

Real-time semantic compensation in patients with agrammatic comprehension: Electrophysiological evidence for multiple-route plasticity

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To understand spoken language requires that the brain provides rapid access to different kinds of knowledge, including the sounds and meanings of words, and syntax. Syntax specifies constraints on combining words in a grammatically well formed manner. Agrammatic patients are deficient in their ability to use these constraints, due to a lesion in the perisylvian area of the language-dominant hemisphere. We report a study on real-time auditory sentence processing in agrammatic comprehenders, examining their ability to accommodate damage to the language system. We recorded event-related brain potentials (ERPs) in agrammatic comprehenders, nonagrammatic aphasics, and age-matched controls. When listening to sentences with grammatical violations, the agrammatic aphasics did not show the same syntax-related ERP effect as the two other subject groups. Instead, the waveforms of the agrammatic aphasics were dominated by a meaning-related ERP effect, presumably reflecting their attempts to achieve understanding by the use of semantic constraints. These data demonstrate that although agrammatic aphasics are impaired in their ability to exploit syntactic information in real time, they can reduce the consequences of a syntactic deficit by exploiting a semantic route. They thus provide evidence for the compensation of a syntactic deficit by a stronger reliance on another route in mapping sound onto meaning. This is a form of plasticity that we refer to as multiple-route plasticity.

In listening to language, qualitatively different syntactic and semantic constraints are combined to derive the message from the speech signal. The basic distinction between syntax and semantics can be observed in electrophysiological recordings of brain activity, where this distinction is reflected in two qualitatively different brain signals: the P600/SPS and the N400, respectively (1–4). In this study, we used these two language-related event-related brain potential (ERP) effects to investigate the language deficit of agrammatic comprehenders and the nature of possible compensatory processes resulting from brain damage.

It is a well established finding in the ERP literature on language comprehension that varying the meaning relation between words affects the amplitude of a negative-going potential with an onset at ≈ 250 ms and a maximal amplitude at ≈ 400 ms after word onset. This potential is known as the N400. Although the grammatical structure of the sentence “The pizza is too hot to drink” is identical to that of the sentence “The pizza is too hot to eat,” *drink* elicits a larger negative-going potential than *eat* because of the semantic mismatch between *drink* and the sentence context. The amplitude of the N400 is a sensitive manifestation of the binding of word meanings into an overall interpretation of the utterance (3, 5, 6). In aphasia research, this ERP component has been used to track real-time comprehension deficits in brain-damaged patients, where it has revealed processing deficiencies in the time course of meaning activation and integration (7–10). In aphasic patients, the onset latency of the N400 can be delayed by ≈ 150 ms relative to control subjects, and the distribution of the component over the scalp can deviate

somewhat from that found in normal controls (possibly associated with changes in volume conduction due to the brain lesion). Nevertheless, the overall electrophysiological pattern is consistent with that of the standard N400 effect.

A qualitatively different brain response is observed to violations of syntactic constraints, as in, for instance, “The boy are throwing the ball,” in which the singular noun-phrase *the boy* mismatches in the grammatical feature of number with the plural verb form *are*. This violation of a syntactic constraint results in a positive-going effect that starts at ≈ 500 ms after the onset of the word that renders the sentence ungrammatical. This effect is known as the P600/SPS (1, 4).

It is important to note that we do not claim that the N400 effect and the P600/SPS are language-specific. In fact, for none of the language-relevant ERPs can one make the claim that they are language-specific (11). For instance, N400 effects also have been reported with pictures and meaningful environmental sounds as input (12, 13). The P600/SPS is not only observed for violations of syntactic structure, but also of musical structure (14). With language as input, however, the brain seems to honor the distinction between semantic and syntactic processing, in that semantic violations usually result in an N400 effect and syntactic violations in a P600/SPS, sometimes accompanied by an earlier anterior negativity (LAN) (15). For our purposes, this outcome is sufficient to evaluate the consequences of brain damage in agrammatic aphasics for their on-line processing of syntactic information.

