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RESEARCH ARTICLE

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Syntactic and semantic processing in the healthy and aphasic human brain

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Abstract A syntactic and a semantic task were performed by German-speaking healthy subjects and aphasics with lesions in the dominant left hemisphere. In both tasks, pictures of objects were presented that had to be classified by pressing buttons. The classification was into grammatical gender in the syntactic task (masculine or feminine gender?) and into semantic category in the semantic task (man- or nature made?). Behavioral data revealed a significant Group by Task interaction, with aphasics showing most pronounced problems with syntax. Brain event-related potentials 300–600 ms following picture onset showed different task-dependent laterality patterns in the two groups. In controls, the syntax task induced a left-lateralized negative ERP, whereas the semantic task produced more symmetric responses over the hemispheres. The opposite was the case in the patients, where, paradoxically, stronger laterality of physiological brain responses emerged in the semantic task than in the syntactic task. We interpret these data based on neuro-psycholinguistic models of word processing and current theories about the roles of the hemispheres in language recovery.

Keywords Event-related potentials · Aphasia · Language production · Lemma access · Brain plasticity

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Introduction

Language processes are lateralized to the left hemisphere in most right-handed subjects. However, not all language processes are lateralized in the same way. According to current neurocognitive models, language processes are *differentially lateralized* (Pulvermüller 1999b; Zaidel 1976) in that the processing of phonology, syntax, or grammatical function words is lateralized to the dominant hemisphere, whereas processes related to the word meaning and pragmatic aspects of language involve both hemispheres. This hypothesis of differential laterality of semantic and syntactic brain processes was examined in the present study by two tasks requiring syntactic and semantic processing of word-related linguistic information, respectively. In addition, it was examined whether focal damage in the perisylvian regions of the left dominant hemisphere in aphasics would affect the differential laterality.

It has been suggested that, in right-handers in whom the left hemisphere is dominant, left-hemispheric damage and rehabilitative efforts in aphasics trigger the recruitment of right-hemispheric resources, including the homotopic areas of the lesioned regions on the left (Zaidel 1998). Such amplification of right hemispheric activation is assumed to contribute to recovery from aphasia (Kinsbourne 1998). Recent neuroimaging data are consistent with this view (Weiller et al. 1995; Weiller and Rijntjes 1999; Musso et al. 1999; Moore 1984, 1986; Papanicolaou et al. 1987). Furthermore, the relevance of right-hemispheric processes for language processing has been proven by neuropsychological studies. (1) Patients with almost complete lesion of the left hemisphere and patients with left-sided hemispherectomy demonstrated basic language processing (e.g., Zaidel 1983; Pulvermüller 1995). (2) Patients who had recovered from aphasia following a left-hemispheric stroke became aphasic again after an additional right hemispheric stroke (Lee et al. 1984; Cambier et al. 1983; Basso 1989; Cappa et al. 1994). (3) Aphasics showed speech arrest following right-sided intracarotid Amytal injections (Kinsbourne

1971; Czopf 1972), whereas healthy subjects normally show this effect only after left-sided injection. These findings suggest that the right becomes particularly relevant after lesion of the left-hemispheric language areas. We will call this the *right substitution hypothesis of language*.

As an alternative, it is possible that areas in the lesioned dominant hemisphere itself, rather than those in the other hemisphere, are particularly relevant for language recovery. This *left substitution hypothesis* is supported by more recent data indicating that, although right-hemispheric activation is observed in many aphasics during language tasks, those patients who recover particularly well from their language deficits show an increase over time of activity levels in the lesioned dominant left hemisphere. This is interpreted as an indication of reintegration into the functional network (Karbe et al. 1998; Heiss et al. 1997, 1999). Thus, the data available so far suggest the relevance of both left- and right-hemispheric processes for language recovery.

Nevertheless, restitution processes in the two hemispheres may contribute differentially to different kinds of linguistic processing. The present syntactic and semantic tasks were performed with aphasics to shed light on this issue. Based on the right substitution hypothesis, one would expect an absence of laterality patterns for all language tasks, or even stronger activation on the right than left hemisphere in right-handed aphasics. In contrast, the left substitution hypothesis would predict left-lateralized language-related activity in aphasics. As a third alternative, it is possible that different linguistic functions which show differential laterality in normals will change their laterality patterns in different ways after lesion of the language areas. This latter proposal implies that, also in the aphasic population, laterality of brain activity depends on the particular language task. Neurophysiological processes reflected in the event-related brain potential (ERP) were used as the dependent variable.

