

COGNITIVE SCIENCE

Cognitive Science 28 (2004) 383-407

http://www.elsevier.com/locate/cogsci

Artificial syntactic violations activate Broca's region

Karl Magnus Petersson a,b,c,*, Christian Forkstam b,c, Martin Ingvar c

^aNeurocognition of Language Research Group, Max-Planck-Institute for Psycholinguistics, Nijmegen, The Netherlands

^bCognitive Neurology and Memory Research Group, F.C. Donders Centre for Cognitive Neuroimaging, University of Nijmegen, Nijmegen, The Netherlands ^cCognitive Neurophysiology Research Group, Department of Clinical Neuroscience, N8 Karolinska Institutet, Stockholm, Sweden

Received 22 July 2003; received in revised form 8 December 2003; accepted 12 December 2003

Available online 20 March 2004

Abstract

In the present study, using event-related functional magnetic resonance imaging, we investigated a group of participants on a grammaticality classification task after they had been exposed to well-formed consonant strings generated from an artificial regular grammar. We used an implicit acquisition paradigm in which the participants were exposed to positive examples. The objective of this study was to investigate whether brain regions related to language processing overlap with the brain regions activated by the grammaticality classification task used in the present study. Recent meta-analyses of functional neuroimaging studies indicate that syntactic processing is related to the left inferior frontal gyrus (Brodmann's areas 44 and 45) or Broca's region. In the present study, we observed that artificial grammaticality violations activated Broca's region in all participants. This observation lends some support to the suggestions that artificial grammar learning represents a model for investigating aspects of language learning in infants [TICS 4 (2000) 178] and adults [Proceedings of the National Academy of Sciences of United States of America 99 (2002) 529].

© 2004 Cognitive Science Society, Inc. All rights reserved.

Keywords: Artificial grammar; Language; Functional neuroimaging; FMRI; Broca's region

1. Introduction

The human capacity to learn and communicate through language is an outstanding scientific challenge to understand (Chomsky, 2000; Hauser, Chomsky, & Fitch, 2002; Jackendoff, 2002)

E-mail address: karl.magnus.petersson@fcdonders.kun.nl (K.M. Petersson).

0364-0213/\$ – see front matter © 2004 Cognitive Science Society, Inc. All rights reserved. doi:10.1016/j.cogsci.2003.12.003

^{*} Corresponding author.

and Chomsky, following von Humboldt, has suggested that natural language processing is a paradigmatic example of the 'infinite use of finite means' (Chomsky, 1965; von Humboldt, 1836). Since the 1950s a fundamental problem in theoretical linguistics has been to construct explicit models reflecting this intuition (Chomsky, 1965; Newmeyer, 1995). The simplest formal model incorporating the idea of 'infinite use of finite means' is represented by the family of regular (right-linear phrase structure) grammars (Chomsky, 1957). Furthermore, it has been suggested that the task of learning an artificial grammar is a potentially relevant model for investigating aspects of language learning in infants (Gomez & Gerken, 2000), exploring key differences between human and animal learning relevant to the narrow faculty of language (Hauser et al., 2002), as well as second language learning in adults (Friederici, Steinhauer, & Pfeifer, 2002). The seminal work of Reber (1967) indicated that humans can learn artificial grammars in an implicit fashion and suggested that relevant information was abstracted from the environmental input. Reber (1967) also suggested that this process represented a mechanism that is intrinsic to natural language learning. From a cognitive neuroscience perspective it is therefore of interest not only to understand the nature of the knowledge, its representation, and the functional role acquired during learning, but also to characterize the neural infrastructure subserving these aspects of artificial grammar processing. This enterprise includes both charactering the end-state of artificial grammar learning as well as the learning process itself using different functional neuroimaging approaches as well as behavioral measures. This makes it possible to compare natural and artificial language processing in the human brain and to address important questions related to the characteristics of the learning mechanism(s) involved, the nature of the knowledge acquired, and how this knowledge is represented and put to use.

Humans appears to be equipped with acquisition mechanisms that have the capacity to extract structural information implicitly without induction of an explicit model from the experience of observed exemplars (Reber, 1967; Stadler & Frensch, 1998). It has been suggested that such acquisition mechanisms play an important role in several types of information extraction processes or forms of learning (e.g., Cleermans & McClelland, 1991; French & Cleeremans, 2002; Lewicki, 1986; Stadler & Frensch, 1998). In the present study we employed the classical artificial grammar learning (AGL) paradigm (Stadler & Frensch, 1998), which includes an acquisition phase and a classification phase. During the acquisition phase, participants were engaged in a short-term memory task using an acquisition sample of symbol sequences generated from an artificial grammar. Subsequent to the acquisition phase the subjects were informed that the items (i.e., symbol sequences) were generated according to a complex system of rules and they were asked to classify new items, not previously encountered, as grammatical or non-grammatical guided by their immediate intuitive impression ('gut feeling'). Typically, subjects perform reliably above chance on this task (Reber, 1967; Stadler & Frensch, 1998).

One component in the definition of a formal language is its finite lexicon (alphabet) V of terminal symbols, $V = \{t_1, t_2, \ldots, t_N\}$. The set of all possible finite symbol strings that can be generated from the alphabet V is given by Kleene-star operator $V^* = \{\emptyset, t_1, t_2, \ldots, t_N, t_1t_1, t_1t_2, t_1t_3, \ldots, t_{k1}t_{k2}, \ldots, t_{km}, \ldots\}$. A formal language L over V is then defined as a subset of V^* , $L \subseteq V^*$; a symbol string $s = t_{k1}t_{k2}, \ldots, t_{km}$ is well-formed or grammatical if and only if $s \in L$ (e.g., Davis, Sigal, & Weyuker, 1994; Lewis & Papadimitriou, 1981; Taylor & Taylor, 1997). This way of introducing formal languages amounts to an extensional definition, an E-language,

where the language is identified with its string set. This is adequate for formal investigations but is, perhaps, of limited interest from a cognitive point of view. In the context of natural language grammars it has been questioned whether an extensional definition is meaningful (Chomsky, 1986, 2000). A more fruitful approach takes as its point of departure an intentional definition of language (cf. Chomsky & Lasnik, 1995). This entails the specification of a generating mechanism, including principles of combinations and additional non-terminal symbols, capable of generating all grammatical (well-formed) strings and only those in a given language (e.g., Davis et al., 1994; Lewis & Papadimitriou, 1981; Taylor & Taylor, 1997). The generating mechanism serves as an intentional definition of the language, an I-language, and a string s is grammatical ($s \in L$) if and only if the formal mechanism (or machine) can generate it. Here, it should be noted that the term 'language' in formal language, do not entail anything beyond what is outlined above and that a formal (or artificial) grammar represents a specification of a mechanism that generates (or recognizes) certain types of structural regularities.

As noted above, a simple formal model incorporating the idea of the 'infinite use of finite means' is represented by a family of artificial grammars called regular grammars (Partee, ter Meulen, & Wall, 1990). A regular grammar (Fig. 1) generates right-branching phrase structure trees and the class of regular grammars has a generative capacity equivalent to the class of regular languages and can be implemented in the finite state machine architecture (see, for example, Davis et al., 1994; Savage, 1998; Taylor & Taylor, 1997). A finite state machine can be viewed either as a language generator (Chomsky, 1957; Lasnik, 2000) or language recognizer for a given regular language (Cohen, 1997; Davis et al., 1994; Savage, 1998). Recent developments in the theory of transformational grammar suggest that two important processing devices may capture human syntactic competence, namely, Merge and Move (Chomsky, 1995; Radford, 1997) The family of right linear phrase structure grammars is closely related to and can be implemented by a constrained Merge operator. They are equally easy to implement within the framework of unification grammars (Jackendoff, 1997; Shieber, 1986) by for example a

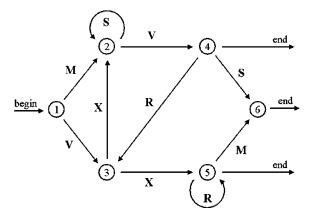


Fig. 1. The transition graph representation of the Reber grammar. MSSVRXV is a grammatical string and this can be seen by starting in the initial state 1 and successively read one symbol at the time moving from one internal state to the next according to the symbols labeling the arrows (legal transitions; in the present case: 1-2-2-2-4-3-2-4) ending in the final state which can be reached from $\{4, 5, 6\}$ after having read the whole string. In contrast, MSSVSXV is non-grammatical.

constrained unification operation (Vosse & Kempen, 2000), or within most common formal approaches to grammar (Sag, Wasow, & Bender, 2003).

A recent meta-analysis of functional neuroimaging studies of syntactic processing (Indefrey, in press, briefly reported in Indefrey, 2001; see also the reviews of Bookheimer, 2002; Friederici, 2002) reported that the most reliably replicable finding related to syntactic parsing across imaging techniques, presentation modes, and experimental procedures, was localized to the left inferior frontal gyrus (Brodmann's areas (BA) 44 and 45), consistent with what is known from brain lesion data (Caplan, 1992; Caramazza & Zurif, 1976; see also Friederici, 2002; Zurif, 1990). The left inferior frontal region is part of the prefrontal cortex, which has been related to different aspects of language processing, including phonological, syntactic, semantic, pragmatic, as well as non-linguistic contextual information (Bookheimer, 2002; Duncan, 2001; Mesulam, 2002). The prefrontal cortex has also been related to different short-term working memory and long-term memory processes (Baddeley, 2003; Simons & Spiers, 2003). In Baddeley's model of working memory (Baddeley, 1992, 2003), the 'phonological loop' has been associated with the left temporo-parietal and left inferior frontal regions. Recently it was suggested that the 'phonological loop' may have evolved to facilitate the acquisition of language and in support of this notion, its capacity appears to be a good predictor of second language learning (Baddeley, 2003; Baddeley, Gathercole, & Papagno, 1998). The prefrontal cortex has been investigated in several primate studies at the neuronal level in a wide range of complex tasks, including categorization, working memory, rule learning and rule switching, as well as cross-modal integration (Duncan, 2001; Duncan & Miller, 2002). The response properties of prefrontal neurons are highly adaptable and any given neuron can be driven by different kinds of input, perhaps through the dense interconnections that exist within the prefrontal cortex as well as reciprocal connections to a majority of cortical and subcortical structures (Fuster, 1997; Mesulam, 2002; Stuss & Knight, 2002).

