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Research report

Ventral premotor cortex lesions disrupt learning of sequential grammatical structures

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Introduction: Recent functional magnetic resonance imaging (fMRI) evidence shows differential involvement of the inferior frontal gyrus (IFG) and the ventral premotor cortex (PMv) in syntactic processing. Our main goal is to specify the precise role of the PMv in the processing of sequential structures and whether these processes are a necessary prerequisite for the successful acquisition of grammatical structure.

Methods: We tested patients with PMv lesions in an artificial grammar (AG) learning task, including correct sentences and sentences with violations of local (referring to adjacent elements within an AG string) and long-distance dependencies (incorporating recursive structures). In addition to performance measures event-related potentials to these violations were recorded.

Results and conclusions: Compared to matched controls, patients displayed impaired acquisition of the AG. This impairment was more pronounced for local than for long-distance dependencies. This effect was paralleled by a selective reduction of the P600 component in response to violations of local dependencies. Most importantly, the P600 elicited by violations of long-distance dependencies was comparable between groups. Together, behavioral and ERP results indicate a PMv involvement in processing local sequential information.

1. Introduction

Human language can be defined as a sequence of symbols that is formed according to a hierarchy of rules with increasing generative power. The lowest-level grammar consists of a sequence of local dependencies between neighboring elements (e.g., words) and therefore, can be fully specified by their transition probabilities. In contrast, more complex grammars, such as so-called phrase structure grammars, are characterized by the licensing of complex hierarchical structures and long-distance dependencies. Recent neuroimaging studies have shown that the processing of local phrase structure dependencies and long-distance dependencies have different neural correlates. Local structural violations elicit activation in the left frontal operculum, while the processing of long-distance dependencies activates Broca's area (Friederici et al., 2003, 2006b; Röder et al., 2002). Similar results have been obtained when investigating artificial grammar (AG) systems. While the posterior part of the inferior frontal gyrus (IFG) (BA44) seems to play an important role in the processing of long-distance or hierarchical dependencies, the ventral premotor cortex (BA6, PMv) seems to subserve the processing of local

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dependencies (Friederici et al., 2006a; Opitz and Friederici, 2007). In a previous functional magnetic resonance imaging (fMRI) study (Opitz and Friederici, 2007), participants were trained and subsequently tested in an AG (a modified version of the AG called BROCANTO, Friederici et al, 2002b). Two types of structural dependencies (local *vs* long-distance) were contrasted. The local dependency consisted of two neighboring syntactic elements, whereas the long-distance dependency constituted an embedding of a complementizer structure within a local phrase structure. When contrasting brain activations associated with violations of local and long-distance dependencies against their respective baselines, the left PMv responded to the processing of local dependencies whereas the opercular part of the IFG (Brocas area, BA 44) showed activation when processing long-distance dependencies.

Differential processing of local and hierarchical dependencies has also been shown in electrophysiological (ERP) studies (Bahlmann et al., 2006; Jiang and Zhou, 2009). One of these studies was carried out on an artificial language, in which two types of AG systems consisting of meaningless syllable sequences were learned and then tested (Bahlmann et al., 2006). One type of structure formed local transitions, while another type was based on long-distance dependencies. Violations of either structure elicited a late positive ERP component. Based on its spatio-temporal characteristics this component closely corresponds to a late positivity called the P600, representing syntactic reanalysis or integration (Kaan and Swaab, 2003; Hagoort, 2008; Hahne and Friederici, 1999). The amplitude of the late positivity varied as a function of syntactic hierarchy[1] and may thus reflect enhanced integration costs for long-distance as compared to local dependencies.

The second study investigated the comprehension of different levels of the hierarchical syntactic structure in Chinese. Violation of both types of dependencies elicited an anteriorly distributed negativity, with a left hemispheric maximum for violations of local dependencies and right hemispheric distribution for hierarchical dependencies. Contrary to the findings by Bahlmann et al. (2006) neither type of violation evoked a late positivity. The absence of the P600 effect was interpreted as being due to the absence of explicit task demands. However, both studies report processing differences for local and long-distance dependencies, confirming previous fMRI evidence.

Although all studies reviewed so far suggest that the PMv is involved in the detection of violations of sequential information [see Section 4 for a detailed discussion], the temporal dynamics of the neuronal modifications during the acquisition of non-motor, perceptual sequences are less clearly understood. Recent studies provided evidence that motor-related brain areas were activated in the course of learning of sequential finger movements (Jenkins et al., 1994; Lafleur et al., 2002) and of visuo-motor associations (Praeg et al., 2006; Toni et al., 2001). However, this does not imply that the learning of linguistic sequences relies on the PMv as does the learning of motor sequences. Thus, it is not clear whether this cortical region is necessarily involved in the acquisition of local linguistic dependencies in a domain-general manner.

A second issue that is currently discussed regards the relationship between the processes subserved by BA44 and BA6. On the one hand it is assumed that the PMv matches a sentence with an appropriate default template and Broca's area contributes to the generation of hierarchical organization in language that operates on serially organized representations provided by the adjacent PMv (Fiebach and Schubotz, 2006). This view implies a gradient of complexity from simple sequential structures processed in the PMv toward complex hierarchical dependencies handled by Broca's area. On the other hand, results from several fMRI experiments suggest an independence of the processes subserved by the two regions. In most experiments activity in either region is observed (Opitz and Friederici, 2003, 2004) and both regions differentially respond to experimental variables (Musso et al., 2003; Tettamanti et al., 2002). In these studies it has been consistently demonstrated that Broca's area is involved when processing natural and artificial languages that meet the universal principles of natural grammars, but not when a rule system that cannot exist in any natural language was to be learned (Musso et al., 2003).