To investigate the real-time consequences of brain damage that has resulted in a syntactic deficit, subjects listened to sentences containing either one of two syntactic violations. One violation concerned the number agreement between subject and verb (e.g., “The girls pay the baker and *takes* the bread home”). The other one violated word-order constraints (e.g., “The thief steals the *expensive very clock* from the living room”). Both kinds of violation elicit a P600/SPS in intact language listeners. However, agrammatic comprehenders are limited in their ability to use grammatical information such as morphosyntactic features (e.g., the suffix *-s* on the verb form *take*) and word-order constraints during on-line sentence interpretation (16). These patients could nevertheless derive a (partly) adequate interpretation by recognizing and combining the individual word meanings in their linear order (17, 18). In this case, the adequacy of the interpretation is determined by the semantic coherence of the individual words in their left-to-right order. Here then, the linear order of the input string, rather than the hierarchical phrase structure, determines the ease of interpretation. This linear string hypothesis predicts for the agrammatic aphasics a difference in the electrophysiological records for word-order violations and their correct counterparts, but not for the agree-

Abbreviations: ERP, event-related brain potential; AAT, Aachen Aphasia Test.

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Table 1. Individual patient information for the aphasic patients

Patient	Age, years	Sex	Token Test	Comprehension score AAT	Syntactic comprehension score	Lesion
1 Broca NA	68	M	24	105/120	88/144	Fronto-temporal
2 Broca NA	50	F	10	97/120	95/144	Fronto-temporo-parietal including insula
3 Broca NA	74	F	7	108/120	115/144	Frontal including insula
4 Broca NA	65	F	18	91/120	111/144	Fronto-temporal including insula
5 Broca NA	51	M	20	109/120	113/144	Fronto-temporo-parietal including insula
6 Broca A	63	M	38	67/120	52/144	Frontal including insula
7 Broca A	42	M	17	94/120	74/144	Temporo-parietal
8 Broca A	67	M	18	103/120	47/144	Fronto-temporal including insula
9 Broca A	70	M	50	90/120	59/144	Fronto-temporal including insula
10 Broca A	48	M	42	89/120	51/144	No adequate information available

Information on the nonagrammatic (NA) and agrammatic (A) Broca's aphasics. The patients were classified as nonagrammatic or agrammatic on the basis of their scores on a specific test of their syntactic comprehension. Scores were computed on a 3-point system: 2 points for a correct response, 1 point for a correct response after repetition or self-correction, and 0 points for an incorrect response. Maximum score is 144 (72 items × 2 points). Nonagrammatic aphasics have a score of above 85. Agrammatic aphasics have a score of below 75. The agrammatic aphasics showed chance-level performance on the most complex structures (see Fig. 1). The overall severity of the aphasia is indicated by the score on the Token Test: no/very mild disorder (0–6), light (7–23), middle (24–40), and severe (>40). The severity of the language comprehension disorder is indicated by the score on the AAT subtest for comprehension (which includes word and sentence comprehension in both the auditory and visual modality): no/very mild disorder (107–120), light (90–106), middle (67–89), and severe (1–66). In addition, information on the lesion site in the left hemisphere is presented.

ment violation and their correct counterparts. In the latter case, the linear order of the input string remains the same under the violation.

Materials and Methods

Participants and Patient Selection. Ten aphasic patients with a lesion in the left perisylvian area resulting from a cerebrovascular accident, and 12 age- and education-matched controls (mean age 59 years, range 49–72 years, SD 7.8 years) participated in this study. All subjects gave informed consent, in accordance with the declaration of Helsinki. The patients were tested at least 9 months post-cerebro-vascular accident. All patients showed slow, effortful speech and omissions and/or reductions of morphosyntactic elements in their speech output. They were administered the Dutch version of the Aachen Aphasia Test (AAT) (19) and were classified as Broca's aphasics (see Table 1). To select the aphasic patients who were severely agrammatic in their comprehension, we administered a Dutch version of a sentence-picture matching test (20). The participants listened to a total of 72 spoken sentences and selected one of four pictures that matched each sentence. The test contained five levels of syntactic complexity, ranging from active, semantically irreversible sentences (e.g., "The man with the tie carries the ball") to sentences containing an embedded subject-relative clause in the passive voice ("The child that is sought by the man carries a ball"). Correct matching for complexity levels 2–5 could only be based on syntactic information. Five patients showed a level of performance that was just above or not different from chance (25% on this test) for sentence structures that were more complex than simple active sentences (see Fig. 1). These patients were classified as agrammatic comprehenders. The remaining five aphasic subjects also showed a complexity effect. However, even for the most complex structures their performance level was still above chance, demonstrating some remaining sensitivity to syntactic cues. These patients were classified as nonagrammatic comprehenders on the basis of their remaining capacity for processing syntax.