A number of recent FMRI studies have investigated implicit (Seger, Prabhakaran, Poldrack, & Gabrieli, 2000; Skosnik, Mirza, Gitelman, Parrish, & Mesulam, 2002) and explicit learning of material generated from artificial grammars (Fletcher, Büchel, Josephs, Friston, & Dolan, 1999; Strange, Henson, Friston, & Dolan, 2001), artificial language (Opitz & Friederici, 2003), and natural languages different from the native language of the subjects (Musso, Moro, Glauche, Rijntjes, & Reichenbach, 2003). Opitz and Friederici (2003) used the experimental paradigm outlined by Fletcher et al. (1999) and Strange et al. (2001). The task used in these studies can be characterized as explicit problem solving with performance feedback. In this set-up, the participants are explicitly instructed to extract the underlying grammatical rules during the learning condition, while during the classification task the participants receive performance feedback after each trial. In the study by Musso et al. (2003), the subjects were explicitly taught three natural language rules and three rules not observed in natural language grammars. In the present study, using functional magnetic resonance imaging (FMRI) in an event-related fashion, we investigated a group of participants on a grammaticality classification task after they had been exposed to well-formed consonant strings generated from the Reber grammar (Fig. 1). We used an implicit acquisition paradigm in which the participants were exposed to positive examples. The objective of this study was to investigate whether brain regions related to language processing overlap with the brain regions activated by the grammaticality classification task used in this study. Thus, we specifically tested the hypothesis that brain

regions related to syntactic comprehension are also engaged in processing of input strings generated from an artificial grammar as well as strings that violated this grammar. We were interested in the behavior of the left inferior frontal gyrus (BA 44, 45) during processing of the input strings. Several of the studies reviewed in Indefrey (in press) used grammar violation paradigms, in which non-grammatical items were compared with grammatical items, yielding activations in the left inferior frontal region or Broca's region (Amunts, Schleicher, Burgel, Mohlberg, & Uylings, 1999) specifically related to the non-grammatical versus grammatical comparison. Thus, we specifically hypothesized that non-grammatical compared to grammatical items, reflecting artificial grammar violations, would activate Broca's region during the grammaticality classification task. It should be noted that we are using the terms 'grammatical' and 'non-grammatical' in a descriptive sense reflecting their generative origin.

2. Materials and method

2.1. Participants

Twelve right-handed healthy university students volunteered to participate in the study (3 female and 9 male subjects with mean age $\pm SD = 24\pm3$ years). They were all pre-screened and none of the subjects used any medication, had a history of drug abuse (including nicotine), head trauma, neurological or psychiatric illness, or a family history of neurological or psychiatric illness. The local Ethics committee at the Karolinska Institutet/Hospital approved the study. All subjects gave written informed consent.

2.2. Stimulus material

The stimulus material was generated from the regular (right linear) grammar as implemented by the finite-state machine of Reber (Reber & Allen, 1978), Fig. 1. Of the 110 possible grammatical (G) consonant strings of 2–8 letters, 56 randomly chosen items were allocated to the acquisition/training set and the remaining 54 items were included in the classification set. The non-grammatical (NG) strings were generated from the grammatical strings by randomly re-arranging the order of letters to render them non-grammatical. The NG strings were included in the classification set so that this set included 108 items in total, 50% G- and 50% NG-items.

2.3. Experimental procedure

2.3.1. Implicit acquisition task

The acquisition or training phase consisted of a short-term memory task using the acquisition set. In a self-paced paradigm, each subject was instructed to attend to the consonant strings as they were presented on a computer screen for 5 s, and then as the string disappeared, to recall the string and type it into the computer. Subjects were allowed to correct themselves. The acquisition set was presented three times. The acquisition phase lasted approximately 40 min.

2.3.2. Classification task

Following the training phase, the subjects were informed that the previously studied strings followed a complex set of rules. The participants were instructed to classify a new set of consonant strings, half of which were generated from the same underlying structure while the other half in many aspects were similar but violate the grammar in some respect, as grammatical and non-grammatical, respectively. The subject were asked to make their classification judgement based on their immediate intuitive impression/impulse ('gut-feeling' or guessing inclination), and were informed that this strategy would yield the best performance. During the classification task event-related FMRI data were acquired. A sensorimotor classification control task was also included in the FMRI study, in which the subjects had to decide whether the presented string consisted of only P:s or L:s (same average length as the consonant strings). The subjects indicated their response by pressing one of two different buttons with their middle-(NG, L) or index finger (G, P). During the FMRI experiment, the different stimulus types were presented in random order on a screen for 3 s, during which time the subjects responded by pressing a keypad, followed by a fixation-cross for 4s. A minimum of approximately 1.5h separated the acquisition- and the classification phase. The computer screen was displayed to the subject through a LCD-projector standing inside the MR-scanner room, projecting onto a semi-transparent projection screen that the subject viewed comfortably through a binocular device mounted on the head-coil.

2.4. MRI data acquisition

During both the acquisition and classification task, the consonant strings were presented visually using the ERTS software (http://www.erts.de). During the classification task, whole head T2*-weighted EPI-BOLD FMRI data were acquired with a GE Signa 1.5T MR-scanner using an sequential slice acquisition EPI sequence (volume TR = 4.2 s, TE = 100 ms, 90° flip-angle, 42 axial slices, slice-matrix size = 64×64 , slice thickness = 3 mm, slice gap = 0.5 mm, FOV = 224 mm, isotropic voxel-size = $3.5 \, \text{mm} \times 3.5 \, \text{mm} \times 3.5 \, \text{mm}$) in a randomized event related fashion. For the structural MR image volume a high-resolution T1-weighted 3D SPOILED-GRASS2 sequence was used (volume TR = $24.0 \, \text{ms}$, TE = $6 \, \text{ms}$, 35° flip-angle, 124 coronal slices, slice-matrix size = 256×256 , slice thickness = $1.5 \, \text{mm}$, slice gap = 0 mm, voxel-size = $0.859 \, \text{mm} \times 1.5 \, \text{mm} \times 0.859 \, \text{mm}$ interpolated to 1 mm \times 1 mm \times 1 mm).

2.5. MR image pre-processing and statistical analysis

Image pre-processing and statistical analysis was performed using the SPM99 software (http://www.fil.ion.ucl.ac.uk). The functional EPI-BOLD images were realigned, slice-time corrected, and the subject-mean functional MR images were co-registered with the corresponding structural MR images. These were subsequently spatially normalized (i.e., the normalization transformations were generated from the structural MR images and applied to the functional MR images) and transformed into a common approximate Talairach space (Talairach & Tournoux, 1988), as defined by the SPM99 MNI T1 template, and finally spatially filtered by convolving the functional image volumes with a isotropic 3D spatial Gaussian filter kernel (10 mm FWHM). The FMRI data was proportionally scaled to account for global effects and

analyzed statistically using the general linear model and statistical parametric mapping (Friston et al., 1995). The linear model included explanatory variables, modeling G- and NG-items separated in terms of correct and incorrect responses. The explanatory variables were temporally convolved with the canonical hemodynamic response function. In addition, the linear model included the time derivative of the convolved regressors, specifying a design matrix incorporating the condition effects as effects of interest and, as effects of no-interest, the session/subject-effects, and a temporal high-pass filter to account for various low-frequency effects (e.g., related to different physiological effects such as heart-rate and respiration, and slow MR-scanner drifts). In order to account for temporal autocorrelation, the FMRI data were convolved with a Gaussian (FWHM = 4s) temporal kernel and effective degrees of freedom estimated (Worsley & Friston, 1995). In the statistical analysis relevant contrasts, corresponding to null-hypotheses, were used to generate statistic images SPM[T]:s, which were all thresholded at T = 3.11 (p = .001, uncorrected). The cluster size was used as the test statistic and only clusters significant p < .05 (corrected for multiple non-independent comparisons) are described. All p-values reported are corrected for multiple non-independent comparisons based on the theory of smooth 3D random field theory (Adler, 1981; Worsley, Marrett, Neelin, Vandal, & Friston, 1996). The significant clusters were subsequently resolved into peak-height of local maxima with Z-score >3.09 and p-values were corrected for multiple non-independent comparisons based on the false discovery rate (Genovese, Lazar, & Nichols, 2002). In addition we investigated commonalities over subjects using minimum T-field theory (Worsley & Friston, 2000). The terms of activation and deactivation are used as synonyms for a relative increase and decrease in BOLD signal, respectively. For reasons of portability of data the tables of local maxima use the Talairach nomenclature (Talairach & Tournoux, 1988).

3. Results

All subjects showed for each classification session, during which event-related FMRI data were acquired, a significant above-chance correct classification performance on the classification task (mean \pm $SD=73\pm7\%$, range = 61–92%, whereas 50% correct is expected by chance) consistent with the original result reported by Reber (1967). Thus the subjects were able to reliably differentiate between grammatical and non-grammatical items.

A significantly activated set of regions (set-level inference p < .001; see Table 1 and Fig. 2) were observed in the grammaticality classification (CL) task compared to the sensorimotor baseline (B) task and included 5 significant clusters: The left middle-inferior frontal gyrus (p < .001) centered on BA 44/45 extending into BA 6/9 and BA 45/47, the anterior cingulated cortex (p = .007; BA 32), the left inferior parietal cortex (p = .012) centered on the supramarginal gyrus (BA 40) extending into the inferior parts of the superior parietal cortex, and bilateral middle-inferior occipital and occipito-temporal cortex (left: p < .001, right: p < .001; BA 18, 19).

