Nouns and Verbs in the Intact Brain: Evidence from Event-related Potentials and High-frequency Cortical Responses

Friedemann Pulvermüller, Werner Lutzenberger[1] and Hubert Preissl[1]

Department of Psychology, Universität Konstanz, 78457 Konstanz and [1]Institut für Medizinische Psychologie, Universität Tübingen, 72074 Tübingen, Germany

Lesion evidence indicates that words from different lexical categories, such as nouns and verbs, may have different cortical counterparts. In this study, processing of nouns and verbs was investigated in the intact brain using (i) behavioral measures, (ii) stimulus-triggered event-related potentials and (iii) high-frequency electrocortical responses in the gamma band. Nouns and verbs carefully matched for various variables, including word frequency, length, arousal and valence, were presented in a lexical decision task while electrocortical responses were recorded. In addition, information about cognitive processing of these stimuli was obtained using questionnaires and reaction times. As soon as ~200 ms after stimulus onset, event-related potentials disclosed electrocortical differences between nouns and verbs over widespread cortical areas. In a later time window, 500–800 ms after stimulus onset, there was a significant difference between high-frequency responses in the 30 Hz range. Difference maps obtained from both event-related potentials and high-frequency responses revealed strong between-category differences of signals recorded above motor and visual cortices. Behavioral data suggest that these different physiological responses are related to semantic associations (motor or visual) elicited by these word groups. Our results are consistent with a neurobiological model of language representation postulating cell assemblies with distinct cortical topographies as biological counterparts of words. Assemblies representing nouns referring to visually perceived objects may include neurons in visual cortices, and assemblies representing action verbs may include additional neurons in motor, premotor and prefrontal cortices. Event-related potentials and high-frequency responses are proposed to indicate two different functional states of cell assemblies: initial full activation ('ignition') and continuous reverberatory activity.

Introduction

Nouns and verbs may have different neuronal counterparts. It has been proposed that areas in the frontal lobe play a role in processing of verbs and temporo-occipital cortices are relevant for processing nouns (Warrington and McCarthy, 1987; Damasio and Damasio, 1992; Pulvermüller, 1999). This idea is based on observations of patients suffering from lesions in the vicinity of the classical perisylvian language areas. While lesions in temporal and/or occipital regions sometimes selectively affect processing of nouns, lesions in frontal areas have been reported to be associated with deficits in processing verbs (Miceli *et al.*, 1984, 1988; Damasio and Tranel, 1993; Goodglass *et al.*, 1966).

Differences in meaning between the classes of nouns and verbs may be of particular relevance for their cortical representations. Warrington and McCarthy (Warrington and McCarthy, 1987) proposed that the meaning of most verbs is related to the motor modality, while the meaning of concrete nouns is related to the visual modality. Cortical processing of these words should, therefore, involve motor and visual cortices respectively. This is a necessary assumption in any associationist framework. According to Hebb (Hebb, 1949) and more recent work related

to his ideas (Palm, 1982; Gerstein *et al.*, 1989; Aertsen and Arndt, 1993; Fuster, 1995; Braitenberg, Schüz, 1998), the cortex is an associative memory in which frequent co-activation of neurons leads to formation of strongly connected neuron ensembles. These cell assemblies may form functional units while being distributed over various cortical areas. A cell assembly representing a meaningless word or syllable, such as an infant's babble, would be distributed over perisylvian areas. However, if the word is frequently presented together with visual stimuli and therefore acquires meaning, co-activation of neurons in perisylvian and visual cortices would lead to the formation of cell assemblies distributed over these perisylvian and temporo-occipital sites. Assemblies of this kind may represent nouns with concrete and well-imaginable meaning related to the visual modality, such as 'rat'. A similar point can be made for word forms frequently co-occurring with movements of the own body. In this case, co-activation of neurons in motor and perisylvian cortices may lead to the formation of cell assemblies distributed over perisylvian and additional areas in the frontal lobe related to the action. Assemblies of this kind are assumed to be the cortical equivalent of action verbs, such as '(to) write'. Accordingly, cell assemblies representing words have different cortical distributions and assembly topographies reflect semantic properties of the words (see Fig. 1) (Braitenberg and Pulvermüller, 1992; Pulvermüller, 1992, 1996, 1999). This model does not only allow for an explanation of various neuro-psychological double dissociations (Pulvermüller and Preissl, 1991), but also leads to predictions regarding topographies of cortical activity during word processing (Pulvermüller *et al.*, 1995). Noun/verb differences in cortical activity should be visible primarily in and close to motor and visual cortices.

After adequate stimulation, a Hebbian cell assembly may first become fully active ('ignition') and this process may be followed by a state in which the assembly exhibits sustained activity [in which it 'holds' (Braitenberg, 1978)]. Ignition and sustained activity may lead to specific changes of fine-grained measures of electrocortical activity in the intact brain. Electrocortical activity during cognitive tasks can be measured non-invasively using high-resolution electroencephalography (EEG). While event-related potentials calculated from EEG-recordings provide only a rough picture of actual activity in the cortex [for extensive discussions of this point, see Coles (Coles, 1989) and Rockstroh *et al.* (Rockstroh *et al.*, 1989)], recent data indicate that this picture is, however, fine-grained enough to disclose processing differences between vocabulary classes, for example content and function words (Neville *et al.*, 1992; Nobre and McCarthy, 1994; Pulvermüller *et al.*, 1995) or concrete and abstract nouns (Kounios and Holcomb, 1994). Besides event-related potentials, another measure of electrical activity in the brain, high-frequency electrocortical responses, may provide important information about specific cognitive neuronal processes.
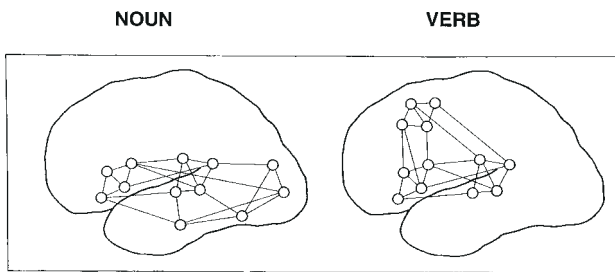
Figure 1. Sketch of possible cortical representations of nouns eliciting visual associations and verbs leading to association of body movements.

