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Brain Activity During Syntactic and Semantic Processing—A Magnetoencephalographic Study

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Summary: Drawings of objects were presented in series of 54 each to 14 German speaking subjects with the tasks to indicate by button presses a) whether the grammatical gender of an object name was masculine ("der") or feminine ("die") and b) whether the depicted object was man-made or nature-made. The magnetoencephalogram (MEG) was recorded with a whole-head neuromagnetometer and task-specific patterns of brain activity were determined in the source space (Minimum Norm Estimates, MNE). A left-temporal focus of activity 150-275 ms after stimulus onset in the gender decision compared to the semantic classification task was discussed as indicating the retrieval of syntactic information, while a more expanded left hemispheric activity in the gender relative to the semantic task 300-625 ms after stimulus onset was discussed as indicating phonological encoding. A predominance of activity in the semantic task was observed over right fronto-central region 150-225 ms after stimulus-onset, suggesting that semantic and syntactic processes are prominent in this stage of lexical selection.

Key words: Magnetoencephalography; Gender decision; Lemma retrieval; Semantic classification; Phonological encoding.

Introduction

Although there is fundamental agreement that language processes are primarily lateralized to the left hemisphere in most right-handed subjects, neurocognitive models assume different degrees of left-hemispheric dominance for different language processes (e.g., Pulvermüller 1999b). For instance, processes related to phonology, syntax, or grammatical function words are mainly attributed to the dominant hemisphere, whereas processes related to semantic and pragmatic aspects of language are assumed to involve both hemispheres. Evidence from electrophysiological studies that challenged hemisphere-specific language processes by violation of the rules and principles (Kutas and Hillyard 1984; Friederici et al. 1993, 1996), and electroencephalographic and magnetoencephalographic evidence on word recognition (Neville et al. 1992; Walla et al. 2001a), semantic word encoding (Walla et al. 2001b), gender decision (Dobel et al. 2001) or (Japanese) character reading (Kuriki

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et al. 1996; 1998) support this view (overviews by Friederici 1999; Kutas and van Petten 1994; Segalowitz and Chevalier 1998; Pulvermüller 1996, 1999a,b).

The hemisphere-specific focus of cortical activity may vary with the sequence of processes in speech production, which Levelt (1989; Levelt et al. 1999) conceived as a staged process. Measuring the magnetoencephalogram (MEG) in a picture naming task Levelt et al. (1998) related distinct stages of word production to the time course of evoked magnetic activity starting with conceptual preparation and lexical selection (0-150 ms), followed by the retrieval of lemma information (150-275 ms), and phonological encoding (275-400 ms), before stages of phonetic encoding and articulation are reached (400-600 ms). Levelt (1989;Levelt et al. 1999) describes the lemma as part of the lexical selection process, in that it contains syntactical information about the word like the lexical category, tense or gender, whereas other authors characterize the lemma as purely lexical representations that specify the meaning of a word (Garrett 1982; Zorzi and Vigliocco 1997).

The present study used a gender decision task to trigger brain activity during the retrieval of syntactic information. According to Levelt and colleagues (1999), gender decision of depicted objects requires access to the semantic representation of the depicted object, and access to its grammatical information (lemma), while a semantic decision requires the first but not the latter. By adding a semantic classification task with the identical stimulus material, we expected to amplify potential contrasts in hemisphere-specific processing. In a recent ERP-study

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Accepted for publication: May 21, 2002.

Research was supported by the Deutsche Forschungsgemeinschaft and the Volkswagen-Stiftung.

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with the same two tasks (Dobel et al. 2001) we found a predominantly left-anterior negative slow wave 300-600 ms following picture-onset in the gender decision task, whereas the semantic task produced symmetric responses over the hemispheres. Since this result was based on sampling with a rather low rate of 200 Hz and averaging over 300 ms, the present study employed magnetoencephalography with high temporal resolution to explore stages in the course of speech production and to test the hypothesis that the retrieval of lemma information, as provoked by a gender decision task, is indicated by brain activation around 200 ms after stimulus-onset. Since access to syntactic information has been assigned to left-hemispheric activity, we expected this peak of activity to predominate in the left hemisphere. These accentuations were hypothesized to show up in the comparison with the control task that focused on semantic processes only. By examining these hypotheses, the present study should complement the temporal-spatial specification of speech production stages provided by Levelt et al. (1998) in their picture naming task.