Materials and methods

Subjects

Eighteen patients and 23 normal controls participated in the study. Patients were recruited from the local rehabilitation center (Schmieder Kliniken Allensbach). The study was approved by the local ethics committee. All subjects successfully completed both the syntactic and the semantic tasks above chance level and provided the minimum number of artifact free ERP data sets. The mean age of the patients (6 females, 12 males) was 49±11 years, and their mean level of education 11±2 years. Sixteen of the 18 patients had suffered from a left hemispheric cerebrovascular insult. One patient suffered from aphasia following a cerebral trauma including subdural bleeding in the temporal-parietal area and compression of the left lateral ventricle; one had suffered from a left-temporal skull fracture. The time interval since the insult varied between 1 and 62 months around a mean of 21±20 months. The presence of aphasia and the aphasia subtypes were based on clinical criteria and confirmed in each case by the Aachener Aphasie Test [AAT (Huber et al. 1983); see also Table 1 for neuropsychological information]. According to AAT guidelines, the diagnosis of an aphasic syndrome was given with a probability >70% in all patients, eight of them being classified as Broca's, five as Wernicke's and five as amnestic aphasics.

Of the 23 control subjects (13 females, 10 females; mean age 49±10 years, mean level of education 11±2 years), 14 were healthy controls and 9 were neurological patients with disorders not affecting the brain (e.g., prolapsed intervertebral disks), who were treated in the same rehabilitation center as the aphasics. The patient and normal control groups did not significantly differ in their age or levels of education. All subjects were right handed as verified by a modified version of the Edinburgh Handedness Questionnaire (Oldfield 1971).

Materials

Fifty-four line drawings of concrete objects were selected from the Snodgrass and Vanderwart (1980) picture series. All selected objects had been proven to elicit highly consistent naming responses. The object's names were all frequent German nouns (word frequencies: mean token lemma frequencies: 56/million). Fifty percent of the objects were nature-made, and the other 50% were man-made. The object names also fell into different syntactic groups, half of them having masculine grammatical gender and the other half feminine nouns (see task below). The same set of drawings was presented in both the syntactic and the semantic tasks to exclude stimulus-related differences.

Tasks

A syntactic and a semantic task were designed, similar to a task used by Jescheniak and Levelt (1994). The syntactic task took advantage of the fact that, in German, nouns have a grammatical gender which is overtly represented by the definite articles that frequently accompany a noun in its noun phrase. The chosen articles indicating grammatical gender were ''*der*'' for masculine nouns and ''*die*'' for feminine nouns. For competent speakers of German, it is an easy task to determine for each noun its respective definite article. Subjects were asked to indicate by pressing one out of two buttons whether the grammatical gender of an object name was masculine (''*der*'') or feminine (''*die*''). In the semantic classification task, the same stimuli were presented and subjects were asked to decide whether the presented object was man-made or naturally made. The sequence of tasks (syntactic vs semantic) was balanced across subjects. Different randomized sequences of the 54 pictorial stimuli were assembled for each block. Stimuli were presented using the STIM system (NEUROSCAN) and presented on a 14-inch monitor, placed at a distance of about 1.50 m in front of the subject (visual angle of stimuli about 8.6°). The response buttons were easily manageable microswitches integrated into a response pad that was mounted on the left armrest of the subject's chair.

The subjects responded with their left hand, because of the high probability of right-sided paralysis in aphasic patients. In the gender decision task, subjects had to respond with the left index finger to masculine gender and with the left middle finger to feminine gender. In the semantic classification task, subjects had to respond with the left index finger to man-made and with the left middle finger to naturally made objects. Stimulus presentation lasted until the button press. The subsequent trial started after a response stimulus interval (RSI) of 3 s. Practice trials ensured that instructions were adequately understood. Response times and accuracy of responses were recorded by a pentium computer. Differences between groups and tasks in these measures were evaluated by an analysis of variance with the between-subjects factor Group (comparing aphasics and controls) and the within-subjects factor Task (comparing the syntactic and the semantic task). Performance differences between aphasics with fluent speech (Wernicke's and amnestic aphasia, N=10) and non-fluent (Broca's aphasia, N=8) were evaluated by an additional ANOVA comprising the between-subjects factor Syndrome.