High-frequency cortical responses in the range >20 Hz, the so-called gamma-band, have been proposed to be related to the activation of stimulus-specific cortical representations relevant for cognitive processing [for review, see Aertsen and Arndt (Aertsen and Arndt, 1993), Lopes da Silva (Lopes da Silva, 1991) and Singer and Gray (Singer and Gray, 1995)]. Consistent with this idea, high-frequency responses recorded in EEG and magnetoencephalography (MEG) disclosed differences between processing of Gestalt-like visual stimuli and matched meaningless arrays (Lutzenberger *et al.*, 1995; Tallon *et al.*, 1995), and between meaningful words and matched meaningless pseudowords (Lutzenberger *et al.*, 1994; Pulvermüller *et al.*, 1994, 1995b, 1996a, 1997). Because event-related potentials and high-frequency EEG responses may provide rather specific information not only about the cortical loci of cognitive processes, but, in addition, about their physiological properties, both measures were investigated in subjects processing nouns and verbs matched for length, word frequency and other variables (see Materials and Methods). In an earlier study (Pulvermüller *et al.*, 1996b), we found differential high-frequency responses to nouns in verbs. Here, we address the question how high-frequency responses relate to specific cognitive processes and electrocortical activity as revealed by event-related potentials.

Before the actual EEG experiment was carried out, effort was spent to study cognitive differences between the processing of noun and verb stimuli. This was done to investigate empirically whether processing of these stimuli primarily led to associations involving the visual and motor modalities [as proposed by Warrington and McCarthy (Warrington and McCarthy, 1987)], subjects were asked to rate motor and visual associations elicited by presentation of a particular set of nouns and verbs. This pre-experiment made it possible to select nouns and verbs strongly differing in the motor and visual associations they elicit. For the EEG experiment verbs with relatively strong motor associations and nouns with relatively strong visual associations were selected.

Materials and Methods

Subjects
Thirty right-handed monolingual native-speakers of German (16 females) with at least 14 years of formal education were paid for their participation in the EEG experiment (15 DM/h). Their age ranged between 20 and 31 years (mean 25). None of them had a history of neurological illness or drug abuse. Their vision was normal or corrected-to-normal. All of them were strongly right-handed, as assessed by Oldfield's handedness inventory (Oldfield, 1971). Six subjects reported to have ambidexters or left-handers among their closest relatives. Data from two subjects were excluded from the analysis, due to large numbers of artifact trials. Fifteen additional subjects participated in a pre-experiment. They exhibited the same age range as the EEG participants, but no additional restrictions were applied.

Stimuli
Eighty concrete German nouns and 80 verbs referring to actions were selected. Note that most German nouns cannot be used as verbs and that the use of nouns homophonous to verbs ['das Gehen' (noun) generated from 'gehen' (verb)] occurs quite rarely. Thus, it may appear plausible that the words presented in isolation are classified as nouns or verbs respectively. Cognitive processes elicited by individual words were assessed in the pre-experiment. Subjects were asked to rate each word on separate five-point scales. They had to indicate whether they found the word meanings arousing (arousal ratings), and whether they judged them as positive or negative (valence ratings). Motor and visual associations elicited by the stimuli were assessed by asking (i) whether words reminded subjects of visually perceivable objects or scenes (visual ratings), and (ii) whether words reminded subjects of activities they could perform themselves (action ratings). Note that a question about motor associations may leave it unclear whether associations of movement perceptions or actual actions performed by the subject are to be rated. Therefore, it was made clear by the instruction that motor activities performed by the experiment participants were meant.

For the EEG experiment, 100 stimuli — 50 nouns and 50 matched verbs — were selected from the pre-evaluated vocabulary. All words were 4–9 letters long. Average lengths were 6.4 (nouns) and 6.6 (verbs) letters. As revealed by a *t*-test, the difference was not significant. All words consisted of two syllables. All were common words in German with moderate word frequency, i.e. they occur between 1 and 50 times per million words according to the CELEX database (Baayan *et al.*, 1993). Group averages of word frequencies were 7.9 (nouns) versus 7.3 (verbs) per million. Again, a *t*-test failed to reveal a significant between-group difference. Thus, the two word groups were closely matched for both word length and word frequency. This is important, because earlier psychophysiological work indicated that both of these variables can strongly affect word-evoked electrocortical responses [for discussion, see Pulvermüller (Pulvermüller, 1999)]. In addition, these stimulus groups were matched for arousal and valence values obtained in the pre-evaluation. However, motor and visual ratings for nouns and verbs were significantly different (see Results).

Procedure
The 100 stimuli words — 50 nouns and 50 verbs as detailed above — were presented together with 100 matched pseudowords, in a lexical decision task. Pseudowords were generated from word stimuli by exchanging letters within or between words. All pseudowords were in agreement with the phonological and orthographic rules of German. We ascertained that pseudowords were not meaningful words in English or French (because in the state of Baden-Württemberg where the experiment took place, most children learn both of these languages at school).

Words and pseudowords written in large black uppercase letters were presented on a gray video screen 2.5 m away from the subjects' eyes. Each stimulus was displayed for 100 ms with an stimulus onset asynchrony randomly varying between 3.5 and 4.5 s. Stimuli were presented in pseudorandom order. Not more than four words or pseudowords, and not more than two words of one of the categories (noun, verb) were allowed in direct succession. A new pseudorandom sequence of stimuli was created for each individual. Subjects were asked to decide as quickly and as accurately as possible whether a stimulus was a word in German or not, and to push a switch to the left or right accordingly. Switch direction for word/pseudoword responses and response hand were counterbalanced between subjects.

Immediately after the EEG experiment, all experiment participants were asked to rate their conscious motor and visual associations elicited by the stimuli presented in the experiment. The procedure was the same as in the pre-experiment performed for stimulus selection.

EEG Recording
Electrocortical activity was recorded through 29 sites of the extended international 10/20 system. These included 10/20 positions over the frontal lobes (F7, F3, Fz, F4, F8), the central sulcus and anterior temporal lobes (T3, C3, Cz, C4, T4), the parietal and posterior temporal lobes (T5,

P3, Pz, P4, T6), and the occipital lobes (O1, O2) (Jasper, 1958; Towle *et al.*, 1993). Additional electrodes were placed anterior and posterior to the central electrode lines (at recording sites T13, FC5, FC1, FC2, FC6, T24, and T35, CP5, CP1, CP2, CP6, T46), on the mastoids, above and below the left eye and lateral to both eyes. The two latter electrode pairs were used for recording the vertical and horizontal EOG. All other channels were recorded against C_z reference, converted off-line to a linked mastoid reference and submitted to current source density (CSD) analysis as described below. Note that data recorded in this way allow for the computation of any alternative reference (Picton *et al.*, 1995), and for the estimation of local current source densities (Perrin *et al.*, 1987). Furthermore, it is recommended to choose an electrode from the midline as an on-line reference in digital EEG recordings (Picton *et al.*, 1995). All impedances were kept <5 kΩ throughout the experiment. Signals were recorded in the 0.0796–70 Hz band and sampled with 200 Hz. The EEG was recorded for 1.28 s/trial (256 data points), starting 0.1 s before word onset (100 ms baseline).