Stimulus Materials. The materials consisted of 480 spoken sentences. Half of these sentences were fillers. The other half consisted of 120 sentence pairs. Each sentence pair consisted of a sentence with a syntactic violation and its correct counterpart. Sixty sentences contained an agreement violation, where the

grammatical subject of a sentence does not agree in number with the finite verb of the matrix clause (e.g., "The girls pay the baker and takes the bread home"; the violation is underlined). These sentences were paired with 60 correct counterparts. Sixty sentences contained a word-order violation (e.g., "The thief steals the expensive very clock from the living room"; the violation of word-order preference is underlined) and also were paired with 60 correct counterparts. All materials were spoken at a normal rate by a female speaker. With the word-order stimuli, care was taken to ensure that the correct and incorrect versions were matched on prosody and rhythm. In Dutch, the critical regions of the word-order sentences (i.e., *very expensive clock* and *expensive very clock*) can be realized with a natural neutral

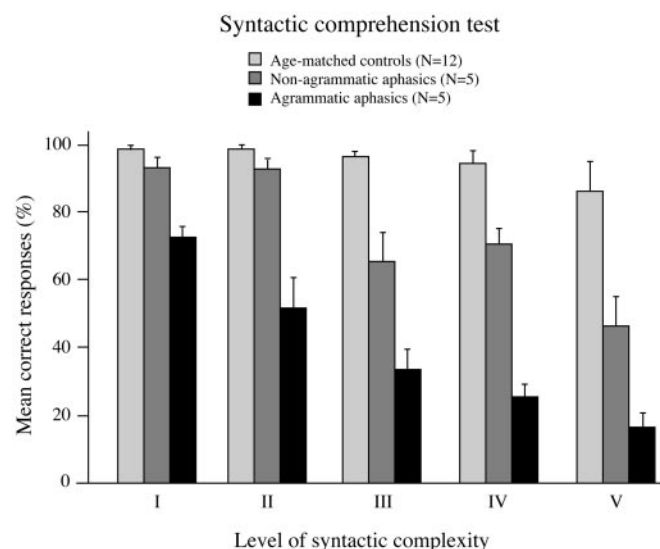


Fig. 1. Syntactic comprehension test. Mean percentage correct responses for the age-matched controls, the nonagrammatic aphasics, and the agrammatic aphasics, for five different sentence types: (I) active, semantically irreversible sentences; (II) active, semantically reversible sentences; (III) simple passive sentences; (IV) sentences with an active subject-relative clause; and (V) sentences with a passive subject-relative clause. The syntactic complexity of the sentences increases from II to V.

prosodic contour, without intonational breaks or differential stress patterns. This is the contour that we used.

Experimental Procedures. Participants were tested individually in a sound-attenuated booth. Sentences were presented via a digital audio tape (DAT) recorder (300ES; Sony, Tokyo). The participants listened to the stimuli via closed-ear headphones (HD-224; Sennheiser, Wedemark, Germany) while fixating their eyes on a fixation cross on the monitor in front of them. Participants were told that they would hear sentences, some of which had language errors in them, but they were given no information concerning the kinds of errors that would occur. Participants were informed that they would occasionally be asked a question about the last presented sentence. All questions were related to the content of the correct sentences. For example, after the presentation of the sentence, “The thief steals the very expensive clock from the living room,” the question asked was, “What did the thief steal?” The total number of questions was 24, 4 per block. The answers to these questions should certify that the participants were actively engaged in processing the sentences. The participants were tested in two sessions separated by at least 4 weeks. Correct and incorrect versions of a particular item were tested in different sessions, with each session containing the same number of correct and incorrect trials. Each session started with a practice list. The total duration of stimulus presentation was 40 min per session.

Electrophysiological Recording and Data Analysis. ERPs were recorded from 13 scalp sites, each referred to the left mastoid. Three electrodes were placed over the midline (Fz, Cz, and Pz), and three pairs were placed over the left and right hemispheres (F7, F8, FT7, FT8, PO7, and PO8), according to the standard convention of the American Electrophysiological Society. Four electrodes were placed over nonstandard intermediate locations: a temporal pair (LT and RT) placed 33% of the interaural distance lateral to Cz, and a temporo-parietal pair (LTP and RTP) placed 30% of the interaural distance lateral to Cz and 13% of the inion-nasion distance posterior to Cz. Vertical eye movements were monitored via a supra- to suborbital bipolar montage. A right-to-left canthal bipolar montage was used to monitor for horizontal eye movements. Activity over the right mastoid bone was recorded on an additional channel to determine whether there were differential contributions of the experimental variables to the presumably neutral mastoid site. No such differential effects were observed.