Testing our critical hypothesis of artificial grammatical violations in a random effects model, that is, comparing the brain activity related to non-grammatical (NG) versus grammatical (G) items, showed a significant activation (p = .01, corrected) in the left inferior frontal gyrus (BA 44 with local maximum at $[x \ y \ z] = [-48 \ 16 \ 22]$, and BA 45 with local maximum at

Table 1
The significantly activated set of regions observed in the grammaticality classification task compared to the senso-rimotor control task

| Region (Brodmann's area) | Cluster p-value | Z | T_{11} | Voxel <i>p</i> -value | $[x \ y \ z]$ |
|--|-----------------|------|----------|-----------------------|-------------------|
| Left middle-inferior frontal cortex | <.001 | | | | |
| BA 6/9 | | 4.29 | 7.17 | .016 | $[-56\ 2\ 36]$ |
| BA 6/44 | | 4.12 | 6.63 | .016 | $[-58\ 0\ 32]$ |
| BA 44 | | 4.09 | 6.53 | .016 | $[-48 \ 8 \ 22]$ |
| BA 44 | | 4.05 | 6.41 | .016 | $[-52\ 10\ 16]$ |
| BA 45/47 | | 3.56 | 5.05 | .021 | $[-56\ 10\ -2]$ |
| BA 9/44 | | 3.54 | 5.01 | .021 | $[-50\ 16\ 28]$ |
| BA 6/44 | | 3.41 | 4.71 | .025 | $[-58\ 10\ 8]$ |
| Anterior cingulated cortex | .004 | | | | |
| BA 32 | | 4.01 | 6.26 | .016 | [6 28 36] |
| BA 32 | | 3.56 | 5.04 | .021 | $[-6\ 26\ 44]$ |
| Left inferior parietal cortex | .023 | | | | |
| BA 40 | | 4.25 | 7.06 | .016 | [-30 - 50 42] |
| BA 40/7 | | 3.56 | 5.73 | .016 | [-26 - 64 44] |
| Left middle-inferior occipital and occipito-temporal cortex | <.001 | | | | |
| BA 18 | | 4.36 | 7.42 | .016 | [-20 - 88 - 2] |
| BA 19 | | 4.28 | 7.14 | .016 | [-30 - 88 6] |
| BA 18/19 | | 4.20 | 6.89 | .016 | [-36 - 84 - 6] |
| BA 19 | | 4.17 | 6.79 | .016 | $[-32 - 86 \ 16]$ |
| BA 18/19 | | 3.90 | 5.94 | .016 | [-32 - 88 - 12] |
| BA 19/37 | | 3.57 | 5.08 | .020 | [-40 - 66 - 10] |
| Right middle-inferior occipital and occipito-temporal cortex | <.001 | | | | |
| BA 19 | | 4.69 | 8.77 | .016 | [40 - 78 8] |
| BA 18 | | 4.62 | 8.47 | .016 | $[44 - 80 \ 10]$ |
| BA 19 | | 4.43 | 7.68 | .016 | [40 - 78 - 4] |
| BA 19 | | 4.24 | 7.00 | .016 | [24 - 94 - 10] |
| BA 19 | | 4.19 | 6.85 | .016 | [40 - 72 - 12] |
| BA 18 | | 4.06 | 6.42 | .016 | [26 - 82 - 2] |

All p-values are corrected for multiple non-independent comparisons. The T_{11} -scores relate to the T-distribution on 11 degrees of freedom and the voxel p-values are corrected based on the false discovery rate.

[$-40\ 22\ 22$]; see Fig. 3 and Table 2). At a lower level of thresholding we also observed a local maximum at [$-44\ 26\ 10$] in BA 45 (p=.01, uncorrected). This effect was observed in each of the 12 subjects (minimum T-field conjunction over subjects >0 with local maxima at [$-44\ 12\ 22$], Z=4.37; BA 44/45; [$-46\ 16\ 24$], Z=4.32, BA 44; [$-40\ 22\ 22$], Z=3.71, BA 45). We also investigated the effects of (C) versus incorrect (NC) responses and the interaction G/NG \times C/NC in the random effects analysis. No significant effects related to these contrasts were observed in the left inferior frontal gyrus. However, we did observe a significant interaction [GC-GNC] versus [NGC-NGNC] in the left ventero-lateral thalamus ([$-12\ -18\ 12$], Z=5.00, p=.05, corrected).

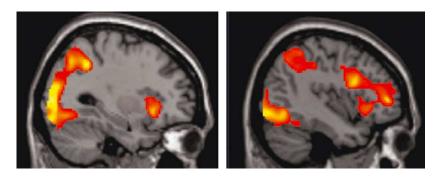


Fig. 2. Grammaticality classification compared to the sensorimotor baseline task, see Table 1 for coordinates of the local maxima. Significant activations were observed in the left middle-inferior frontal region (centered on BA 44 extending into BA 6/9 and BA 45/47), the anterior cingulated cortex (BA 32), the left inferior parietal cortex centered on the supramarginal gyrus (BA 40) extending into the inferior parts of the superior parietal cortex (BA 7), and bilateral middle-inferior occipital and occipito-temporal cortex (left BA 18/19/37 and right BA 18/19).

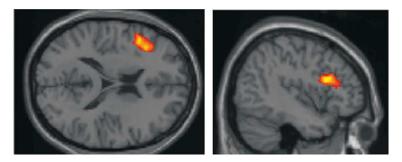


Fig. 3. Artificial syntactic violations were related to a significant activation in the left inferior frontal gyrus centered on BA 45 and extending into BA 44.

In order to further investigate the effects in the inferior prefrontal region with greater statistical power we used a minimum T-field approach (Worsley & Friston, 2000) to test different contrasts as conjunctions over subjects. In the minT-conjunction over grammaticality classification versus baseline & correct versus incorrect ([CL-B] & [C-NC]), we observed a significant effect in a superior–posterior sub-region of the left inferior prefrontal region described above (BA 44, [-52 8 26], Z = 6.01, p < .001, corrected), and in the minT-conjunction over [grammatical classification vs. baseline] & [correct vs. incorrect] & [non-grammatical vs. grammatical]

Table 2 Significant non-grammatical vs. grammatical effects in the left inferior frontal gyrus, Broca's region (Brodmann's area 44 and 45)

| Region ($p = .01$, corrected) | Brodmann's area | Z | T_{11} | [x y z] |
|---------------------------------|-----------------|------|----------|-------------|
| Left inferior frontal gyrus | BA 44 | 4.41 | 7.62 | [-48 16 22] |
| Left inferior frontal gyrus | BA 45 | 3.70 | 5.40 | [-40 22 22] |

Local maxima with a Z-score >3.7 (p = .0001, uncorrected) are listed.

([CL-B] & [C-NC] & [NG-G]) we observed significant effects in the same left inferior prefrontal sub-region (BA 44, [-50 10 26], Z = 5.72, p < .001, corrected, and BA 44/45, [-48 12 20], Z = 4.51). There was also a small sub-region that showed a significant interaction effect between the factors grammaticality and correctness (BA 44, $[-44\ 10\ 20]$, Z=5.18, p = .02, corrected) in the minT-conjunction over [grammatical classification vs. baseline] & [grammaticality × correctness interaction] ([CL-B] & [[GC-GNC] – [NGC-NGNC]]) related to the fact that the response was greater in correct grammatical versus incorrect grammatical compared to correct non-grammatical versus incorrect grammatical. However, this interaction effect was not observed in the whole region related to the grammaticality violation effect (i.e., [GNC-GC]). This was determined by an exclusive masking procedure in which we masked away the effects related to the conjunction of [grammatical classification vs. baseline] & [correct vs. incorrect] & [interaction] ([CL-B] & [C-NC] & [[GC-GNC] - [NGC-NGNC]]). Thus we observed a significant effect in $[-44\ 12\ 22]$, BA 44, (Z=5.18, p=.02, corrected) related to ([CL-B] & [C-NC] & [NG-G])/([CL-B] & [C-NC] & [[GC-GNC] - [NGC-NGNC]]) close to the local maxima [-48 16 22] observed in [NG-G]. In summary, these results indicate that there might be a regional functional sub-specialization within the left BA 44 and 45.

4. Discussion

The primary objective of the present study was to investigate whether brain regions activated by the grammaticality classification task described here would overlap with regions related to natural language processing. The present results indicate that the use of the knowledge acquired from an artificial grammar in an implicit acquisition paradigm using only positive examples is subserved by the same neural processing infrastructure that has most consistently been related to human syntactic processing (Figs. 3 and 4). We note that the effect of artificial syntactic violations was stimulus-locked rather than response-locked (when time-locking on the subject responses we did not observe the effect). More specifically, we observed that artificial syntactic violations specifically activate Broca's region, that is, the Brodmann's areas 44 and 45 of the left inferior frontal gyrus (Amunts et al., 1999). This was observed in all subjects as revealed by minimum *T*-field conjunction over subjects >0 in this region. The observation that artificial syntactic violations activate Broca's region thus lends some support to the suggestions that artificial grammar learning represents a model for investigating aspects of language learning in infants (Gomez & Gerken, 2000) and adults (Friederici et al., 2002), and perhaps exploring differences between human and animal learning relevant to the narrow faculty of language (Hauser et al., 2002). It should be noted that we take no particular position on the characteristics of the knowledge acquired by the subjects in the present study but we outline a number of possibilities in the discussion below.

