

# Role of the Corpus Callosum in Speech Comprehension: Interfacing Syntax and Prosody

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## SUMMARY

The role of the corpus callosum (CC) in the interhemispheric interaction of prosodic and syntactic information during speech comprehension was investigated in patients with lesions in the CC, and in healthy controls. The event-related brain potential experiment examined the effect of prosodic phrase structure on the processing of a verb whose argument structure matched or did not match the prior prosody-induced syntactic structure. While controls showed an N400-like effect for prosodically mismatching verb argument structures, thus indicating a stable interplay between prosody and syntax, patients with lesions in the posterior third of the CC did not show this effect. Because these patients displayed a prosody-independent semantic N400 effect, the present data indicate that the posterior third of the CC is the crucial neuroanatomical structure for the interhemispheric interplay of suprasegmental prosodic information and syntactic information.

## INTRODUCTION

Spoken language comprehension requires a timely coordination of a number of different information types. The processing system has to identify phonemes, words, and the syntactic relation between them as well as to extract the suprasegmental information conveyed by the intonational contour of a spoken utterance. The different hemispheres seem to contribute to these aspects of processing differentially (Poeppel, 2003; Scott and Johnsrude, 2003). The former processes are thought to be based on neural networks implemented mainly in the left hemisphere (LH) (Friederici, 2002). The neural implementation of prosodic information, however, is less straightforward (Friederici and Alter, 2004; Gandour et al., 2004). While there is converging evidence from patient studies that emotional prosody is processed in the right hemisphere (RH) or bilaterally (Pell, 1998), the findings for a neural basis of linguistic prosody are more heterogeneous.

Some patient studies suggest that the RH plays a major role in linguistic processing (Brádvik et al., 1991; Weintraub et al., 1981), whereas other studies indicate that LH and RH patients are impaired in processing prosody of spoken sentences (Bryan, 1989; Emmorey, 1987). However, when using filtered speech that only carries prosodic information or degraded speech a clear RH involvement was reported (Blumstein and Cooper, 1974; Perkins et al., 1996). The RH involvement finds support in imaging studies that show a stronger RH activation in the temporal and frontal opercular cortices for the processing of sentences in which segmental information is filtered out, leaving the intonational contour intact (Meyer et al., 2002, 2004). The combined findings suggest that linguistic prosody is mainly lateralized to the RH but that the LH comes into play when phonemic segmental information is present in the speech signal and whenever prosody is segmentally bound (Behrens, 1985; Pell and Baum, 1997; Van Lancker and Sidtis, 1992).

This, however, means that the LH and the RH interact during normal on-line spoken language comprehension. If so, the pure logic suggests a crucial involvement of the corpus callosum (CC) as the neural basis for interhemispheric information exchange. Up to now, however, it has been unclear which part of the CC is the functionally relevant structure for this information exchange. A case study links a lesion in the anterior portion of the CC to the processing of affective and linguistic prosody (Klouda et al., 1988). In contrast, recent studies using imaging as well as lesion approaches indicate that the posterior quarter of the CC is the relevant part for the interhemispheric transfer of auditory information (Rumsey et al., 1996; Pollmann et al., 2002) and for the development of verbal abilities (Nosarti et al., 2004). Thus, which part of the CC provides the neural basis for the interhemispheric exchange of segmental and suprasegmental linguistic information is debatable. Here, we report data providing the ultimate test for this open issue by investigating patients with lesions in the anterior or posterior portions of the CC, respectively.

The experimental paradigm of the present study has been shown to be sensitive to functional interaction of segmental information and linguistic prosody. Focusing on verb argument structure information as the crucial syntactic parameter, and intonational phrase boundary as the

**Table 1. Examples of Stimuli**

Experimental Items		
(A) Prosodically Correct		
Prosody-argument structure match condition (intransitive verb)		
<i>[Peter verspricht Anna <b>zu arbeiten</b>]<sub>IPH1</sub></i>	<i>[und das Büro zu putzen.]<sub>IPH2</sub></i>	
<i>[Peter promises Anna to work]</i>	<i>[and to clean the office.]</i>	
(B) Prosodically Incorrect		
Prosody-argument structure mismatch condition (intransitive verb)		
<i>*[Peter verspricht]<sub>IPH1</sub></i>	<i>[Anna <b>zu arbeiten</b>]<sub>IPH2</sub></i>	<i>[und das Büro zu putzen.]<sub>IPH3</sub></i>
<i>[Peter promises]</i>	<i>[Anna to work]</i>	<i>[and to clean the office.]</i>
(C) Prosodically Correct		
Prosody-argument structure match condition (transitive verb)		
<i>[Peter verspricht]<sub>IPH1</sub></i>	<i>[Anna <b>zu entlasten</b>]<sub>IPH2</sub></i>	<i>[und das Büro zu putzen.]<sub>IPH3</sub></i>
<i>[Peter promises]</i>	<i>[to support Anna]</i>	<i>[and to clean the office.]</i>

In sentence A, no intonational phrase boundary (IPH) is present after the first verb (*verspricht/promises*), indicating a structure asking for an intransitive verb, i.e. a verb without a direct object, such as the verb *zu arbeiten/to work*. Sentence B contains the same verb *zu arbeiten/to work*, but the prior prosodic structure mismatches this verb's argument structure, as an IPH is present after the first verb, indicating a structure asking for a transitive verb, i.e. a verb with a direct object, such as *zu entlasten/to support*, as in sentence C. Bracketing indicates the respective IPHs and thereby the syntactic phrase boundaries. The critical verb relevant for the subsequent analysis is marked in bold. The incorrect prosodically marked sentences (B) were cross-spliced from two correct ones, such as (A) and (C), by cross-splicing the underlined part of (C) into (A).

crucial prosodic parameter, the paradigm uses sentences with a mismatch between the syntactic and prosodic structure as the relevant test sentence condition (Steinhauer et al., 1999). In this condition, the prosodic structure of the initial sentence part triggers expectations of a particular syntactic verb class, namely transitive verbs (i.e., verbs like *to support*) that obligatorily take a direct object argument (*He supports someone*), but the actual verb presented is an intransitive verb (i.e., a verb like *to work*) that takes no direct object (*He works*). For a German example of an experimental sentence from the prosody-syntax mismatch condition see Table 1B.