The electroencephalogram (EEG) and electrooculogram (EOG) recordings were amplified by a SynAmp model 5083 EEG amplifier system, using a band-pass filter of 0.02 to 30 Hz. Impedances were kept below 3 k Ω . The EEG and EOG signals were digitized on-line with a sample frequency of 200 Hz. The waveforms were screened for amplifier and movement artifacts, which were rejected (the overall rejection rate was 21.7% for the age-matched controls, 23.5% for the nonagrammatic aphasics, and 20.0% for the agrammatic aphasics). Datasets with a substantial number of eye blinks were corrected for blink artifacts (21).

The waveforms were normalized on the basis of the EEG activity 150 ms before the onset of the word that violates word-order preferences or number agreement. Repeated measures ANOVAs were performed on the mean amplitudes in the 600- to 1,500-ms latency range after the onset of the word that has been shown to elicit the P600/SPS in normal populations (1), and on additional latency ranges when necessary.

Results

Behavioral Data. The mean average of the correct responses to the content questions was 98% for the elderly control subjects (range 91–100%), 97% for the nonagrammatic patients (range 96–

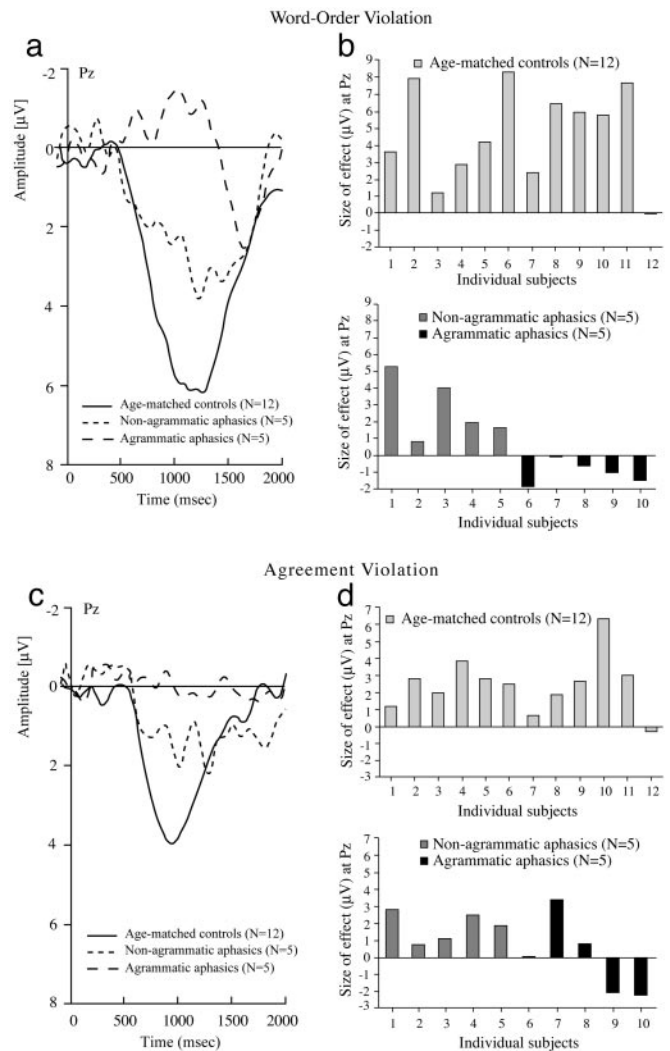


Fig. 2. Difference waveforms (obtained by subtracting the waveforms for the correct from the incorrect condition) and individual subject effect sizes at electrode site Pz. Waveforms are averaged over participants for the group of age-matched controls ($n = 12$, solid line), nonagrammatic aphasics ($n = 5$, light dashed line), and agrammatic aphasics ($n = 5$, heavy dashed line). The waveforms are aligned at zero on the onset of the word that violates word-order preferences (a) or number agreement (c). (a) Word-order violation, difference waveforms. (b) Word-order violation effect sizes for individual subjects. Effect size (mean area amplitude in μ V) at electrode site Pz per subject in the 600- to 1,500-ms window. (c) Agreement violation, difference waveforms. (d) Agreement violation effect sizes. Effect size (mean amplitude in μ V) at electrode site Pz per subject in the 600- to 1,500-ms window. Negativity is plotted upwards.

100%), and 81% for the agrammatic patients (range 63–92%). Although the agrammatic patients had a lower score than the nonagrammatic aphasics and the elderly controls, their level of performance indicates that they actively processed the sentences. Answering the questions did not require a syntactic analysis of the sentence and was therefore unrelated to the scores on the syntactic comprehension test.

