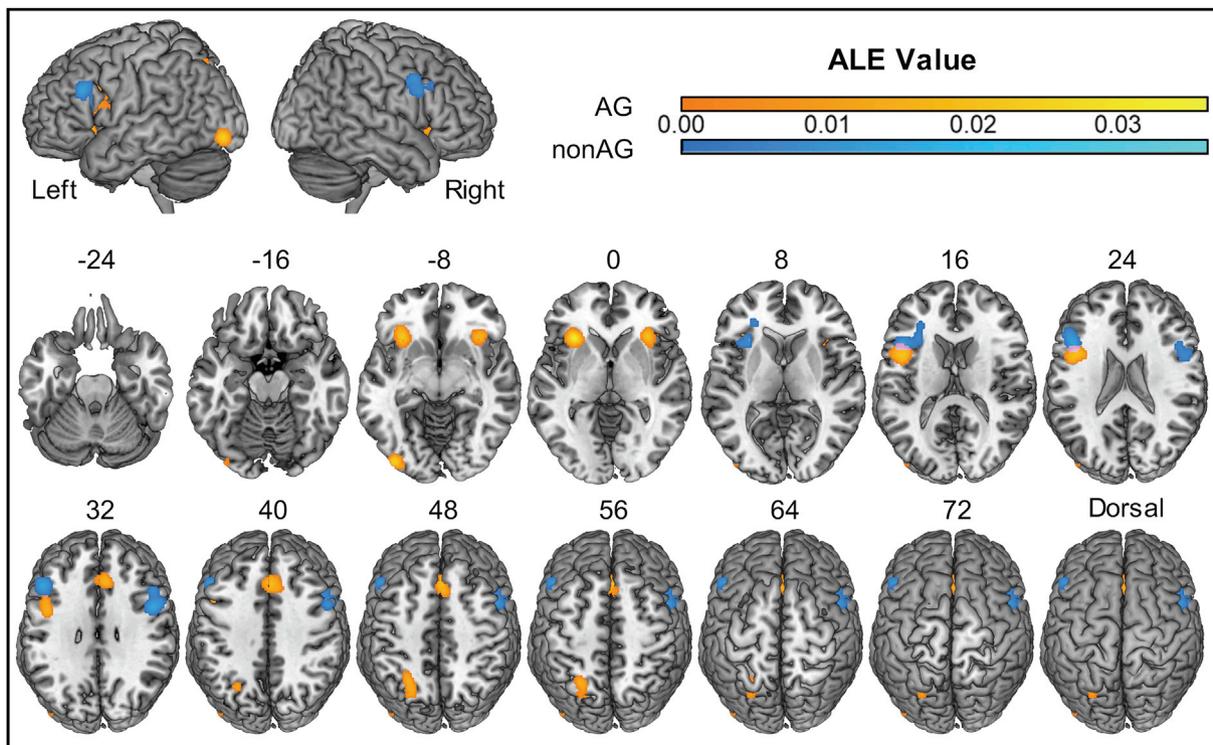


Fig. 7. ALE maps for Artificial Grammar Learning (AG), non-Artificial Grammar Learning (nonAG), and their conjunction (pink).

learning, which included all relevant contrasts focusing on either lexical or grammatical targets. We also ran conjunction and subtraction ALE analyses to reveal overlap and differences in activation between these two sets of contrasts. Here we focus on key findings from these analyses.

4.1.1.1. Overlapping activation for lexical/grammatical learning in frontal and parietal cortex. For both lexical and grammatical learning, significant ALE results were found bilaterally in and around the IFG, including the pars opercularis (BA 44) and pars triangularis (BA 45), as well as the precentral gyrus (BA 6) and the anterior insula (BA 13). ALE results for both lexical and grammatical learning were also observed in the SMA, though this midline activation was more dorsal and posterior for lexicon and more ventral and anterior for grammar. Additionally, both analyses yielded ALE results in the left posterior parietal lobe, including the superior parietal lobule and the angular gyrus of the inferior parietal lobule. Indeed, all of these areas emerged as significant areas of convergence in the conjunction analysis of lexicon and grammar, underscoring that they may be important for adult learning of both language domains.