In an event-related potential (ERP) comprehension experiment with young healthy participants, Steinhauer et al. (1999) found an N400 followed by a P600 for the prosody-syntax mismatch condition. The N400 known to correlate with lexical integration difficulties (Brown and Hagoort, 1993) was interpreted as reflecting integration difficulties due to the mismatch between the prosodically expected verb's argument structure and the actually perceived verb's argument structure. The P600 taken to correlate processes of syntactic revision (Osterhout and Holcomb, 1992) was interpreted to indicate syntactic revision processes necessary to perform the task-required comprehension question in this study. A more recent ERP study in Dutch, using comparable material but a sentence verification task, only found the N400 (S. Bogels et al., 2006, AMLAP, paper presentation), suggesting that the occurrence of the P600 may be task dependent.

We hypothesized that the observed prosody-syntax mismatch that results consistently in an N400 pattern has its neural basis in the successful interaction of the LH and the RH (Friederici and Alter, 2004). This hypothesis was put to test by examining a rare patient group, namely patients with lesions in the CC. One subgroup displayed lesions in the posterior third of the CC (henceforth called "posterior CC"), and one had lesions in the anterior two-thirds of the CC (henceforth called "anterior CC") (see Table 2). Figure 1 provides detailed information about the individual patients' lesion sites and the lesion overlap of the five patients within each group.

It was predicted that a differential ERP pattern in the prosody-syntax mismatch paradigm should occur as a function of the lesion site. This hypothesis is based on recent neuroanatomical studies specifying the location of the interhemispheric fiber tracts by means of diffusion tensor imaging. Projections between the temporal lobes and thereby the auditory cortices of the two hemispheres are located within the posterior third of the CC (Styner et al., 2005; Huang et al., 2005), whereas the anterior two-thirds are described as being occupied by orbital and frontal fiber connections instead (Huang et al., 2005).

These two patient groups and age-matched healthy controls were examined in two experiments. Experiment 1 investigated the effect of prosodic phrase structure on the processing of a verb whose argument structure either matches or does not match the prior prosody-induced syntactic structure (Tables 1A and 1C) (Table 1B). In (A)

**Table 2. Patients' History**

Patient ID	Gender	Age	Callosal Lesion	Additional Lesions
<b>Anterior CC Group (Involving the Anterior Two-Thirds of the CC)</b>				
104	f	65	rostrum, anterior c-body	pontine, left basal ganglia
142	f	43	anterior c-body, Isthmus	midline structures after transcallosal surgery
197	f	60	rostrum, middle c-body	frontolateral and temporopolar contusion, parietal necrosis, left basal ganglia
286	m	62	anterior c-body	CMA with pontine lacune
521	m	48	anterior knee, left middle c-body, EVD	basal forebrain lesion, right temporopolar lesion
<b>Posterior CC Group (Involving the Posterior Third of the CC)</b>				
126	m	68	chronic ischemic posterior CC lesion	CMA, lacunar thalamic infarct, right occipital bleeding
339	m	55	posterior c-body (presplenial)	post SAH, post EVD
422	m	40	presplenial lesion	parietal atrophy
432	f	23	posterior CC lesion	embolized AVM, lesion left posterior thalamus
675	m	20	small presplenial lesion	left preinsular region, left cerebral peduncle (midbrain)

Abbreviations: posterior CC group is used as an abbreviation for posterior CC/presplenial group; AVM, arteriovenous malformation; CMA, cerebral microangiopathy; EVD, external ventricular drainage; SAH, subarachnoid hemorrhage.

the absence of a prosodic break after the first verb induces the syntactic expectation of an intransitive verb (i.e., verb without object), whereas in sentences B and C the presence of a prosodic break induces the expectation of a transitive verb (i.e., verb with direct object). This prosody-induced syntactic expectation is fulfilled in (C), but not in (B). We predicted that if the prosody-syntax mismatch effect observed in normal listeners (Steinhauer et al., 1999) is due to the interaction between LH and RH, and in particular to fibers crossing through the posterior portion of the CC (Huang et al., 2005), then a prosody-induced mismatch effect should be absent in patients with lesions in the posterior third of the CC. In these patients, the prosodic information processed in the RH should not influence syntactic processes in the LH. As the present experiment used a prosody judgment task not necessarily requiring a syntactic reanalysis, we expected the mismatch effect to be realized as an N400 effect at the critical verb. Experiment 2 was conducted in order to be able to interpret the predicted absence of an N400 mismatch effect in experiment 1 as being due to an impaired interaction between prosodic and syntactic information. This experiment investigated the presence of an N400 effect during auditory sentence processing when the mismatch between the crucial verb and the prior context is based purely on semantic information (Holcomb et al., 1992; Friederici et al., 1993).

## RESULTS

### Experiment 1: The Prosody-Induced Mismatch Effect

The comparison between conditions A and B allowed us to keep the verb constant (same verb) and to ensure that any finding at the verb would be attributable to the pro-

