Abstract

The study investigated the neuronal basis of the retrieval of words from the mental lexicon. The semantic category interference effect was used to locate lexical retrieval processes in time and space. This effect reflects the finding that, for overt naming, volunteers are slower when naming pictures out of a sequence of items from the same semantic category than from different categories. Participants named pictures blockwise either in the context of same- or mixed-category items while the brain response was registered using magnetoencephalography (MEG). Fifteen out of 20 participants showed longer response latencies in the same-category compared to the mixed-category condition. Event-related MEG signals for the participants demonstrating the interference effect were submitted to a current source density (CSD) analysis. As a new approach, a principal component analysis was applied to decompose the grand average CSD distribution into spatial subcomponents (factors). The spatial factor indicating left temporal activity revealed significantly different activation for the same-category compared to the mixed-category condition in the time window between 150 and 225 msec post picture onset. These findings indicate a major involvement of the left temporal cortex in the semantic interference effect. As this effect has been shown to take place at the level of lexical selection, the data suggest that the left temporal cortex supports processes of lexical retrieval during production.

INTRODUCTION

Producing spoken words involves a train of mental operations. Figure 1 presents the stages distinguished by Levelt, Roelofs, and Meyer (1999) in their theory of lexical access. When a picture is named, say of a tiger, you must first recognize the depicted object (the tiger). Next you must decide how you want to refer to it in the present communicative situation (specifically as a tiger, or more generally as an animal). This is called “conceptual preparation.” Let us assume you go for the tiger reference. Then you must zoom in on the appropriate item (“lemma”) in your mental lexicon (“tiger”), which is under competition of semantically related items (such as “lion”). This is the operation of “lexical selection” in Figure 1. Next you must access the selected item’s word form information or “phonological code” (/taiɡ/); this is essentially the string of segments (consonants, vowels) that make up the word. You then syllabify the word by successively composing its syllables from the segments (/tai_/ɡa/) and assign stress to them. This is the operation of “phonological encoding” in Figure 1. For each of these syllables, you access a stored motor instruction (or “gestural score”) or you generate the score base on segmental information; it specifies the articulatory gesture that will produce the spoken syllable. Finally, you execute these gestures, with overt speech (the spoken word “tiger”) as output. There is one additional operation involved in any speech production. As in any other complex motor action, we continuously monitor our own performance. We will return to this mechanism of self-monitoring in the discussion.

The present study is concerned with the operation of lexical selection. Our aim was to gather detailed information on the time course and location of the brain activations underlying this operation. We approached this by magnetoencephalography (MEG) measurement during picture naming. To focus on lexical selection in such a task we used an interference effect repeatedly observed in behavioral studies of picture naming, the “semantic context effect.” Kroll and Stewart (1994) observed for English speakers that when a series of pictures was to be named, latencies were longer when pictures appeared within lists of items from the same semantic category than when they appeared in lists of items from various semantic categories. For instance, speakers are slower to name a picture of a “tiger” when the other pictures within the experimental block are animals, than when they stem from various categories such as vehicles, fruits, and furniture. A similar
effect was obtained by Kroll and Stewart with bilingual English–Dutch speakers in a single-word translation task. The semantic context effect has also been shown in a picture-naming task with German speakers (Damian, Vigliocco, & Levelt, 2001) and in a translation task with Dutch speakers that required the production of noun phrases (Vigliocco, Lauer, Damian, & Levelt, in press). The effect is highly reliable, producing a latency difference of 30–40 msec between same- and mixed-category conditions. Complementary, in a button experiment that arguably requires conceptual, but not lexical, access, no effect of semantic context was found, implicating a language locus (Damian et al., 2001). The semantic context effect arises during lexical selection. According to the abovementioned theory of lexical access (Levelt et al., 1999), semantically related concepts, such as tiger and lion, coactivate one another through activation spreading in a semantic network. Each concept activates its own lemma in the mental lexicon. Coactivated lemmas compete for lexical selection, and competition affects selection latency. This predicts that latencies should be relatively slow if semantically related items are active during naming. This has been confirmed in a host of experimental studies (see Levelt et al., 1999, for a review). It is also what happens in the same-category condition of the paradigm used in the present experiment. When the subject names a semantically homogeneous set of pictures, there will be a stronger semantic coactivation among the items in the response set than when the set is semantically heterogeneous (for examples, check Figure 2). As a consequence, there will be more competition among activated lemmas in the same-category condition than in the mixed-category condition, with the critical difference in selection latency as a result.