Our main goal is two-fold. Firstly, we seek to specify the precise role of PMv in the acquisition of linguistic sequential structures and, secondly, we are interested to find out whether these processes operate independently in successful grammar learning. For this purpose patients with lesions centered in the PMv were trained on the modified version of BROCANTO (Friederici et al., 2002b; Opitz and Friederici, 2007) that allowed directly comparing local phrase structure dependencies (e.g., such as word category information) and hierarchical, long-distance dependencies. Firstly, if the PMv is, indeed, involved in learning sequential information in a domain-general fashion, we expect impaired acquisition of BROCANTO by patients as compared to matched controls. Secondly, if these processes subserved by both structures operate independently, a selective impairment in learning local dependencies should be observed. In contrast, if the processes mediated by the PMv are a necessary prerequisite for successful grammar learning, we also expect patient's processing of hierarchical structures to be impaired. Lastly, a respective reduction of the P600 is expected, i.e., a selective reduction of the P600 to violations of local dependencies in case of independent processes subserved by the PMv and Broca's area, but an equally reduced P600 to violations of both, local and long-distance dependencies, when the processing of hierarchical structures depends upon the intact processing of serially organized representations provided by the adjacent PMv.

In order to ascribe possible changes in the P600 component to syntactic processing deficits and not to varying attentional demands, ERPs were also recorded in a visual classification (i.e., oddball) task. It has been previously shown, that patients with focal vascular basal ganglia lesions and patients without basal ganglia lesions both displayed a P300 in a classic non-linguistic oddball paradigm, while no P600 was elicited by morphosyntactic violations (Frisch et al., 2003) and argument-structure violations (Kotz et al., 2003) in the patients with basal ganglia lesions. This single dissociation between the P600, normally

[1] The term hierarchy refers here to phrase structure grammars. Although this use is different from the original formulation introduced by Chomsky and Schützenberger (1963) it is formally correct as phrase structure grammars can generate such hierarchical sequences. However they are not necessary, a context free grammar is sufficient for generating such sequences, and is lower in the Chomsky hierarchy of languages (see Moro, 2008, for a very recent and updated illustration).

elicited in a broad range of syntactic anomalies, and the P300 indicates that the P600 is not simply a P300-like component, i.e., that it reflects the same process of detecting a task-relevant and unexpected event (Kotz et al., 2009b). Consequently, by comparing the P300 oddball effect and the P600 effect elicited by violations of linear and hierarchical dependencies in patients and their age matched controls we are able to examine the extent to which lesions to the PMv have a general effect on ERP components evoked in cognitive tasks or can be ascribed to a specific syntactic processing deficit in these patients.

2. Methods

2.1. *Subjects*

Eight chronic patients with lesion centered in the PMv were invited to participate in the current study. Individual patient case histories are displayed in Table 1 and a lesion overlap is depicted in Fig. 1. Furthermore, eight healthy controls were tested. Participants were matched for gender (three females), age (M ± one standard deviation: patients = 53.8 ± 4.8, controls = 56.2 ± 5.7, $t(14) = -.94$, $p = .361$), and education. In order to explore whether elderly controls perform comparable to healthy young participants in an AGlearning task, 16 young volunteers (seven males, mean age 23.5 ± 2.3), recruited among students at Saarland University participated in a behavioral version of the combined EEG/behavioral experiment. All participants gave informed consent prior to the experiment in accordance with the declaration of Helsinki. This clinical study was also approved by the ethics committee of the medical department at the University of Leipzig.

2.2. *Materials*

2.2.1. *Visual oddball*

The material in the visual oddball task consisted of 16 differently shaped objects (circle, triangle, etc.). One-quarter of the objects, designated as targets, were easily discernible by an opening (round), while the remaining 75% were not (see Mecklinger et al., 1998, for details).

2.2.2. *AG learning*

The stimulus material is based on a modified version of the artificial language BROCANTO (Friederici et al., 2002b; Opitz and Friederici, 2007). BROCANTO is formed based on the universal principles of natural languages (i.e., it consists of different syntactic word categories and defines phrase structure rules). Each sentence of the artificial language contains three to eight words and represents a subject–verb–[object] structure. A complementizer structure (C) is used that allows the direct comparison of local phrase structure dependencies and hierarchical, long-distance dependencies. The stimulus set consists of 100 correct sentences, half of them including local dependencies and the other half including long-distance dependencies. Another 100 sentences contain a syntactic violation: a long-distance violation, a word category repetition, or a local phrase structure violation, both composing local violations (see Table 2 for examples).

2.3. *Experimental procedure*

Participants engaged in two experiments, a visual oddball experiment followed by an AGlearning experiment. The oddball experiment was conducted in order to estimate unspecific reductions of ERP components in patients compared to controls. In this experiment participants were presented with a total of 300 stimuli, including 25% targets. Stimulus duration was 200 msec and the inter stimulus interval (ISI) was 1200 msec, resulting in approximately 7 min of experimental time. Participants were instructed to fixate the center of the screen and to silently count the targets.

With regards to the AGlearning experiment participants were trained on a modified version of the miniature AG system

Table 1 – Patient's history and localization of lesions.