Methods

Subjects

Fourteen healthy subjects (7 female, mean age 25.9, SD = 4.7 years, range 18-37 years, all students) received a financial bonus for participating in the study that lasted about 2 hours. Subjects were right-handed, as assessed by the Edinburgh-Handedness-Questionnaire (Oldfield 1971; mean index: 96.8, range: 75-100), and none of the subjects reported to have a left-handed or ambidextrous first-degree relative. All subjects were native speakers of German and had normal or corrected to normal vision. Subjects were informed about the measurement and experimental procedure and signed a written consent before the start of the session.

Material and methods

Fifty-four line drawings of concrete objects that represented frequent German nouns (word frequencies: mean token lemma frequencies: 56/million) were selected from the Snodgrass and Vanderwart (1980) picture series. The noun for half of the objects had a masculine, the other half a feminine gender, and 50% of the objects were nature-made, the other 50% man-made. Pictures were transformed in a digital picture-format with foreground color white and background color black. In the syntactic task subjects were asked to indicate, whether the grammatical gender of an object name was masculine or feminine by pressing one of two buttons with the index or middle finger of the left hand for

the German articles "der" defining masculine and "die" feminine nouns. In the semantic classification task, subjects decided, whether the presented object was man-made or nature-made. Stimulus presentation was terminated by the button press and followed by a response-stimulus-interval of 2.5–3.0 s (example of stimuli and design in figure 1).

The same set of drawings was presented in both tasks though in a different order. Tasks were repeated following Jescheniak and Levelt (1994), who found the automatic retrieval of syntactic information to become increasingly prominent over time. Thus, the series of 54 object pictures was presented a total of four times with the task sequence semantic – semantic – syntactic – syntactic. Within each run, the sequence of stimuli varied randomly. Prior to the experiment the pictures were shown to the subject in order to assure that all the objects were recognized without problem. In addition, ten practice trials of each task ensured that subjects had understood the instructions.

Stimuli were projected via a mirror system onto a screen (transparent layer) positioned 1.5 m in front of the seated subject. This resulted in a maximal visual angle of about 5.7 degrees. Subjects were instructed to focus their gaze on a white fixation point in the middle of the black screen. With the disappearance of the fixation point the stimuli appeared at the same position.

Data acquisition and analysis

Response latencies of the button presses were stored to the nearest millisecond. Differences of the mean medians of response latencies between tasks and between the two trial series within each task (semantic 1st 2nd, syntactic 1st 2nd) were evaluated by one-way analyses of variance with the within-subjects factors TASK and SERIES.

The MEG was recorded with a 148-channel whole head magnetometer (MAGNES® 2500WH, 4D NEUROIMAGE, San Diego, USA) in a magnetically shielded room (Vacuumschmelze, Hanau, Germany), while the subject was in a seated position. Data were recorded continuously with a sampling-rate of 508.6 Hz and a 0.1-100 Hz band-pass filter. The electrooculogram (EOG) and the electrocardiogram (EKG) were recorded and stored together with the MEG-data for offline analysis. Silver-silverchloride electrodes were placed on the outer canthi for the monitoring of horizontal eye movements, and above and below the right eye for vertical eye movements. EKG electrodes were placed on right collarbone and below left costal arch.

Single runs were submitted to a standard NEUROIMAGE noise-reduction algorithm, which calculates weight factors from the correlation between MEGand reference-channels and subtracts the (weighted) ref-



Figure 1. Example of the stimuli and stimulus sequence: The picture of an object (e.g., a hat) is presented, until the subject presses the button for response. In the gender decision task, a button press with the left index finger was correct, because the German article "der" defines the masculine grammatical gender of the object, while pressing a button with the left middle finger would incorrectly relate the German article "die" to the feminine gender of hat. The next object picture is presented 2.5 - 3.0 s after the button press. In this example the picture of a cow asks for button press with the left middle finger to correctly assign the German article "die" to the feminine grammatical of the object. In the semantic classification task, the same object drawings required the decision, whether the object is man-made (like a hat) or nature-made (like a cow). The relationship of task ("der"/"die" or man-made/nature-made) and finger (index/middle) was balanced across subjects.

erence signal from the MEG signal. The reference channels are placed in relative distance to the head with 8 from 11 reference-channels being used for the reduction algorithm. After conversion into binary format (BESA99) the continuous data were divided into 1500-ms epochs, including 500 ms before and 1 s after stimulus-onset. Eye-movement and blink artifacts, as well as artifacts caused by the magnetic fields emerging from the heart were corrected using the "Multiple Source Eye Correction Method" (Berg and Scherg 1994). Individual thresholds of amplitude and gradient for artifact-rejection were determined on every run. Artifact-contaminated channels were interpolated by the Spherical Spline Method (Perrin et al. 1989). For trials with correct response, artifact-free epochs (46.5 for both tasks in the 1st, 47.1 for the 2nd run; F(1,13) = 0.76, p = 0.39) were high-pass filtered at 0.1 Hz, baseline-corrected (referenced to the 500-ms pre-stimulus baseline), and the averaged epochs were transformed into average reference.