Data Analysis

Behavior
Accuracies of lexical decisions and response times were compared between word categories using analyses of variance. Ratings of cognitive processes elicited by word stimuli were compared between categories using *t*-tests and analyses of variance.

EEG
Only trials with correct lexical decisions were submitted to the evaluation of electrocortical responses. Trials including artifacts >100 μV caused by blinks and eye movements, and trials including obvious muscle activity were excluded. Small artifacts caused by blinks or vertical or horizontal eye movements were removed using the method proposed by Gratton *et al.* (Gratton *et al.*, 1983).

Current Source Densities (CSDs). To interpolate potential distributions over the head, all recording sites were projected on a sphere approximating the standard head shape. Average spherical coordinates of electrodes were taken or calculated from Lagerlund *et al.* (Lagerlund *et al.*, 1994). Potential distributions were interpolated on the sphere using spherical splines (Perrin *et al.*, 1987, 1989; Perrin, 1992). The interpolation between two adjacent projections of recording sites was based on the angle between them and the weighted sum of Legendre polynomials. Next, two-dimensional spherical Laplacians were calculated and current source densities (CSDs) were estimated for all recording sites. CSDs were obtained for each time point of each trial. Compared to raw EEG data, CSD analysis makes it possible to calculate activity at critical electrodes independently of the activity at the reference electrode. In addition, this procedure enhances the contribution of local brain activity to the signal, while global contributions of distant sources are minimized (Hjorth, 1975; Perrin *et al.*, 1987; Law *et al.*, 1993). Note that it is sometimes difficult to determine whether EEG responses are generated at the critical electrode or at the reference, and whether they are influenced by generators distant from the electrodes. The calculation of CSDs minimizes these problems (Hjorth, 1975; Perrin *et al.*, 1987; Law *et al.*, 1993).

Event-Related Potentials. After CSD analysis, stimulus-triggered event-related potentials and normalized spectral responses were calculated for each subject, recording site and condition. [Note that, strictly speaking, it is inappropriate to speak of event-related or evoked potentials (μV) here, because, in fact, CSDs (A/cm^2) were calculated and analyzed – for reasons detailed above. However, since it is less common to speak about 'evoked current source densities', we will sometimes use the more established term.] Average values of evoked/event-related potentials were obtained in the following five time windows: I, 60–90 ms (P1); II, 120–140 ms (N1); III, 200–230 ms; IV, 280–310 ms; V, 500–800 ms. These time windows were chosen because global field power exhibited peaks in these intervals.

Spectral Responses. Normalized evoked spectral activity was calculated in the following way. Signals (256 data points corresponding to 1.28 s of recording) were first padded to zeros by using cosines, and then submitted to fast Fourier transformation (FFT). Amplitudes of the FFT-transformed signal were multiplied by cosine-shaped windows. The filtered signals were then restored by inverse FFTs and rectified by calculating root mean squares. These spectral power values were then averaged over trials. Finally, all data points were normalized, i.e. divided by the respective baseline value. Mean log power of spectral responses relative to baseline was evaluated for all recording sites in two time windows and four frequency windows. Mean values were calculated in the intervals 200–500 and 500–800 ms after stimulus onset. The following bands were chosen: 10–20, 25–35, 35–45 and 52.5–67.5 Hz. Additional analyses of high-frequency spectral responses >20 Hz were performed for the intervals 160–260 and 200–300 ms.

Statistical Analysis. A regions-of-interest (ROI) analysis was performed, because the model summarized in the Introduction allows for straightforward predictions on the recording sites where between-stimulus differences can be expected. Recording sites C3/C4 and O1/O2 were selected, because they are located close to motor and visual cortices. In addition, recordings from FC5 and FC6 were compared to the occipital sites, because earlier work indicated that processing differences between action- and visually-related words may be pronounced in the inferior premotor cortex [Brodmann area 44 and adjacent area 6 (Martin *et al.*, 1996)], and FC5 appears to be closest to this region. Three-way analyses of variance were carried out with the following design: Word Class (nouns versus verbs) × ROI (central versus occipital) × Hemisphere (left versus right). Additional analyses were performed as detailed in the Results.

Results

Behavioral Data

Ratings
Initial screening of mean ratings of all 80 noun and 80 verb stimuli indicated that nouns were rated to evoke stronger visual associations than motor associations while the opposite was the case for most verbs. Only 11 out of 80 verbs received higher vision than action ratings, and there was no noun in the sample that primarily reminded subjects of motor activities they could perform by themselves. Note that these data did not reveal a sufficiently large number of visually-related verbs or action-related nouns to allow for an investigation of electrocortical activity evoked by these categories. However, the ratings made it possible to find 50 verbs and 50 nouns that were matched for the variables word length, word frequency, arousal and valence, but significantly differed in their ratings regarding motor and visual associations.

When ratings of these matched stimuli were compared, motor associations were stronger for the verbs than for the nouns [mean ratings: 3.2 versus 0.9; $F(1,49) > 100$, $P < 0.001$], and visual association scores were higher for nouns than for verbs [means: 2.9 versus 3.6; $F(1,49) = 79.9$, $P < 0.001$]. Thus, for stimuli used in the EEG study subjects of the pre-experiment had reported stronger motor associations for verbs relative to nouns, and stronger visual associations elicited by nouns relative to verbs.