Table 1 Demographical and clinical data of the patient group. Maximal value of "spontaneous speech" is 5, denoting "no dysfunction." Maximal values of AAT subtests denoting "no dysfunction": repetition 150, written language 90, naming 120, comprehension 120. Values of token test denote number of errors made (max: 50) (handedness: *l* left, *r* right)

Patient	Sex	Age	Handedness	Years of education	Months since lesion	Verbal output	Type of aphasia	Spontaneous speech						AAT subtests				
								Communication behavior	Articulation and prosody	Automatic speech	Semantic structure	Phonetic structure	Syntactic structure	Token test	Repetition	Written language	Naming	Comprehension
1	M	46	R	13	11	Non-fluent	Broca's	3	2	5	4	3	4	5	119	75	115	111
2	M	52	R	13	62	Non-fluent	Broca's	1	4	4	3	4	1	30	134	60	64	100
3	F	42	R	9	34	Non-fluent	Broca's	2	3	2	3	3	1	10	107	56	90	86
4	M	57	R	13	47	Non-fluent	Broca's	3	4	5	3	4	2	13	140	52	95	115
5	F	58	R	9	54	Non-fluent	Broca's	2	3	5	3	4	2	17	118	67	105	84
6	F	52	R	9	18	Non-fluent	Broca's	4	5	4	4	4	2	20	142	62	109	115
7	F	51	R	9	7	Non-fluent	Broca's	3	5	3	4	2	2	17	116	71	104	90
8	F	22	R	13	3	Non-fluent	Broca's	2	2	5	3	4	1	30	145	70	45	71
9	M	51	R	13	20	Fluent	Amnestic	3	5	5	4	4	4	17	124	86	97	102
10	M	48	R	13	20	Fluent	Amnestic	3	5	5	3	4	3	8	130	90	103	113
11	M	36	R	9	51	Fluent	Amnestic	4	4	5	5	5	5	16	145	70	108	89
12	M	59	R	9	3	Fluent	Amnestic	3	4	5	4	3	4	9	147	72	98	103
13	M	69	R	13	2	Fluent	Amnestic	4	4	5	3	4	4	14	134	74	104	108
14	M	34	R	13	25	Fluent	Wernicke's	2	5	4	4	4	4	30	136	85	83	98
15	M	51	R	9	1	Fluent	Wernicke's	3	5	5	3	3	4	29	96	71	70	72
16	M	67	R	13	11	Fluent	Wernicke's	3	4	5	3	3	3	5	120	77	89	79
17	M	50	R	10	7	Fluent	Wernicke's	3	5	5	3	3	3	37	108	66	82	91
18	F	40	R	13	3	Fluent	Wernicke's	3	5	5	3	2	3	22	82	59	66	116

EEG recordings

The EEG was recorded with a DC amplifier (MES, Munich) using an electrode cap (Electrocap Inc.) that included the positions Fz, Cz, Pz, Fp1, C3, F3, F7, T3, T5, P3, O1, Fp2, C4, F4, F8, T4, T6, P4, O2, M1, and M2 (left and right mastoid). The vertical and the horizontal EOG was recorded for correction of movement artifacts in the ERPs with two electrodes placed about 1 cm below the eyes (VE1, VE2), two electrodes on the outer canthi (HE1, HE2) and one on the forehead between the eyes. Bandwidth ranged from DC to 30 Hz (6 dB/octave). Electrode impedance was kept below 5 kΩ by cleaning the skin below the electrode with Omniprep and rubbing in electrolyte. Data were digitized at 1 bin/μV, 16-bit A/D, and sampled at 100 Hz with filter settings DC–30 Hz. Data were recorded continuously and stored for offline analysis. Prior to the experiment a run of standardized vertical and horizontal eye movements and of blinks was carried out to develop a template for later eye movement correction of the event-related potentials. Following the recording, electrode positions and the four reference points nasion, inion, and left and right preauricular points were digitized in three dimensions using a 3D digitizer (Polhemus Inc.).

The continuously recorded data were first corrected for slow DC shifts by polynomial correction over the whole recording. Epochs starting 1 s before stimulus onset and ending 2 s after stimulus onset were determined. Data from each epoch were referred to a 500-ms pre-stimulus baseline. Data were transformed to average reference. Epochs were corrected for eye movement and blink artifacts following the method by Berg and Scherg (1994) that allows the electrodes to be used around the eyes also as EEG electrodes. This method distinguishes between ocular and brain activity and corrects for ocular artifacts. After the automatic correction each trial was visually inspected and excluded if there were remaining artifacts of any kind (muscle potentials, large drifts, etc.).