For each averaged epoch cortical sources were evaluated using the minimum norm estimate (MNE), an inverse method reconstructing the primary current that underlies an extracranially recorded brain response (for details see Hämäläinen and Ilmoniemi 1984; Grave de Peralta Menendez et al. 1997; Hauck et al. 1999). The present procedure and set of parameters followed exactly the method described in Hauck et al. (1999). The MNE amplitudes were computed for 197 dipole-locations on a shell at 80% radius of the head relative to its center (assessed by individual head-shapes) as the best solution to compensate for the dependence of the accuracy of inverse solutions and the depth of the source, and averaged across 25-ms epochs. For each 25-ms epoch the differences of the MNEs at each of the 197 locations were compared between tasks by single-sided paired t-tests. T-maps were verified by additional t-tests for the mean MNE averaged for sensor groups with significant task differences.

Results

Performance

Subjects made 1.7% errors in the gender, and 1.5% in the semantic task (n.s.). Subjects were slower to respond in the gender decision (M = 929 ms, SD = 117 ms) than in the semantic task (M = 796 ms, SD = 139 ms; TASK: F(1,13) = 10.4, p < .01). Responses became faster with the repetition of each task (SERIES: F(1,13) = 15.7, p < .01; 1st series: M = 912 ms, SD = 154 ms; 2nd series: M = 814 ms, SD = 117 ms), while the interaction TASK × SERIES did not reach significance (F(1,13) < 1).

Magnetic activity

An example of the time course of MNE across 700 ms following stimulus onset at 35 locations is illustrated for the grand mean in figure 2A. An increase in MNE scores relative to baseline around 100 ms after stimulus onset indicates an increase of brain activity at this latency. This increase in activity is obvious for both tasks, its amount differing between sensors. Figure 2B illustrates the distribution of the MNE, averaged across subjects, for the original and the repetition of each task. Overall activity is largely similar between the two original tasks and between repetitions, while different topographical accentuations become evident between tasks and repetitions.

For the first presentation of each task (semantic 1^{st} , syntactic 1^{st}), differences and t-maps of the 197 MNE disclosed more pronounced activity in the semantic than the gender task 125-200 ms following stimulus onset. Averaged across this epoch, a significant task difference between the average MNE of the respective sensor groups was confirmed by t(13) = 3.33 (p<.01).

When presented for the second time, the comparison of the task-related MNE patterns (semantic 2nd, syntactic 2nd) indicated two activity peaks after stimulus onset relative to baseline. The first peak was prominent between 150 and 275 ms, the second between 275 and 450 ms. Statistically significant differences between tasks were found between 150-275 ms and between 300 and 625 ms following stimulus onset (figure 3A). In the first epoch (150-275 ms, figure 3B) task differences were confined to left fronto-temporal sensors with more activity in the gender than the semantic task. The post hoc t-test

for the mean MNE of this group of sensors confirmed this task difference with t(13) = 2.14, p < .05). In contrast, significant t-values between 150 and 225 ms at right-frontal sensors verified more activity in the semantic compared to the gender task (for the post hoc t-test of the mean MNE of this group of sensors: t(13) = 1.97, p < .05).

A second epoch of task-dependent activity patterns became evident between 300 and 400 ms (figure 3C). Significant differences with more activity during gender than semantic task were restricted to the left hemisphere, and comprised more sensors over left frontal, temporal and central areas (for the mean MNE of the sensors with significant t-values: t(13)=3.54, p<0.01). After this period, areas with significantly more activity in the gender than the semantic task became prominent in both hemispheres up the end of the recording period (400-625 ms, figure 3C). For the mean MNE of left temporal and parietal group of sensors the task effect was verified by t(13)=3.34, p<0.01), for the group sensors over the right temporal area t(13)=3.12, p<0.01).