No.	Sex	Hand	AaT	TsL	Etiology	Site of lesion	Lesion description	Affected Brodmann areas
1	f	R	47	10	Angioma, postoperatively	B	Left MFG, IFG, IFGPOp, IFGPTr, aIn, EC; bilateral Th	08 09 44 45 46
2	m	L	67	7	PMI	L	MFG, IFGPOp, PrG	06 43 44 45 47
3	m	R	32	6	PMI	L	IFGPOr, IFGPTr, IFGPOp, PrG, aIn	06 43 44 45 47
4	m	R	39	6	PMI	L	IFGPOp, PrG	04 06 44
5	m	R	56	5	PMI, noncompressive temporal arachnoid cyst	L	MFG, IFGPOr, IFGPTr, IFGPOp, PrG, aIn	06 08 09 44 45 46 47
6	f	R	51	4	SAH	B	Right PrG PrG IFGPOp, left LOrG, POrG, CC	L 11 47 R 06 44
7	f	L	46	6	BZI	B	Left PoG, right PrG, bilateral SPL, Cu	L 01 02 03 R 04 06 B 07 19
8	m	R	52	4	PMI	L	IFGPOr, WM of IFG, LOrG, WM of PrG, aIn	06 11 47

Abbreviations: f = female; m = male; L = left; R = right; B = bilateral; PMI = partial middle cerebral artery infarction; SAH = subarachnoidal hemorrhage; BZI = border–zone infarction.
Orbital region: MOrG = medial orbital gyrus; LOrG = lateral orbital gyrus; POrG = posterior orbital gyrus.
Frontal region: IFG = inferior frontal gyrus; IFGOr = inferior frontal gyrus, orbital part; IFGTr = inferior frontal gyrus, triangular part; IFGOp = inferior frontal gyrus, opercular part; MFG = middle frontal gyrus; SFG = superior frontal gyrus; PrG = precentral gyrus.
Occipital region: Cu = Cuneus.
Subcortical: Th = thalamus; CI = internal capsule; EC = external capsule; CC = corpus callosum.
Age and time since lesion (at test) in years. AaT = Age at Test; TsL = Time since Lesion; Hand = Handedness.

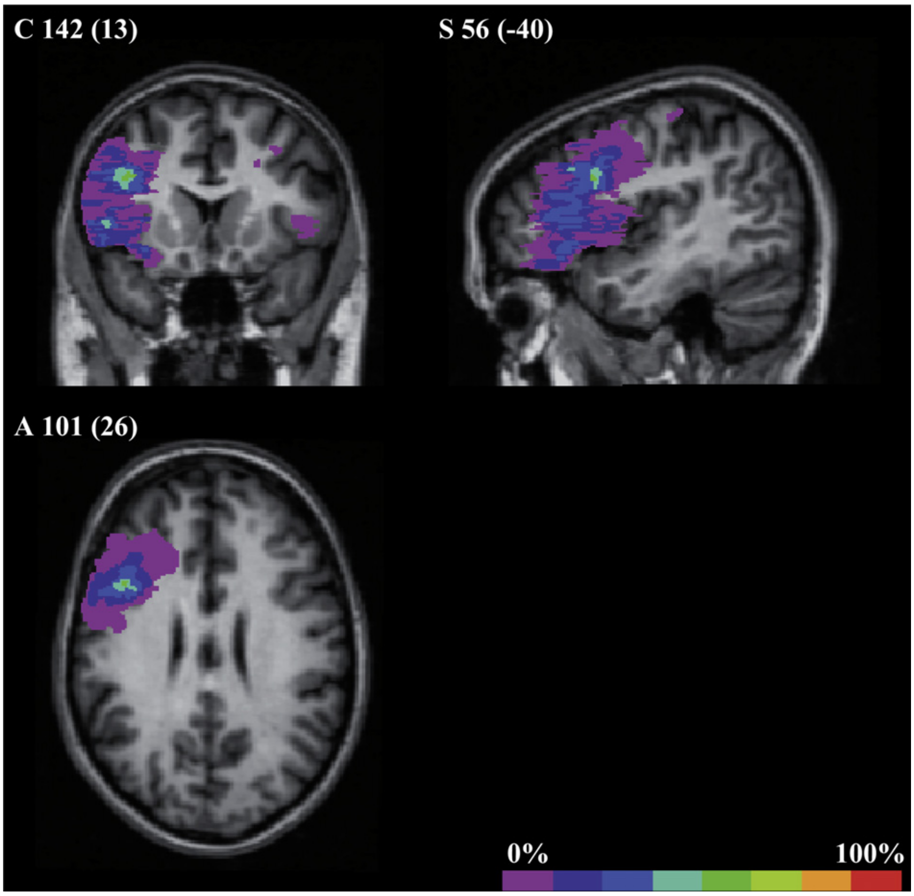

Fig. 1 – Lesion overlap. Displayed are representative coronal C, sagittal S and axial A slices with corresponding Talairach coordinates (y, x, and z, respectively) in brackets. ROI of the eight patients described in Table 1 are overlapped on a reference image (healthy control, female, 23 years of age). In the color bar the colors indicate the number of overlapping ROIs. The leftmost (dark violet) color indicates the index for a single ROI, while the rightmost (bright red) color shows the index for all the ROI's overlapping. Here maximal lesion overlap is found at precentral gyrus at junction with middle frontal gyrus, indicated by turquoise/green shades.