The mean number of artifact-free trials with correct responses (out of the total of 54) were: for aphasics: gender decision: 28±9; semantic classification: 29±7; for controls: gender decision: 37±9; semantic classification: 34±8. For these trials, the distribution of the average amplitude was determined for the time segment for 300–600 ms after stimulus onset. This interval was determined from visual inspection of the grand average curves and indicated evidence of a prominent asymmetry between left- and right-hemispheric recordings, as well as group- and task-related differences (Fig. 1). Several ERP components can contribute to the potential recorded in this time range, including late parts of the Left Anterior Negativity associated with syntactic violations and function word processing (Neville et al. 1992), the N400 associated with the integration of semantic meaning into context (Kutas and Hillyard 1984), and the Slow Wave associated with stimulus encoding, conceptual processes and verbal working memory (Rösler et al. 1998; Ruchkin et al. 1997, 1988). For the present report, the component was labeled Slow Wave (SW).

Since the present study focussed on topographies of event-related potentials, the comparison of the SW topographies between groups did not consider the differences in the overall amplitude of brain responses. Therefore, data were normalized as suggested by Picton et al. (2000). For each subject and task, the amplitude obtained at each electrode was divided by the respective standard deviation across electrodes. Differences in the topography of the ERP component between groups were evaluated by analyses of variance with the between-subject factors Group (aphasics vs controls) and the within-subject factors Task (syntax vs semantics), Gradient (anterior vs posterior areas) and Hemisphere (left vs right hemisphere). The latter comparisons were based on amplitudes averaged across five electrodes from each of the following four regions: left anterior: HE1, Fp1, F7, F3, C3; right anterior: HE2, Fp2, F8, F4, C4; left posterior: P3, T3, T5, M1, O1; and right posterior: P4, T4, T6, M2, O2. Differences in the ERP distributions between aphasics with fluent and non-fluent speech were examined by additional ANOVAs with the between-subject factor Syndrome.

The relationship between performance and SW was examined by assigning subjects of each group and for each task to a group of "good performers" and "bad performers" (above or below median of latencies). On each task the SW pattern of "good" and "bad" performers was compared in an ANOVA. In addition, the aphasics were assigned to a group of "early" (below median of elapsed months since lesion) and "late" (above median of elapsed months since lesion) aphasics. Pearson correlations were calculated for months since lesion and performance (number of errors, latencies), as well as correlations between response latencies and SW