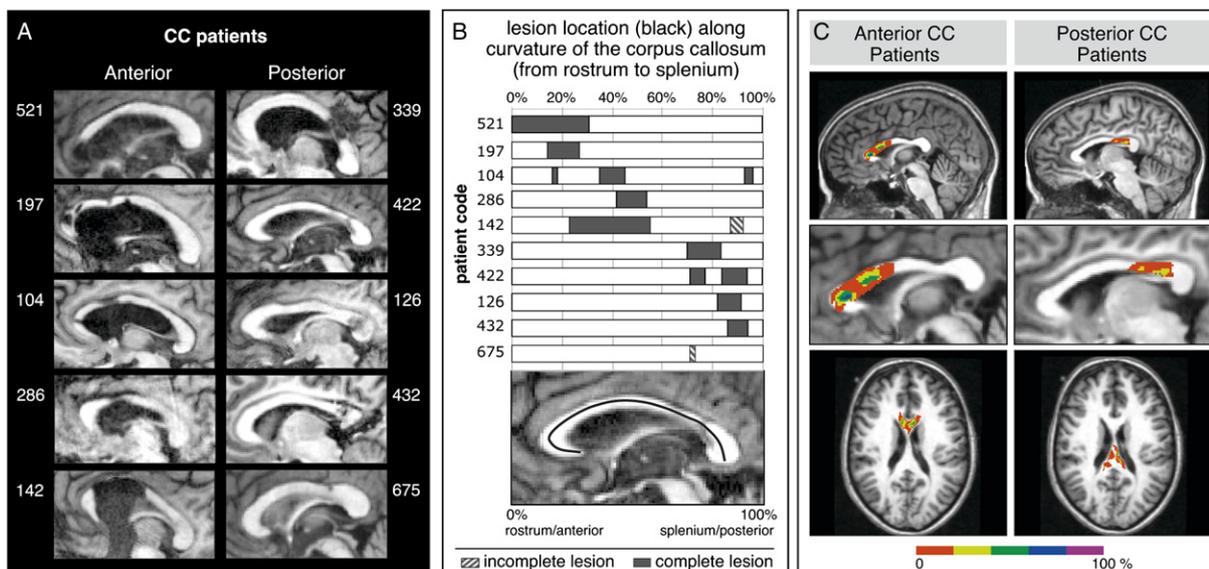
cessing of the prior prosodic information and not to the different verb types (transitive versus intransitive verbs). Keeping the verb constant is of particular importance, as verb complexity has been shown to play a role in sentence processing in healthy (Shapiro et al., 1987) and aphasic (Shapiro et al., 1993) subjects. The comparison between conditions C and B can provide additional evidence for a prosody-induced mismatch effect, as here the prosodic structure is held constant and the verb types vary, but it has to be kept in mind that in this comparison the target words differ (different verb).

### Performance Data

The omnibus ANOVA for the correctness judgment (% correct) of conditions A versus B revealed no significant main effects of group, condition, or interactions of these factors (all  $p > .1$ ). The ANOVA comparing conditions B and C revealed a main effect of group ( $F[1,18] = 6.02$ ,  $p = 0.02$ ) and a main effect of condition ( $F[1,18] = 5.67$ ,  $p = 0.03$ ) but no interaction indicating a better performance for condition B compared to condition C in all groups (see Table 3).

### ERP Data

The analysis of experiment 1 focused on the prosody-induced N400 mismatch effect. For this analysis, ERPs time locked to the critical second verb of the different conditions were compared in two separate analyses: one analysis compared conditions A and B, i.e., the two conditions with the same verb in the critical position (henceforth "same verb analysis"), and the other analysis compared conditions B and C, i.e., the two conditions in which the target verbs differ (henceforth "different verb analysis"). To define the crucial time windows (TWs) for these analyses, we initially conducted analyses for successive TWs of 50 ms between 0 and 800 ms separately for the same verb comparison and the different verb comparison. For the same verb analysis, main effects of group and interaction



**Figure 1. Lesion Location of Corpus Callosum Patients**

(A) Midsagittal section of the CC of the ten patients listed in Table 1. Numbers represent patient numbers.  
 (B) Quantitative measures of lesions in the CC, applying the rostrum-posterior CC procedure by Sugishita et al. (1995).  
 (C) Lesion density maps of anterior versus posterior lesion contributions in the CC. Midsagittal (top and middle) and axial (bottom) slices are shown, cutting the location of maximal lesion overlap. For each voxel, the percentage of lesion overlap is depicted. The color scale shows five levels: each bar represents 20% increments.

effects with group were found between 200 and 350 ms and between 300 and 500 ms, and for the different verb analysis between 300 and 500 ms and between 600 and 750 ms. These TWs were used for further analyses.

**Same Verb Analyses**

**200–350 ms.** An ANOVA over correctly answered trials with the factors group (controls, CC patients) × condition ([A] and [B]) × hemisphere (left and right) × region of interest (ROI; anterior and posterior) was performed. This analysis revealed a main effect of condition (Cond) ( $F[1,18] = 6.97, p = 0.01$ ), a Cond × group × ROI interaction ( $F[1,18] = 7.26, p = 0.01$ ), and a Cond × group × ROI × hemisphere

(Hem) interaction ( $F[1,18] = 8.27, p = 0.01$ ). To resolve the interactions with the factor group, separate analyses were carried out for each group.

Healthy controls showed an N400-like effect comparing prosodically incorrect and correct conditions (Figure 2A). Statistical analyses confirmed this observation. The ANOVA revealed a significant main effect of Cond ( $F[1,9] = 8.20, p = 0.01$ ) and a significant interaction of Cond × ROI ( $F[1,9] = 7.27, p = 0.02$ ) and a Cond × Hem × ROI interaction ( $F[1,9] = 7.99, p = 0.01$ ). The interaction of Cond × ROI was due to a significant Cond effect at anterior ROIs ( $F[1,9] = 13.39, p = 0.00$ ) and the absence of such an effect at posterior ROIs ( $p = 0.10$ ). The respective ROI effects of Cond were not qualified by Hem (all  $p > .1$ ).

Anterior CC patients (Figure 2B) displayed a mismatch effect for the critical verb in the prosodically incorrect compared to the correct condition. The negativity observed for the anterior CC patients was less widely distributed than the effect found for the age-matched controls. This was tentatively supported by statistical analysis. Statistical analyses for anterior CC patients revealed a trend toward Cond × ROI interaction ( $F[1,4] = 4.00, p = 0.11$ ). When analyzing the Cond effects for the different ROIs, a significant Cond effect was found for the posterior ROI ( $F[1,4] = 13.74, p = 0.02$ ), but not for the anterior ROI ( $p = 0.80$ ).