Discussion

The goal of the present study was to examine whether the retrieval of lemma information, provoked in a gender decision task, was indicated by brain activation around 200 ms after stimulus-onset with predominance in the left hemisphere, compared to the control task that focused on semantic processes only. Thereby, we followed Levelt's model (1989, 1999) of stages in speech production, in which the 150-275-ms epoch is related to processes of syntactic lemma retrieval, the 275-400-ms epoch to phonological encoding, and the 400-625-ms epoch to phonetic encoding. Using equivalent current dipole (ECD) modeling as method of source analysis, Levelt et al. (1998) described for the 150-275-ms window a clustering of sources of activity in the right parietotemporal cortex. In contrast, a left-frontotemporal activity focus dominated in the present MNE analysis. Differences in the design and analyses may account for the different results. Compared to the picture naming task employed by Levelt and colleagues, the present design emphasized the retrieval of syntactic information by introducing a gender decision task. Detailed analysis of magnetocencephalographic activity across 25-ms epochs in the source space (MNE) disclosed the left frontotemporal dominance for the difference between tasks, that is, activity dominance during gender over semantic processing, while activity over posterior areas with right-hemispheric focus was evident for both tasks (see figure 2). This suggests that processes involved in the gender decision task involve left-anterior brain areas (Pulvermüller 1999b) more than processes involved in semantic categorization.



Figure 2A (top insert): Illustration of typical averaged evoked magnetic response of a subject (arbitrarily selected), superimposed for the 148 sensors during an 800-ms recording epoch. Below: Time course of Minimum Norm Estimates (MNE) across 100 ms before and 700 ms after stimulus onset averaged across all subjects separately for the gender decision (solid) and the semantic classification (dotted) task (second repetition of each task). MNE in nAm (increase in activity up) are depicted for 35 of the 197 MEG locations. A vertical black line marks stimulus-onset for each sensor. Vertical lines across sensors demarcate the time of interest around 200 ms, for which task differences are examined.

B: Top views (covering 110°, nose pointing upwards marked by triangle) of the distribution of Minimum Norm Estimates (MNE) averaged for three time epochs (from left to right: 150-275 ms, 300-400 ms, 400-625 ms) during the first (1st) and the second (2nd) presentation of the gender decision (top) and the semantic categorization (bottom) task. Shadings in gray indicate the scaling of MNE, isocontour lines representing steps of 0.0025-nAm.



Figure 3. A: Distribution of MNE score differences (view from top on the head, nose upwards) during the second task presentations, plotted separately for successive 25-ms epochs starting 125 ms after stimulus onset. Top rows: Areas shaded in red depict areas with higher MNE scores for semantic classification than gender decision, areas shaded in green areas with MNE scores for gender decision exceeding those for semantic classification. Isocontour lines represent steps of 0.001-nAm differences between MNE. Rows below: t-statistic with black areas indicating areas of non-significant difference between tasks, green areas indicating MNE differences with significantly (p<.05) higher MNE during gender decision than semantic classification, red areas indicating MNE differences with significantly higher MNE during semantic than gender decision. B: Difference maps and t-maps averaged for the epoch 150-275 ms after stimulus onset, displayed for the top view (left) and the left-hemispheric view (right), and for the epoch 150-225 ms after stimulus onset, displayed for the top view (lower left) and the front view (lower right). C: Same as B for the time intervals 300-400 ms and 400-625 ms following stimulus onset.

In a similar time range, the semantic classification task provoked more pronounced activity in right-frontal areas. The different task-dependent activity patterns in the same latency range may suggest the early retrieval of concept together with syntactic information, as suggested by Levelt et al. (1999). Both aspects of the lexical selection process may have been differentially emphasized by task instructions, the instruction for gender decision emphasizing the stage of lemma retrieval, the instruction for semantic categorization the retrieval of a semantic feature. This task-dependent asymmetry differs from the previous report of bilateral activity induced by semantic categorization (Dobel et al. 2001). The difference between studies may be explained by the different temporal resolution of EEG (sampling rate 200 Hz, ERP averaged for the 300-600-ms interval) and MEG (sampling rate 500 Hz, averages across 25-ms epochs): Responses before 300 ms were not analyzed in the ERP study, and the specific balance of left- and right-hemispheric processes in this early time window may be disclosed only by the high temporal resolution. Moreover, the relative difference in the predominance of activity reported here does not rule out left-hemispheric activity in the semantic task, but stresses that the right-hemispheric activity was larger than the left-hemispheric in the semantic task.

It has to be considered whether the anterior signals represent sources of eye movement activity. Visual stimuli were used for the comparison with the previous ERP (Dobel et al. 2001) and MEG studies (Levelt et al. 1998). A visual stimulus-evoked response (VEP) may be inferred from the increase in activation around 100 ms after stimulus onset (see figure 2). Although eye movements were carefully controlled, an influence of blinks and eye movements on early visual evoked responses cannot be ruled out completely. However, the early anterior activity peaks (150-275 ms) differed between tasks. Since task-dependent eye-movements are hardly conceivable, given that the same stimuli were used in both tasks, a crucial influence of VEPs on the task-specific activity pattern seems unlikely.