The presence of ALE results in the frontal and insular regions for both lexical and grammatical learning suggests that these areas may represent components of a broader language learning network. Indeed, models of first language (L1) processing networks widely implicate the IFG as well as (though less consistently) premotor cortices (Eickhoff et al., 2009a; Friederici, 2011; Guenther, 2006; Hickok and Poeppel, 2007), so it is not entirely surprising that these regions might also be involved in aspects of adult language learning. Indeed, it has been suggested that the IFG and premotor regions play roles in adult-learned language both for grammar (see below) and vocabulary (Davis and Gaskell, 2009; Gupta and Tisdale, 2009; Rodriguez-Fornells et al., 2009). Additionally, the substantial activation that we see in the anterior insula is consistent with recent research suggesting that the anterior insula serves as an “integration hub” that coordinates higher-order cognitive processes involved in speech and language processing (Oh et al., 2014). Given its anatomical connections to the IFG (Jakab et al., 2012), one might in fact expect that the anterior insula should have a place in a language network – a view that is supported by a recent meta-analysis of expressive language processing (Eickhoff et al., 2009a).

The observed ALE results in the left posterior parietal lobe for both Lexicon and Grammar, including in the conjunction analysis, is an intriguing finding that deserves some attention. Though its place in language networks is not as prominent as frontal regions, some evidence suggests that parietal cortex may be involved in both first and second language (Golestani et al., 2002; Lee et al., 2007; Mechelli et al., 2004; Rodriguez-Fornells et al., 2009). The left posterior inferior parietal lobe has been found to show increased grey-matter density in bilinguals as compared to monolinguals, and within bilinguals, grey-matter density in this region is increased for individuals who learned a second language at a younger age or who attained higher second language proficiency (Mechelli et al., 2004). In monolinguals, grey-matter density is positively correlated with vocabulary scores in the right and left posterior inferior parietal lobe (Lee et al., 2007). White matter density in this area has also been shown to be related to language, with greater white matter density being positively associated with novel word pronunciation abilities (Golestani et al., 2002). These findings support a role for posterior parietal cortex in language, in particular in lexical aspects.

Both the frontal and parietal findings are relevant to the claims of the declarative/procedural (DP) model, which predicts that declarative memory should be involved in both lexical and grammatical learning in adults (Ullman, 2004, 2005, 2015, 2016; see also Gupta and Tisdale, 2009; Paradis, 1994, 2009). The IFG, in particular BA 45, has been associated with the selection and retrieval of lexical and semantic knowledge (Binder et al., 2009; Dapretto and Bookheimer, 1999; Friederici et al., 2002; Thompson-Schill et al., 1998; Vigneau et al., 2006), as well as more generally with declarative memory (Eichenbaum, 2012; Ullman, 2004, 2016). Parietal cortex has also been implicated in

declarative memory (Wagner et al., 2005). In particular, posterior parietal cortex seems to be important for encoding and retrieving information learned in declarative memory (Wagner et al., 2005), though more recent evidence suggests that even within posterior parietal cortex, there are specialized regions for different episodic memory functions (Sestieri et al., 2017). Therefore, the apparent role(s) of the IFG and posterior parietal lobe in lexical aspects of language may not be specific to language, but rather may reflect the involvement of declarative memory. Thus, the joint lexical and grammatical activation observed in BA 45 and posterior parietal cortex is expected by the model. However, the involvement of BA 44 and motor-related regions is predicted by the DP model mainly for (later stages of) grammar learning, not lexical learning (Ullman, 2015). One possible explanation for this finding is that activation in these regions reflects articulatory processes (e.g., Hernandez, 2009), which may be linked to procedural memory and may be expected to underlie the learning and processing of word forms (Klein et al., 2015). Indeed, Gupta and Tisdale (2009) argue that both declarative and procedural memory systems are involved in all types of learning, including word learning. Regarding the anterior insula, neither the DP model nor other models that we are aware of make specific predictions about how this region fits into adult language learning. Note that most other models of adult-learned language focus on comparisons of L2 and L1, the latter of which is not examined here, and/or do not make specific functional neuroanatomical predictions regarding BA 45, BA 44, or posterior parietal cortex that would allow them to be easily evaluated in the context of our findings (Abutalebi, 2008; Bley-Vroman, 1989; Clahsen and Felser, 2006; Ellis, 2007; Green, 2003; MacWhinney, 2001; Paradis, 1994, 2009; Perani and Abutalebi, 2005).

4.1.1.2. Ventral occipito-temporal activation for lexical learning. Our analyses suggest that ventral occipito-temporal cortex may be particularly important when adults learn new lexical information. Specifically, lexical (but not grammatical) learning yielded ALE results in the inferior temporal gyrus and inferior occipital gyrus, bilaterally. In the left hemisphere, this activation included a subpeak in the fusiform gyrus. The subtraction analysis of Lexicon > Grammar revealed that there was significantly greater likelihood of activation for lexical than grammatical learning in the left inferior temporal gyrus, with a subpeak in the left fusiform gyrus (as well as the middle temporal gyrus). The activation in the right hemisphere homologues of this cluster, though significant in the Lexicon analysis on its own, was not significant in the Lexicon > Grammar analysis, so this activation seems to be at least somewhat left-lateralized.