When comparing grammaticality classification with the sensorimotor baseline we observed a significantly activated network of regions including the left middle-inferior frontal gyrus (centered on BA 44/45 extending into BA 6/9 and BA 45/47), the anterior cingulated cortex (BA 32), the left inferior parietal cortex (centered on the supramarginal gyrus BA 40 extending into the inferior parts of the superior parietal cortex), and the bilateral middle-inferior occipital and the ventral occipito-temporal cortex (BA 18, 19). This is consistent with previous studies

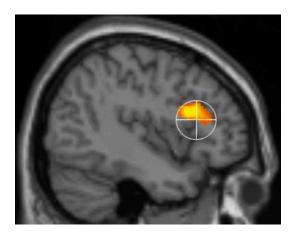


Fig. 4. The cross-hair is localized at the mean coordinates (approximately $[x\ y\ z] = [-44\ 19\ 12]$) of the natural syntax FMRI studies reported in the review of Bookheimer (2002). The mean distance of the individual local maxima reported in Bookheimer (2002) to the mean coordinates is approximately 13 mm indicated by the radius of the circle in the figure. Artificial syntactic violations specifically activated the left inferior frontal gyrus centered on BA 45 and extending into BA 44.

of implicit artificial grammar learning (Seger et al., 2000; Skosnik et al., 2002). Furthermore, this indicates that the left inferior frontal region is actively interacting in the context of an extensive functional brain network, consistent with the common insight from functional neuroimaging suggesting that cognitive functions are implemented in functional networks (Ingvar & Petersson, 2000).

4.1. Functional neuroimaging studies of natural and artificial grammars

The classical model for language organization in the brain (Broca, 1861; Wernicke, 1874) relates language production to the anterior language areas in the dominant hemisphere, most commonly the left, centered on the posterior left inferior frontal region, and language comprehension to the posterior language areas centered on the posterior left superior temporal (restricted Wernicke's area) and surrounding parieto-temporal regions (extended Wernicke's area). However, this simple mapping of production and comprehension components onto anterior and posterior language related brain regions have since been re-examined and shown to be oversimplified (see, e.g., Caplan, 1992; Kaan & Swaab, 2002; Zurif, 1990, 1998). Cortical electrical stimulation mapping has indicated that aspects of syntactic processing is related to the left middle-inferior frontal, posterior superior temporal, and inferior parietal regions (Ojemann, 1983; Ojemann & Mateer, 1979). Also, several neuroimaging studies (for recent reviews see, e.g., Bookheimer, 2002; Kaan & Swaab, 2002) have indicated that these regions may be associated with different aspects of syntactic processing, including the syntactic complexity of sentences (Caplan, Alpert, & Waters, 1998; Caplan, Alpert, & Waters, 1999; Caplan, Alpert, Waters, & Olivieri, 2000; Cooke et al., 2001; Inui et al., 1998; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Stromswold, Caplan, Alpert, & Rauch, 1996), grammatical error detection (Embick, Marantz, Miyashita, O'Neil, & Sakai, 2000; Kang, Constable, Gore, &

Avrutin, 1999; Ni, Constable, Mencl, Pugh, & Fulbright, 2000), or sentence matching under a syntactic/lexical manipulation (Dapretto & Bookheimer, 1999). A recent study by Indefrey, Hagoort, Herzog, Seitz, and Brown (2001) reported data on brain activations during language processing in an experiment requiring the subjects to detect grammatical errors in meaningless sentences. The study of Indefrey et al. (2001) distinguished syntactic processing from several other cognitive and linguistic functions and the data revealed that syntactic error detection was specifically related to a region of the left dorsolateral prefrontal cortex in or adjacent to Broca's region. A recent meta-analysis of functional neuroimaging studies of syntactic processing concluded that the most reliably replicable finding related to syntactic parsing is localized to the left inferior frontal gyrus (BA 44, 45) representing evidence for an involvement of Broca's region in aspects of syntactic processing (Indefrey, in press), while the overview of Kaan and Swaab (2002) appears to argue for a different conclusion. However another recent meta-analysis of natural language FMRI studies indicated that there are evidence for a functional specialization with respect to the left inferior frontal region related to phonology, syntax, and semantics (Bookheimer, 2002). Despite considerable overlap, there seemed to be general trends indicating that the anterior-inferior part of the left inferior frontal gyrus (centered around BA 47) is related to aspects of semantic processing, while the posterior-superior part (centered on the posterior parts of 44 and extending into the anterior parts of BA 6) is related to aspects of phonological processing. Activations related to aspects of syntactic processing were centered on the middle part of the left inferior frontal gyrus centered on BA 44 and 45. A simple descriptive analysis of the coordinates listed by Bookheimer (2002) yields mean coordinates [-46 11 26], [-44 19 12], and [-42 25 4] for phonology, syntax, and semantics, respectively (the mean distances of the local maxima to the mean coordinates are 10, 13, and 15 mm, respectively). In terms of spatial extent, the effect of artificial grammaticality violations we observed in the present study was localized to the middle portion of the left inferior frontal gyrus centered on BA 45 and extending into BA 44 (Fig. 4).

The results from the minimum *T*-field analysis indicated a complex response pattern within this region with respect to the factors correct/incorrect and grammatical/non-grammatical. These included effects of correct versus incorrect responses, non-grammatical versus grammatical items, as well as interactions related to the fact that the response was greater in correct grammatical versus incorrect grammatical compared to correct non-grammatical versus incorrect grammatical. These results indicate that there may be a regional functional sub-specialization within the left inferior frontal region (BA 44, 45). However, the precise interpretation of these results is at present unclear. It should also be noted that the issue of precise spatial localization in functional neuroimaging is complex and related to, among other things, inter-individual residual anatomical variability (i.e., residual variability after anatomical normalization), threshold effects, and the choice of test statistic (Petersson, Nichols, Poline, & Holmes, 1999). It appears that spatial precision in group studies of higher cognitive functions is on the order of approximately 10 mm (cf. Brett, Johnsrude, & Owen, 2002; Petersson et al., 1999). The descriptive results of the data reported in Bookheimer (2002) are thus in line with this estimate. For example, the mean spatial spread of the individual local maxima reviewed in Bookheimer (2002) related to the FMRI studies of natural syntactic processing is approximately 13 mm (Fig. 4).

As noted in the introduction, a number of recent FMRI studies have investigated explicit learning of material generated from artificial grammars (Fletcher et al., 1999; Strange, Fletcher,

Henson, Friston, & Dolan, 1999; Strange et al., 2001), artificial language (Opitz & Friederici, 2003), and from natural languages different from the native language of the subjects (Musso et al., 2003). One difference between these studies and the present is that we contrasted grammatical and non-grammatical items while the other studies focused on learning related effects (time × condition interactions). Another difference is that we employed an implicit acquisition task, exposing the subjects only to positive examples. In contrast, Fletcher et al. (1999), Strange et al. (1999, 2001), and Opitz and Friederici (2003) used experimental tasks which can be characterized as explicit problem solving with performance feedback, while Musso et al. (2003) explicitly taught their participants the rules to be learned. For example, the observation of learning related effects in the medial temporal lobe in the studies of Opitz and Friederici (2003) and Strange et al. (1999) is likely related to the explicit character of the task. The medial temporal lobe memory system is critically involved in declarative and episodic memory (Cohen, Ryan, Hunt, Romine, & Wszalek, 1999; Eichenbaum & Cohen, 2001; Squire, 1992; Squire, Knowlton, & Musen, 1993). Furthermore, studies conducted with amnesic patients indicate that patients and normal controls performed similarly on both the classical and the transfer version of the AGL task, despite the fact that the amnesic patients showed no explicit recollection of either whole-item or fragment information (Knowlton & Squire, 1994, 1996, cf. the discussion below). The explicit problem solving character of the tasks may also provide an explanation for the observation of learning related effects in the anterior prefrontal/frontal pole region (centered on BA 9/10) in several of these studies (Fletcher et al., 1999; Strange et al., 2001). In addition, Strange et al. (2001) suggest that the experimental paradigm they used is similar to the Wisconsin Card Sorting Test which has also shown to activate this fronto-polar region following a rule sorting switch (Rogers, Andrews, Grasby, Brooks, & Robbins, 2000). However, Opitz and Friederici (2003) observed learning related changes in the left posterior BA 44 bordering on BA 6. They suggested that this might relate to the fact that they used a small artificial language incorporating rules that can be found in natural languages. However, they also noted that the artificial vocabulary used was composed of pronounceable items that do not exist in German or other natural languages known to the participants. It appears possible that their subjects engaged explicit and implicit learning processes in phonological learning. Thus it is unclear that their finding is related to the rules of the artificial language, as conceptualized by them. In addition they observed similar learning related changes in bilateral middle occipital (BA 19), left inferior occipital region (BA 18), and the right posterior parietal (BA 7) regions to the one observed in the left inferior frontal region. Hence, it appears that the learning process engaged during the task is related to a complex set of brain regions in both hemispheres, and it is not clear how or which of these regions are specifically related to the structural regularities of the artificial language.

Noam Chomsky has argued that children's capacity to acquire natural languages depends on an innate universal grammar (UG) that constrains the form of possible human languages (Chomsky, 1965, 1986; Chomsky & Lasnik, 1995). In a recent study, Musso et al. (2003) attempted to investigate the neural correlate of acquiring new linguistic competence by teaching adult participants two types of rules, UG consistent and rules which have not been found in any known natural language. They reported relative activation over time in Broca's region for the former and relative decreased activation for the latter. These results are broadly consistent with the observations of Opitz and Friederici (2003). However, the effect reported by Musso

et al. (2003) was related to the middle portion of the left inferior frontal gyrus and thus more anterior to the one observed by Opitz and Friederici (2003). Musso et al. (2003) speculated that biological constraints and language experience interact in Broca's region to enable new linguistic competence to develop. However, Chomsky posited the existence of a language acquisition device (instantiating universal principles and parameters) because, he argued, the impossibility of acquiring a language (which takes place largely implicitly) and almost entirely from unlabeled positive information alone (i.e., without explicit feedback as well as negative evidence; cf. discussion below). Chomsky has also argued for sometime that there are no language rules (cf. e.g., Chomsky, 2000). He states that the 'Principle and Parameters' approach (cf. e.g., Chomsky & Lasnik, 1995) rejects the concept of rules and grammatical constructions entirely (Chomsky, 2000, p. 8). Instead, he argues, there are only general principles or linguistic constraints that interact to yield the properties of linguistic expressions. Furthermore, these principles are not learned or acquired but innate (cf. Chomsky, 1995, 2000). The variation between natural languages is accounted for by different parameter settings which are acquired (or triggered) during the acquisition process (cf. Radford, 1997, 2000). Similarly, the universal framework of 'Optimality Theory' (Kager, 1999; Prince & Smolensky, 1997), the tripartite framework of Jackendoff (1997, 2002) as well as the lexicalist unification framework of Vosse and Kempen (2000) specify linguistic constraints rather than rules. The subjects in the study of Musso et al. (2003) were explicitly taught the rules they had to learn, information was provided describing each rule with example sentences clarifying the rule. The subjects then practiced on correct and incorrect examples and performance feedback were provided. However, they were not provided with any information about phonological aspects of the new vocabulary. Thus, as noted by Marcus, Vouloumanos, and Sag (2003), one may ask whether the results reported reflect any aspect of language acquisition as such. Marcus et al. (2003) suggest a number of alternative interpretations in terms of working memory, complexity demands, or linguistically independent domain-general rule learning.