BROCANTO. The training procedure was highly similar to the one described in Opitz and Friederici (2004, 2007). It comprised alternating learning and test blocks. A brief instruction (7 sec) started each block. During learning, participants viewed 20 correct sentences for 7 sec each on a computer monitor and were instructed to extract the underlying grammatical rules. During test blocks, participants were presented with 20 new sentences that were either grammatical (half of the sentences)

Table 2 – Examples of grammatical and non-grammatical sentences of the modified version of BROCANTO.

		Grammatical sentences								Non-grammatical sentences						
Long-distance dependencies	(a)	aak D	gum N	prez V	caf C	aak D	trul N	rix V	(b)*	aak D	gum N	prez V	nöri M	aak D	trul N	rix V
Local dependencies	(c)	aak D	plox N	glif V	rüfi M	aak D	böke A	gum N	(d)*	aak D	plox N	glif V	pel V	aak D	böke A	gum N

D – determiner, N – noun, V – verb, M – verb modifier, A – adjective, C – complementizer.
Violations that rendered sentences non-grammatical are in italics. Note that the non-grammatical version of the long-distance dependency condition (b) is ungrammatical as the sequence D–N–V at the end of the sentence is only licensed after a C-element as in its grammatical counterpart (a). In case of local dependencies ungrammaticality is realized by two successive elements of the same class (V-elements in the present example), not allowed by the grammar. An example of each of these sentences for English would be the following:
(a) The man wondered whether the boy lied. (b) * The man wondered slowly the boy lied. (c) The man greeted enthusiastically the young girl. (d) * The man greeted saw the young girl.

or ungrammatical. Following a fixation cross (500 msec) each sentence was presented in a word-by-word fashion in the center of a computer screen. The duration of the word presentation was 500 msec with an interval of 500 msec between words. Participant's judged the grammaticality of each sentence. Visual feedback was given for each response. This procedure was repeated 10 times with different sentences.

2.4. *Data acquisition and analysis*

Electroencephalograms (EEG) were continuously recorded from 29 Ag/AgCl scalp electrodes positioned at FP1/2, F7/8, F5/6, F3/4, Fz, FT7/8, FC3/4, T7/8, C3/4, Cz, TP7/8, CP5/6, P7/8, P3/4, Pz, O1/2. The EEG from all sites was recorded with reference to the left mastoid electrode. An additional channel recorded EEG from the right mastoid, allowing the scalp recordings to be re-referenced off-line to linked mastoids. Vertical and horizontal electrooculograms (EOG) were recorded with additional electrodes located above and below the right eye and outside the outer canthi of both eyes. Inter electrode impedances were kept below 5 kΩ. The EEG was digitized at a sampling rate of 250 Hz with a band-pass from DC to 40 Hz.

Off-line data processing included a digital high-pass filter set to .1 Hz (−3 dB cutoff) to eliminate low frequency signal drifts. An automatic rejection criterion (voltage variation of more than 30 μV within a 200 msec sliding time window) was applied to the EOG channels to mark segments contaminated by eye movement artifacts. These recording epochs were corrected using a linear regression approach (Gratton et al., 1983). Furthermore, all channels were scanned manually for additional artifacts.

In the oddball experiment artifact-free epochs ranging from −200 msec to 1000 msec with respect to stimulus onset were averaged separately for each participant, and stimulus type, with a 200 msec pre-stimulus baseline. Based on visual inspection of the grand average waveform, electrode sites exhibiting the largest effects were pooled into two topographical regions of interest (ROIs): an anterior ROI (Fz, FP1, FP2) and a posterior region (Cz, Pz, O1, O2). Peak latency and mean amplitudes in a time window between 350 and 500 msec were used for the quantification of the ERP effects. A repeated-measure analysis of variance (ANOVA) was performed with the within-subject factor stimulus type (standard *vs* target) and the between-subject factor group.

In the AGlearning experiment, ERPs of the second half of the experiment were analyzed time-locked to the onset of the critical violated word and its corresponding correct word. A 200 msec pre-stimulus interval was taken for baseline correction. The respective items were averaged only for behaviorally correct responses, for each participant, and violation type. Based on visual inspection, suggesting a broad distribution of the P600, ERPs were quantified for statistical analysis in a left hemispheric ROI (F3, FC3, C3, CP5) and a right hemispheric ROI (F4, FC4, C4, CP6) in the time window from 550 msec to 700 msec post-stimulus onset. Data were analyzed with repeated-measures ANOVA (alpha level = .05). Condition (correct, local violation, hierarchical violation) and hemisphere (LH *vs* RH) were treated as within-subject factors while group was considered a between-subject factor. The Greenhouse–Geisser adjustment for nonsphericity was used whenever appropriate and the corrected *p*-values are reported together with the uncorrected degrees of freedom.

3. Results

3.1. *Oddball experiment*

Overall neither healthy controls nor patients had any difficulty to detect target stimuli. Out of a total of 75 targets, healthy controls on average detected all 75 targets and PMv patients detected 73 targets.

As apparent from Fig. 2 targets elicited a P300 component in patients and normal controls. This was confirmed by a main effect of stimulus type (target *vs* standard) ($F_{(1,14)} = 62.69$, $p < .0001$) in an omnibus ANOVA. Neither the main effects of ROI and group nor any interaction involving these factors reached significance (all $p > .2$). The same analysis was carried out for the peak latency. Here no main effects or any interaction reached significance (all $p > .2$), indicating that PMv patients like healthy controls elicited a normal P300.