The inferior occipital lobe and inferior temporal lobe constitute part of the ventral stream (“what pathway”), a somewhat left-lateralized network of neural structures that plays a role in visual (Goodale and Milner, 1992; Lamme et al., 1998) and perhaps auditory processing (Rauschecker, 1998; Rauschecker and Scott, 2009; Scott, 2005). Regarding language, it has been proposed that the ventral stream is particularly important for mapping sounds to meanings, and is therefore crucial for lexical/semantics (Davis and Gaskell, 2009; Hickok and Poeppel, 2007; Ripollés et al., 2017; Rodriguez-Fornells et al., 2009). In view of this connection to lexical/semantics, Ullman (2004, 2016) suggests that the ventral stream is strongly linked to the declarative memory system. Specifically, “what” knowledge is posited to depend on both the ventral stream (for processing) and declarative memory (for learning). Thus, this somewhat left-lateralized inferior occipito-temporal activation for lexical learning suggests the involvement of the ventral stream and the related declarative memory system in this language domain, consistent with the predictions of the DP model.

The presence of ventral stream activation in the absence of MTL activation in our ALE results for lexical learning seems somewhat surprising at first, as several theories of and evidence pertaining to adult language learning implicate the hippocampus/MTL in adult lexical/semantic learning (Davis and Gaskell, 2009; Gupta and Tisdale, 2009; Ripollés et al., 2017; Ullman, 2005, 2015). However, this finding is

consistent with evidence suggesting that aspects of word learning can rely on ventral stream and perhaps other neocortical regions even without MTL involvement (Merhav et al., 2015; Sharon et al., 2011; but see Smith et al., 2014; Warren and Duff, 2014). Note, though, that the absence of ALE results in the MTL/hippocampus may also be due to lower BOLD sensitivity in these structures (Ekstrom, 2010), as discussed above (see section 2.6.2). Furthermore, there is at least some evidence of MTL/hippocampal involvement in lexical learning from our included studies (Breitenstein et al., 2005; Krönke et al., 2013; Mestres-Missé et al., 2008; Stein et al., 2009; Takashima et al., 2014), as well as in more recent papers (e.g., Berens et al., 2018), suggesting further examination of this issue is warranted. Finally, note that the absence of ventral stream activation for grammar learning may be primarily due to a greater importance of semantics for lexical than grammatical aspects of language.

4.1.1.3. Basal ganglia activation for grammatical learning. For grammar – but not lexical – learning, there was consistent activation across studies in the left caudate nucleus and the left putamen of the basal ganglia. This activation was found in anterior portions of both of these striatal structures, that is, in the caudate head/body and the anterior putamen. These findings are predicted by the DP model, which posits that the basal ganglia – in particular anterior portions of the striatum – play a critical role in grammar due to their underlying role in procedural memory. Specifically, the model predicts that these basal ganglia regions underlie the learning rather than the later processing of grammar, since these regions subserve procedural learning rather than the later processing of automatized skills (Ullman, 2015, 2016). In contrast, such activation is not predicted for lexical learning. A recent neuroanatomical meta-analysis of procedural learning, specifically of early stages of implicit sequence learning (of studies employing the Serial Reaction Time task), also obtained ALE results in the head/body of the caudate and the anterior putamen (Janacek et al., in prep), underscoring the likelihood that the activation observed in these structures for early stages of grammar learning, as observed here, may have been due to underlying procedural learning mechanisms. Note that the absence of anterior caudate/putamen activation for lexical learning does not preclude the possibility that portions of the basal ganglia can indeed be involved in certain aspects of lexical learning. For example, tasks that emphasize articulatory learning or control might be expected to yield basal ganglia activation, perhaps especially in the putamen (Abutalebi et al., 2013; Bradley et al., 2013; Hernandez and Fiebach, 2006; Menon et al., 2000; Wildgruber et al., 2001; Wise et al., 1999), as might word learning tasks examining the role of reward, which is associated with the ventral striatum (Ripollés et al., 2014). These issues seem important topics for future investigation.