The behavioral studies of lexical access have provided a rough estimate of the time windows (TWs) for the operations depicted in Figure 1. The evidence is reviewed by Levelt, Praamstra, Meyer, Helenius, and Salmelin (1998). In picture naming, lexical selection was estimated to take place during the 150–275-msec interval post picture onset. It is preceded by object recognition and conceptual preparation; it is followed by phonological code retrieval and syllabification. The estimate for the temporal window of the latter two operations was 275–400 msec post picture onset.

Neuronal studies of this time course are scarce. van Turenout, Hagoort, and Brown (1998) examined the time course of word production using lateralized readiness potentials as the dependent variable. They found lemma selection to precede phonological code retrieval by some 40 msec. This measurement, however, did not allow conclusions about the locus of the relevant processes in the brain. A first attempt at localization of the subsequent operations, including lexical selection, was made in the abovementioned study by Levelt et al. (1998). They conducted an MEG experiment on picture naming and computed peak activity of dipole sources in the individual magnetic response patterns. These showed a clear progression from early occipital activation via parietal and temporal to frontal activation. During the predefined TW for lexical selection (150–275 msec), dipole sources were found active in the right parietal lobe, whereas left posterior temporal dipoles were found active during the next TW of phonological processing (275–400 msec). The activation in the right parietal lobe was tentatively interpreted as

Figure 1. Core processing stages in the production of words.
an effect of visual attention or visual memory. The subsequent activation of the Wernicke’s area was taken to reflect aspects of phonological processing.

Most localization studies of spoken word production have used PET and fMRI neuroimaging. They typically reported activation in a range of temporal areas in addition to left inferior frontal activation. The former regions are generally taken to involve semantic operations, whereas the latter, inferior frontal region is taken to reflect phonological/phonetic aspects of spoken word preparation (e.g., Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Wiggs, Ungerleider, & Haxby, 1996; Vandenbergh, Price, Wise, Josephs, & Frackowiak, 1996). However, as pointed out by Indefrey and Levelt (2000), the poor temporal resolution of these brain imaging techniques as well as the particular tasks used in these studies make it difficult to identify the different subprocesses (such as the ones depicted in Figure 1) involved in picture naming. Thus, it is still an open matter which brain regions are involved in the operation of lexical selection. There are, however, a number of brain lesion–behavioral studies that suggest an involvement of the left temporal region in lexical retrieval processes, as subjects with lesions in this region demonstrate word finding problems as well as semantic substitution errors (for a review, see Friederici, 1999). Different from all previous studies, the present experiment specifically targets the operation of lexical selection by manipulating it as an independent experimental variable. Any concomitant variation in dependent magnetic activation of the brain will be indicative for both the time course and the cerebral localization of the neuronal processes involved in lexical selection.

RESULTS

Performance Data

In an overall analysis of the naming latencies, the predicted inhibitory effect of semantic context was obtained, with a mean response latency of 739 msec in

Figure 2. The picture stimuli used in the experiment, consisting of five semantic categories with five exemplars each. Stimuli were repeatedly presented in small sets corresponding either to the rows (same category/semantically homogeneous) or to the columns (mixed category/semantically heterogeneous) of the matrix. For each picture, the German target name and its English translation are given.
the same-category condition, and a mean of 713 msec in the mixed-category condition. The difference of 26 msec was highly significant, \( F(1,19) = 27.0, p = .0001 \). The mean error rate was 2%, which was considered too low to allow a meaningful analysis. A post hoc analysis per subject revealed a significant context effect (\( p < .05 \)): for 15 out of 20 subjects. For these 15 subjects, the mean reaction time for the mixed-category condition was 685 msec, and for the same-category condition it was 721 msec; the difference was again highly significant, \( F(1,14) = 57.6, p < .0001 \).

**MEG Data**

A comparison of the elicited overall magnetic field strength between subjects and conditions reveals that evoked activity occurred between 150 and 500 msec. An activity peak shortly before 200 msec was consistently present in all subjects showing a significant context effect. Some subjects had strong earlier responses. This might be due to the variability of the individual structure of the primary visual cortex (see Aine et al., 1996). For some of the subjects, the primary visual cortex is very symmetrical and as the stimulation was centered to subject’s visual field, the equivalent dipoles may then cancel each other.