To investigate whether subjects actually taking part in the EEG experiment exhibited the same dissociation with regard to these stimuli, ratings of visual and movement associations were also obtained from these same subjects after the EEG experiment had been performed (see Materials and Methods). A two-way analysis of variance revealed significant main effects of both factors, Word Class (noun versus verb) and Modality of Associations (visual versus motor). Overall ratings were higher for verbs than for nouns [average values: 4.2 versus 2.1 points; $F(1,29) = 79.5$, $P < 0.001$], and visual ratings were higher
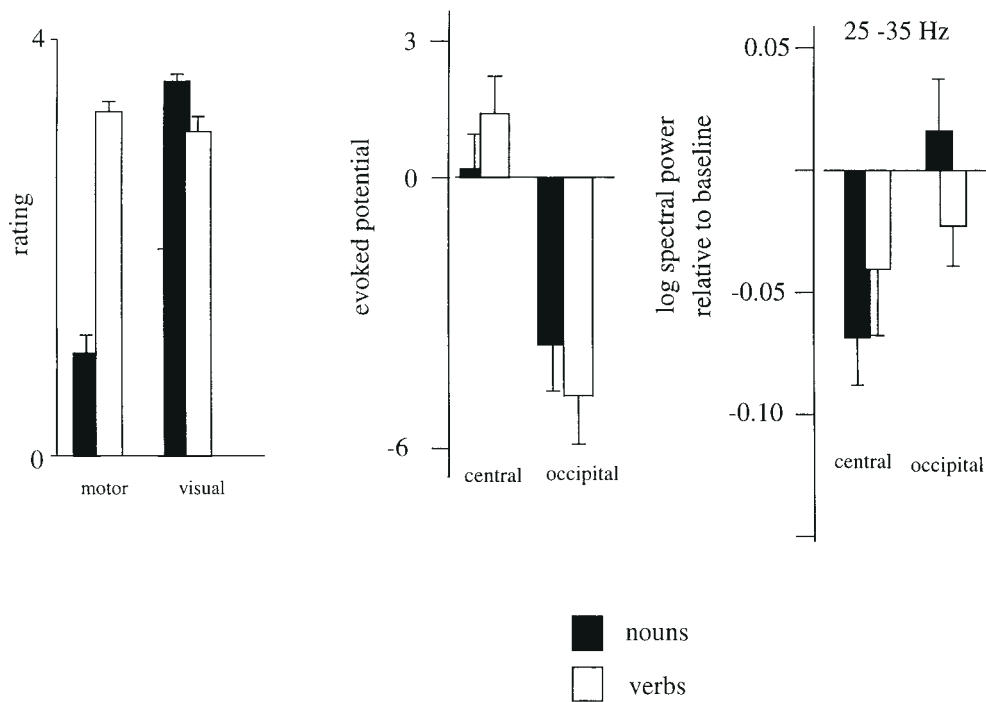
Figure 2. (Left) Ratings of the associations of actions and visual perceptions elicited by noun and verb stimuli on a five-point scale (0 = low, 4 = high). Ratings were obtained from the same subjects from whom EEGs were recorded. (Middle) Average event-related potentials submitted to current source density (CSD) analysis recorded from central (C3/C4) and occipital (O1/O2) sites 200–230 ms after presentation of nouns and verbs. (Right) Average log spectral power in the high-frequency range between 25 and 35 Hz recorded from central (C3/C4) and occipital (O1/O2) sites 500–800 ms after presentation of nouns and verbs. The double dissociation (cross-over interaction) between nouns and verbs regarding associations of actions and visual perceptions is paralleled by both amplitudes of event-related potentials and strengths of high-frequency responses recorded at central and occipital recording sites.

compared to motor ratings [3.4 versus 2.3 points; $F(1,29)$ = 105.7, $P < 0.001$]. Importantly, there was a significant inter-action of the factors Word Class and Modality of Association [$F(1,29)$ = 195.6, $P < 0.001$]. This interaction is displayed in the left diagram of Figure 2. Visual ratings were clearly higher than motor ratings for the nouns [average values: 4.3 versus 1.0; $F(1,29)$ = 191.2, $P < 0.001$] and the opposite effect for verbs approached significance [4.1 versus 4.3; $F(1,29)$ = 2.9; $P = 0.09$]. Visual associations were reported to be stronger for the nouns compared to the verbs [$F(1,29)$ = 18.2, $P < 0.001$] and associations of actions were stronger for the verbs compared to the nouns [$F(1,29)$ = 189.5, $P < 0.001$]. Notice that according to the hypothesis to be tested in the physiological experiment, differences in association modalities relate to activity changes in the respective cortices. Thus, it was important to ascertain that for each of the modalities of association (motor/visual) there was a significant word category-difference. The present data strongly support this.

Furthermore, the additional ratings of arousal and valence revealed similar values for both word classes, consistent with the view that noun and verb stimuli did not differ on these dimensions. Noun stimuli included names of animals, plants and large man-made objects. All verbs referred to motor activities and actions that can be performed by humans.

Lexical Decision
Behavioral data obtained during the EEG experiment did not reveal any differences between nouns and verbs. Average response times (727 versus 721 ms) and accuracies (>98%) of responses did not significantly differ for these word categories (F values < 1; P values > 0.2).

Physiological Data

Event-Related Potentials
The time-course of grand average event-related 'potentials' obtained after CSD analysis are displayed in Figure 3 (see also lower diagrams in Fig. 5). The earliest peak evidencing ingoing currents (i.e. electrons entering the head) was present 60–90 ms after stimulus onset at occipital recording sites (window I). This earliest wave corresponds to the P1 component. It was followed by a strong outgoing current also maximal at occipital recording sites in the interval 120–140 ms (window II), the equivalent of the N1. This wave exhibited polarity reversal at anterior recording sites. After these waves, CSDs tended to return towards the baseline. Around 200–230 ms there was a smaller peak revealing outgoing currents at occipital sites and ingoing currents at anterior sites (window III). These three earliest waves are referred to as 'components' in the text below. At 280–310 ms (window IV), there were again a posterior (parieto-occipital) focus of ingoing activity and more anterior outgoing currents. In the late time interval 500–800 ms after stimulus onset (window V), ingoing activity was again present at anterior sites.

Analysis of the three early components (but not of later time windows) revealed differences between CSDs obtained at central and occipital recording sites [component I: $F(1,29)$ = 21.0, $P < 0.001$; II: $F(1,29)$ = 79.3, $P < 0.001$; III: $F(1,29)$ = 12.4, $P < 0.001$]. There was also evidence that in time windows III and IV signals were larger over the left hemisphere compared to the right [III: $F(1,29)$ = 17.5, $P < 0.001$; IV: $F(1,29)$ = 10.4, $P = 0.003$].