The predictions of the DP model regarding basal ganglia activation are similar to those of Paradis's neurocognitive model of bilingualism (Paradis, 1994, 2004, 2009, 2013). This model suggests that implicit aspects of grammar learning in adults may eventually rely on procedural memory, and thus basal ganglia activation might be expected. However, the model posits that such proceduralization is rare and occurs only after extensive practice (Paradis, 1994, 2004, 2009, 2013), and thus would be unlikely in the early phases of learning explored in the present study.

While the basal ganglia findings observed here are consistent with the procedural memory-related predictions of the DP model and perhaps Paradis' model, they do not seem inconsistent with other potential explanations. For example, it has been suggested that basal ganglia activation in adult-learned languages is due to the increased effort and cognitive control required to process a language learned later in life, particularly for the grammar of that language (Abutalebi, 2008; Abutalebi et al., 2013; Green, 2003; Perani and Abutalebi, 2005). Additionally, Stocco and colleagues propose that during rule learning, the basal ganglia are involved in overriding preexisting connections within the cortex ('conditional routing'; Stocco et al., 2010; Stocco et al., 2014; Stocco and

Prat, 2014). Both of these views also seem in line with the basal ganglia findings observed here.

4.1.2. Declarative grammar learning analyses

Our next set of analyses probed grammar learning that was predicted by the DP model to rely on declarative memory. For ease of exposition, here we first summarize the key findings from these analyses and then interpret them in the context of the DP model.

4.1.2.1. Frontal and parietal cortex: overlapping and distinct activation for declarative/non-declarative grammar learning. While both Declarative Grammar Learning and non-Declarative Grammar Learning analyses yielded results in bilateral IFG (BA44/45), this activation was more extensive, including peaks in the anterior insula, for non-Declarative Grammar Learning. Non-Declarative Grammar Learning also yielded extensive bilateral activation in premotor regions, whereas Declarative Grammar Learning only yielded a right hemisphere subpeak in BA 6. Both analyses also yielded activation in left posterior parietal cortex, in the angular gyrus and/or superior parietal lobule, and this region was also significant in the conjunction analysis of these two types of learning. However, only Declarative Grammar Learning showed right posterior parietal activation (in the precuneus, the medial continuation of the superior parietal lobule). The conjunction analysis of Declarative and non-Declarative Grammar Learning revealed the left and right IFG, centered on BA 44, as a significant area of convergence between these two analyses. However, the subtraction analyses indicated that there was greater likelihood of activation in the left IFG, centered on BA 44, for non-Declarative Grammar Learning. The reverse subtraction analysis did not yield any significant results.

4.1.2.2. Basal ganglia activation only in non-declarative grammar learning. The non-Declarative Grammar Learning analysis additionally yielded significant ALE results in the head/body of the caudate, with subpeaks in the anterior putamen as well as the thalamus. Declarative Grammar Learning did not yield any basal ganglia activation.

4.1.2.3. MTL involvement only in declarative grammar learning. We hypothesized that grammar learning paradigms predicted to promote learning in declarative memory should activate the MTL, but we also expected that ALE analyses might not be well-suited to yield results in this region (see section 2.6.2 in Methods). Indeed, no ALE results in the MTL were obtained. We also ran ROI cross-tabulation analyses to directly test our predictions regarding the involvement of MTL in declarative grammar learning. This analysis showed that no subject group whose contrasts were classified as non-Declarative Grammar Learning showed activation in the MTL, whereas 27% of subject groups whose contrasts were classified as Declarative Grammar Learning did show activation in the MTL, in all cases in the hippocampus. This difference was significant.

4.1.2.4. Interpretation. This set of analyses was designed to directly test the DP model regarding grammar training that is or is not expected to rely particularly on declarative memory. The results indeed elucidate this issue.

The overlapping activation suggests that grammar learning predicted to rely importantly on declarative memory and grammar learning that is not predicted to rely particularly on this system, but rather primarily on procedural memory, both in fact depend to some extent on both learning and memory systems. This view is supported by overlapping activation found both in structures implicated in procedural memory (BA 44) and in structures implicated in declarative memory (posterior parietal cortex).

While the similarities in converging activation observed between declarative grammar learning and non-declarative grammar learning are informative, the differences are particularly interesting, and support specific predictions of the DP model, though we emphasize that the low power in our exploratory analyses warrants cautious interpretation. First

of all, non-declarative grammar learning yielded significantly greater ALE results as compared to declarative grammar learning in procedural memory substrates, in particular BA 44, as well as more extensive activation in premotor regions. Moreover, only non-declarative grammar learning yielded basal ganglia activation, specifically in anterior portions of the caudate nucleus and the putamen. Conversely, declarative grammar learning yielded more extensive activation in declarative memory substrates, in particular in posterior parietal cortex (in the precuneus, which has been implicated in declarative memory; Wagner et al., 2005). Moreover, only declarative grammar learning yielded activation in the MTL, specifically in the hippocampus.