The root mean square signals (RMS) of magnetic field strength per hemisphere are separately plotted in Figure 3. The RMS signals were calculated on the basis of 64 MEG channels per hemisphere. The sensors positioned at the midline of the whole array were excluded. This rather coarse analysis was done to check whether the evoked overall field strength reveals the interference effect already. As can be seen, the evoked magnetic field strengths did not differ significantly between conditions, which means that the elicited field strength for both conditions is approximately identical. Although the sum of the currents is identical, the composition of its parts might be different. Hence, a current source density (CSD) localization may provide a more direct measure for the spatio-temporal characteristics of the cortical activity. As noted above, lemma selection was expected to fall in the TW of 150–275 msec post picture onset (Levelt et al., 1991, 1999).

**Spatial Principal Component Analysis (PCA)**

The transformation of magnetic data into CSD data sharpens the problem of a direct statistical analysis because the number of available channels increases from 147 (MEG sensors) up to 251 (current dipoles). A spatial PCA was therefore performed to replace the multichannel spatio-temporal activation pattern by a few virtual spatial current channels and their corresponding time courses aligned to the experimental conditions. Like all statistical techniques, PCA must be applied and interpreted with caution. Wood et al. (1984) have pointed out that under certain circumstances PCA may lead to a misallocation of the variance among the components. However, as they noted, when PCA misallocates variance, so would windowed amplitude measurement. As Dien (1998) pointed out, PCA provides useful information about the underlying structure of the evoked responses. Within the framework of this article, the PCA is based on current density data. The PCA is used to figure out which brain regions are activated synchronously. Here the estimated current density distribution of each condition is decomposed into nine factors and a residual. The spatial loadings of these factors are identical between conditions. It is the potentially different time course that reveals differences between conditions.

We have applied the spatial PCA in the following way. First, a rectangular matrix was constructed that had a column for each CSD node and a row for each time instant between 150 and 500 msec, condition, block, and subject. The covariance matrix of the current density matrix was submitted to PCA. The nine spatial factors (SFs) that accounted for 74% of the total variance were extracted and finally rotated using promax rotation. The first nine factors of the PCA decomposition explained variance according to the following table:

<table>
<thead>
<tr>
<th>Factor</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variance</td>
<td>37.6</td>
<td>11.4</td>
<td>7.4</td>
<td>6.4</td>
<td>3.2</td>
<td>2.8</td>
<td>2.2</td>
<td>1.7</td>
<td>1.4</td>
</tr>
</tbody>
</table>

The next table displays variance explained by each factor after promax rotation eliminating other factors. Since promax rotation is an oblique rotation, the sum of variances is higher than the sum of the explained variances of the PCA factors.

<table>
<thead>
<tr>
<th>Factor</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>Variance</td>
<td>14.7</td>
<td>14.2</td>
<td>10.8</td>
<td>12.4</td>
<td>6.1</td>
<td>7.0</td>
<td>5.5</td>
<td>4.9</td>
<td>4.6</td>
</tr>
</tbody>
</table>

All reference axis correlations were less than .29. The rotated SFs reflect characteristic topographic patterns in the data set. They were plotted in Figure 4.

The time courses of the nine SFs are displayed in Figure 5. Separate ANOVAs for each SFs were carried...
out with the factors’ TWs (14 consecutive TWs of 25 msec) and condition (same/different) between 150 and 500 msec. SF6, representing left temporal activation, showed a significant TW by condition interaction, $F(1,13) = 3.01, p < .05$. No other TW yielded a significant difference.

Analyses of SF6 effects for each of the 14 TWs showed a significant condition effect in the following TWs: 150–175 msec, $F(1,14) = 6.85, p < .05$; 175–200 msec, $F(1,14) = 9.59, p < .01$; 200–225 msec, $F(1,14) = 4.98, p < .05$; and 450–475 msec, $F(1,14) = 5.49, p < .05$.

**DISCUSSION**

The present article set out to investigate the neuronal basis of a particular subprocess during production, namely semantically driven lexical selection. We used a specific behavioral effect, the semantic interference ef-
fect, to temporally locate lexical selection during picture naming. The brain responses of those 15 subjects who demonstrated the interference effect, that is longer picture-naming latencies in same-category blocks than in mixed-category blocks, were analyzed. The MEG measures provided the high temporal resolution needed for a TW analysis of these subjects' cerebral activations during picture naming.

The subjects showed a significant difference in their brain responses between the same- and mixed-category conditions in a TW ranging from 150 to 225 msec post picture onset. The spatial distribution of this difference indicated that the left temporal region supports the processes underlying the semantic interference effect. This is indicated by SF6, which is strongest over the left temporal regions. The analysis used here does not provide the real extent and shape of the activated region for two reasons. First, it is still a matter of debate how to retrieve the spatial extent of an activated region from the current density solution. Second, the SFs of the PCA have to fulfill additional restrictions that may vary the apparent shape of strongest activity. Our result does not exclude the possibility that other areas may also be involved, but the area found to be active here is the main area carrying the effect most markedly. The induced change in current strength was too small to yield a significant difference.