4.2. The possible roles of the left inferior frontal region

An important general problem for models entailing that Borca's region, or more generally, that the left inferior frontal region, is specifically related to different aspects of language processing is that neither neuropsychological lesion studies nor functional neuroimaging data appear to support such a strong hypothesis (Caplan, 1992; Dronkers, 2000; Kaan & Swaab, 2002; Marcus et al., 2003; Zurif, 1990, 1998). For example, Kaan and Swaab (2002) suggest that recent insights from aphasia research require a re-evaluation of the classical interpretation of the structure—function relationship based on the apparent double dissociation between Wernicke's (traditionally associated with left temporo-parietal lesions) and Broca's aphasia (traditionally associated with left middle-inferior frontal lesions). They argue that Broca's region is neither necessary nor sufficient to induce syntactic deficits; these patients do not completely lack syntactic processing capacities and they also exhibit some semantic deficits. Kaan and Swaab (2002) also suggest that Broca's aphasia can alternatively be interpreted as a processing deficit in contrast to a knowledge deficit. In other words, Broca's aphasia, may at least partly, be understood in terms of difficulties with certain aspects of temporal processing and integration of information, or alternatively, in terms of short-term memory capacities. This suggestion is

consistent with functional neuroimaging data indicating an important role of the prefrontal cortex, including the left inferior frontal region, in both short-term working memory and long-term memory (Cabeza, Dolcos, Graham, & Nyberg, 2002; Fletcher & Henson, 2001; Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002; Nyberg et al., 2003; Simons & Spiers, 2003). In addition, functional neuroimaging studies comparing syntactically complex and simple sentences can be interpreted in terms of memory load and integration/unification of information (cf. Kaan & Swaab, 2002, for a review of the literature supporting this interpretation).

Furthermore, several recent studies have indicated that Broca's region or left inferior frontal region might have a broader role in cognition and appears to be engaged in several cognitive domains in addition to the ones already mentioned (Marcus et al., 2003), including musical syntax (Maess, Koelsch, Gunter, & Friederici, 2001), absolute pitch perception (Zatorre, Perry, Beckett, Westbury, & Evans, 1998), and human imitation (Iacoboni, Woods, Brass, Bekkering, & Mazziotta, 1999). A growing body of evidence from functional neuroimaging suggests an overlap in the processing of structural relations in language and music. This include investigations using EEG (Patel, Gibson, Ratner, Besson, & Holcomb, 1998), MEG (Maess et al., 2001), and FMRI (Koelsch, Gunter, Cramon, Zysset, & Lohmann, 2002; Tillmann, Janata, & Bharucha, 2003), for a recent review, see Patel (2003). Recently, the similarities between music and language have been stressed (Hauser & McDermott, 2003; Patel, 2003; Peretz & Coltheart, 2003; Trehub, 2003). It has been suggested that music is a human universal, that like language, organizes discrete elements into hierarchically structured sequences according to syntactic principles (Lerdahl & Jackendoff, 1983), see also (Jackendoff, 2002; Patel, 2003). For example, Patel (2003) suggests that the commonalities between structural processing in language and music can be understood in processing terms. The idea is that brain regions engaged in processing these commonalities provide the neural infrastructure for structural integration. According to this view, the neural infrastructure engaged in structural integration are 'processing regions' that serve to rapidly and selectively bring low-activation items in 'representation regions' up to the activation threshold needed for integration to take place. This suggestion is similar to the framework recently proposed by Hagoort (2003) in which integration of various sources of linguistic information (phonological, syntactic, semantic/pragmatic) operate in parallel in a workspace where incremental unification takes place. The workspace is hypothesized to be related to the left inferior frontal region and it is suggested that lexically specified structures enter the unification space according principles outlined by Vosse and Kempen (2000) during parsing. Cross-talk between different sources of information can, when necessary, immediately influence the integration process. It is also of interest to note that there seems to be a considerable overlap between regions implicated in the perception/production of music and the perception/production of abstract sequences, including the left inferior frontal region (Janata & Grafton, 2003). However, as already noted, there are indications of functionally segregated subdivisions within the left inferior frontal region (Bookheimer, 2002). In addition, Marcus et al. (2003) suggest that syntactic processing may engage the pars triangularis of the left inferior frontal gyrus (BA 45), while studies of Jabberwocky sentences, musical syntax and imitation of actions tend to activate the more posterior pars opercularis subdivision (BA 44) of the left inferior frontal gyrus.

There is also a growing body of evidence indicating that Broca's region is not the only area related to the processing of syntactic information. Other brain regions which have been related

to syntactic processing include the left superior anterior temporal lobe, the left middle and posterior parts of the superior and middle temporal gyri, as well as right hemisphere regions (Bookheimer, 2002; Friederici, 2002; Kaan & Swaab, 2002). According to Kaan and Swaab (2002), none of these regions are uniquely activated by syntactic processing. Thus it is not unreasonable to suggest that syntactic natural language processing, or more generally the faculty of language, is in fact dependent on a functional network of interacting brain regions, none perhaps which is uniquely involved in syntactic processing only. This perspective seems to hold for higher cognitive functions more generally (Ingvar & Petersson, 2000). With respect to this latter perspective, one might suggest that particular brain regions, for example, the prefrontal cortex (cf. e.g., Dehaene, Kerszberg, & Changeux, 1998; Duncan, 2001; Duncan & Miller, 2002; Fuster, 1997; Mesulam, 2002; Stuss & Knight, 2002), are computationally or processing specific (e.g., detecting and recognizing structural regularities; interpreting, integrating or unifying hierarchical regularities, or recognizing dependencies between related elements) independently of particular content domains. As noted by Marcus et al. (2003), on this view, specific brain regions may genuinely participate in a range of tasks, including Broca's region, with specialized function emerging from unique configurations of domain-general mechanisms.

4.3. Learning artificial grammars, the question of knowledge representation, and learnability

A complementary perspective on artificial grammar learning views this as a model for investigating implicit learning. Reber (1967) defined implicit learning as the process by which an individual comes to respond appropriately to the statistical structure in the input. Thus, he argued, the capacity for generalization subjects show in the grammaticality classification task is based on the implicit acquisition of regularities reflected in the input strings. Reber (1967) suggested that humans can acquire implicit knowledge of aspects of the underlying structure through an inductive statistical learning process and that this is put to use during grammaticality classification. Support for the implicit character of artificial grammar learning comes from lesion studies on amnesic patients. Knowlton and Squire (1996) investigated amnesic patients and normal controls on a classical and a transfer version of the AGL task. The patients and their normal controls performed similarly on both AGL tasks while the amnesic patients showed no explicit recollection of whole-item or fragment (i.e., bi- or tri-gram) information. Knowlton and Squire argued that these results indicate that the explicit recollection in the normal controls reflects an epiphenomenon not necessary for adequate performance on the classification task. Instead, AGL depends on the implicit acquisition of both abstract and exemplar-specific information, the latter indicating the acquisition of distributional information of local sequential regularities (Knowlton & Squire, 1996). They also argued for the existence of abstract representations (i.e., 'rule-based' representations) based on the results from the transfer version. It thus appears that humans are able to transfer knowledge acquired from exemplars in one domain to a different domain (Gomez & Schvaneveldt, 1994). Similarly, Skosnik et al. (2002) suggest that AGL involve the non-conscious consolidation of complex rules and structures. Furthermore, it has been shown that infants have the capacity to learn and generalize over local regularities. Recent studies indicate rapid (on the order of 2–10 min) 'rule-abstraction' (Marcus, Vijayan, Bandi Rao, & Vishton, 1999), learning of transition probabilities in artificial syllable sequences

(Saffran, Aslin, & Newport, 1996), and artificial grammar learning (Gomez & Gerken, 1999) in young infants. In the study of Gomez and Gerken (1999), infants also demonstrated some transfer capacity, suggesting that they were abstracting beyond the transitional probabilities holding between particular items in the grammar. However, it is an issue under discussion whether transfer studies demonstrated 'rule-based' learning. It is unclear whether this conclusion follows, or more specifically, this depends on the assumption that transfer performance is critically dependent on abstract representations and it is unclear whether this is necessarily the case. Transfer performance is dependent on a mapping from the representation of the acquired knowledge to the new surface form which by necessity has to be established during the initial phase of the transfer task. Whether this mapping is generated from an abstract knowledge representation or a surface based knowledge representation is at present unknown (cf. Redington & Chater, 1996). For example, it has been demonstrated that transfer results could be explained by similarity judgements and knowledge of substring regularities (Redington & Chater, 1996, 2002). On the other hand, the results of Knowlton and Squire (1996) are compatible with an abstract representation, given the observation that the classification performance did not correlated with associative chunk strength when the participants had reached the late acquisition phase. This may indicate that at least some form of abstraction of grammatical structure takes place. In addition, learning of long distance dependencies has been demonstrated in sequence learning as well as in artificial grammar learning (Ellefson & Christiansen, 2000; Poletiek, 2002). It has been suggested that induction cannot be explained entirely in terms of the acquisition of local sequential regularities, as argued by, for example, Meulemans and Van der Linden (1997). While Reber (1967) originally argued that the implicit learning process abstracted 'rule-based' knowledge (see Reber, 1993 for a modification of his position), these more recent studies indicate that dual mechanisms may be at play (for an alternative perspective, see Channon, Shanks, Johnstone, Vakili, & Chin, 2002; Johnstone & Shanks, 2001). In summary, it is reasonably clear from these studies that distributional information of local sequential regularities are acquired and used in grammaticality classification.