This conforms to the predictions of the DP model. Explicit grammar training, explicitness of developed grammatical knowledge, and the extent to which the grammatical target emphasizes similarity- or chunk-based (as opposed to rule-based) learning, all appear to promote learning in declarative memory. Interestingly, the individual grammar learning studies that showed activation in the MTL each involved different factors that might promote learning in declarative memory, such as high chunk strength (Lieberman et al., 2004), surface similarity between the training and testing sets (Opitz and Friederici, 2004), and explicit training conditions (Yang and Li, 2012). Within the MTL, the hippocampus seems to be particularly important, perhaps not surprisingly given its role in associating different types of information (Eichenbaum, 2012; Ullman, 2004; Wixted and Squire, 2011), which should be critical in learning the idiosyncratic information found in the lexicon, such as form-meaning pairings.

In contrast, when grammar learning does not occur in declarative memory-promoting conditions, in particular when rule-governed grammar is learned in more implicit training conditions, it does not appear to depend importantly on declarative memory. Indeed, not a single activation focus was observed in the MTL across all non-declarative grammar learning studies. Rather, as predicted by the DP model, such implicit rule-governed grammar learning yielded ALE results in the basal ganglia. Specifically, anterior portions of the caudate nucleus and putamen were implicated, as expected given their role in early learning in procedural memory (Janacsek et al., in prep). Thus, while our analyses on declarative grammar learning versus non-declarative grammar learning are exploratory and should be interpreted with caution, the direction of the above-mentioned findings are supportive of the DP model, and should lay the groundwork for future research.

4.1.3. Artificial grammar analyses

We now turn to our analyses of artificial grammar learning. Because of the volume of interest in artificial grammars, and conflicting evidence regarding the extent to which they serve as valid models of natural language grammar learning (Fitch and Hauser, 2004; Forkstam et al., 2006; Friederici et al., 2006; Petersson et al., 2012), we ran separate ALE analyses on studies from our Grammar analysis that trained participants on artificial grammars and those that trained participants on other grammatical targets, all of which included meaning (artificial languages, miniature languages, and reduced natural languages).

4.1.3.1. Converging artificial grammar/non-artificial grammar activation in frontal cortex, particularly in BA 44. Our ALE analysis of artificial grammar learning revealed significant ALE results in the left pars opercularis (BA 44) with a subpeak in the precentral gyrus (BA 6), as well as in the anterior insula (BA 13), bilaterally. The ALE analysis of non-artificial grammar learning yielded results bilaterally in the IFG, centered in pars triangularis (BA 45) with a subpeak in pars opercularis (BA 44) in the left hemisphere, and in the precentral gyrus (BA 6) with subpeaks in pars triangularis (BA 45) and pars opercularis (BA 44) in the right hemisphere. The conjunction analysis showed convergence between artificial grammar and non-artificial grammar studies only in the left pars opercularis (BA 44).

This overlapping activation for artificial grammar and non-artificial

grammar studies is consistent with previous research indicating a relationship between artificial grammar and natural language grammar processing (Christiansen et al., 2010; Conway et al., 2007; Forkstam et al., 2006; Petersson et al., 2012; Silva et al., 2017). In particular, the converging activation in left BA 44 is highly consistent with research that has implicated this region in syntactic processing in natural languages (Dapretto and Bookheimer, 1999; Friederici, 2011; Friederici and Kotz, 2003; Friederici et al., 2000) as well as in artificial grammar learning (Friederici et al., 2006; Petersson et al., 2012). Thus, the current study lends further support to the hypothesis that left BA 44 is particularly important for grammar, even in paradigms that do not include meaning. The finding also supports the view that even in language learning tasks, brain structures implicated in processing can play a role. The presence of BA 44 activation across both types of grammar learning paradigms is consistent with the DP model, which specifically posits that BA 44 is involved in procedural memory, in particular in aspects of grammatical processing (Ullman, 2004, 2016).