Importantly, the ROI × Word Class interaction reached significance when event-related potential data from the 200–230 ms window were analyzed [C3/4 versus O1/2: $F(1,29)$ = 11.0,
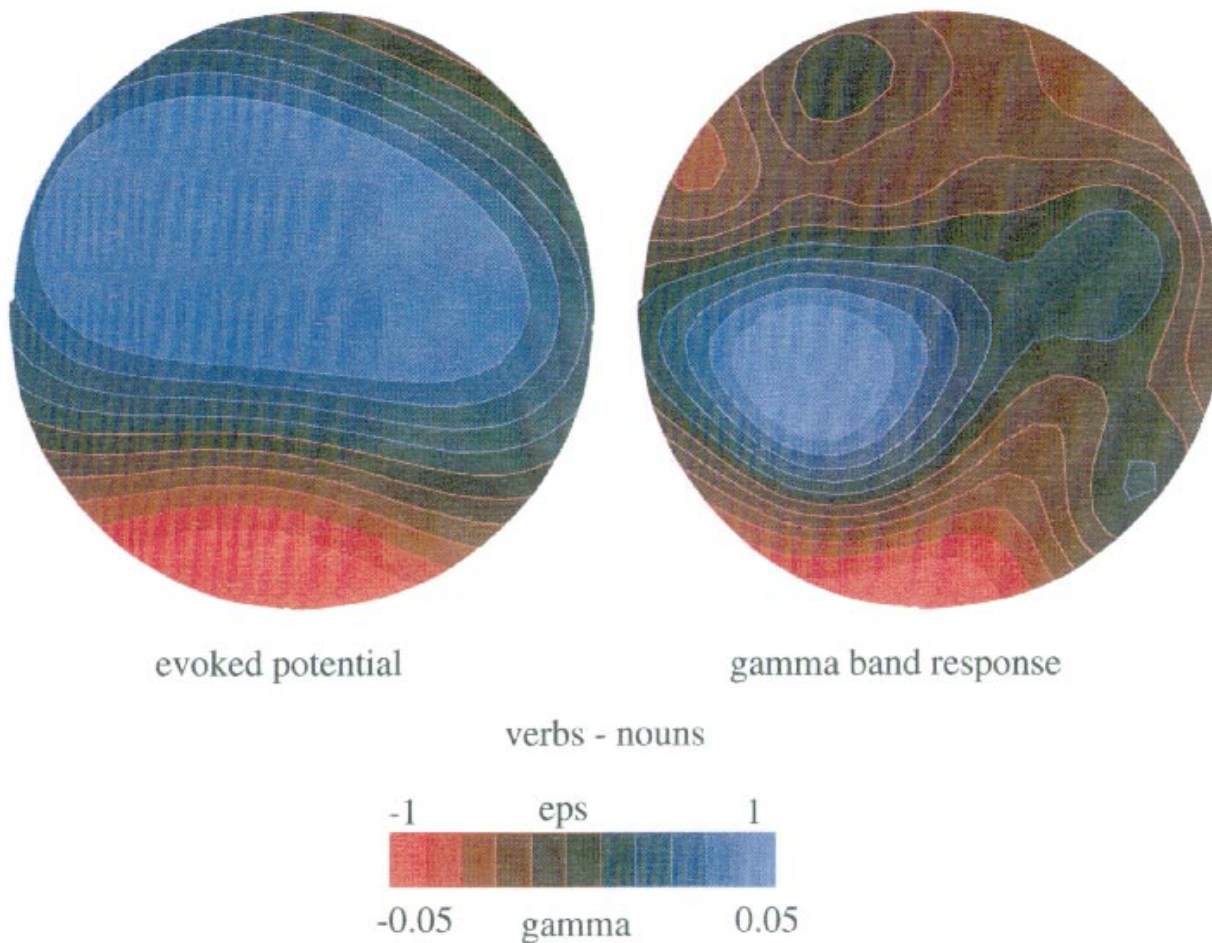
Figure 3. Topographies of grand average word-evoked potentials (after CSD analysis) recorded in five time windows (as indicated). Circles represent the head seen from above. Anterior is up and Left is left.

$P < 0.002$; FC5/6 versus O1/2: $F(1,29) = 8.3$, $P < 0.01$]. Comparison of noun- and verb-evoked potentials revealed that above premotor and motor cortices action verbs elicited more ingoing activity than nouns [$t(29) = 2.51$, $P < 0.02$], while the nouns produced more ingoing (less outgoing) activity at occipital recording sites [$t(29) = 2.25$, $P < 0.03$]. This *physiological double dissociation* is displayed in the middle diagram of Figure 2.

The cortical topography of differences between CSD-analyzed average event-related potentials elicited by nouns and verbs in the 200–230 ms time window is depicted in Figure 4 (map on the left). This map evidences that noun/verb differences in event-related potentials were largest around the ROIs chosen, i.e. at recording sites above motor and visual cortices [recording sites C3/C4 (FC5/6) and O1/O2]. There was no evidence of additional foci where the word categories diverged in their event-related responses.

Spectral Responses
Spectral responses in the earlier time interval (200–500 ms) failed to revealed any significant main effects or interactions of the variables Word Class, ROI or Hemisphere.

In the late time interval, at 500–800 ms after stimulus onset, there was a significant main effect of the ROI factor (central versus occipital) when log normalized power between 10 and 20

Hz was analyzed [$F(1,29)$, $P < 0.006$]. There was stronger power reduction at recording sites close to motor cortices. A significant interaction of the Word Class and ROI factors was revealed by the analysis of spectral power between 25 and 35 Hz [$F(1,29) = 5.5$, $P < 0.02$]. Spectral responses around 30 Hz following verbs were enhanced at central sites (C3/C4), but reduced at occipital sites (O1/O2) relative to noun-evoked activity. The bar diagram on the right in Figure 2 displays the significant interaction and double dissociation. No significant interaction was found for the comparison of data from CP5/6 and O1/2. Analysis of the frequency bands 35–45 Hz and 52.5–67·5 Hz failed to reveal significant main effects or interactions when data from the same time window were analyzed. Additional analyses failed to reveal significant word category differences in spectral responses recorded over inferior prefrontal cortices (F7/8) or posterior temporal cortices (T5/T6, T35/46).

To further investigate whether word class-differences were present around the time interval when event-related potentials evidenced such differences (200–230 ms), additional analyses were carried out. Spectral power in all three high-frequency bands (25–35, 35–45, 52.5–67.5 Hz) were calculated in the intervals 160–260 and 200–300 ms. These analyses failed to reveal word class-differences in high-frequency activity. This suggests that at the time of significant differences in event-related