Electrophysiological Data. Difference waveforms (obtained by subtracting the averaged waveforms of the correct from the incorrect condition) for the word-order violation and the agreement violation are shown in Fig. 2 a and c, respectively, for a representative posterior midline electrode site (Pz). Both the age-matched control subjects and the nonagrammatic aphasics showed a sizeable P600/SPS effect to this syntactic violation.

WORD ORDER VIOLATION

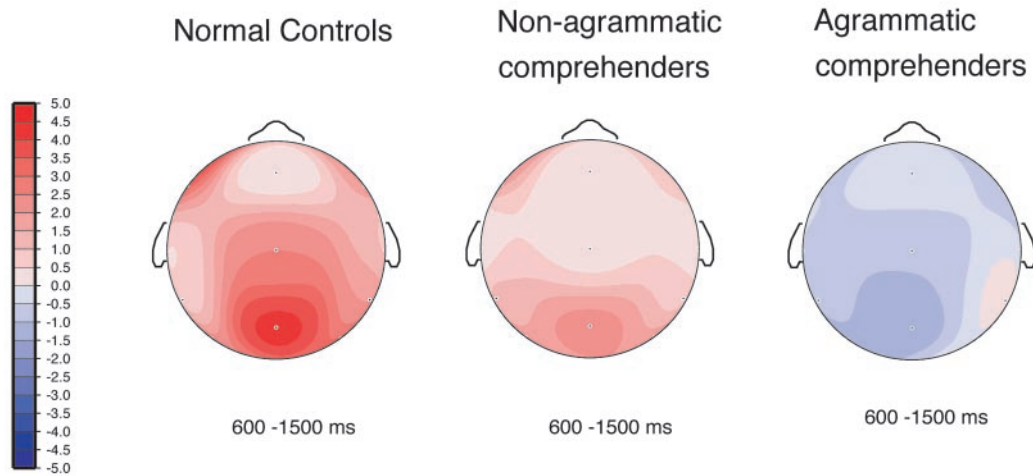


Fig. 3. The scalp distribution of the ERP effects that were obtained for the word-order violation in the normal controls, the nonagrammatic comprehenders, and the agrammatic comprehenders. Effects were based on mean amplitudes in the 600- to 1,500-ms latency window. Positive polarity effects are in red, negative-going effects are in blue. Scale values are in μV .

Fig. 3 shows the topographic distribution of the word-order violations. As can be seen, in both normal controls and nonagrammatic aphasics the effect was strongest over posterior electrode sites. This posterior distribution is standardly observed for the P600/SPS to syntactic violations (1, 4). Both subject groups showed the same P600/SPS effect to the agreement violations (see Fig. 2c). The onset latency of the violation effects was at ≈ 500 ms for the word-order violation and slightly later for the agreement violation. Both subject groups showed the same onset latency of the effects, but the amplitude of the syntactic violation effects was larger in the normal controls than in the nonagrammatic aphasics. As can be seen in Fig. 2b and d, 11 of the 12 normal subjects showed the P600/SPS effect, as did all 5 nonagrammatic aphasics. In short, despite some variation in the size of the effects, normal controls and nonagrammatic aphasics showed a P600/SPS to the two types of syntactic violations that were used in this study.

Repeated measures ANOVAs were done for the three subject groups separately on the mean amplitudes in the 600- to 1,500-ms latency range over all 13 electrode sites. The ANOVA for the elderly controls showed an overall significant P600/SPS effect (word-order violation, $P < 0.0002$; agreement violation, $P < 0.003$). A significant P600/SPS effect also was obtained for the nonagrammatic Broca's aphasics (word-order violation, $P < 0.007$; agreement violation, $P < 0.02$). For the word-order violations, analyses on individual electrode sites revealed significant effects, for both groups, at electrode sites Cz, Pz, RT, RTP, PO7, and PO8. For the agreement violation, significant effects were obtained for both groups at electrode sites Fz, Cz, Pz, LT, and PO8.