More left-temporal activity during gender decision than semantic categorization was also evident in the subsequent epoch. Levelt et al. (1998) related a source cluster in the region of the left temporal gyrus in the 275 - 400 ms interval to phonological encoding. Studies employing different methods like EEG, imaging or transcranial magnetic stimulation also attributed phonological encoding and rehearsal to left-hemispheric functions (Banich and Nicholas 1998; Zaidel 1998; Zaidel and Peters 1978; Kuriki et al. 1996; Stromswold et al. 1996; Stewart et al. 2001). The converging evidence suggests that the presently observed left-temporal focus in the 300-400 ms epoch may be an indication of phonological encoding.

Activity predominance in the gender over the semantic task extended to bilateral temporal and parietal areas in the interval 400-625 ms. Since subjects were not required to articulate, this late left-temporo-parietal focus of activation is difficult to compare with Levelt's model, which describes phonetic encoding and preparation for articulation during this epoch. However, Levelt et al. (1998) found sources in this time window to be "quite scattered" (p.560) in parietal and temporal lobes, in particular in the vicinity of the sensory motor face area. This topography may be compared with the present bilateral activity. Right-hemispheric temporal activation was also described by McGuire et al. (1996) in a self-monitoring task. It is possible that similar processes were evoked by the present task. Although no overt picture naming was required silent naming of the object's gender including phonological encoding or monitoring may have served to verify the earlier automatic retrieval of the grammatical gender.

The task-specific activity patterns became prominent with the repetition of each task. Although this is in line with the notion of Jescheniak and Levelt (1994) that lemma retrieval might overrule other task-inherent processes like concept retrieval only, when those become less effort consuming and automatic, alternative explanations have to be considered. General activity was similar in the two original tasks, which would argue against an impact of task order. Still, consequences of task repetition like habituation, priming or a change in the strategy of task completion have to be considered. Habituation and repetition priming have been reported to result in activity reduction. For instance, van Turennout et al. (2000) found repetition priming in an object naming task to be associated with a decrease of functional neural activity (assessed by fMRI for immediate, 30-sec, and longer, 3-day, repetition) over posterior and left inferior frontal regions. Sekiguchi et al. (2001) found a decrease of the magnetic response to word (but not for non-word) repetition 300-500 ms post-stimulus. Task repetition in the present study produced only a slight decrease of overall activity on the present semantic task, but a change in the task-specific activity patterns. The conclusion that an activity decrease with repetition indicates the formation of sparser, yet specific neural networks, might explain the task-specific accentuation of activity patterns with task repetition.

Priming may also be considered in a more general sense as familiarization with the task, which allows a change from controlled to automatic processing. Such a familiarization and potential change in strategies may have been indicated in the present study by increasing response speed as well as by a change in task-specific activity patterns. Semantic categorization of object pictures – as the first task – should have activated processes like the visual analysis of objects, episodic memory, lexical concept retrieval, implicit item learning. All these processes have been related to right-frontal or bilateral activation

(Tulving et al. 1996; Seeger et al. 2000; Fletcher et al. 1999). The same processes, however, should have been activated also in the gender decision task. Thus, the pattern of activation in the first task presentation may have been determined more by these shared processes than by the task specific retrieval of syntactic information. Semantic categorization may have emphasized episodic memory and conceptual retrieval more than the gender decision instruction, accentuating this task-specific activity pattern in the difference maps. When less effort for priming of episodic memory was required during the task repetition, the task-specific activity patterns favoring lemma retrieval and phonological encoding became prominent.

Magnetic source imaging served in the present study to elucidate hemisphere-specific activity in the course of speech production. This deduction of regions of cortical activity, derived from the Minimum Norm Estimate, should substantiate the assignment of language processes to their cortical generator structures. MNE, which allows the inference of distributed cortical activity, seemed more suitable to map cortical activity expected for the present tasks than the fitting of single equivalent current dipole, as complex processes provoked by the present tasks are more likely to activate distributed sources of an unknown number. However, the similarity of the present results with those obtained by Levelt et al. (1998) using the ECD approach suggests that both methods are suitable to explore brain activation during speech production.

In conclusion, the high temporal and spatial resolution magnetoencephalography employed in the present study allowed the testing of specific hypotheses derived from the stage-model of language production (Levelt et al. 1999) and provided new evidence on the temporally distinct and hemisphere-specific brain processes involved in retrieval of syntactic information and phonological encoding.

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