I: 60 - 90 msec   II: 120 - 140 msec   III: 200 - 230 msec

IV: 280 - 310 msec   V: 500 - 800 msec
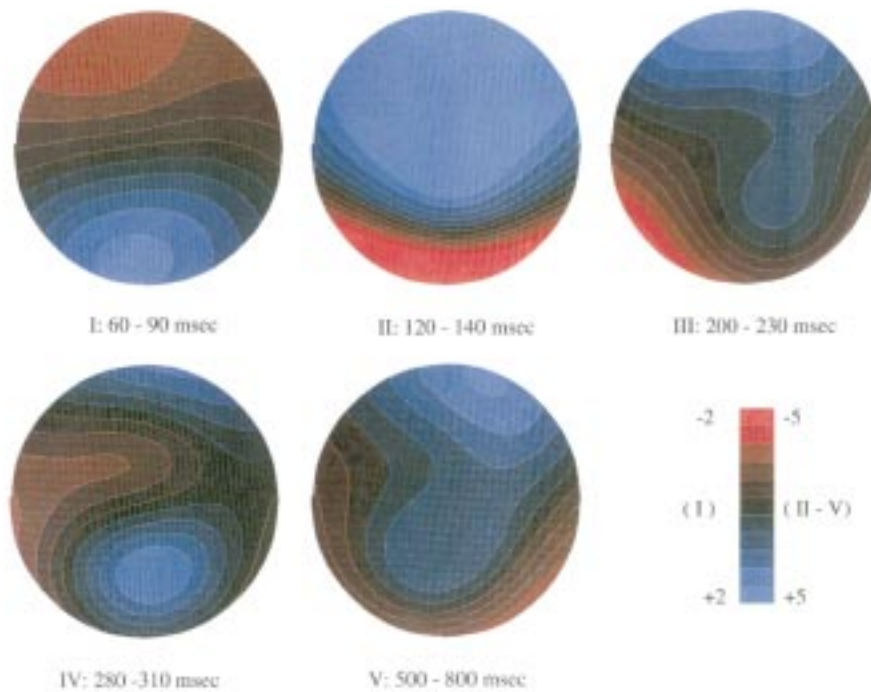
Figure 4. Word-class differences in average event-related potentials 200–230 ms after stimulus onset (left diagram) and in 30 Hz activity 500–800 ms after stimulus onset (right diagram) are displayed. Activity patterns elicited by verbs was subtracted from the activity patterns elicited by nouns. Blue (red) areas indicate stronger high-frequency responses and more ingoing current densities for the verbs (nouns).

potentials, there were no word class-differences in high-frequency brain responses.

Discussion

EEG signals elicited by the presentation of action verbs and nouns with strong visual associations revealed electrocortical differences between these word categories. Significant differences were seen early on, 200 ms after stimulus onset, in event-related potentials submitted to CSD analysis, and much later, 500–800 ms after stimulus onset, in high-frequency spectral responses around 30 Hz (25–35 Hz). Compared to nouns, 30 Hz responses to verbs led to stronger high-frequency activity at central recording sites located close to motor cortices (C3/C4), whereas nouns elicited stronger high-frequency activity than verbs at occipital sites over visual cortices (O1/O2). A similar double dissociation was revealed by event-related potentials (see difference maps in Fig. 4). Because there was no evidence for early word class-differences in high-frequency responses or for late word class-differences in event-related potentials, the two measures are probably not two sides of the same coin: they appeared in temporal succession with significant differences in high-frequency responses developing after the difference in event-related potentials. The crossover interactions revealed by both physiological measures (event-related potential and high-frequency responses) were paralleled by a cognitive double dissociation, the conscious visual and movement associations reported by experiment participants (see Fig. 2).

Electrocortical differences between nouns and verbs have been reported earlier (Brown and Lehmann, 1979; Samar and Berent, 1986; Dehaene, 1995; Preissl et al., 1995). In these studies, event-related potentials calculated relative to a linked mastoid reference (or to a global average reference) yielded significant word-class differences primarily at anterior recording
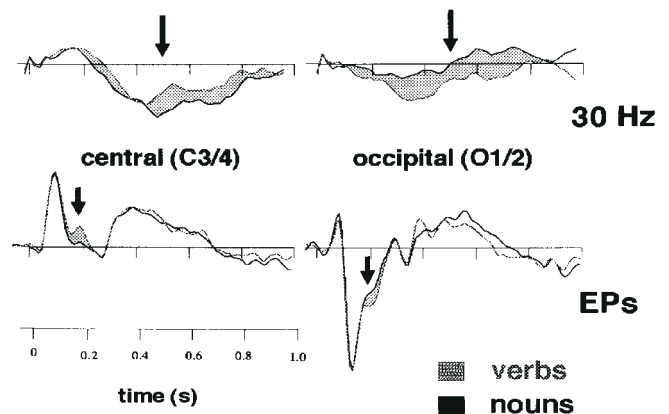
Figure 5. Time-course of 30 Hz activity and event-related potentials recorded at central and occipital sites (C3/C4 and O1/O2). Significant word-class differences are present early-on in the event-related potential (short arrows), but much later in high-frequency responses (long arrows).

sites. However, when CSD analysis was used in the present analysis, to maximize the contribution of local cortical generators to the signal (Hjorth, 1975; Perrin et al., 1987; Law et al., 1993), noun/verb differences over occipital visual cortices became significant as well. This indicates that the difference over occipital lobes is more local and perhaps less pronounced than the one observed over motor cortices. To uncover both differences, it is advantageous to use high-resolution EEG and sophisticated analysis techniques.

Specific Physiological Responses at Different Latencies

Importantly, the word class-difference in event-related potentials appears as soon as around 200 ms after stimulus onset. This is

consistent with earlier findings of electrocortical differences between other word classes, e.g. content and function words (Pulvermüller *et al.*, 1995a). As detailed in this earlier publication, exact matching of word stimuli for variables such as word length and frequency and, in addition, low variances of these measures within each stimulus category, may be crucial for obtaining these early physiological indicators of word class-specific processes (Pulvermüller, 1999).

It was not possible to find a word category-difference in high-frequency activity in early time windows. Analysis of high-frequency responses in 100 ms intervals including the window where event-related potentials uncovered differences did not lead to significant results. This suggests that the early difference was specific to the event-related potential measure. One may argue, however, that the analyses performed are not sufficient to rule out possible brief differences in 30 Hz activity occurring simultaneously with the observed dynamics in evoked potentials. However, the following must be noted. (i) Using exactly the same 30 ms window (200–230 ms) to analyze 30 Hz responses cannot lead to meaningful results, because this window would hardly include one sine wave (of 360°) of 30 Hz activity. (ii) High-frequency activity revealed by animal studies (Murthy and Fetz, 1992, 1996) usually lasts for several cycles, so that any difference in 30 Hz activity should be present over a period of at least 100 ms. Thus, the performed analyses should have revealed any detectable difference. Still, the time-course of average 30 Hz activity (Fig. 5), which suggests strong category differences around half a second after stimulus onset, may still nourish the suspicion that there was a small, non-significant difference starting together with the difference in event-related potentials. This speculation is, of course, possible, but nevertheless the conclusion is that the present data set does not provide strong evidence for word class-differences in high-frequency responses at the point in time of significant differences in event-related potentials.

In a late time window, 500–800 ms after stimulus onset, noun/verb differences were revealed by spectral responses in the low part of the high-frequency range (25–35 Hz). The analysis of average event-related potentials calculated for this same time window failed to reveal any word class-differences. In the late window, only the evaluation of high frequencies led to significant word-class differences, while the opposite was true at an earlier point in time. Thus, we conclude that the dynamics of event-related potentials and high-frequency responses followed different time courses.