In a previous MEG study (Levelt et al., 1998), the TW of 150–275 msec post picture onset was estimated to reflect the core process of conceptually driven lemma selection. The semantic interference effect has been theoretically attributed to the competition of semantically related lexical entries during the stage of lexical selection (see Levelt et al., 1999; Roelofs, 1992). This TW corresponds closely to the critical TW in our present data. In addition, the data show that it is only in the left temporal region where the critical activation difference arises during this temporal window. This suggests an involvement of this area in the process of conceptually driven lexical selection.

How does this correspond to other brain imaging data? Most imaging studies of word production have been PET and fMRI studies, which do not provide the temporal resolution needed for a TW analysis of the kind presented here. However, Levelt and Indefrey (2000) provided a meta-analysis of 58 neuroimaging experiments of word production, which sheds light on the brain regions involved in the operation of successive core processes in spoken word generation. Systematic comparison of naming tasks that do or do not involve a particular core process (such as lexical selection, phonological retrieval, phonological encoding) provided a coherent picture of brain regions involved in these processing steps. A comparison of naming tasks involving or not involving the core process of conceptually driven lexical selection, that is, the relevant process in the present experiment, showed the mid-region of the left middle temporal gyrus to be the one distinguishing region for that operation. As Vandenberghe et al. (1996) put it, this region is a “common semantic system” for word and object stimuli. This is in excellent agreement with our present findings, which provide the additional information that the critical region is engaged in the 150–225-msec TW post picture onset. It should be added, though, that the previous MEG studies of picture naming (e.g., Levelt et al., 1998; Salmelin, Hari, Lounasmaa, & Sams, 1994) did not show marked left temporal activation during the same TW. Instead, dipolar activity was detected in the parietal, in particular, the right parietal areas, during this TW. However, only the present experiment was specifically designed to examine semantic lexical competition as an independent variable.

The present data show a second TW, 450–475 msec post picture onset, during which a significant difference in activation arises between the same- and the mixed-category conditions. This is again localized in the left temporal region (see Figure 5, SF6). Is it possible to have different functions hosted within the same brain region? In principle, this is possible. Either the same brain region may host different functions as parts of different networks or two functionally different brain regions may overlap to a considerable degree resulting in a common factor in the PCA. Given the present data, we suggest that both functions share a considerable amount of activated brain tissue.

Which of the core processes (Figure 1) could be involved here? We assume that the relevant process is self-monitoring. We do not only monitor our own overt speech for appropriateness or errors, but also our “internal speech.” That allows us to correct ourselves even before the trouble word is fully produced (as in the following example: “We can go straight on to the ye-, to the orange node”). Data from Wheeldon and Levelt (1995) show that monitoring is based on a syllabified representation of word forms. The syllabic representation of the target word is available when phonological encoding is completed. Under the present experimental conditions, it might be completed at about 350 msec post picture onset and may be continued without clear limit over articulation (Indefrey & Levelt, submitted). The main target of our self-monitoring is semantic appropriateness/correctness. In this respect, the two experimental conditions are critically different. In the same-category condition, the subject might want to verify whether indeed the correct alternative has been chosen from the competing items; this check is less relevant in the mixed-category condition as there are no competing items. Which cortical regions are involved with self-monitoring? In a PET study of monitoring overt self-produced speech and speech produced by others, McGuire, Silbersweig, and Frith (1996) found bilateral activation of the lateral
temporal cortex, and in particular of the left superior temporal sulcus (BA 21/22). In a PET study involving different degrees of internal self-monitoring Paus, Perry, Zattore, Worsley, and Evans (1996) showed the involvement of the left auditory cortex, in particular, a region on the planum temporale and a region in the left posterior perisylvian cortex. Finally, Levelt and Indefrey (2000) provide evidence from their meta-analysis for the possibility that the mid-region of the left superior temporal gyrus is activated during both overt and covert self-monitoring. These results suggest that the left temporal effect of our independent variable during the late TW of 450–475 msec is due to internal self-monitoring.

METHODS

Subjects

Twenty (aged 19 to 28 years, mean age 22.5, 10 women) right-handed volunteers participated in this study. All of them had normal vision or corrected to normal using contact lenses. The vision was checked by a vision performance test board in a distance of about 5 m. All participants had a score of at least 50 according to the Edinburgh Handedness Test (Oldfield, 1971).