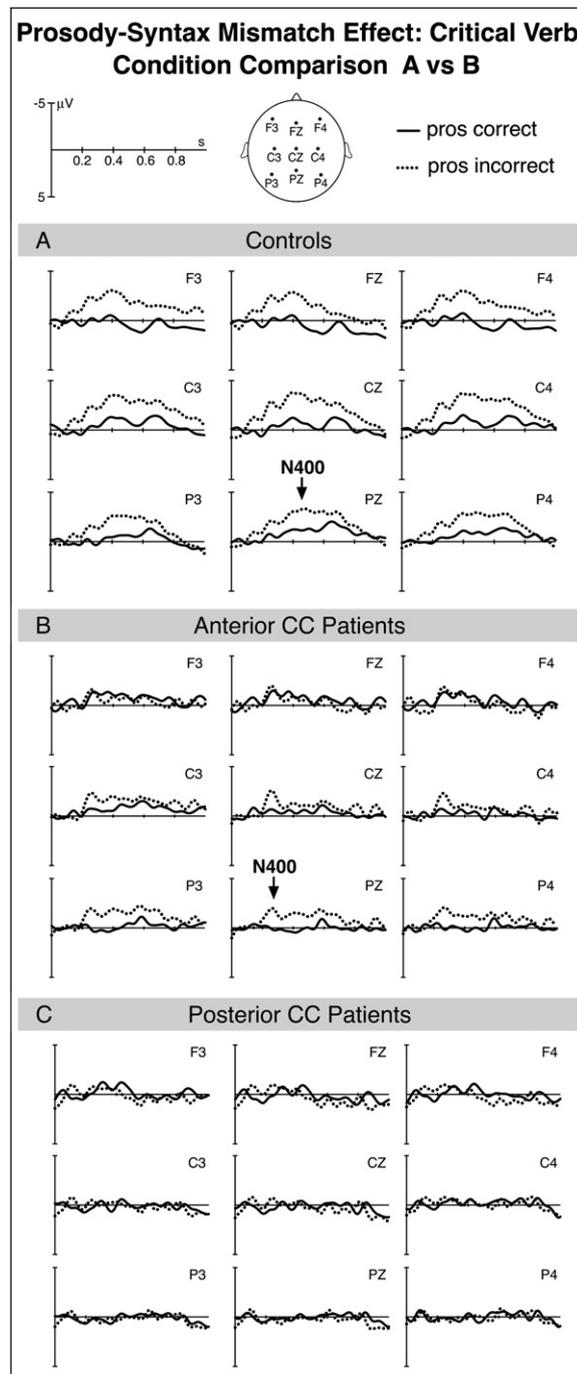
Posterior CC patients (Figure 2C), in contrast, did not show a Cond × ROI interaction ( $F[1,4] = 0.00, p > 0.94$ ).

**300–500 ms.** The ANOVA with the same factors as analyzed in the previous TW showed a main effect of group

**Table 3. Performance Data Experiment 1, Percent Correct**

	Condition A	Condition B	Condition C
Controls	71.66	74.37	66.45
Anterior CCs (excluding 286 <sup>a</sup> )	59.89	71.87	39.06
Posterior CCs	65.41	74.99	35.41

<sup>a</sup> Patient 286 was excluded from the behavioral analysis because he was dramatically low in his performance: 35.42% for correct (A) and 29.17% for incorrect (B) sentences and 25.00% for correct (C) sentences. His performance was significantly below chance for all conditions as tested by  $\chi^2$  test of equal distribution (condition A,  $p = 0.04$ ; condition B,  $p = 0.004$ ; condition C,  $p = 0.001$ ) and suggests the same strategic tendency in the prosody judgment task.



**Figure 2. Prosody-Syntax Mismatch Effect: Comparison A versus B**

Verb-specific ERPs of experiment 1 for normal age-matched controls (A), anterior CC group (B), and the posterior CC group (C). The solid line indicates the prosodically correct verb, and the dotted line indicates the prosodically guided incorrect verb.

( $F[1,18] = 5.21, p = 0.03$ ) and Cond ( $F[1,18] = 5.27, p = 0.02$ ). There were also two interactions: Cond  $\times$  group ( $F[1,18] = 4.90, p = 0.04$ ) and Cond  $\times$  group  $\times$  ROI

( $F[1,18] = 10.11, p = 0.00$ ). To resolve the interactions with the factor group, separate analyses were carried out for each group.

Healthy controls showed a negative brain response in the classical N400 TW comparing prosodically incorrect and correct conditions (Figure 2A). Statistical analyses confirmed this observation. The ANOVA revealed a significant main effect of Cond ( $F[1,9] = 7.98, p = 0.01$ ), though no interaction between Cond  $\times$  ROI ( $F[1,9] = 3.05, p = 0.11$ .)

Anterior CC patients appeared to show an extended negativity for the critical verb in the prosodically incorrect compared to the correct condition, although it was reduced in amplitude (Figure 2B). There was no main effect of Cond ( $p > .1$ ), though there was a strong trend toward interaction of Cond  $\times$  ROI ( $F[1,4] = 6.12, p = 0.06$ ). When analyzing the Cond effects for the different ROIs, however, no significant Cond effect was found for the posterior ROI ( $F[1,4] = 1.93, p = 0.23$ ) or for the anterior ROI ( $p = 0.56$ ). The results indicate that anterior CC patients show a comparable early negative response to critical verbs in the prosodically incorrect condition, but not in a later TW.

Posterior CC patients did not show a Cond effect or a Cond  $\times$  ROI interaction (all  $p > .1$ ).

**Different Verb Analyses**

300–500 ms. An ANOVA with the factors group (controls, CC patients)  $\times$  Cond ([B] and [C])  $\times$  Hem  $\times$  ROI indicated a main effect of group ( $F[1,18] = 6.44, p < 0.02$ ). Given our predictions, we conducted planned analyses for each group separately, but none of these analyses revealed a statistically significant effect (all  $p > 1$ ).