The results of the agrammatic aphasics were clearly very different from those of the two other subject groups (see Figs. 2 and 3). For the word-order violation, the early part of the waveform is dominated by a negative-going shift. The scalp distribution of this negative shift has a posterior maximum with a left-scalp preponderance (see Fig. 3). This distribution is quite standard for auditory N400 effects and compares well with normal subject populations (22). No N400 effect is seen over right-scalp electrodes. Although deviant from normal populations in this latter topographical aspect, the overall pattern is consistent with the N400 literature on aphasic patients, where

N400 effects tend to have a left-scalp preponderance (9). Over electrode site LTP, where the N400 effect was maximal (see Fig. 4), the onset of the N400 effect is at ≈ 300 ms. As has been previously observed in agrammatic patients (9), the onset of the N400 effect was (slightly) later than usually found in normal populations. In addition, the N400 effect lasted for a relatively long period, until $\approx 1,500$ ms. As is shown in Fig. 2b, at least four of the five agrammatic aphasics showed that their waveforms for

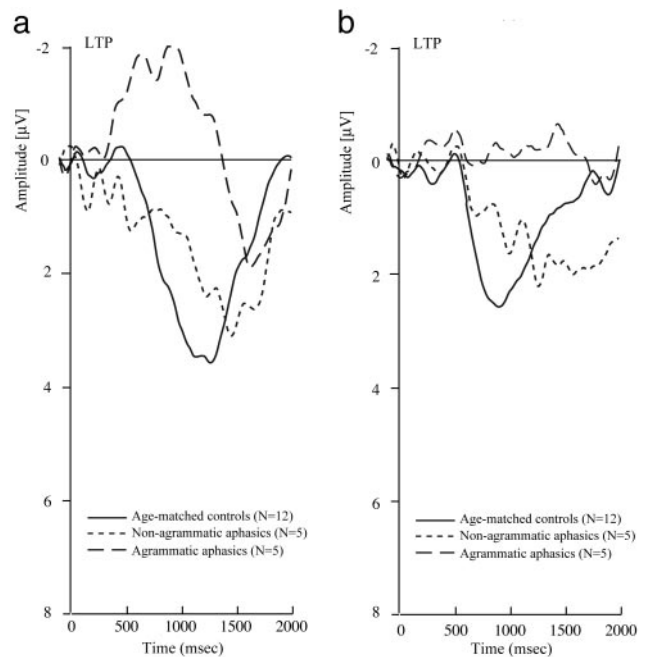


Fig. 4. Difference waveforms (obtained by subtracting the waveforms for the correct from the incorrect condition) at a left temporo-parietal electrode site (LTP). Waveforms are averaged over participants for the group of age-matched controls ($n = 12$, solid line), nonagrammatic aphasics ($n = 5$, light dashed line), and agrammatic aphasics ($n = 5$, heavy dashed line). The waveforms are aligned at zero on the onset of the word that violates word-order preferences (a) or number agreement (b). Negativity is plotted upwards.

the word-order violation were dominated by the N400 effect. An ANOVA with Patient Group (agrammatics vs. nonagrammatics) as the additional factor resulted in a highly significant Group by Word Order interaction ($P < 0.001$), resulting from the qualitatively different ERP responses to the word-order violation in the agrammatic aphasics compared with the nonagrammatic aphasics.

As can be seen in Figs. 2*a* and 4, the N400 effect for the word-order violation was followed by a late positivity that started at $\approx 1,400$ ms. This positivity was seen only over posterior electrode sites. An analysis for the 13 electrode sites on the mean amplitudes in the 1,500- to 1,800-ms latency window failed to reach significance ($P = 0.45$). However, the positivity became significant in an analysis over the five posterior electrode sites (LTP, Pz, RTP, PO7, and PO8; $P = 0.015$).

In contrast to the word-order violation, the agrammatic aphasics did not show any effect for the agreement violation (see Figs. 2*c* and 4*b*). The repeated measures ANOVA on the mean amplitudes in the 600- to 1,500-ms latency window for the 13 electrode sites failed to show a significant effect of this syntactic violation ($P = 0.73$). Analyses on individual electrode sites also failed to show sensitivity to the agreement violation (minimum $P = 0.49$). Analyses on the individual effect sizes demonstrated that the agrammatic patients, in contrast to the other two subject groups, showed variable and inconsistent performance on the agreement violations. This finding is shown in Fig. 2*d*. The differences shown here do not reflect any statistically significant pattern: the agrammatic aphasics showed a profile of random positive and negative ERP differences over electrode sites, without any consistency within a single patient. Moreover, when the same patients were tested on a different set of agreement violations (not reported on here), each of the agrammatic patients again showed a completely variable pattern of differences over electrode sites. In addition, individual patients were highly variable in their performance on the two sets of agreement violations, with no consistency between the sets. The random performance on agreement violations is characteristic of this patient group. However, on other linguistic and nonlinguistic tests, these agrammatic aphasics do show consistent behavior. The word-order violation effect reported here is an example in point. In addition, other language-related ERP recordings with these patients demonstrate that they do exhibit a standard N400 effect when confronted with semantic violations.