4.1.3.2. Activation specific to artificial grammar. Beyond frontal cortex, our ALE analysis of artificial grammar studies showed consistent activation in the left posterior superior parietal lobule, left inferior occipital gyrus, and premotor areas. Non-artificial grammar studies did not show consistent activation in any brain structures other than the frontal regions discussed above. Subtraction analyses between Artificial Grammar and non-Artificial Grammar yielded null results in both directions. At this point it remains unclear why the regions mentioned just above should be active in artificial grammar learning but not in non-artificial grammar learning. However, it should be noted that our Artificial Grammar analysis included nearly twice as many subject groups as the non-Artificial Grammar analysis, the latter of which was fairly underpowered given current ALE recommendations (Eickhoff et al., 2016). Thus, a power differential could at least partly explain the additional activation in the Artificial Grammar analysis, so these regions seem ripe for further exploration.

4.2. Implications

The findings from the current study have basic research, theoretical, and applied implications pertaining to adult language learning. Independent of particular theoretical perspectives, our study reveals a network of structures that seem to be broadly involved in language learning, that is, for both lexical and grammatical learning. These regions include the bilateral IFG (BA 44/45), BA 6, anterior insula, and SMA, as well as the left superior parietal lobule and the left angular gyrus. Several of these regions have been included in various proposed (first) language processing networks (Eickhoff et al., 2009a; Friederici, 2011; Guenther, 2006; Hickok and Poeppel, 2007). Intriguingly, our findings also provide support to the somewhat smaller chorus of voices that suggest that the insula (Eickhoff et al., 2009a; Oh et al., 2014) and parietal cortex (Golestani et al., 2002; Lee et al., 2007; Mechelli et al., 2004) may also play a role in language networks. More generally, our findings suggest that brain regions that are involved in L1 processing may also be recruited for aspects of adult language learning and processing.

The results also have implications for neurocognitive theories of language learning. In particular, the findings are largely consistent with the predictions of the DP model. The ventral occipito-temporal (ventral stream) activation found only for lexical learning and the anterior caudate/putamen activation found only for grammar learning are expected by this model, and strengthen the view that lexical learning relies importantly on declarative memory, while grammar depends more on procedural memory. Moreover, the joint activation for lexical and grammatical learning in BA 45 and posterior parietal cortex is consistent with the model's claims that in adults grammatical learning should also rely to some extent on declarative memory. The presence of BA 44 activation for lexical learning was not predicted, but may be accounted

for by the assumptions of the model. While some of the findings appear to be at least somewhat consistent with other neurocognitive theories of adult language learning and processing (Abutalebi, 2008; Green, 2003; Paradis, 1994, 2004; 2009; Perani and Abutalebi, 2005), the relative lack of specificity about neural structures and language domains, as well as the absence of L1 activation in the studies examined here, preclude fuller evaluation of these accounts in the present study.

In our exploratory analyses, when grammar studies were separately analyzed according to whether or not they were expected to promote learning in declarative memory (e.g., explicit versus implicit training conditions), our findings led to even clearer support for the DP model. In particular, only grammar learning that is predicted by the DP model to rely particularly on declarative memory showed hippocampal involvement (in the ROI cross-tabulation analyses), while only grammar learning predicted by the model to rely particularly on procedural memory showed basal ganglia (anterior caudate/putamen) activation (in the ALE analyses). These patterns are specifically predicted by the model. To further probe this theory, as well as other theories in the field of Second Language Acquisition (SLA; e.g., Abutalebi, 2008; Bley-Vroman, 1989; Clahsen and Felser, 2006; DeKeyser, 2015; Ellis, 2007; Green, 2003; MacWhinney, 2001), one could examine how the neurocognition of language learning changes with exposure or proficiency, how it is impacted by factors such as attention (López-Barroso et al., 2016), and how it compares to the neurocognition of L1 processing. Such analyses were either impossible to run due to limited power or beyond the scope of the current study.

At least partly as a consequence of its theoretical implications for adult language learning, this study may also have practical implications for applied linguistics and language pedagogy. First, the results underscore the view that both declarative and procedural memory are involved in adult grammar learning. This finding has important implications for the field of SLA, which has long debated the degree to which adult language learning can involve implicit learning and knowledge. Since the declarative memory system involves explicit memory and the procedural memory system appears to be an implicit memory system, activation of structures in both systems suggests that both explicit and implicit processes may be involved in adult language learning (for a discussion of the explicit/implicit and declarative/procedural memory distinctions, and confusions between these, see Ullman, 2015). Indeed, such redundancy is not uncommon among biological systems (Tononi et al., 1999). However, this challenges foundational assumptions about the explicitness of adult language learning and processing (Bley-Vroman, 1989; Krashen, 1981), and supports research suggesting that adults can indeed learn and process language both implicitly and explicitly (Ellis, 2005; Norris and Ortega, 2001; Spada and Tomita, 2010). Second, our findings demonstrate a role for declarative memory in both lexical and grammatical learning, so it stands to reason that approaches that enhance the performance of the declarative memory system could improve learning in both domains. These may include both behavioral and pharmacological approaches, such as explicit training, retrieval practice (the testing effect), and the administration of pharmacological agents such as memantine (Laine and Salmelin, 2010; Ullman and Lovelett, 2018; Ullman and Pullman, 2015). Third, the involvement of procedural memory structures demonstrates that this system is also important for adult grammar learning. The goal of adult language teaching, then, might not only be to increase scores on language tests, but also to determine what sorts of training conditions and cognitive abilities can facilitate the involvement of these automatic processes in the brain.