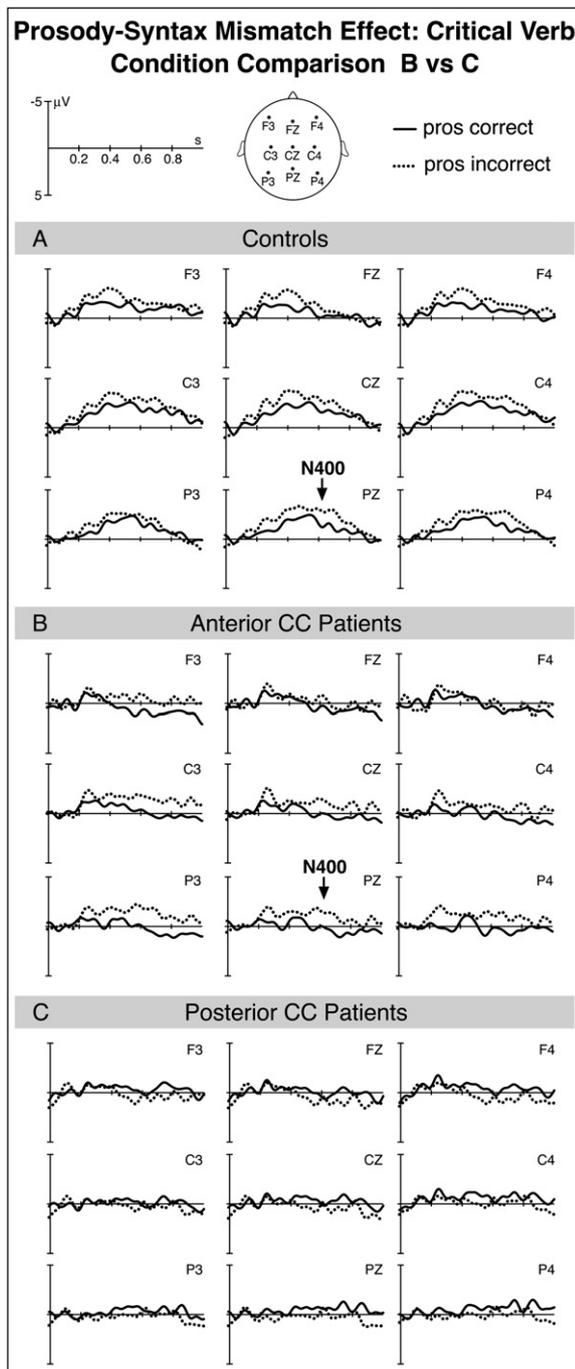
600–750 ms. An ANOVA with the same factors for this TW revealed a main effect of Cond ( $F[1,18] = 4.44, p = 0.04$ ), a trend-significant effect of group ( $F[1,18] = 2.95, p = 0.10$ ), and a Cond  $\times$  ROI interaction ( $F[1,18] = 5.56, p = 0.02$ ). Again, planned separate analyses for each group were conducted.

Healthy controls demonstrated a marginally significant effect of Cond ( $F[1,9] = 3.76, p = 0.08$ ) and a trend interaction of Cond  $\times$  ROI ( $F[1,9] = 3.41, p = 0.09$ ). Resolution by ROI revealed a posterior effect ( $F[1,9] = 5.41, p = 0.04$ ), but not an anterior effect ( $p > 1$ ) (Figure 3A).

Anterior CC patients also showed a significant Cond effect ( $F[1,4] = 7.73, p = 0.04$ ) (Figure 3B).

Posterior CC patients showed no significant Cond effect ( $F[1,4] = 1.94, p = 0.23$ ) (Figure 3C).

The data from the same verb and different verb analyses revealed that patients with lesions in the posterior third of the CC, in contrast to the other two groups, did not show any prosody-induced verb argument structure mismatch effect, indicating an insensitivity to prosodic information during sentential processing. The absence of such a mismatch effect was found both in the same verb analyses that varied the prosodic context while holding the targets identical and the different verb analyses that varied the verb class of the targets while holding the prosodic context constant. The mismatch effect observed in the other two groups was significant in both analyses but differed



**Figure 3. Prosody-Syntax Mismatch Effect: Comparison B versus C**

Verb-specific ERPs of experiment 1 for normal age-matched controls (A), anterior CC group (B), and the posterior CC group (C). The solid line indicates the prosodically correct verb, and the dotted line indicates the prosodically guided incorrect verb.

in latency. The N400-like mismatch effect is much earlier in the same verb than in the different verb analysis. The later occurrence in the different verb analysis (conditions

B versus C) compared to the same verb analysis (conditions A versus B) could be due to the fact that in condition C 35.4% of the verbs were prefixed compared to only 8.3% in the other two conditions ([A] and [B]). As these prefixes can in principle be part of intransitive verbs, the processing system must await the verb stem before a mismatch of the verb argument structure in condition (C) can be detected, thereby delaying the mismatch effect.

It is interesting to note that no group by condition interaction was found for the behavioral data. This may be due to the fact that these data reflect a prosody judgment task performed off-line after each sentence, whereas the ERP data clearly reflect on-line processes. The apparent difference between on-line and off-line could either be taken to indicate that the off-line task is not sensitive enough to uncover possible differences between groups or that the posterior portion of the CC is crucial only for on-line inter-hemispheric communication, allowing off-line processes to use other pathways. However, given the finding that even controls show difficulties in the off-line prosody judgment task (with an overall error rate of 29.17%), we refrain from a final interpretation of the behavioral data. Relative good performance was observed for both patient groups (when compared to normals) in conditions A and B. All groups showed poorer performance for condition C, which used transitive verbs. This result is in line with psycholinguistic work considering transitive verbs (C) to be more complex than intransitive verbs (B) (Shapiro et al., 1987, 1993).

The conclusions that can be drawn from the ERP patient data with respect to the interhemispheric communication will be considered in detail in the Discussion section. Before, however, discussing the patient findings in more detail, we need to demonstrate that CC patients, in particular those with lesions in the posterior part of the CC, do show an N400 effect when the mismatch is based solely on semantic information and is thus independent of prosodic information.

### Experiment 2: The Lexical-Semantic Mismatch Effect

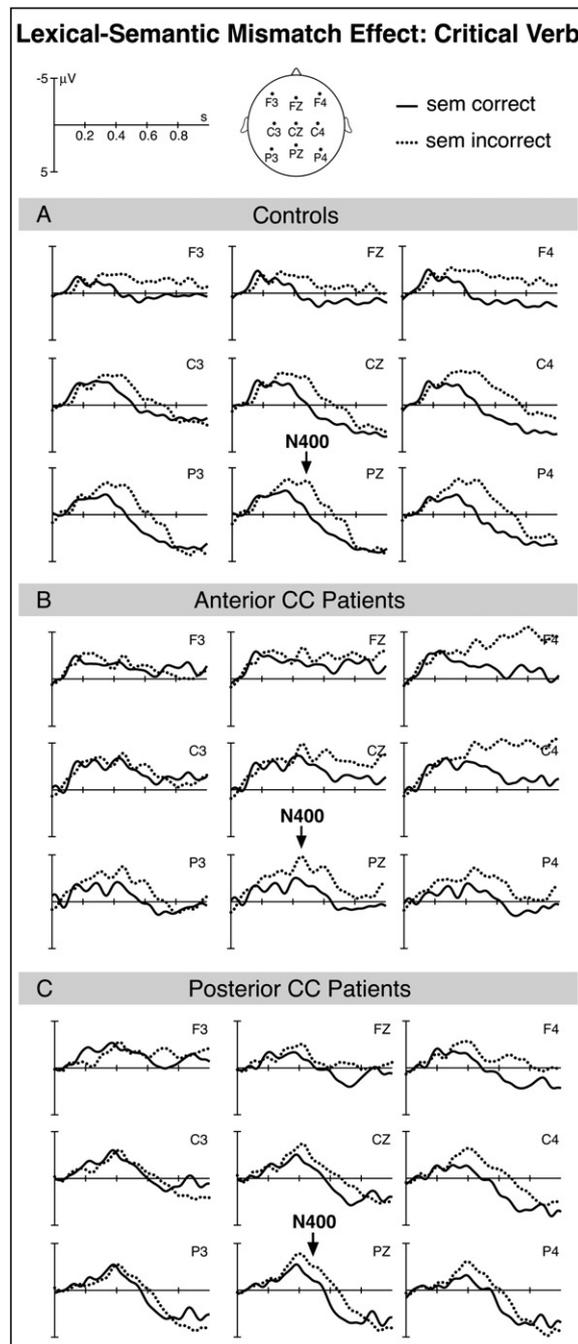
Experiment 2 was designed to examine the presence of an N400 effect independent of prosodic information. In this experiment, the lexical-semantic N400 effect was investigated by means of sentences in which the critical verb mismatched the prior context with respect to the verb's selection restrictions.