As can be seen in Table 1, the agrammatic aphasics had a lower score than the nonagrammatic aphasics on not only the syntactic off-line test, but also the Token Test and the AAT comprehension test. One can, therefore, ask whether the ERP results reflect a syntactic deficit or, more generally, the severity of the aphasia. Because syntactic cues contribute to the performance on both the Token Test and the AAT comprehension test, it is to be expected that these scores correlate with the performance on the syntactic off-line test. Thus, to address the issue of the specificity for syntax, we have to look at an aspect of comprehension that does not invoke sentential-syntactic cues. This aspect is provided by a part of the AAT comprehension test that measures single-word comprehension. In this part of the comprehension test, single words are presented either auditorily or visually. The patients have to select one picture (from an array of four pictures) that matches the presented word. The test results showed an average score for the agrammatic comprehenders of 50 (range 40–59) that is very similar to the average score of the high comprehenders, which was 53 (range 50–57). A median split of the single-word comprehension scores resulted in a group of high single-word comprehenders consisting of two agrammatic aphasics and three nonagrammatic aphasics (subjects 1, 3, 5, 7, and 8 in Fig. 2*b*) and a group of low single-word comprehenders consisting of three agrammatic aphasics and two nonagrammatic aphasics (subjects 2, 4, 6, 9, and 10 in Fig. 2*b*). The ERP results

for the individual patients indicate that the grouping of patients on the basis of single-word comprehension does not pattern with the N400 and P600/SPS effects that were obtained for the word-order violation in the agrammatic and nonagrammatic aphasics, respectively. It is, therefore, more likely that the ERP results reflect impairments that are relatively specific for on-line syntactic processing than a relatively unspecific impairment in on-line processing of verbal material in general.

Discussion

The present results provide electrophysiological evidence that agrammatic comprehenders are severely impaired in the ability to exploit syntactic information in real-time spoken-language understanding. In their on-line processing profile, as revealed in the ERP waveforms, agrammatic comprehenders were insensitive to agreement violations. Sensitivity to these violations requires the processing of morphosyntactic features such as number marking on the verb. Nevertheless, these same patients showed sensitivity to another type of syntactic violation, namely a violation of word order. However, in this case their brain activity was qualitatively different from the nonagrammatic aphasics and control subjects. These latter subject groups showed the ERP response that, in the context of language processing, usually is seen to syntactic violations (the P600/SPS). In contrast, the ERP of the agrammatic aphasics was dominated by the N400 effect that usually is observed to semantic binding operations during on-line language processing. Although the late positivity after the N400 effect might indicate some remaining capacity for syntactic processing, it more likely reflects a general taxing of processing resources after a semantic binding problem. A similar positivity after the N400 effect has been observed for aphasic patients in a study with semantic violations only (9). In summary, although word-order violations trigger a syntax-related ERP response in normal controls and nonagrammatic comprehenders, the same violations trigger an ERP response related to semantic binding in Broca's aphasics with agrammatic comprehension.

We offer the following explanation for this semantic ERP response in agrammatic aphasics. The absence of a P600/SPS in combination with chance performance in an off-line syntactic judgment task for sentences that were more complex than simple actives suggests that the agrammatic aphasics are no longer able to exploit syntactic information during sentence comprehension. The N400 effect for the word-order violations suggests that these sentences were processed through another (compensatory) processing route that was not available for the agreement violation. The lack of a syntax-related ERP effect suggests that the agrammatic comprehenders did not interpret these sentences through a hierarchically organized phrase-structure representation. Instead, word meanings were incrementally integrated in the semantic representation of the linear string of preceding words, where the interpretation process was more difficult when the adjective preceded the adverb (*thief steal expensive very*) than in the reverse order (*thief steal very expensive*). In the adjective-before-adverb word order, the internal event structure is less coherent than in the correct order, due to the reversal of the semantic arguments of the denoted event (23). That is, in the semantic context of *thief steal expensive*, the canonical structure of events is better matched by mentioning what is being stolen, than by further expanding the meaning of *expensive* (as in *thief steal expensive very*). The results indicate that agrammatic patients still have access to this level of semantic information and are able to use this during real-time processing. This is not to say that their usage of semantic information is optimal, but it is certainly less affected than syntactic processing operations. As such, the relative preservation of a semantic processing route presumably results in the N400 effect.