No word category-differences were obtained in any of the other frequency bands analyzed. Responses in the alpha/beta band (10–20 Hz) indicated stronger reduction of spectral power at central compared to posterior recording sites. This topographical difference may be due to alpha desynchronization, a well-known phenomenon accompanying motor and cognitive activity (Pfurtscheller and Klimesch, 1991). Recall that subjects had to respond to each stimulus by moving one of their index fingers. In contrast, analyses of the alpha/beta band failed to reveal any difference between stimulus classes. Therefore, the stimulus-specific differences in the high-frequency range around 30 Hz are, most likely, not related to the dynamics in lower bands (Lutzenberger *et al.*, 1997).

While desynchronization of rhythms in the 10–20 Hz window may reflect movement preparation, it appears unlikely that movement preparation contaminated word class-differences in high-frequency responses. Responses with the left or right index finger (counterbalanced over subjects) had to follow both kinds

of words, and response times and accuracies were very similar for these stimuli. Thus, there is no indication that differences in movement preparation were present for the two word types. However, the fact that high-frequency responses at C3/C4 were reduced relative to the baseline may well be related to the global power reduction in lower frequencies [for further discussion, see Pulvermüller *et al.* (Pulvermüller *et al.*, 1995b)].

Spectral responses in the highest frequency-band analyzed (60 Hz) did not reveal significant noun/verb differences either. This is relevant, because muscle artifacts which may contaminate EEG recordings would lead to pronounced power changes in frequencies above 50 Hz (Cacioppo *et al.*, 1990; Lutzenberger *et al.*, 1997). The absence of such changes in the present data argues against a contribution of muscle activity. Furthermore, muscle activity would produce maximal artifacts close to the muscles causing them (in particular the M. occipito-frontalis and the M. temporalis). A topographical difference maximal at the vertex (Cz) is unlikely to be produced by muscle artifacts. Thus, both the particular frequency range (30 Hz) and the topography of the observed word class-differences speak against a contamination by muscle activity.

In conclusion, the two electrophysiological indicators of word class-differences followed different time courses. Early (~200 ms) and late (>500 ms) differences were present in average potentials and high-frequency spectral power respectively. When significant differences became manifest in one of the measures the other measure did not reveal such differences, and vice versa. This provides a strong argument in favor of the view that different physiological processes are reflected by these measures.

Differences in Topographies of Electrocortical Responses

The topographical differences in brain responses can be used to draw careful conclusions on cortical generators differentiating between nouns and verbs. Although there are exceptions to this rule [see, for example, Brunia and Vingerhoets (Brunia and Vingerhoets, 1980)], cortical sources are in many cases located close to recording sites where strong electrocortical effects can be recorded [see Rockstroh *et al.* (Rockstroh *et al.*, 1989) for elaborate discussion of this issue]. To further increase the likelihood that local cortical generators are primarily seen in the physiological response, we applied CSD analysis — a technique which is known to maximize the contribution of local generators to the signal and to minimize the influence of distant sources (see Materials and Methods). Therefore the present data are consistent with the view that generators in or close to motor and visual cortices underlie the electrocortical differences between word categories. Verbs may have elicited stronger electrocortical activity in or close to primary motor, premotor and adjacent prefrontal cortices, while nouns may have mobilized additional generators in primary and/or higher-order visual cortices. Clearly, the present EEG data cannot provide a more fine-grained localization. For example, it is not possible to draw conclusions about whether activity in primary motor cortices or in premotor areas contributed to noun/verb differences. Notably, however, stimulus-specific differences in event-related potentials and high-frequency responses exhibited quite similar difference maps and may, therefore, be caused by the same or strongly overlapping neuronal generators.

For a more exact localization of the cortical generators distinguishing between noun and verb processing, it is necessary to use metabolic imaging studies. Earlier positron emission

tomography (PET) studies in which experimental subjects had to read nouns and generate verbs revealed that both prefrontal and temporo-parietal areas were activated by a verb-generation task relative to noun reading (Petersen *et al.*, 1989; Wise *et al.*, 1991; Fiez *et al.*, 1996). However, it is difficult to decide which of the many aspects of the verb-generation task (e.g. lexical, attention or search processes) is most crucial for the activation of additional areas. In a PET study of nouns and verbs, Warburton *et al.* (Warburton *et al.*, 1996) found stronger activation in inferior frontal and inferior temporal areas during verb generation compared to generation of nouns. However, as these authors indicate, this result could reflect the fact that the noun generation task was subjectively 'easier' for experiment participants (p. 163), rather than reflecting differences in the processing of comparable words from different lexical classes. These studies failed to provide strong evidence for word category differences.

Recent PET studies using naming paradigms indicate that different cortical areas are involved in semantic processes related to action words, color words, tool names and animal names (Martin *et al.*, 1995, 1996; Damasio *et al.*, 1996). For example, naming of animals led to additional enhancement of metabolic rates in visual cortices in the occipital lobes (including primary visual cortices in the calcarine fissure located below recording electrode O1), while tool naming activated additional areas in the premotor cortex and in the posterior temporal lobe (Martin *et al.*, 1996). Because animal names represented a substantial fraction of the concrete nouns used in this study, and because tool names, like action verbs, can be assumed to elicit movement associations, it is possible to relate these findings to the present results. Martin *et al.*'s study and the present results both suggest additional generators in occipital visual cortices contributing to semantic processes elicited by words with visual associations. The present results are also consistent with additional generators in the frontal lobe sparked by words related to movements, as indicated by Martin *et al.*'s finding of premotor activation during processing of tool names. The present data do not address the issue of whether motor, premotor or even more anterior prefrontal sites are most relevant. However, in contrast to Martin *et al.*'s results this study did not provide evidence for additional left-temporal generators distinguishing between word categories. This may reflect limitations of the EEG, or of the present experiment, but it is noteworthy to recall that such temporal differences were also absent in a study using intracranial recordings (Nobre *et al.*, 1994; Nobre and McCarthy, 1995).

Importantly, PET results indicated that primarily areas in the left language-dominant hemisphere distinguished between word categories, while EEG data revealed similar noun/verb differences over both cortical hemispheres which are difficult to explain by left-hemispheric generators alone. The idea that the right hemisphere contributes to the processing of action verbs has received further support by our recent finding of reduced accuracy of action verb processing in patients with right-frontal lesions (Pulvermüller *et al.*, 1998). However, the common findings of the PET and EEG studies provide evidence that aspects of the meaning of words determine activation of cortical generators outside the left perisylvian region. The differences in results may, in part, be due to differences in the experimental paradigms applied. For example, the task to be performed (word generation and naming versus word perception and judgement) may lead to differential involvement of the hemispheres. More research is necessary to decide the issue of word class-specific activity in the right hemisphere (Pulvermüller, 1999).