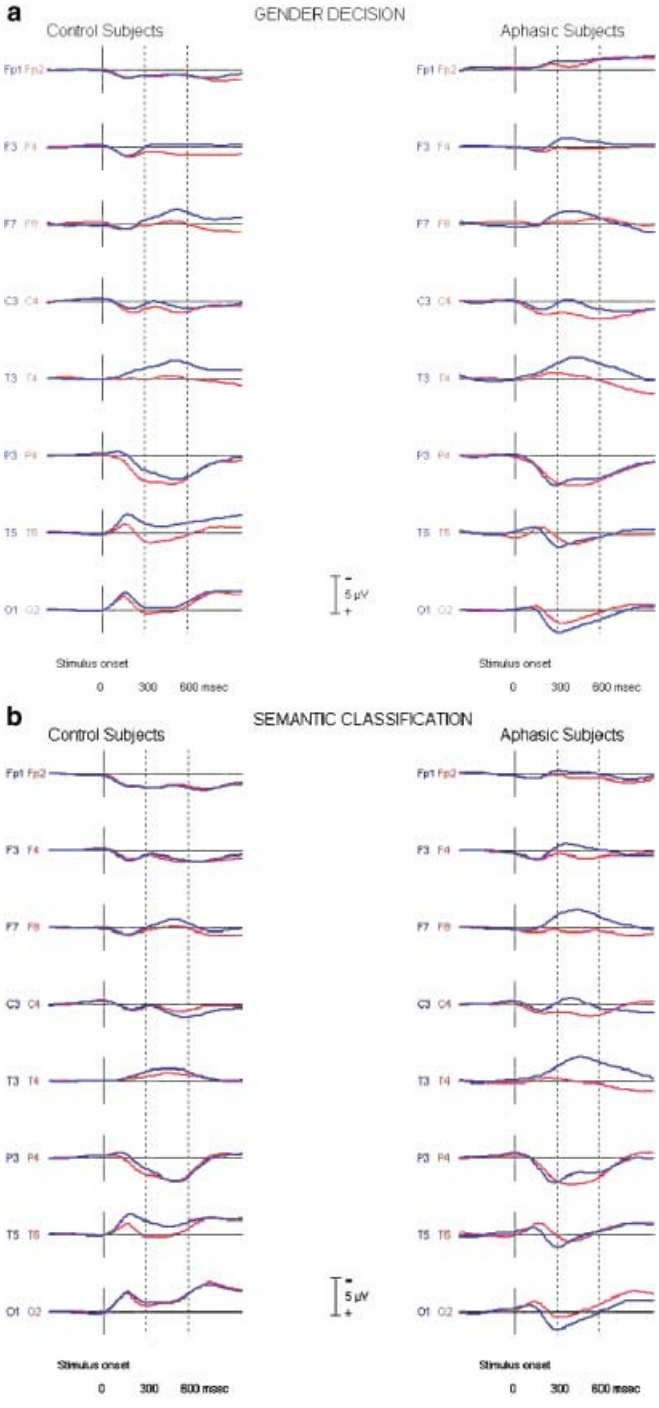

Fig. 1a, b Event-related potentials for both tasks and groups. ERP waveforms during 500 ms pre-stimulus and 1 s poststimulus are superimposed for selected recordings for left- (*blue*) and right- (*red*) hemispheric recordings averaged separately for the control group (*left*) and the aphasic group (*right*). Negativity up, average reference, DC to 5 Hz

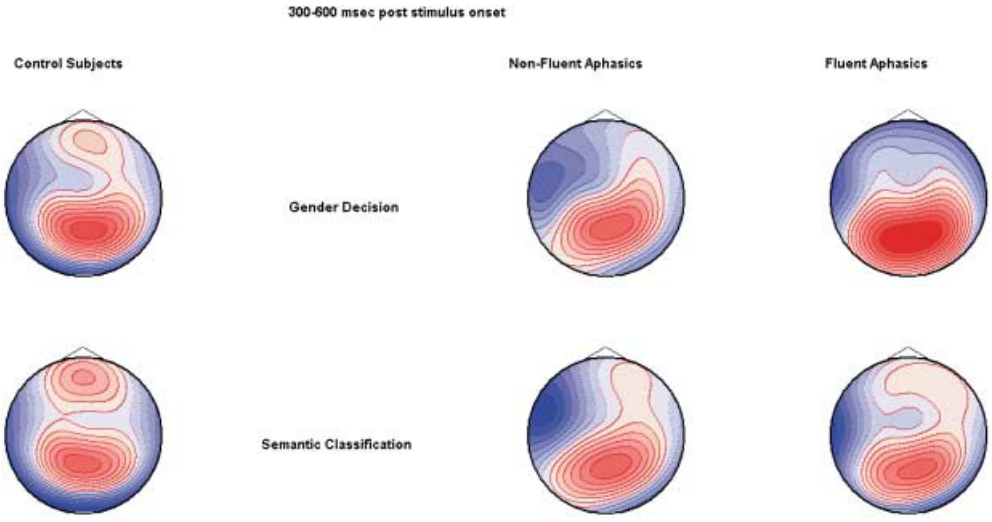

Fig. 2 Scalp distribution of the ERP between 300 and 600 ms following stimulus onset (Slow Wave) averaged separately for both tasks and the three groups (*left* controls, *middle* non-fluent aphasics, *right* fluent aphasics). *Shades of blue* indicate negative amplitudes of the SW, *shades of red* color positive amplitudes (relative to baseline, average reference). *Each line and step in color*, respectively, corresponds to 0.5 µV. Distributions are based on non-normalized data

Table 2 Mean % number of errors (± SD) and mean of median response latencies (s) (± SD) averaged separately for groups and tasks

	Gender decision		Semantic classification	
	Response latency	Mean of % errors	Response latency	Mean of % errors
Aphasics	2.7±1.5	13.8±15.3	1.1±0.3	6.0±7.1
Controls	0.9±0.3	3.8±3.8	0.7±0.2	3.2±11.1

in the four regions. Only response latencies of correct trials were chosen, and trials with incorrect responses were excluded from the ERP analysis.

Results

In both tasks, the aphasics made more errors and responded more slowly than the controls (Group, errors: $F_{(1,39)}$=7.2; P<0.01; latencies: $F_{(1,39)}$=37.7; P<0.01; see Table 2 for mean values). The main effect Task indicated that both groups were less accurate ($F_{(1,39)}$=4.1; P<0.05) and slower ($F_{(1,39)}$=39.5; P<0.01) in the syntax task compared to semantic classification. A significant interaction Task × Group was explained by particular slowing of responses of aphasics in the syntactic task ($F_{(1,39)}$=23.7; P<0.01). This effect appeared as a trend for number of errors ($F_{(1,39)}$=3.0; P<0.1). Aphasics with fluent and non-fluent speech did not differ in performance.

(Planned comparisons confirmed the group differences in the gender decision task for latencies: $F_{(1,39)}$=32.0; P<0.01, and number of errors: $F_{(1,39)}$=9.2; P<0.01, and in semantic classification for latencies: $F_{(1,39)}$=28.3; P<0.01, but not for number of errors: $F_{(1,39)}$=0.8; NS. Planned comparisons also confirmed the task differences for controls (latencies: $F_{(1,22)}$=39.6; P<0.01, number of errors $F_{(1,22)}$=0.05; NS), and aphasics (latencies: $F_{(1,17)}$=24.6; P<0.01; number of errors: $F_{(1,17)}$=4.9; P<0.05).