The situation is different for the agreement violation. In contrast to the word-order violation, in the agreement violation the event structure of the sentence violating the subject-verb agreement remains the same as in the correct counterpart. In the absence of the capacity to process the morphosyntactic marker for plural in establishing agreement between the subject and the finite verb, the two sentence versions are identical. This might explain why an N400 effect is observed for word-order violations but no such effect is seen for the agreement violations. The latter type of sentence did not offer the possibility for a compensatory processing route.

The data therefore speak to the real-time functioning of the language system under impairment: the way in which different sources of linguistic information are combined to derive an interpretation seems to be tailored to the processing options that are still available to the impaired language comprehension system. The results that we obtained suggest that a semantic

processing stream provides an optimization of language comprehension within the limitations imposed by a syntactic deficit resulting from brain damage. Although this finding does not imply that semantic processing is fully optimal in agrammatic aphasics, it is relatively more preserved than syntactic processing. Under impairment, the comprehension system seems to weigh the remaining information differently or more strongly. This multiple-route plasticity instantiates the potential for on-line adaptation to impairments in the language comprehension system.

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1. Hagoort, P., Brown, C. M. & Groothusen, J. (1993) *Lang. Cognit. Proc.* **8**, 439–483.
2. Kutas, M. & Hillyard, S. A. (1980) *Science* **207**, 203–205.
3. Kutas, M. & Van Petten, C. K. (1994) in *Handbook of Psycholinguistics*, ed. Gernsbacher, M. A. (Academic, San Diego), pp. 83–143.
4. Osterhout, L. & Holcomb, P. J. (1992) *J. Mem. Lang.* **31**, 785–806.
5. Brown, C. M. & Hagoort, P. (2000) in *Architectures and Mechanisms for Language Processing*, eds. Crocker, M., Pickering, M. & Clifton, C. (Cambridge Univ. Press, Cambridge, U.K.), pp. 213–217.
6. Van Petten, C., Coulson, S., Rubin, S., Plante, E. & Parks, M. (1999) *J. Exp. Psychol. Learn. Mem. Cognit.* **25**, 394–417.
7. Brown, C. M., Hagoort, P. & Swaab, T. Y. (1996) in *Aphasietherapie im Wandel*, eds. Widdig, W., Ohlendorf, I. M. & Malin J.-P. (Hochschul Verlag, Freiburg, Germany), pp. 89–122.
8. Hagoort, P., Brown, C. M. & Swaab, T. (1996) *Brain* **119**, 627–649.
9. Swaab, T., Brown, C. M. & Hagoort, P. (1997) *J. Cogn. Neurosci.* **9**, 39–66.
10. Swaab, T., Brown, C. M. & Hagoort, P. (1998) *Neuropsychologia* **36**, 737–761.
11. Osterhout, L. & Hagoort, P. (1999) *Lang. Cognit. Proc.* **14**, 1–14.
12. McPherson, W. B. & Holcomb, P. J. (1999) *Psychophysiology* **36**, 53–65.
13. Van Petten, C. & Rheinfelder, H. (1995) *Neuropsychologia* **33**, 485–508.
14. Patel, A. D., Gibson, E., Ratner, J., Besson, M. & Holcomb, P. J. (1998) *J. Cogn. Neurosci.* **10**, 717–733.
15. Friederici, A. D., Pfeifer, E. & Hahne, A. (1993) *Cognit. Brain Res.* **1**, 183–192.
16. Linebarger, M. C., Schwartz, M. F. & Saffran, E. M. (1983) *Cognition* **13**, 361–392.
17. Caplan, D. (1987) *Neurolinguistics and Linguistic Aphasiology* (Cambridge Univ. Press, Cambridge, U.K.).
18. Caplan, D. & Hildebrandt, N. (1988) *Disorders of Syntactic Comprehension* (MIT Press, Cambridge, MA).
19. Graetz, P., De Bleser, R. & Willmes, K. (1992) *De Akense Afasie Test* (Swets & Zeitlinger, Lisse, The Netherlands).
20. Huber, W., Klingenberg, G., Poeck, K. & Willmes, K. (1993) *Neurolinguistik* **7**, 43–66.
21. Gratton, G., Coles, M. G. H. & Donchin, E. (1983) *Electroencephalogr. Clin. Neurophysiol.* **55**, 468–484.
22. Hagoort, P. & Brown, C. M. (2000) *Neuropsychologia* **38**, 1518–1530.
23. Sirigu, A., Cohen, L., Zalla, T., Pradat-Diehl, P., Van Eckhout, P., Grafman, J. & Agid, Y. (1998) *Cortex* **34**, 771–778.