#### Performance Data

The omnibus ANOVA for the correctness judgment revealed no main effects of group, Cond, or an interaction of the two factors (controls: semantically correct [sem corr], 98.37%; semantically incorrect [sem incorr], 98.61%) (anterior CCs: sem corr, 97.50%; sem incorr, 95.41%) (posterior CCs: sem corr, 97.91%; sem incorr, 95.62%).

#### ERP Data

The lexical-semantic N400 mismatch effect was expected for all groups. Age-matched controls showed an N400 effect that was more pronounced over RH- than



**Figure 4. Lexical-Semantic Mismatch Effect**

Verb-specific ERPs from the semantic condition of experiment 2 for age-matched controls (A), for the anterior CC group (B), and for the posterior CC group (C). The solid line indicates the semantically correct verb, and the dotted line indicates the semantically guided incorrect verb.

LH-electrode sites (see Figure 4A). Anterior CC patients also showed an N400 effect with a maximum over RH sites, as did the posterior CC patients (see Figures 4B and 4C).

An ANOVA with the factors group (healthy controls, CC patients)  $\times$  Cond (corr and incorr)  $\times$  Hem (left and right)  $\times$  ROI (anterior and posterior) conducted for the TW 400–700 ms revealed a significant main effect of Cond ( $F[1,17] = 22.03, p = 0.00$ ), a significant Cond  $\times$  Hem interaction ( $F[1,17] = 16.12, p = 0.00$ ), and a Cond  $\times$  Hem  $\times$  ROI interaction ( $F[1,17] = 13.85, p = 0.00$ ). The interaction was due to the Cond effect in the left posterior ROI ( $F[1,17] = 13.83, p = 0.00$ ), in the right posterior ROI ( $F[1,17] = 32.27, p = 0.00$ ), and in the right anterior ROI ( $F[1,17] = 33.80, p = 0.00$ ) and to its absence in the left anterior ROI ( $F[1,17] = 2.99, p = .1$ ). The factor group did not interact with any other factor or factor combination (all  $p > .1$ ), indicating that both anterior CC patients and posterior CC patients did not differ from healthy controls with respect to a semantic N400 effect.

Data from experiment 2 clearly demonstrate that both patient groups and healthy controls show a comparable N400 elicited for a semantic mismatch independent of prosodic information.

The semantic N400 is present between 400 and 700 ms, whereas the prosody-induced mismatch effect varied in latency as a function of the same verb versus different verb analysis. The latency difference between the latter two effects was attributed to the morphological differences in the stimuli of the two verb classes. The difference between the same verb analysis in experiment 1 and the analysis for the same verbs in experiment 2 observed for both healthy controls and anterior CC patients may be due to different processes underlying the two effects. In contrast to the detection of a semantic mismatch requiring the retrieval of the verb's meaning and its integration into the preceding context, the detection of a prosody-verb argument structure mismatch is based on a prosody-induced prediction of an obligatory argument structure against which the incoming verb is checked. The present data may suggest that, when keeping the verb class constant, the latter process is faster than the former.

## DISCUSSION

The present study demonstrates that the posterior third of the CC plays an essential role during the interplay of linguistic prosody and syntactic structure during on-line sentence comprehension. An intact posterior third of the CC connecting temporal regions is a necessary precondition for a prosody-induced N400 mismatch effect. Lesions in the anterior two-thirds of the CC that connect frontal regions, in contrast, can cause a modulation of the prosody-induced mismatch effect but cannot eliminate the effect.

The prosody-induced N400-like mismatch effect observed for healthy controls signals lexical integration difficulties for the verb that belongs to a verb class whose argument structure (intransitive verbs, i.e., verbs without object) is unexpected given the prosody-induced syntactic context upon which a transitive verb (a verb with a direct object) is expected. Prior studies using similar material

reported an N400-P600 (Steinhauer et al., 1999) or an N400 effect (S. Bogels et al., 2006, AMLAP, paper presentation) depending on whether or not the task induced a syntactic revision process. The present prosodic judgment task not necessarily requiring a syntactic revision elicited only an N400-like mismatch effect in healthy listeners, suggesting that no syntactic revision process was initiated.

The prosody-induced mismatch effect observed for the anterior CC patient group indicates that these patients process prosodic information and use it to build up expectancies about the upcoming verb class. The observed negativity in the anterior CC patients was modulated both in distribution and timing when comparing the effect of different prosodic context on the identical verb. A possible interpretation of this result can be based on the finding that the neural network of the N400 is not restricted to temporal regions but also includes frontal brain regions (Halgren et al., 2006; Maess et al., 2006). Anterior CC lesion affecting the connecting fibers of the frontal lobes may have influenced the morphology of the N400-like mismatch effect. The present finding that a lesion in the anterior two-thirds of the CC modulates the prosody-induced mismatch effect, in turn, suggests that the prosody-induced N400-like mismatch effect as observed in healthy controls may require an interhemispheric communication of not only the temporal regions but also of the frontal regions.