Finally, our results pertaining to artificial grammar learning show critical neural overlap between grammar learning in this classic paradigm and in more natural paradigms (i.e., those that involve meaning), such as miniature languages, artificial languages, and reduced natural languages. This is particularly true for left BA 44, which has been implicated in syntactic processing in both first and second language (Dapretto and Bookheimer, 1999; Friederici, 2011; Friederici and Kotz, 2003; Friederici et al., 2000; Morgan-Short and Ullman, 2012; Tagarelli

et al., in prep; Wartenburger et al., 2003). These results therefore validate the use of artificial grammars in exploring questions about grammar learning in natural languages.

4.3. Open questions and limitations

Although the present study has clarified a number of important issues regarding the functional neuroanatomy of language learning, and has a range of implications, various open questions remain. In addition, the study has a number of limitations, several of which are related to power.

First, this study does not include any analyses on aspects of language learning beyond lexicon and grammar, such as phonology, prosody, or pragmatics. We did originally consider a broader set of studies in our search, but given the focus of our paper on grammar and lexical/semantics, and the relatively small number of relevant studies in each of these other linguistic domains, we decided not to include these in our paper. However, we believe they warrant examination in future meta-analyses.

Second, more fine-grained analyses within lexical and grammatical learning could have been informative. For example, several theoretical accounts suggest distinct roles for the hippocampus/MTL and neocortical areas in word learning, including regarding their involvement in early versus later encoding and consolidation processes, respectively (Davis and Gaskell, 2009; Gupta and Tisdale, 2009; Laine and Salmelin, 2010; Ullman, 2005, 2016). Sleep-based consolidation may also affect aspects of rule learning (López-Barroso et al., 2016). Thus, meta-analyses probing areas that increase or decrease in activation over the course of learning, or that are differentially involved before or after sleep-based consolidation, could tell us more about how the involvement of different brain regions changes as learning progresses, and therefore inform such views. Additionally, comparisons of areas involved in the processing of ungrammatical versus grammatical artificial grammar strings might shed light on some interesting questions in artificial grammar research about the processes underlying the unification of structural elements in language (Pettersson et al., 2012). These and other more fine-grained analyses were not conducted because we did not have sufficient power, but suggest areas for future research (for a recent though somewhat underpowered ALE examination of ungrammatical vs. grammatical strings, see Udden & Männel, 2018).

Third, and along these lines, more fine-grained analyses probing basal ganglia activation could help further elucidate the role(s) of the basal ganglia in language learning. The basal ganglia, as discussed above, underlie not only procedural memory but also other cognitive functions that could play roles in language learning, such as cognitive control (Abutalebi, 2008; Green, 2003; Paradis, 1994, 2004; 2009; Perani and Abutalebi, 2005) and conditional routing (Stocco et al., 2010, 2014; Stocco and Prat, 2014). Thus, different processes could help explain why basal ganglia involvement was observed in grammar learning in our analyses. Furthermore, the basal ganglia comprise a set of structures, each of which may make somewhat different contributions to language learning. For example, Bradley et al. (2013) found that during a word learning task, monolinguals activated a broad network of brain regions, including the caudate, whereas bilinguals activated the putamen. They interpreted this as evidence for the recruitment of cognitive control mechanisms for monolinguals and motor control mechanisms for bilinguals during learning (see also Abutalebi et al., 2013; Hernandez and Fiebach, 2006). Our analyses did not examine substructures of the basal ganglia as a function of variables such as prior language experience, due to insufficient power. Such issues are ripe for further research.

Fourth, our analyses collapsed contrasts with a fairly broad range of baselines, including rest, sensorimotor control tasks, and the task of interest itself (e.g., in posttest > pretest contrasts). This was necessary for reasons of power, and a reasonable approach because the ALE technique is designed to identify similar activation across contrasts, and thus should identify areas related to learning among all of these types of contrasts. However, because we included less well-controlled baselines, such as

rest, some of the converging activation that we observed may have been due to processes beyond learning, such as attention or effort.