3.2. *AGlearning task – behavior*

The performance (endorsement rates) of patients and both control groups in the last two blocks is depicted in Table 3. As apparent from the figure, the endorsement rates (i.e., the proportion of sentences rated as grammatical) for grammatical sentences did not differ between groups, whereas non-grammatical sentences were endorsed more frequently as grammatical by patients as compared to both control groups. Crucially, this was especially the case for sentences containing violations of local dependencies. This visual impression was confirmed in an ANOVA with the repeated-measure factor condition (correct, local violation, hierarchical violation) and the between-subject factor group. This analysis revealed a main effect of group ($F_{(2,29)} = 10.48$, $p < .001$) , a main effect of condition ($F_{(2,58)} = 63.36$, $p < .001$), and a condition by group interaction ($F_{(4,58)} = 10.09$, $p < .001$) indicating a different response pattern for the three groups. In particular, the patients' endorsement rates were different from both control groups ($p < .001$, post hoc Tukey's honestly significant difference (HSD)) that did not differ from each other ($p > .5$). Subsidiary analysis tested whether all three groups were able to distinguish between grammatical and non-grammatical sentences by means of a Wilcoxon Signed-Ranks test[2]. These tests indicated that all three groups could distinguish between grammatical and non-grammatical sentences (patients: $T = 1.82$, $p < .05$; elderly controls: $T = 2.52$, $p < .01$; young control subjects ($T = 3.52$, $p < .001$). However, for patients this analysis revealed a significant effect only for violations of hierarchical dependencies ($T = 2.1$, $p < .05$) and a non-significant result for local violations $T = 1.12$, $p > .3$) suggesting a rather selective impairment of this group in learning local dependencies.

[2] The Wilcoxon Signed-Ranks test for dependent samples was used because of the very small sample size of the patients and the age matched control group. Especially in this case the Wilcoxon Signed-Ranks test has a considerable power advantage over the dependent samples *t*-test (Blair and Higgins, 1985).

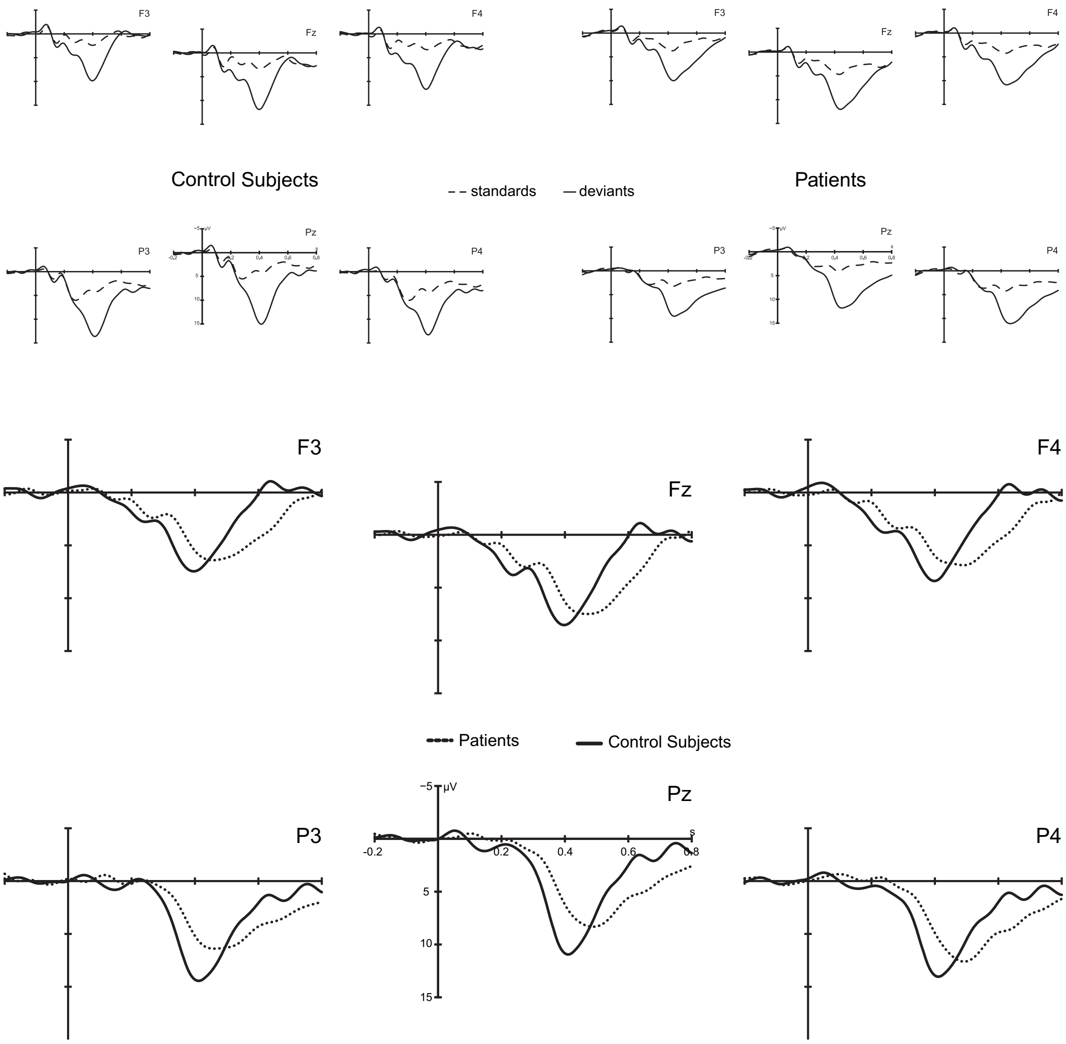

Fig. 2 – P300 oddball effects in healthy controls (upper left panel) and PMv patients (upper right panel). Dotted lines represent standard stimuli, solid lines the targets. The lower panel depicts the target – standard difference waveform for healthy controls (solid line) and patients (dotted line).