The absence of a prosody-induced N400-like mismatch effect in posterior CC patients in experiment 1 suggests that on-line syntactic processes in these patients are not influenced by the prosodic information. In particular, the results show that syntactic predictions for a particular verb class (i.e., with a particular argument structure) based on prosodic information (i.e., the IPh boundary in the prior context) do not influence the processing of the target verb. This result indicates that the posterior CC in particular is necessary for the interplay between prosodic information and the verb argument structure as the relevant syntactic information. This conclusion is based on two additional findings. First (experiment 1), patients with lesions in the anterior two-thirds of the CC display a prosody-induced mismatch effect. Second (experiment 2), patients with lesions in the posterior third of the CC do demonstrate a semantic N400 effect, suggesting that the absence of the prosody-induced N400-like mismatch effect for these patients in experiment 1 is due to the ineffective processing of prosodic information that normally guides expectations of the upcoming verb's argument structure, and not to an inability to process verbs in sentential context.

The role of the CC has long been discussed with respect to interhemispheric transfer of cognitive information (Kirkbride et al., 1994). Its particular role in language processing has been hypothesized for the pathogenesis of developmental language disorders (Fabbro et al., 2002; Nijokiktjen, 1990), and dyslexia (Duara et al., 1991; Rumsey et al., 1996). A correlational study using behavioral

measures indicated that the posterior quarter of the CC is crucial for verbal skills (Nosarti et al., 2004). Dichotic listening studies with CC patients specified the splenium as the relevant part of the CC through which the auditory commissures project (Pollmann et al., 2002; Sugishita et al., 1995).

With respect to the functional neuroanatomy of language processing, the present findings specify that the posterior third of the CC, including the splenium and the presplenial part, is crucial for the interplay between prosodic and syntactic information. Thus, the transfer between the LH and the RH with respect to the integration of prosodic and syntactic information may not be restricted to the splenium itself, whose superior region, in particular, has been described neuroanatomically as the location of the fibers connecting the temporal lobes (e.g., Huang et al., 2005). As the processing of prosodic and syntactic information involves the most posterior parts of the left and right temporal lobe, respectively (e.g., Perkins et al., 1996; Meyer et al., 2003), it is likely that the interhemispheric transfer has a broader basis including the presplenial part of the CC. A study examining the degeneration in the CC as a consequence of temporal lesions supports this view by finding that the lesions in the posterior temporal lobe led to degeneration in the splenium and in the posterior trunk of the CC (De Lacoste et al., 1985). Thus, it appears that the posterior CC, i.e., its splenial and presplenial part, is responsible for the interplay between left and right hemispheric functions during auditory sentence processing.

## EXPERIMENTAL PROCEDURES

### Experiment 1

#### Participants

From our patient databank of 1300 patients, ten patients with lesions in the CC were selected. Individual patient histories of these rare cases are displayed in Table 1. Patients were grouped according to their lesion site within the CC. Following Sugishita et al. (1995), we categorized lesions affecting the posterior third of the CC as posterior CC patients and within the anterior two-thirds as anterior CC patients. All patients reported normal hearing and were right-handed. In addition, ten age-matched right-handed healthy controls (four female) were tested. All participants gave informed consent to be in the study.

#### Lesion Measurement

High-resolution, whole-head 3D modified driven equilibrium Fourier transform (Lee et al., 1995; Ugurbil et al., 1993) magnetic resonance scans were obtained in 128 sagittal slices, with 1.5 mm thickness and a data matrix of 256 × 256 voxels. Figure 1A shows midsagittal sections of the CC of each patient. In addition, we ran a T<sub>2</sub>\*-weighted protocol in order to visualize microbleeds in patients with traumatic brain injury (TBI; Fazekas et al., 1999; Roob et al., 1999). To measure the length of the CC quantitatively, we adopted the rostrum-posterior CC procedure by Sugishita et al. (1995). In the midsagittal plane, a curve was constructed manually by means of a segmentation software program (Krugel and Lohmann, 1996), midway between the dorsal and the ventral aspects of the CC from the tip of the rostrum to the end of the posterior CC. The length of this segmented curve was defined as the total length of the CC. The anterior and posterior limits of the callosal lesions were marked on this curved line, and the extent of the lesion was calculated as a percentage of the total CC length. Patients were classified into two groups. One group consisted

of patients with lesions affecting the posterior third of the CC, labeled posterior CC patients. The second group consisted of patients with lesions within the anterior two-thirds of the CC, labeled anterior CC patients. For individual quantitative information in the CC, see Figure 1B. The figure also lists all patients' additional lesions, which, however, were localized outside the crucial left and right perisylvian cortex and were thus considered to have no direct impact on the processes under investigation. With respect to the CC lesion, all posterior CC lesions included the superior region of the splenium, a region described as being occupied by fiber connections of the temporal lobes (Huang et al., 2005) extending to the presplenial part of the CC.

The group of anterior CC patients is more variable with respect to lesion site. There are two patients with lesions in the anterior third of the CC (197 and 521), which, according to Huang et al. (2005), is occupied by orbital and frontal fiber connections. For three patients (104, 142, and 286), the lesion is located in the anterior half of the CC, but the rostrum through which the orbital lobes are connected remained intact.

#### Materials

The experimental sentence material consisted of 48 prosodically correct sentences of type A and 48 of type C, plus 48 prosodically incorrect sentences (B) constructed from prosodically correct sentences, i.e., (A) and (C) (see Table 1). In sentence A, the noun phrase *Anna* is the object of the first verb and thus belongs to the first intonational phrase (IPH<sub>1</sub>), which is not divided by any prosodic break. In sentence C, the prosodic break of IPH<sub>1</sub> indicates a syntactic structure in which *Anna* is the object of the second verb and thus belongs to the second intonational phrase. In the critical experimental condition B, the two sentence types were cross-spliced with the first three words coming from (C) and the rest of the sentence from (A). Thus in (B), the prosodic break (IPH<sub>1</sub>) signals a syntactic structure in which *Anna* is the object of the second verb, which consequently should be a transitive verb. The actual verb in (B), however, is an intransitive verb without a direct object, thus mismatching the prior prosodic information. All sentences were produced by a trained female native speaker of standard German and recorded in a soundproof chamber. The digitized speech signals (44.1 kHz/16 bit sampling rate) of each sentence were measured with respect to word and pause duration, fundamental frequency (pitch contour), and loudness (amplitude squares), and the differences were statistically analyzed in paired Student's *t* tests or with ANOVAs. The additional IPH boundary in (C) was signified prosodically by a pause before *Anna* ( $p < 0.00$ ), as well as by a significant lengthening of the first constituent, *Peter verspricht* ( $p < 0.00$ ). Whereas a major accent occurred on the verb *zu arbeiten* in (A), accentuation was shifted to the noun phrase *Anna* in (C). These differences in accent positions were confirmed by a locally rising pitch contour in the loudness maximum ( $p < 0.01$ ; for more details see Steinhauer et al. [1999]). The 48 prosodically incorrect sentences (B) were derived by cross-splicing the first part of (C) and the second part of (A) in the silent phase of the affricate /ts/ of the infinitive marker *zu/to* (compare Table 1). This procedure plus an amplitude normalization protected against detectability of the signal manipulation at the splicing point.