Figure 2 illustrates the scalp distribution for both tasks separately in controls and in non-fluent and fluent aphasics. In both tasks and subject groups, the SW was more negative over the left than the right hemisphere (Hemisphere: $F_{(1,39)}$=19.7, P<0.01). This interhemispheric difference varied as a function of group and task (Group × Task × Hemisphere: $F_{(1,39)}$=9.7; P<0.01). Controls exhibited a left hemispheric asymmetry in the gender decision task (Hemisphere: $F_{(1,22)}$=21.9; P<0.01), but a more bilateral distribution of negativity in the semantic task (Hemisphere: $F_{(1,22)}$=2.8, NS). In contrast, aphasics showed the opposite pattern, a pronounced lateralization in the semantic task (Hemisphere: $F_{(1,17)}$=14.1, P<0.01), but no significant lateralization in the syntactic task (Hemisphere: $F_{(1,17)}$=2.6, NS). When the left-hemispheric SW of aphasics was compared between tasks, the main effect Task fell short of significance ($F_{(1,17)}$=3.8; P<0.07), indicating a more pronounced negativity in the semantic task. For the right-hemispheric SW the Task effect was not significant ($F_{(1,17)}$=0.6, NS). It seems interesting that the noticeable negativity in the semantic task was primarily pronounced in "late" compared to "early" aphasics, as indicated by the interaction Group ("early"–"late aphasics) × Task ($F_{(1,16)}$=6.2, P<0.05) and the post hoc ANOVAs revealing a significant effect Task only in the late aphasics ($F_{(1,8)}$=8.5, P<0.05; for early aphasics $F_{(1,8)}$<1).

In both groups, the gender decision task evoked more anterior, the semantic task more posterior negativity (Task × Gradient: $F_{(1,39)}$=4.7, P<0.05), and the negative-going SW was larger in the semantic than in the gender decision task (Task: $F_{(1,39)}$=9.0, P<0.01).

Independent of the task, aphasics displayed the more pronounced left anterior negativity than controls (Group × Hemisphere × Gradient: $F_{(1,39)}$=6.9, P<0.01;

Gradient × Hemisphere for aphasics: $F_{(1,17)}$=4.0, P<0.07; for controls: $F_{(1,22)}$=2.5, NS). Within the group of aphasics this pattern tended to be more prominent in non-fluent than in fluent aphasics (Syndrome × Gradient × Hemisphere: $F_{(1,16)}$=3.8, P<0.07; Gradient × Hemisphere for non-fluent aphasics: $F_{(1,8)}$=22.3, P<0.01, for fluent aphasics NS).

When the relationship of performance level and evoked response was evaluated, the ANOVAs comparing good and bad performers did not show any significant results for the semantic task and the syntactic task, neither for aphasics nor for controls. There were also no significant correlations between response latencies and evoked responses over the four regions.

Neither in the syntactic nor in the semantic task did the SW differ significantly between "good" and "bad" performers. There were also no significant correlations between response latencies and evoked responses over the four regions. Further, no correlation was found between months post onset of the disease and performance. Also the grouping of aphasics according to their syntactic functioning in spontaneous speech (as measured by the AAT) did not reveal any significant results.

Discussion

As expected, aphasics exhibited better performance on a semantic than on a syntactic task. Although overall performance was reduced in aphasics compared to controls, aphasics showed particularly attenuated responses when making gender decisions on concrete German nouns, but only moderately impaired performance on a semantic classification task involving the same nouns. Also the pattern of event-related brain responses differed between groups. The expected pattern of laterality with more pronounced laterality during syntactic than during semantic processing was displayed by controls, whereas aphasics exhibited the more pronounced laterality during the semantic task. Nonetheless, a relationship between performance and SW pattern was not supported by correlations or by comparing "good" and "poor" performers within each group.

Interestingly, the left-anterior negativity obtained in both tasks was more prominent in patients than in controls, particularly in non-fluent aphasics. Within the group of aphasics, those with a longer time elapsed since the lesion exhibited the larger negativity over all areas in the semantic task.