In this context it is of interest to note that no super-finite class of languages, including the class of regular languages, is in general learnable from positive examples alone without additional constraints on the specific learning paradigm. This is for example the case in the formal learning theory framework of Gold (1967). At a first glance this appears to exclude the possibility of learning an artificial grammar from positive examples alone. It has also been suggested that this is the case when statistical learning mechanisms (cf. e.g., Cherkassky & Mulier, 1998; Duda, Hart, & Stork, 2001; Vapnik, 1998) are employed (Nowak, Komarova, & Niyogi, 2002). In the classical learning framework of Gold (1967), cf. Jain, Osherson, Royer, and Sharma (1999) it was assumed that the learning system had to identify the target language exactly based on only positive examples (i.e., well-formed strings); in addition it was assumed that the environment provides, and that the learning system has access to, an arbitrarily large number of examples (while issues related to computational complexity were ignored). However, already Gold (1967) noted that under suitable circumstances, that is, with additional constraints on the learning paradigm, this (un)learnability paradox might be avoided. These may for example include the existence and effective use of explicit negative feedback, prior restrictions on the class of possible languages, or prior restrictions on the possible language experiences that can occur (i.e., prior restrictions on the characteristics of the possible language

environments). Recent results in formal learning theory confirm Gold's (1967) suggestion that, if the class of possible languages is restricted, then it is possible to learn infinite languages in infinite classes of formal languages from positive examples (Shinohara, 1994; Shinohara & Arimura, 2000); see also Jain et al. (1999). It should be noted that these prior constraints on the class of possible (or accessible) languages are of a general type and not 'language specific' per se (e.g., restrictions on the maximal number of rules employed by the languages in the class). As noted by Scholz and Pullum (2002), there exists classes of formal languages rich enough to encompass the 'string-sets' of human languages and at the same time being identifiable from a finite sequence of positive examples. Furthermore, the acquisition task becomes potentially more tractable if there are additional structure in the input or if only 'probable approximate' identification is required (cf. e.g., Anthony & Bartlett (1999) for an outline of the probably approximately correct learning paradigm and Engel and Van den Broeck (2001) for an alternative perspective). It has also been also suggested that the acquisition of super-finite classes of languages may be possible given reasonable probabilistic properties of the language environment and the initial language experience of children. Furthermore, negative evidence might be available, based on expectations, without explicit corrections (cf. Rohde & Plaut, 1999). One possibility is to generate expectations or predictions based on an internal model. If the learning system has access to or can acquire a forward model, this can be used for model dependent prediction. This entails the possibility of an unsupervised learning framework in which error information (= difference[input, prediction]) drives the learning process. Simple examples include predictive adaptive time-series models (Haykin, 1998) and predictive simple recurrent neural networks (e.g., Elman, 1990; Haykin, 1998). Recent connectionist modeling suggest that this may be a viable approach to finite recursion (Christiansen & Chater, 1999; for a general overview, see Christiansen & Chater, 2001; see also Seidenberg, 1997; Seidenberg, MacDonald, & Saffran, 2002). Simple recurrent networks may be viewed as a time-discrete analog version of the finite state architecture (i.e., if real number processing is employed). It should be noted that simulations of a simple recurrent neural network, using finite precision numbers, effectively becomes a simulation of a finite state architecture. In summary, as noted by Scholz and Pullum (2002), formal learning theory (Jain et al., 1999) holds open the possibility that language classes of interest, at least in principle, can be acquired from weak environmental input consisting of a finite sequence of un-interpreted positive example (Pullum & Scholz, 2002; Scholz & Pullum, 2002).

Lastly, in the present study we used a regular grammar, the simplest form of phrase structure grammar. This class of grammars can be implemented in the finite state architecture. It is commonly held that the class of finite state machines represents a restrictive class of computational models. However, it should be noted that the computational mechanisms (i.e., the transition function/relation of the computational system) of universal computational architectures like unlimited register machines (Cutland, 1980) and Turing machines (Davis et al., 1994) can be implemented in a finite state architecture (cf. Savage, 1998). In fact, the central processing unit of the register machine as well as the control unit of a Turing machine are examples of finite state machines (cf. Savage, 1998; Tanenbaum, 1990, for concrete examples). The difference in formal language expressivity between regular grammars and context-free/context-sensitive as well as semi-Thue grammars (cf. Davis et al., 1994; Partee et al., 1990) springs necessarily from the memory organization characteristics of the computational system. In particular, formal

language expressivity depends on the interaction between the computational mechanisms and factors like memory access (e.g., stack- or random access) and most crucially on the memory capacity, that is whether this is finite or infinite (cf. Minsky, 1967; Savage, 1998). In a fundamental sense, it is the characteristics of the memory organization that allow the computational architectures to re-use their processing capacities (i.e., computational mechanisms) recursively to generate structurally rich languages (i.e., high expressivity). If finite memory constraints are imposed, it follows that the computational mechanisms of universal architectures are no more powerful than that of the finite state architecture. The finite state machine is the only computational architecture in the Chomsky hierarchy of infinite expressivity with respect to its fundamental recursive construction (i.e., concatenation) and at the same time being finite with respect to both its computational mechanism and its memory organization. In addition, it is possible to implement finite recursion of a general type in a finite state machine. From a neurobiological and cognitive neuroscience perspective it seems reasonable to assume that the human brain instantiate a finite storage capacity, both with respect to short-term working as well as long-term memory. This might indicate the importance of the neurobiological analogue of the finite state architecture.

5. Conclusion

In the present study, we observed that artificial syntactic violations activate the left inferior frontal gyrus (BA 44, 45) or Broca's region in all participants. This observation lends some support to the suggestions that artificial grammar learning represents a model for investigating aspects of language learning in infants (Gomez & Gerken, 2000) and adults (Friederici et al., 2002). Alternatively, the artificial grammar learning paradigm can be viewed as a tool to investigate the implicit acquisition of structured information and may a means to further investigate the role of the inferior frontal region in information processing.

Acknowledgments

This work was supported by the Max Planck Institute for Psycholinguistics, the F.C. Donders Centre for Cognitive Neuroimaging, the Gustav V Research Foundation, the Family Hedlund Foundation, the Swedish Medical Research Council (8246), the Karolinska Institute, the Swedish Bank Tercentenary Foundation and the Knut and Alice Wallenberg Foundation. We also want to thank Professor Peter Hagoort, Dr. Peter Indefrey, Dr. Guillen Fernandez, and Dr. Ivan Toni for commenting on earlier versions of this paper.

References

Adler, R. J. (1981). *The geometry of random fields* (1st ed.). New York: Wiley and sons.

Amunts, K., Schleicher, A., Burgel, U., Mohlberg, H., Uylings, H. B. M., & Zilles, K. (1999). Broca's area revisited: Cytoarchitecture and intersubject variability. *Journal of Comparative Neurology*, 412, 319–341.

Anthony, M., & Bartlett, P. L. (1999). Neural network learning: Theoretical foundations. Cambridge, UK: Cambridge University Press.

Baddeley, A. (1992). Working memory. Science, 255, 556–559.

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience*, 4, 829–839.

Baddeley, A., Gathercole, S., & Papagno, C. (1998). The phonological loop as a language learning device. *Psychological Review*, 105, 158–173.

Bookheimer, S. (2002). Functional MRI of language: New approaches to understanding the cortical organization of semantic processing. *Annual Review of Neuroscience*, 25, 151–188.

Brett, M., Johnsrude, I. S., & Owen, A. M. (2002). The problem of functional localization in the human brain. *Nature Review Neuroscience*, *3*, 243–249.

Broca, P. (1861). Remarques sur le siege de la faculte de langage articulation suivies d'une observation d'aphemie (perte de la parole). *Bulletine Societe d'Anantomie*, *36*, 330–357.

Cabeza, R., Dolcos, F., Graham, R., & Nyberg, L. (2002). Similarities and differences in the neural correlates of episodic memory retrieval and working memory. *NeuroImage*, 16(2), 317–330.

Caplan, D. (1992). Language: Structure, processing and disorders. Cambridge, MA: MIT Press.

Caplan, D., Alpert, N., & Waters, G. (1998). Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow. *Journal of Cognitive Neuroscience*, 10, 541–552.

Caplan, D., Alpert, N., & Waters, G. (1999). PET studies of syntactic processing with auditory sentence presentation. NeuroImage, 9, 343–354.

Caplan, D., Alpert, N., Waters, G., & Olivieri, A. (2000). Activation of Broca's area by syntactic processing under conditions of concurrent articulation. *Human Brain Mapping*, 9, 65–71.

Caramazza, A., & Zurif, E. (1976). Dissociation of algorithmic and heuristic processes in language comprehension: Evidence from aphasia. *Brain and Language*, *3*, 572–582.

Channon, S., Shanks, D., Johnstone, T., Vakili, K., Chin, J., & Sinclair, E. (2002). Is implicit learning spared in amnesia? Rule abstraction and item familiarity in artificial grammar learning. *Neuropsychologia*, 40, 2185–2197.

Cherkassky, V., & Mulier, F. (1998). Learning from data: Concepts, theory and methods. New York: Wiley and Sons.

Chomsky, N. (1957). Syntactic structures. The Hague, The Netherlands: Mouton.

Chomsky, N. (1965). Aspects of the theory of syntax. Cambridge, MA: MIT Press.

Chomsky, N. (1986). Knowledge of language. New York: Praeger.

Chomsky, N. (1995). The minimalist program. Cambridge, MA: MIT Press.

Chomsky, N. (2000). *New horizons in the study of language and mind*. Cambridge, UK: Cambridge University Press.