3.3. *AGlearning task – ERPs*

The ERP patterns for critical words comparing grammatical violations and grammatically correct conditions are displayed in Fig. 3. As can be seen in this figure, both violation conditions elicited more positive going waveforms as compared to correct sentences. This effect was maximal over the right hemisphere in a time interval from around 550 msec to 700 msec (Fig. 4). Moreover, they reveal a striking group difference. An amplitude difference between correct and grammatically incorrect sentences can be observed for healthy controls (Fig. 3), whereas a considerably reduced effect of grammaticality is present in the patient group.

An ANOVA contrasting the ERPs elicited by the critical words in correct sentences and both types of non-grammatical sentences in both hemispheres revealed a main effect of condition ($F_{(2,28)} = 5.22$, $p < .05$) and a marginal significant condition by group interaction ($F_{(2,28)} = 3.04$, $p < .07$). Based on our hypothesis subsidiary analyses were conducted for each group separately. In controls, ERPs elicited by both violation types differed significantly in amplitude from those elicited by correct words ($F_{(1,7)} = 7.61$, $p < .05$) but did not differ from each other (hierarchical violations: 2.75 μV *vs* local violations: 2.87 μV, $F_{(1,7)} < 1$). In contrast, in patients this effect was only

Table 3 – Mean endorsement rates, i.e., the proportion of sentences rated as grammatical (±standard error of means) for grammatical sentences, and sentences containing a violation of either local or hierarchical dependencies. Note that patients endorsed non-grammatical sentences more frequently as grammatical as compared to healthy controls.

	Patients	Elderly control subjects	Young control subjects
Correct sentences	.798 (.036)	.821 (.075)	.843 (.048)
Hierarchical violations	.671 (.046)	.395 (.096)	.513 (.087)
Local violations	.725 (.087)	.229 (.073)	.238 (.039)