The data from healthy control subjects provide another piece of evidence for differential laterality of language processing: left-lateralized activation was seen in a task requiring syntactic processing, contrasting with less lateralized activation elicited by a task requiring semantic processing. We can only speculate which psycholinguistic subprocesses are reflected in the present differential laterality pattern: According to the psycholinguistic model put forward by Levelt et al. (1999), gender decision on names of depicted objects requires: (1) access to the semantic representation of the object name and (2) access to its grammatical information (so-called lemma), while a semantic decision requires (1) but not (2). Thus, the more pronounced laterality to the left of brain responses in the syntactic task may tentatively be related to the access to lemmas, which may be housed in the left-perisylvian areas (Pulvermüller 1999a). As an alternative, a neurobiological approach to language proposed by Pulvermüller (1999b) suggests a different explanation: Since gender decision requires the activation of the neuronal memory traces of both a noun and an article, laterality of brain responses during this task can thus be related to the left-anterior negativity observed for articles and other grammatical function words placed in and out of sentence contexts (Neville et al. 1992; Pulvermüller et al. 1995). In contrast, the semantic classification task requires simultaneous activation of the memory traces of a concrete noun and its attribute, and there is no indication that these item's representations are strongly lateralized. Thus, the present pattern of differential lateralization in a semantic and syntactic task has two possible explanations: First, it can be related to subprocesses of lexical access, in particular lemma access. Second, an explanation is possible based on the word class membership of the words involved in the tasks and the laterality degree of these words' neuronal memory traces, in particular the strongly lateralized memory traces for function words.

It is tempting to interpret the left-anterior negative SW observed in the gender decision task with the Left-Anterior Negativity (LAN) reported in different tasks that require the processing word-category information in phrasal context (for overview see Friederici 1995). The LAN has been found as early as 120 ms in response to reading a word-category error (Neville et al. 1991), but also with peak latency between 300 and 500 ms in tasks including syntactic violations, the processing of a verb's subcategory information, or verb agreement information (Friederici et al. 1996). The presently observed left-anterior negative SW 300–600 ms following the presentation of an object picture to which the noun gender had to be assigned may have activated syntactic processes similar to processes involved in the generation of the LAN. Surface negative ERPs are supposed to reflect cortical excitability and excitation in the respective networks, as they represent depolarization in underlying apical dendrites of cortical pyramidal cells (Elbert and Rockstroh 1987). Accordingly, we may relate the left-anterior negative SW to excitability and excitation in the underlying areas, presumably the perisylvian language cortices. From this perspective, left-anterior negativity may indicate the activation of different networks all involved in syntactic processing and activated by different tasks or syntactic requirements.

In one study the absence of the early LAN in aphasics was reported (Friederici et al. 1999). This study, however, involved a language comprehension task while in the present study processes of language production were investigated. Furthermore, the critical time window was earlier (150–300 ms) and in the present study the apha-

sics were more impaired as measured by the Token Test. These arguments make it hard to compare the two studies directly, but these are issues that should be addressed in future investigations.

Taken together, the present pattern of differential lateralization in a semantic and a syntactic task can be related either to subprocesses of lexical access, in particular lemma access, or to the major lexical categories of the words involved in the tasks and the laterality degree of their neuronal memory traces, in particular strongly lateralized memory traces for function words and less lateralized cell assemblies for content words.

The behavioral results suggest that syntactic processes are more impaired in aphasics than semantic processes. Both tasks seemed to be of similar complexity because (1) they involved the same lexical items, (2) the task instructions were of similar complexity (does it go with *der/die*? does it belong to living/non-living things?), and (3) control subjects made an equal number of errors in both tasks. We may assume that different linguistic processes related to semantic and syntactic knowledge are differentially affected in aphasia. The present data, however, do not justify this conclusion. First, the present study only dealt with aphasia of mild to moderate degree. Severely affected aphasic patients were excluded in order to achieve a high level of accuracy in performance of the linguistic tasks. Second, the syntactic and semantic tasks may reflect special forms of syntactic and semantic processing. A comparison with other syntactic tasks would substantiate the conclusion. Third, it might have been possible to solve the semantic task without knowledge about lexical concepts but only based on so-called world knowledge, that is, episodic memories from one's own experiences. Thus, we may conclude that the present results suggest that syntactic and semantic knowledge access are differentially affected in mild to moderate aphasia, with syntactic processes being much more vulnerable.

The laterality pattern in the aphasics seems intriguing, as it was opposite to that of controls. The laterality during semantic processing is consistent with the *left hemisphere substitution hypothesis* that supposes left-hemispheric circuits are important for the recovery of language functions. Performance data support this view, as the task accompanied by left-lateralized brain responses yielded better behavioral performance. Compared to controls, aphasics were only moderately impaired on the semantic task. It is tempting to relate the SW laterality during this task to this behavioral success, although this hypothesis is not substantiated by correlation between ERP and performance. Compensatory effort may also be deduced from the more pronounced overall negativity in "late" aphasics in the semantic task, although such a hypothesis certainly requires more specific examination.