Chomsky, N., & Lasnik, H. (1995). The theory of principles and parameters. In N. Chomsky, The minimalist program (pp. 13–128). Cambridge, MA: MIT Press.

Christiansen, M. H., & Chater, N. (1999). Toward a connectionist model of recursion in human linguistic performance. Cognitive Science, 23, 157–205.

Christiansen, M. H., & Chater, N. (Eds.). (2001). Connectionist psycholinguistics. Norwood, NJ: Ablex Publishing.
Cleermans, A., & McClelland, J. L. (1991). Learning the structure of event sequences. Journal of Experimental Psychology: General, 120, 235–253.

Cohen, D. I. A. (1997). Introduction to computer theory (2nd ed.). New York: Wiley and Sons.

Cohen, N. J., Ryan, J., Hunt, C., Romine, L., Wszalek, T., & Nash, C. (1999). Hippocampal system and declarative (relational) memory: Summarizing the data from functional neuroimaging studies. *Hippocampus*, 9(1), 83–98.

Cooke, A., Zurif, E. B., DeVita, C., Alsop, D., Koenig, P., Detre, J., Gee, J., Pinango, M., Balogh, J., & Grossman, M. (2001). Neural basis for sentence comprehension: Grammatical and short-term memory components. *Human Brain Mapping*, 15, 80–94.

Cutland, N. J. (1980). *Computability: An introduction to recursive function theory*. Cambridge, UK: Cambridge University Press.

Dapretto, M., & Bookheimer, S. (1999). Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, 24, 427–432.

- Davis, M. D., Sigal, R., Weyuker, E. J., 1994. Computability, complexity, and languages: Fundamentals of theoretical computer science (2nd ed.). San Diego, CA: Academic Press.
- Dehaene, S., Kerszberg, M., & Changeux, J.-P. (1998). A neuronal model of a global workspace in effortful cognitive tasks. *Proceedings of the National Academy of Sciences of United States of America*, 95, 14529–14534.
- Dronkers, N. F. (2000). The pursuit of brain-language relationships. *Brain and Language*, 71, 59-61.
- Duda, R. O., Hart, P. E., & Stork, D. G. (2001). Pattern classification (2nd ed.). New York: Wiley and Sons.
- Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature Review Neuroscience*, 2, 820–829.
- Duncan, J., & Miller, E. K. (2002). Cognitive focus through adaptive neural coding in the primate prefrontal cortex. In R. T. Knight (Ed.), *Principles of frontal lobe function* (pp. 278–292). Oxford, UK: Oxford University Press.
- Eichenbaum, H., & Cohen, N. J. (2001). From conditioning to conscious recollection: Memory systems of the brain. Oxford, UK: Oxford University Press.
- Ellefson, M. R., & Christiansen, M. H. (2000). Subjacency constraints without universal grammar: Evidence from artificial language learning and connectionist modeling. Paper presented at the 22nd Annual Conference of the Cognitive Science Society.
- Elman, J. L. (1990). Finding structure in time. Cognitive Science, 14, 179-211.
- Embick, D., Marantz, A., Miyashita, Y., O'Neil, W., & Sakai, K. L. (2000). A syntactic specialization for Broca's area. *Proceedings of the National Academy of Sciences of United States of America*, 97, 6150–6154.
- Engel, A., & Van den Broeck, C. (2001). Statistical mechanics of learning. Cambridge, UK: Cambridge University Press.
- Fletcher, P., Büchel, C., Josephs, O., Friston, K., & Dolan, R. (1999). Learning-related neuronal responses in prefrontal cortex. *Cerebral Cortex*, *9*, 168–178.
- Fletcher, P. C., & Henson, R. N. A. (2001). Frontal lobes and human memory: Insights from functional neuroimaging. *Brain*, 124, 849–881.
- French, R., & Cleeremans, A. (2002). Implicit learning and consciousness. Hove, UK: Psychology Press.
- Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, 6, 78–84.
- Friederici, A. D., Steinhauer, K., & Pfeifer, E. (2002). Brain signatures of artificial language processing. *Proceedings of the National Academy of Sciences of United States of America*, 99, 529–534.
- Friston, K., Holmes, A., Worsley, K., Poline, J.-B., Frith, C., & Frackowiak, R. (1995). Statistical parametric maps in functional imaging: A general linear approach. *Human Brain Mapping*, 2, 189–210.
- Fuster, J. M. (1997). *The prefrontal cortex: Anatomy, physiology, and neuropsychology of the frontal lobe* (3 ed.). New York: Lippincott-Raven.
- Genovese, C. L., Lazar, N. A., & Nichols, T. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage*, 15, 870–878.
- Gold, E. M. (1967). Language identification in the limit. Information and Control, 10, 447-474.
- Gomez, R. L., & Gerken, L. (1999). Artificial grammar learning by 1-year-olds leads to specific and abstract knowledge. *Cognition*, 70, 109–135.
- Gomez, R. L., & Gerken, L. (2000). Infant artificial language learning and language acquisition. TICS, 4, 178– 186.
- Gomez, R. L., & Schvaneveldt, R. W. (1994). What is learned from artificial grammars? Transfer tests of simple association. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 20, 396–410.
- Hagoort, P. (2003). How the brain solves the binding problem for language: A neurocomputational model of syntactic processing. *NeuroImage*, 20, S18–S29.
- Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science*, 298(5598), 1569–1579.
- Hauser, M. D., & McDermott, J. (2003). The evolution of the music faculty: A comparative perspective. *Nature Neuroscience*, 6, 663–668.
- Haykin, S. (1998). *Neural networks: A comprehensive foundation* (2nd ed.). Upper Saddle River, NJ: Prentice-Hall. Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526–2528.

- Indefrey, P. (2001). The neural architecture of syntactic parsing and encoding. Brain and Language, 79, 106–107.
- Indefrey, P. (in press). Hirnaktivierungen bei syntaktischer sprachverarbeitung: Eine meta-analyse. In G. Rickheit (Ed.), *Neurokognition der sprache*. Tuebingen: Stauffenburg-Verlag.
- Indefrey, P., Hagoort, P., Herzog, H., Seitz, R. J., & Brown, C. M. (2001). Syntactic processing in left prefrontal cortex is independent of lexical meaning. *NeuroImage*, *14*, 546–555.
- Ingvar, M., & Petersson, K. M. (2000). Functional maps—cortical networks. In J. C. Mazziotta (Ed.), *Brain mapping: The systems* (pp. 111–140). San Diego, CA: Academic Press.
- Inui, T., Otsu, Y., Tanaka, S., Okada, T., Nishizawa, S., & Konishi, J. (1998). A functional MRI analysis of comprehension processes of Japanese sentences. *NeuroReport*, 9, 3325–3328.
- Jackendoff, R. (1997). The architecture of the language faculty. Cambridge, MA: MIT Press.
- Jackendoff, R. (2002). Foundations of language: Brain, meaning, grammar, evolution. Oxford, UK: Oxford University Press.
- Jain, S., Osherson, D., Royer, J. S., & Sharma, A. (1999). Systems that learn. Cambridge, MA: MIT Press.
- Janata, P., & Grafton, S. T. (2003). Swinging in the brain: Shared neural substrates for behaviors related to sequencing and music. *Nature Neuroscience*, 6, 682–687.
- Johnstone, T., & Shanks, D. R. (2001). Swinging in the brain: Shared neural substrates for behaviors. *Cognitive Psychology*, 42, 61–112.
- Just, M. A., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, K. R. (1996). Brain activation modulated by sentence comprehension. Science, 274, 114–116.
- Kaan, E., & Swaab, T. Y. (2002). The brain circuitry of syntactic comprehension. Trends in Cognitive Sciences, 6, 350–356.
- Kager, R. (1999). Optimality theory. Cambridge, UK: Cambridge University Press.
- Kang, A. M., Constable, R. T., Gore, J. C., & Avrutin, S. (1999). An event-related fMRI study of implicit phrase-level syntactic and semantic processing. *NeuroImage*, 10, 555–561.
- Knowlton, B. J., & Squire, L. R. (1994). The information acquired during artificial grammar learning. *Journal of Experimental Psychology: Learning and Memory Cognition*, 20, 79–91.
- Knowlton, B. J., & Squire, L. R. (1996). Artificial grammar learning depends on implicit acquisition of both abstract and exemplar-specific information. *Journal of Experimental Psychology: Learning and Memory Cognition*, 22, 169–181.
- Koelsch, S., Gunter, T. C., Cramon, D. Y., Zysset, S., Lohmann, G., & Friederici, A. D. (2002). Bach speaks: A cortical "language-network" serves the processing of music. *NeuroImage*, 17, 956–966.
- Lasnik, H. (2000). Syntactic structures revisited: Contemporary lectures on classic transformational theory. Cambridge, MA: MIT Press.
- Lerdahl, F., & Jackendoff, R. (1983). A Generative theory of tonal music. Cambridge, MA: MIT Press.
- Lewicki, P. (1986). Nonconscious social information processing. San Diego, CA: Academic Press.
- Lewis, H. R., & Papadimitriou, C. H. (1981). *Elements of the theory of computation*. Englewood Cliffs, NJ: Prentice-Hall.
- Maess, B., Koelsch, S., Gunter, T. C., & Friederici, A. D. (2001). Musical syntax is processed in Broca's area: An MEG study. *Nature Neuroscience*, 4, 540–545.
- Marcus, G. F., Vijayan, S., Bandi Rao, S., & Vishton, P. M. (1999). Rule learning by seven-month-old infants. *Science*, 283, 77–80.
- Marcus, G. F., Vouloumanos, A., & Sag, I. A. (2003). Does Broca's play by the rules? *Nature Neuroscience*, 6, 651–652
- Mesulam, M.-M. (2002). The human frontal lobes: Transcending the default mode through contingent encoding. In R. T. Knight (Ed.), *Principles of frontal lobe function*. Oxford, UK: Oxford University Press.
- Meulemans, T., & Van der Linden, M. (1997). Associative chunk strength in artificial grammar learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 23(4), 1007–1028.
- Minsky, M. L. (1967). Computation: Finite and infinite machines. Englewood Cliffs, NJ: Prentice-Hall.
- Musso, M. C., Moro, A., Glauche, V., Rijntjes, M., Reichenbach, J., Buchel, C., et al. (2003). Broca's area and the language instinct. *Nature Neuroscience*, *6*, 774–781.
- Newmeyer, F. J. (1995). Generative linguistics. New York: Routledge.