#### Procedure

In experiment 1, participants were seated in a comfortable chair and listened to the stimuli through loudspeakers. While listening to the sentences, participants were instructed to fixate on a small star in the middle of a computer screen in front of them and to avoid blinking during the presentation of the star. The star occurred 500 ms prior to the presentation of the auditory sentence and remained on the screen until 3000 ms after the completion of the sentence. A response sign appeared for 2000 ms, the time during which they were required to indicate via push buttons whether the sentence was prosodically correct or incorrect. The next trial started after an interstimulus interval of 1000 ms. Correct and incorrect responses were registered for later analyses. Due to the delayed responses necessary to deconfound sentence processing and motor responses, only percent correct data were analyzed.

#### ERP Recordings and Analyses

In both experiments, the electroencephalogram (EEG) was recorded with tin electrodes secured in an elastic cap. Twenty-nine electrodes were placed according to the international 10–20 system with the following locations: Fz, Cz, Pz, FP1, F7, F3, FT9, FT7, FC3, T7, TP7, C3, CP5, P7, P3, O1, FP2, F8, F4, FT10, FT8, FC4, T8, C4, CP6, TP8, P8, P4, and O2 (cf. Sharbrough [1991]). Each EEG channel was amplified with a band pass from DC to 40 Hz. The EEG was recorded continuously and stored for later analysis at a sampling rate of 250 Hz. The impedance was reduced to below 5 k $\Omega$ . Separate ERPs were averaged for each participant at each electrode site. All electrodes were rereferenced to linked mastoids. Both the vertical and the horizontal electrooculogram (EOG) were recorded from electrodes placed above and below the right eye and the outer canthus of each eye, respectively. We removed trials with eye blinks or horizontal eye movements and other artifacts from the raw data prior to averaging the data. The ERPs were averaged over correctly answered trials for all participants of each group. They were time locked to the onset of the critical word in each sentence and then calculated from this onset. In experiment 1, ERPs were time locked to the onset of the verb complex starting with *zu* indicating the infinitival verb form. As this functional element was identical in the two conditions (mean duration of 150 ms), the baseline was set from 0 to 150 ms poststimulus onset of the verb complex. ANOVAs included two posterior ROIs with the following electrode sites: posterior left (CP5, P7, P3, and O1) and posterior right (CP6, P8, P4, and O2); and two anterior ROIs with the following electrode sites: anterior left (F3, F7, FC3, and FT7) and anterior right (F4, F8, FC4, and FT8). Analyses for successive TWs of 50 ms between 0 and 800 ms were conducted. Latencies of TWs for further analyses were defined on the basis of this successive TW analyses as follows: onset of the TW was defined by the first 50 ms TW in which a main effect of group or interaction effects of group were found, and the offset of the TW was defined by the last 50 ms TW in which such effects were found. ANOVAs for the different verb analysis were calculated for the TWs 300–500 ms and 600–750 ms with the within-subjects factors condition, ROI, Hem, and the between-subjects factor group. ANOVAs for the same verb analysis were calculated with the same within—and between—subjects factors with different TWs, namely between 200 and 350 ms and between 300 and 500 ms, due to an earlier onset of the 50 ms TW analysis. The 300–500 ms TW was chosen to allow compatibility between the two types of analyses.

#### Experiment 2

##### Participants and Lesion Measurement

Participants in experiment 2 were identical to those of experiment 1 except for one control participant who was not available for testing in experiment 2.

##### Materials

The language material and the task in experiment 2 were similar to those used in earlier studies with young healthy subjects (Hahne and Friederici, 2002; Gross et al., 1998; Friederici et al., 2000) and with different patient groups and their age-matched controls (Friederici et al., 1999, 2003). The sentence material was produced by a trained female speaker of standard German in a soundproof chamber and digitized (20 kHz/12 bit sampling rate). There were 48 correct sentences (sem corr), e.g., *Das Hemd wurde gebügelt/The shirt was ironed*, and 48 semantically incorrect sentences (sem incorr) due to a selectional restriction violation, e.g., *Das Gewitter wurde gebügelt/The thunderstorm was ironed*. The experiment also included 48 syntactically incorrect sentences and their 48 correct counterparts. Comparable to experiment 1, only data from the lexical-semantic condition known to elicit an N400 was reported. Note, however, that analyses of the syntactic condition did reveal a P600 in each participating group.

##### Procedure

The procedure was generally similar to experiment 1, except for some differences in the timing of the stimulus material and the task. The trial sequences were as in experiment 1: star fixation during sentence

presentation (500 ms before and 3000 ms after the sentence) followed by response sign for 2000 ms, during which subjects were required to indicate via push buttons whether the sentence was correct or incorrect. The interstimulus interval was 1000 ms.

#### ERP Recordings and Analyses

The setup of the ERP recordings and the positioning of the electrodes were the same as in experiment 1. ERPs were averaged over correctly answered trials and time locked to the onset of the verb form starting with the functional element *ge-* indicating the past participle form followed by the verb stem carrying the meaning of the verb. This functional element was the same in the two conditions, with a mean duration of about 100 ms. Therefore, the baseline was set from 0–100 ms poststimulus onset of the element *ge-*. ANOVAs were calculated over the TW 400–700 ms with the within-groups factors condition, region, and Hem and the between-groups factor group.

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