In contrast, the negligible laterality during syntactic processing suggests an equal involvement of the hemispheres in this task and, thus, *a relatively stronger* right-hemispheric recruitment of circuits in aphasics than in controls. However, the bihemispheric activation did not facilitate performance on a genuinely syntactic task. This is in line with other findings suggesting that right hemispheric activation in aphasia is not efficient in improving certain linguistic processes (Heiss et al. 1999). Again, the pronounced left-anterior negativity seen in the patients during both tasks suggests an increased – compensatory? – effort or activation. Such negativity, which has been interpreted as an index of the recruitment of left-perisylvian language cortices (Neville et al. 1992), was most pronounced in the non-fluent patients, who are known to have particular difficulties with syntax and function words. The left anterior activity focus may be an indicator of enhanced processes in the remains of the language processing areas on the left which likely helped to achieve the above-chance performance in our patients. Thus, while the pattern of laterality with more pronounced left-anterior negativity in the semantic task may have indicated substitution enabling adequate performance, the pronounced anterior negativity over both hemispheres in the syntactic tasks may have indicated compensatory effort, which, however, involved inadequate brain areas or was insufficient to improve performance. Alternative explanations have to be considered: Verbal working memory has been associated with the activation of left-anterior brain regions, and aphasic patients have been reported to perform poorly on verbal working memory tasks, but also on other short term memory tasks (Caspari et al. 1998; Meier et al. 1990; Ostergaard and Meudell 1984). Although a non-linguistic control task might have allowed to clarify the contribution of working memory deficits to the present results in aphasics, it may be argued that the present semantic task was indeed a non-linguistic task involving only a semantic categorization and no access to lexical concepts.

To what extent might the ERP-pattern indicate neurophysiological consequences of the lesion? On the one hand, evidence indicates that the periacute, mostly cytotoxic edema is resolved within 2 weeks (O'Brien 1995). Longer lasting extracellular edema, due to disturbance of the blood-brain barrier (O'Brien et al. 1974), seems to have little effect on electric activity and evoked responses (Sutton et al. 1980). Thus, a major impact of the lesion on the present pattern of ERP laterality does not seem likely. In addition, such an influence should have resulted in different patterns in early and late aphasics in the present tasks, which were not found. On the other hand, an impact of the lesion on ERP amplitudes has been demonstrated, for instance, by Yamaguchi and Knight (1991). The authors reported smaller P300 amplitudes following temporal-parietal lesions. Note, however, that we found *increased* amplitudes over the damaged hemisphere and that Swick and Knight (1999) demonstrated unaltered ERPs in patients with dorsolateral prefrontal regions. The latter implies that a lesion per se is not a sufficient condition to result in altered brain topographies. Nevertheless, it is difficult to distinguish whether a reduction in amplitude is the consequence of a lesion precisely in the area of sources of the specific ERP component, or whether a reduction in ERP amplitude is a

non-specific phenomenon following brain damage per se. The same holds for the present results: (1) the topographical pattern of the early anterior lateralized SW may be attributed to the left hemispheric lesion, and (2) due to rigorous and functionally highly specific effort, aphasic patients may show an increased left prefrontal activation during tasks and trials they were able to handle efficiently. Also an increase in ERP amplitudes over the right hemisphere in aphasics might be difficult to explain: Syntactic impairment resulting from the left hemispheric lesion might be compensated by secondary capacities of the right hemisphere. However, the effort of aphasics to solve the task might have led to a generalized activation, which may only be seen over the right hemisphere given the left-hemispheric lesion.

However, the relocation of semantic/syntactic processes discussed within the framework of a language-related model might circumvent this problem of distinction between a functional change as a consequence of language deficit and a general change as a function of brain damage, because a non-specific consequence of brain-damage should not be expected to contribute to this relocation of processes and laterality of ERPs, i.e., it should not be reflected task dependently.

Taken together, the present results suggest the relevance of left-hemispheric circuits in language recovery in aphasia. Stronger left-anterior activity than in controls was found in patients who were able to perform well on a syntactic and a semantic task, the task with the better performance being accompanied by the more pronounced laterality of electrocortical correlates of cognitive and language processing. However, the reversed pattern of laterality across tasks in aphasic patients cannot be explained sufficiently by the left hemispheric substitution hypothesis of language. A more complex interaction between the hemispheres may have been the basis of the lack of laterality during syntactic processing.

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