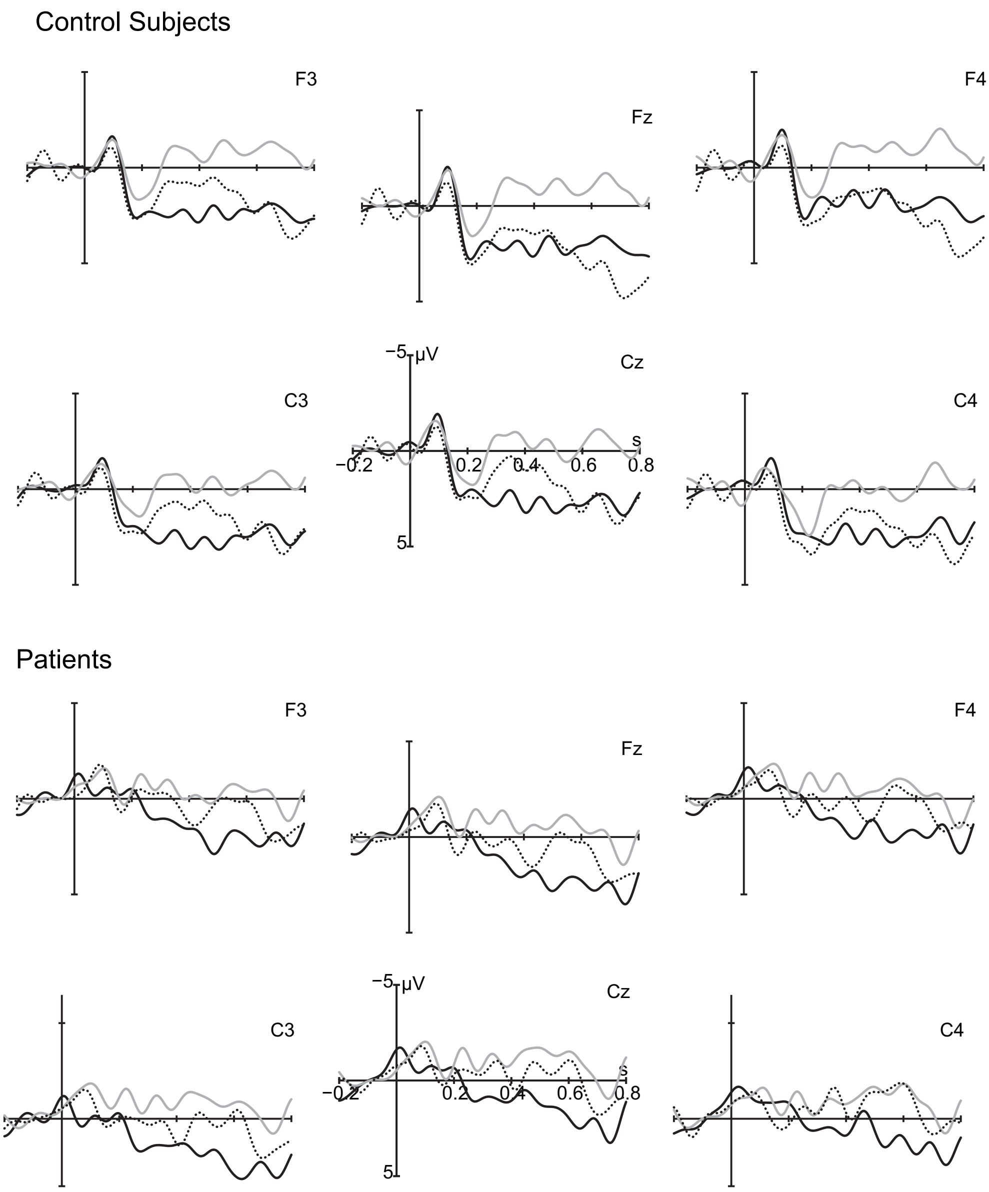

Fig. 3 – ERPs depicted at selected electrodes for correct sentences (gray), hierarchical violations (solid black) and local violations (dotted). The upper panel shows data from healthy controls, the lower panel shows patient data.

observed for hierarchical violations (hierarchical violations: 1.67 μV *vs* local violations: −.42 μV, $F_{(1,7)} = 6.97$, $p < .05$). When comparing both groups directly for each condition patients displayed a reduction of the P600 amplitude in local structures ($F_{(1,14)} = 5.28$, $p < .05$) but not in hierarchical structures ($F < 1$).

In order to verify that the lesion site in PMv patients did not impact differences in ERP effects, the jackknifing procedure (see Obleser et al., 2006; Paulmann et al., 2010, for a similar approach) was applied. Statistics were run iteratively, omitting one patient (and its respective control) each time. If the effects were driven by one particular patient, *F*-values of the respective effects would drop significantly when this patient was omitted. As apparent from Fig. 5 all effects were consistent across patients thereby confirming (i) the homogeneity of the patient group, and (ii) that the effects of interests were not driven by a particular patient.

Taken together, we found a selective impairment of PMv patients in learning local dependencies as indicated by worse performance for local as compared to hierarchical structures that were accompanied by a reduction of P600 amplitude in local as compared to hierarchical structures.

4. Discussion

Behavioral and ERP measures in patients with lesions of the PMv were used to examine the role of the PMv in the processing of sequential linguistic information (local, hierarchical). In the present experiment, PMv patients were impaired in the processing of local dependencies in an artificial language. Taken into account that elderly and young control subjects perform comparably suggests that local dependencies were easier to acquire, and that the acquisition of long-distance, hierarchical

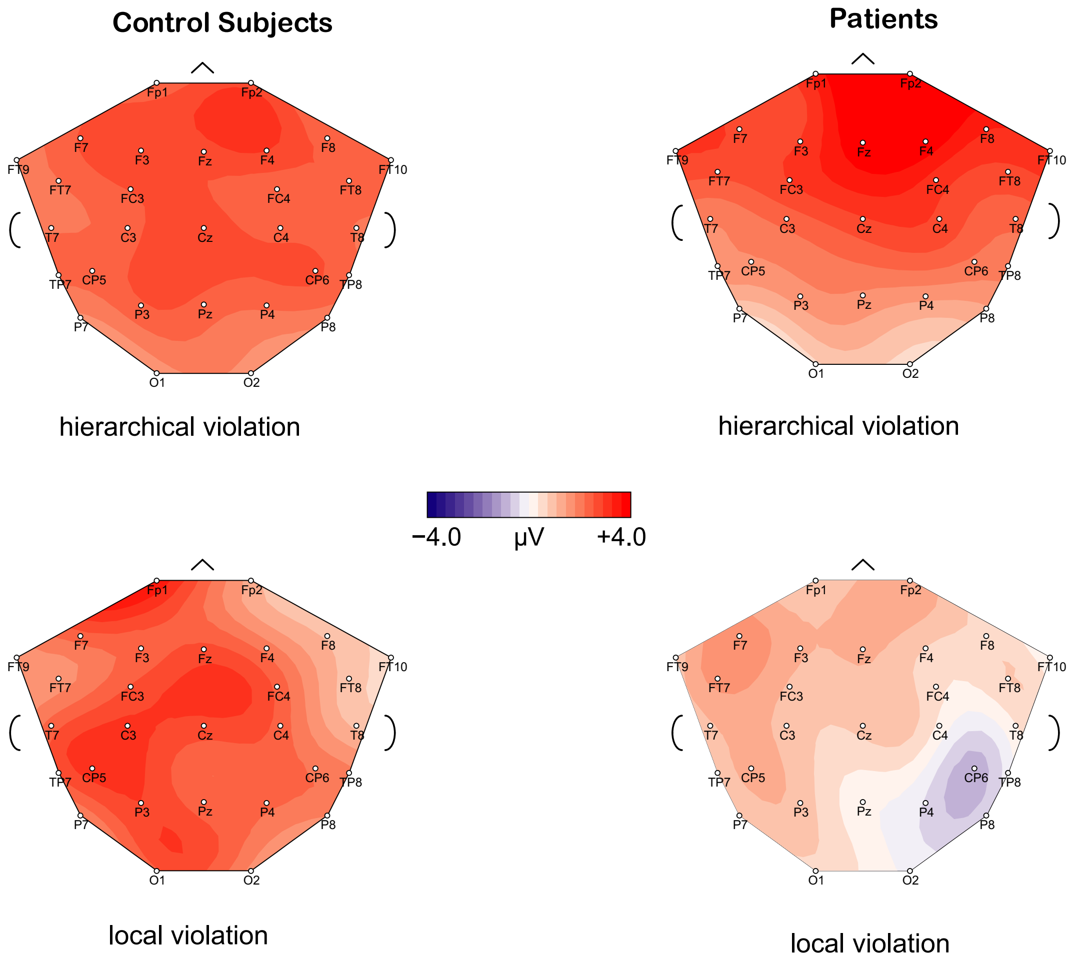

Fig. 4 – Scalp potential maps of the difference waveforms (upper panel: hierarchical violation – correct, lower panel: local violation – correct) in the time window from 550 msec to 700 msec post-stimulus onset depicted for healthy controls (left) and patients with PMv lesions (right). Note the selective reduction of the P600 elicited by local violations in the patient group.