Fifth, we only included contrasts probing areas that were activated, rather than deactivated, during learning. As mentioned in the Methods, this was primarily because deactivations are difficult to interpret, but also because they are not often reported. Thus, while it might be informative to separately analyze activations and deactivations, additional data points would be necessary to allow for such an analysis.

Additional questions arise from activation that was *not* observed. In particular, two regions in the brain that have been implicated in language, but that showed little if any activation in our ALE analyses, are the cerebellum and superior temporal cortex.

We did not observe any activation in the cerebellum. This seems somewhat surprising, given its purported role in language (Argyropoulos, 2016; Fiez, 2016; Lesage et al., 2016; Mariën et al., 2014). One possible reason for the absence of significant ALE results in the cerebellum is that while we only included studies that examined the whole cerebrum, we did not include coverage of the cerebellum as an inclusion criterion. Thus, there might not have been enough studies that examined the cerebellum to show converging activation in this region. Of the 46 papers included in our meta-analyses, 25 reported at least some coverage of the cerebellum and/or reported activation in the cerebellum, 5 did not include the cerebellum in their analyses, and 16 did not report whether analyses included the cerebellum and did not report activation in this region. Thus, the absence of cerebellar activation in our language learning ALE analyses cannot reliably be taken as evidence that this structure is not involved in language learning.

We did not see any activation in the superior temporal gyrus, which is often implicated in aspects of language processing, particularly in speech perception (Binder et al., 2009; Friederici, 2011; Hickok and Poeppel, 2007; Turkeltaub and Coslett, 2010). Perhaps this region is less important for language learning, at least in the learning of lexical and grammatical knowledge, though it has been implicated in learning transitional probabilities between word boundaries (e.g., Karuza et al., 2013) and in novel word learning in adults (Hultén et al., 2010). Another possible explanation for the lack of activation in this region is that many of the studies in the meta-analyses included visual rather than auditory stimuli, and the superior temporal gyrus may be particularly important for auditory aspects of language processing. In any case, this null result leaves the door open for further research.

A final point relevant to activation that was not observed is that in several cases, we obtained ALE results for a particular structure in one analysis but not in its complementary analysis, yet the relevant subtraction analysis did not yield ALE results in that structure. For example, we observed ALE results in the left inferior occipital gyrus for Artificial Grammar but not for non-Artificial Grammar, yet we did not observe activation in this region in the related subtraction. This might suggest that these differences are not particularly robust, but it also may be due to lower sensitivity for ALE subtraction analyses. In general, it is important to be aware of the power imbalances in some of the analyses reported here. Such imbalances were difficult to avoid, given the availability of studies appropriate for each analysis in the current literature, but it may in some cases explain why we observed more activation in higher-powered analyses that is otherwise difficult to explain in the context of neurolinguistic research and theory. On the other hand, these power imbalances further bolster findings such as the involvement of the basal ganglia in grammatical learning, a result that cannot be simply due to power since the Grammar analysis included many *fewer* subject groups than the Lexicon analysis.

Finally, some caution is warranted in concluding that activated brain structures in learning studies are in fact involved in learning, as opposed to aspects of retrieval or processing (e.g., Karuza et al., 2013; Karuza et al., 2014; Orban et al., 2010; Reber, 2013). In particular, any activation associated with learning could be due not only to the engagement of the

underlying structures in learning itself, but also or instead to their involvement in aspects of processing the learned knowledge. For example, as more learning occurs, one's ability to process the learned knowledge increases, and thus processing-related structures may also show activation. Indeed, as we have seen above, activation in BA 44 might reflect aspects of grammatical processing in grammar learning paradigms. In the present study, following the intent of the bulk of studies examining language learning that were included in our meta-analyses, we have discussed the observed activation largely in terms of learning. However, caution is warranted, and it remains likely that at least some of the observed activation may in part be due to aspects of retrieval or processing as well as learning.

5. Conclusion

The results from this study yield the following conclusions. First, the pattern of observed activation has elucidated the functional neuroanatomy of various aspects of adult language learning, independent of any theoretical framework. Second, the findings help clarify the theoretical landscape by providing additional support for particular predictions of the DP model, though the results may not be inconsistent with other models. Third, the results from the artificial grammar analyses provide validation for the use of this paradigm for exploring questions related to grammar learning in natural language. Overall, the study has a range of basic research, theoretical, and applied implications, and should help guide future research.

Declarations of interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuroimage.2019.02.061>.

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