Stimuli

The stimuli were adapted from Damian et al. (2001): Twenty-five white line drawings on black background, depicting well-known objects of the human environment, were selected from five semantic categories (animals, vehicles, clothing, tools, furniture), with five exemplars per category. In Figure 2, these items are arranged in a 5 × 5 matrix such that the rows correspond to the categories and therefore yielded five semantically “homogeneous” sets of five pictures, while the columns form five semantically “heterogeneous” sets.

Objects belonging to the same semantic category tend to be visually similar. To minimize the possibility that larger within- than between-category visual similarity would confound the results, we attempted to match the two conditions by selecting maximally dissimilar exemplars within each category, and by rearranging the items in the matrix. Visual similarity ratings collected on all possible pairwise picture combinations showed a minor difference (2.0 vs. 2.5 on a five-point scale) between the homogeneous and the heterogeneous sets (for details, see Damian et al., 2001). As priority was given to the prevention of a visual confound, overlap between the picture labels regarding their initial phonemes could not be entirely avoided: For both homogenous and heterogeneous picture sets, four out of five sets contained one stimulus pair with identical initial segments. Overall phonological similarity between pairs of picture labels was fully matched across the two conditions by means of an overlap index (see Damian et al., 2001).

Procedure

Participants were instructed to overtly name the pictures displayed with a visual angle of 6°. The entire experiment consisted of four sessions, each containing five experimental blocks of 60 trials, to a total of 20 blocks or 1,200 trials. Within each block, five target pictures corresponding to one of the semantically homogeneous or heterogeneous sets were presented 12 times each in a pseudorandom fashion such that a given picture never appeared on consecutive trials. Type A sessions consisted of semantically homogeneous experimental blocks (same category), while Type B sessions consisted of heterogeneous blocks (mixed category). The sequence of sessions (ABBA, BAAB) was counterbalanced across participants, with an optional break between sessions, which was usually accepted by the participants. To ensure that the intended picture labels were indeed used, participants were asked to practice the names before the first testing session by studying a hard copy of the pictures with their names.

Measurements were done in a shielded room. Subjects were seated in a relaxed position and asked not to move and to avoid eye blinks and eye movements. The signal from the intercom system of the MEG chamber was fed into a voice key, which allowed to measure naming latencies. On each trial, a fixation cross was presented in the middle of the screen for 200 msec, followed by a blank interval for 600 msec. Then, a stimulus picture was presented until the voice key detected an utterance, or for a maximum of 1300 msec. This event was followed by a constant delay of 1300 msec, yielding an interstimulus interval that varied dependent on the speech onset time.

MEG Recording

The MEG raw data were digitized using a sample rate of 508.63 Hz and a passband from DC up to 100 Hz. One hundred forty-seven MEG data channels, 11 MEG reference channels, EOGV, EOGH, and the voice key signal output were recorded using a whole head system WH Magnes 2500 (4D-NeuroImaging). The sensor was positioned symmetrically and as close as possible to fronto-central regions. The coil positions at the head as well as the outer head shape has been measured first by a sensor position indicator. The head position relative to the sensor array was measured by a set of five coils before and after each measurement block.

Data Analysis

Performance Data

Response times on error trials, latencies larger than 1300 msec or smaller than 250 msec, and data points exceeding two standard deviations of a participant’s
conditional mean were excluded from the analysis (7.5% of the entire data set).

MEG Data

Time points were rejected from averaging whenever the standard deviation of a moving time interval exceeded one of the thresholds: EOGV: 100 μV, EOGH: 45 μV, MEG: 1,050 ft. For the purpose of this analysis, an off-line passband filter (1–10 Hz, FIR, 3,247 points) was applied. Epochs without a voice key response were excluded. Averaged signals were calculated for each block and subject by collapsing over all epochs of the same condition. Averaging over blocks was done within the source space, which is based on a generalized method by Knoesche, Maess, and Friederici (1999). A standardized BEM headmodel was adjusted to the subject’s individual head size and position. A layer of dipoles was positioned 15 mm below the inner surface of the scull, which was thought as typical for a description of the cortex. Time window averages from 0 to 500 msec in steps of 25 msec were calculated to enlarge the signal-to-noise ratio. For each instant of the down sampled signal, the CSD distribution corresponding to Gaussian norm was determined. This procedure easily allows for statistical analysis of the dipolar current strengths because the identical source model (identical in number and arrangement of all dipolar currents) is employed for the MEG data analysis of all subjects and all conditions. Finally, the conditions “same category” and “mixed category” were calculated by summing up all averages from blocks of the same type (A, B).

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