dependencies is relatively spared in our patient sample. Nevertheless, there is only a small difference between the patients' incorrect endorsement of hierarchical and local violations. One possible explanation may be the fact that in some of the patients the PMv lesions extend into the neighboring opercular part of the IFG, i.e., into BA44, thereby causing

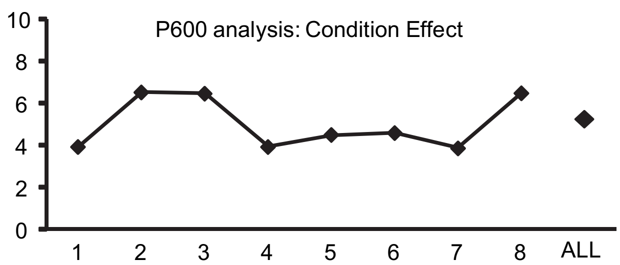

Fig. 5 – Consistency for the significant P600 condition effect. Excluded patients (together with their respective controls) are listed on the abscissa, while the ordinate displays the new observed F-value. The F-value for ALL shows the value obtained when no participant is excluded.

partial deficits in processing hierarchical dependencies. Alternatively, it is also conceivable that the patients' problems in acquiring hierarchical dependencies (that extend across phrase boundaries) are a byproduct of their problems in processing local dependencies within phrase boundaries. As phrase boundaries are the points in a sentence where the predictability of successive words is the lowest, the patients' inability to build-up local sequences that constitute a particular noun or verb phrase in BROCANTO will also derogate their ability to extract the phrase boundaries and, as a consequence, their competence to process hierarchical structures. Support for this view can be derived from the AG learning paradigm using letter strings. In their recent review Perruchet and Pacton (2006) have argued that the computation of transition probabilities between neighboring letters may lead to the formation of chunks that by themselves compose grammatical letter strings. The grammaticality of new letter strings can be assessed by comparing this incoming information against the stored chunk template. According to this view, the formation of chunks is a core process underlying the successful acquisition of an AG. Following this line of arguments the letter chunks can be regarded as an analog of phrases in BROCANTO. Thus, the patients' impaired processing of local dependencies might affect the extraction of phrase boundaries and, consequently, the build-up of hierarchical dependencies. Taken together the present behavioral results are in agreement with recent findings demonstrating that the PMv is involved in the detection of local ungrammaticalities in naturally existing languages (Friederici et al., 2003; Raettig et al., 2010) as well as artificial languages mimicking natural grammars (Tettamanti et al., 2002).

In addition, a reduction of the late positivity (P600) elicited by violations of local dependencies was observed in patients compared to healthy controls. This late positivity elicited by violations in linguistic sequences is in line with previous studies on learning AG systems (Friederici et al., 2002b), syllable sequences (Bahlmann et al., 2006) or letter sequences (Lelekov-Boissard and Dominey, 2002). However, as compared to the 'classical' P600, the positivity in the present experiment has an unusual frontal distribution. The late positivity of the present experiment shares the temporal characteristic of the P600, as well as a partial spatial overlap. A frontal distribution of the P600 has been previously observed in a number of studies and has been interpreted as reflecting the processing of more complex and ambiguous structures (Friederici et al., 2002a; Kaan and Swaab, 2003; Kotz et al., 2009a; Lelekov-Boissard and Dominey, 2002). As participants had to extract the grammatical rules, it seems conceivable that the violation of both types of dependencies was an unexpected, rather than an ungrammatical event (see Fonteneau and van der Lely, 2008, for a similar explanation). An alternative explanation can be derived from the fact that the performance of our participants was not sufficiently high to initiate repair processes, despite their capability of detecting the unusual syntactic structure.

Interestingly, in apparent contrast to previous studies (Bahlmann et al., 2006; Jiang and Zhou, 2009) the present experiment did not reveal a negativity elicited by both violations of local and hierarchical structures. Bahlmann et al. (2006) reported a posteriorly distributed early negativity that was interpreted as a response to expectancy violations toward the incoming constituents (i.e., syllables in this case). However, while Bahlmann et al. used two different categories of syllables (equivalent to a transition probability between neighboring elements of 50%) the present study employed six different word categories leading to much lower transition probabilities (maximally 25% at the critical positions). These different transition probabilities may have caused different participants' expectancies of an upcoming item. Consequently, the violation of expectancies caused by a non-grammatical item may have been less discernible in the present study and, therefore, not reflected as a negativity in the ERP.

In sum, the present data indicate that PMv is required for the acquisition of local dependencies, thereby adding to the evidence that the PMv is a critical brain structure for the processing of perceptual sequences in a domain-general fashion. As the processing of hierarchical structures is also affected in the patients, the present data suggest, that some aspects of the successful utilization of local dependencies are a prerequisite for successful language acquisition. The exact nature of these aspects remains to be elucidated in future research.

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