- Ni, W., Constable, R. T., Mencl, W. E., Pugh, K. R., Fulbright, R. K., Shaywitz, S. E., et al. (2000). An event-related neuroimaging study distinguishing form and content in sentence processing. *Journal of Cognitive Neuroscience*, 12, 120–133.
- Nowak, M. A., Komarova, N. L., & Niyogi, P. (2002). Computational and evolutionary aspects of language. *Nature*, 417, 611–617.
- Nyberg, L., Forkstam, C., Petersson, K. M., Cabeza, R., & Ingvar, I. (2002). Brain imaging of human memory systems: Between-systems similarities and within-system differences. *Cognitive Brain Research*, 13, 281–292.
- Nyberg, L., Marklund, P., Persson, J., Cabeza, R., Forkstam, C., Petersson, K. M., & Ingvar, I. (2003). Common prefrontal activations during working memory, episodic memory, and semantic memory. *Neuropsychologia*, 41, 371–377.
- Ojemann, G. A. (1983). Brain organization for language from the perspective of electrical stimulation mapping. *Behavioral and of Brain Science*, 6, 189–230.
- Ojemann, G. A., & Mateer, C. (1979). Human language cortex: Localization of memory, syntax, and sequential motor-phoneme identification systems. *Science*, 205, 1401–1403.
- Opitz, B., & Friederici, A. D. (2003). Interactions of the hippocampal system and the prefrontal cortex in learning language-like rules. *NeuroImage*, 19, 1730–1737.
- Partee, B. H., ter Meulen, A., & Wall, R. E. (1990). *Mathematical methods in linguistics*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Patel, A. D. (2003). Language, music, syntax and the brain. *Nature Neuroscience*, 6, 674–681.
- Patel, A. D., Gibson, E., Ratner, J., Besson, M., & Holcomb, P. J. (1998). Processing syntactic relations in language and music: An event-related potential study. *Journal of Cognitive Neuroscience*, 10, 717–733.
- Peretz, I., & Coltheart, M. (2003). Modularity of music processing. Nature Review Neuroscience, 6, 688-691.
- Petersson, K. M., Nichols, T. E., Poline, J.-B., & Holmes, A. P. (1999). Statistical limitations in functional neuroimaging II: Signal detection and statistical inference. *Philosophical Transactions of the Royal Society of London B*, 354, 1261–1282.
- Poletiek, F. H. (2002). Implicit learning of a recursive rule in an artificial grammar. *Acta Psychology*, 111, 323–335. Prince, A., & Smolensky, P. (1997). Optimality: From neural networks to universal grammar. *Science*, 275, 1604–1610.
- Pullum, G. K., & Scholz, B. C. (2002). Empirical assessment of stimulus poverty arguments. *Linguistic Review*, 19, 9–50.
- Radford, A. (1997). Syntax: A minimalist introduction. Cambridge, UK: Cambridge University Press.
- Radford, A. (2000). Children in search of perfection: Towards a minimalist model of language acquisition. *Essex Research Reports in Linguistics*, 34, 57–74.
- Reber, A. S. (1967). Implicit learning of artificial grammar. *Journal of Verbal Learning & Verbal Behaviour*, 6, 855–863.
- Reber, A. S. (1993). Implicit learning and tacit knowledge. New York: Oxford University Press.
- Reber, A. S., & Allen, R. (1978). Analogy and abstraction strategies in synthetic grammar learning: A functional interpretation. *Cognition*, 6, 189–221.
- Redington, M., & Chater, N. (1996). Transfer in artificial grammar learning: A reevaluation. *Journal of Experimental Psychology: General*, 125, 123–138.
- Redington, M., & Chater, N. (2002). Knowledge representation and transfer in artificial grammar learning. In A. Cleeremans (Ed.), *Implicit learning and consciousness* (pp. 121–143). Hove, UK: Psychology Press.
- Rogers, R. D., Andrews, T. C., Grasby, P. M., Brooks, D. J., & Robbins, T. W. (2000). Contrasting cortical and subcortical activations produced by attentional-set shifting and reversal learning in humans. *Journal of Cognitive Neuroscience*, 12, 142–162.
- Rohde, D. L. T., & Plaut, D. C. (1999). Language acquisition in the absence of explicit negative evidence: How important is starting small? *Cognition*, 72, 67–109.
- Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical learning by 8-month-old infants. *Science*, 274, 1926–1928.
- Sag, I. A., Wasow, T., & Bender, E. M. (2003). Syntactic theory: A formal introduction (Vol. 152). Stanford, CA: CSLI Publisher.

- Savage, J. E. (1998). Models of computation: Exploring the power of computing. Reading, MA: Addison-Wesley. Scholz, B. C., & Pullum, G. K. (2002). Searching for arguments to support linguistic nativism. Linguistic Review, 19, 185–223.
- Seger, C. A., Prabhakaran, V., Poldrack, R. A., & Gabrieli, J. D. E. (2000). Neural activity differs between explicit and implicit learning of artificial grammar strings: An fMRI study. *Psychobiology*, 283, 283–292.
- Seidenberg, M. S. (1997). Language acquisition and use: Learning and applying probabilistic constraints. *Science*, 275, 1599–1603.
- Seidenberg, M. S., MacDonald, M. C., & Saffran, J. R. (2002). Does grammar start where statistics stop? *Science*, 298, 553–554.
- Shieber, S. M. (1986). An introduction to unification-based approaches to grammar (Vol. 4). Stanford, CA: CSLI, Stanford University.
- Shinohara, T. (1994). Rich classes inferable from positive data: Length-bounded elementary formal systems. *Information and Computation*, 108, 175–186.
- Shinohara, T., & Arimura, H. (2000). Inductive inference of unbound unions of pattern languages from positive data. *Theoretical Computer Science*, 241, 191–209.
- Simons, J. S., & Spiers, H. J. (2003). Prefrontal and medial temporal lobe interactions in long-term memory. Nature Review Neuroscience, 4, 637–648.
- Skosnik, P. D., Mirza, F., Gitelman, D. R., Parrish, T. B., Mesulam, M.-M., & Reber, P. J. (2002). Neural correlates of artificial grammar learning. *NeuroImage*, *17*, 1306–1314.
- Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review*, 99(2), 195–231.
- Squire, L. R., Knowlton, B., & Musen, G. (1993). The structure and organization of memory. Annual Review of Psychology, 44, 453–495.
- Stadler, M. A., & Frensch, P. A. (Eds.). (1998). *Handbook of implicit learning*. Thousand Oaks, CA: Sage Publications
- Strange, B. A., Fletcher, P. C., Henson, R. N. A., Friston, K. J., & Dolan, R. J. (1999). Segregating the functions of the human hippocampus. *Proceedings of the National Academy of Sciences of United States of America*, 96, 4034–4039.
- Strange, B. A., Henson, R. N. A., Friston, K. J., & Dolan, R. J. (2001). Anterior prefrontal cortex mediates rule learning in humans. *Cerebral Cortex*, 11, 1040–1046.
- Stromswold, K., Caplan, D., Alpert, N., & Rauch, S. (1996). Localization of syntactic comprehension by positron emission tomography. *Brain and Language*, 52, 452–473.
- Stuss, D. T., & Knight, R. T. (Eds.). (2002). *Principles of frontal lobe function*. Oxford, UK: Oxford University Press.
- Talairach, J., & Tournoux, P. (1988). Co-planar stereotaxic Atlas of the human brain. Stuttgart: George Thieme Verlag.
- Tanenbaum, A. S. (1990). Structured computer organization (3rd ed.). Englewood Cliffs, NJ: Prentice-Hall.
- Taylor, R. G., & Taylor, S. (1997). Models of computation and formal languages. Oxford, UK: Oxford University Press.
- Tillmann, B., Janata, P., & Bharucha, J. J. (2003). Activation of the inferior frontal cortex in musical priming. *Cognitive Brain Research*, 16, 145–161.
- Trehub, S. E. (2003). The developmental origins of musicality. *Nature Neuroscience*, 6, 669–673.
- Vapnik, V. (1998). Statistical learning theory. New York: Wiley and Sons.
- von Humboldt, W. (1836). Uber die verschiedenheit des menschlichen sprachbaues. Berlin.
- Vosse, T., & Kempen, G. (2000). Syntactic structure assembly in human parsing: A computational model based on competitive inhibition and a lexicalist grammar. *Cognition*, 75, 105–143.
- Wernicke, C. (1874). Der aphasiche symptomen komplex. Breslau: Cohn and Weigart.
- Worsley, K. J., & Friston, K. J. (1995). Analysis of fMRI time-series revisited—again. NeuroImage, 2, 173–181.
- Worsley, K. J., & Friston, K. J. (2000). A test for a conjunction. Statistics and Probability Letters, 47, 135-140.
- Worsley, K. J., Marrett, S., Neelin, P., Vandal, A. C., Friston, K. J., & Evans, A. C. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. *Human Brain Mapping*, 4, 58–73.

- Zatorre, R. J., Perry, D. W., Beckett, C. A., Westbury, C. F., & Evans, A. C. (1998). Functional anatomy of musical processing in listeners with absolute pitch and relative pitch. *Proceedings of the National Academy of Sciences* of United States of America, 95, 3172–3177.
- Zurif, E. B. (1990). Language and the brain. In H. Lasnik (Ed.), *Language: An invitation to cognitive science* (Vol. 1). Cambridge, MA: MIT Press.
- Zurif, E. (1998). The neurological organization of some aspects of sentence comprehension. *Journal of Psycholinguistics Research*, 27, 181–190.