A Putative Explanation of the Present Results

So far, however, these data appear to support the model briefly summarized in the introductory section: cortical representations of words (and other meaningful elements) are represented by widely distributed but tightly connected cell assemblies. Whereas all cell assemblies representing words include neurons in left perisylvian cortices, words with visual associations have assemblies with additional neurons in primary and/or higher-order visual cortices, and words referring to movements of the own body are represented in assemblies that include additional neurons in motor cortices. Therefore, electrocortical and metabolic activity recorded in or close to visual and motor cortices distinguish between action- and visually-related words.

While investigations of metabolic changes during cognitive processes certainly allow for a better localization of brain regions activated, electrophysiological measures do not only provide a much better temporal resolution, but may, in addition, provide valuable information about cortical activity dynamics. Two different physiological measures of cortical activity yielded very similar difference maps when noun- and verb-evoked activity were compared, although they exhibited quite different time courses (see Figs 4 and 5). But what brain processes would these different physiological responses relate to?

Assuming that words are cortically realized as cell assemblies, the fact that word category differences were visible in event-related potentials very early on (200 ms after stimulus onset), while high-frequency cortical responses revealed a similar significant difference only some 300 ms later, may tentatively be explained as follows: Immediately (~200 ms) after presentation of a word stimulus, the respective cell assembly becomes fully active. This process — called 'ignition' of the assembly (Braitenberg, 1978; Palm, 1982) — may lead to an electrocortical change visible in the event-related potential. After its ignition, activity may be retained and may reverberate in the assembly, corresponding to the fact that the cognitive item is kept in *active memory* (Fuster, 1995). Sustained activity in an assembly may cause well-timed and fast-changing activity patterns (Singer and Gray, 1995), leading to a change in high-frequency cortical responses recorded at the surface of the head (Pulvermüller *et al.*, 1997). Thus, initial access to a representation (ignition) and active memory (reverberation) may correspond to changes in event-related potentials and spectral responses in the high-frequency range, respectively. This is in agreement with the temporal course of word-category differences in event-related potentials and high-frequency responses as shown in Figure 5 [for a more extensive discussion of this point, see Pulvermüller (Pulvermüller, 1999)[.

Behavioral and cognitive differences between the noun and verb stimuli used in this study could be documented using ratings of motor and visual associations. In the pre-experiment and after the EEG experiment, subjects reported that nouns elicited stronger visual associations than verbs, and that verbs elicited stronger motor associations than nouns. Conscious processes are necessary for such reports, and it therefore appears adequate to conclude that differences in word-evoked conscious semantic associations are the cognitive correlates of the physiological differences. These results do not exclude the possibility that additional cognitive variables contribute to the electrocortical differences. For example, they may be related to the lexical category or to the grammatical function, which are different for the two word classes. After all, the two groups of words not only differ in their motor and visual associations, but belong to different lexical categories (noun and verb) as

well. Based on the present data, it cannot be concluded with certainty that the semantic associations were the cause of the physiological differences. However, we still believe that this interpretation should be preferred, because it can explain the topography of the physiological word class-differences. Word class-differences over visual and motor cortices were predicted and can be explained by the hypothesis that word semantics is relevant. It is unclear how the hypothesis that the lexical categories *per se* are relevant could explain this topographical difference. Note, furthermore, that other variables, such as word frequency, word length, or their arousal or valence values cannot account for the differences, because stimuli were carefully matched for these variables.

Finally, it should be stressed that the general neuro-cognitive rules which one may want to infer from the present data, i.e. the rules 'verbs → frontal' and 'nouns → temporo-occipital', are problematic for at least four reasons. First, as pointed out by Daniele *et al.* (Daniele *et al.*, 1994), there is lesion evidence revealing exceptions from the 'verbs → frontal' rule: some patients exhibiting deficits in processing verbs do not have any detectable lesion in the frontal lobe. Second, as mentioned in the discussion above, there is PET evidence for specific activity in the middle temporal gyrus related to the processing of words eliciting movement associations (and many verbs elicit such associations). Third, as reported by Hillis and Caramazza (Hillis and Caramazza, 1995), there is at least one patient exhibiting noun deficits in one modality and verb deficits in another modality (selective deficits in producing nouns and in reading verbs). These authors conclude that their case provides evidence for a more fine-grained division of labor so that separate and autonomous neuronal mechanisms can be assumed for orthographic, phonological and semantic representations for a given grammatical class (e.g. the classes of nouns and verbs). Finally, it is by no means clear that the critical variable determining the cortical localization of word representations is their lexical category (i.e. noun versus verb). In the discussion above, we suggested interpreting the topographical differences in physiological measures as an effect of semantic associations elicited by the particular nouns and verbs selected for the experiment (associations with actions and visual percepts). This was motivated by the idea that there may be different cortical distributions of cell assemblies representing words related to actions and visual perceptions, rather than different correlates of nouns and verbs *per se*. To decide the issue finally, it is necessary to compare (i) words of the same lexical category for whom it is clear that there are pronounced differences in semantic associations, and (ii) words of different lexical classes for whom it is evident that they do not differ in their semantic associations. To perform such studies, it is imperative to carefully evaluate cognitive and other psychological properties of linguistic stimuli.

Conclusions

Distinct neuronal activity patterns for nouns with strong visual associations and matched verbs with strong associations to actions were evidenced by electrocortical responses. The topography of event-related potentials and 30 Hz responses distinguishing between nouns and verbs was consistent with the view that neurons outside the classical language centers in the left perisylvian cortex play an important role in language processing. Cortical cell assemblies representing action verbs probably include additional neurons in motor cortices, whereas cell assemblies representing concrete nouns may include additional neurons in visual cortices of both hemispheres. It is hypothesized that event-related potentials 200 ms after stimulus onset indicate initial activation (ignition) of cell assemblies representing words (perception), while differences in high-frequency cortical responses around 30 Hz are caused by sustained activity of such cell assemblies and synchronous and fast reverberation of neuronal activity therein (active memory).

References

Aertsen A, Arndt M (1993) Response synchronization in the visual cortex. Curr Opin Neurobiol 3:586–594.

Baayan H, Piepenbrock R, van Rijn H (1993) The CELEX lexical database (CD-ROM). University of Pennsylvania, PA: Linguistic Data Consortium.

Braitenberg V (1978) Cell assemblies in the cerebral cortex. In: Theoretical approaches to complex systems (Heim R, Palm G, eds), Lecture notes in biomathematics, vol. 21, pp. 171–188. Berlin: Springer.

Braitenberg V, Pulvermüller F (1992) Entwurf einer neurologischen Theorie der Sprache. Naturwiss 79:103–117.

Braitenberg V, Schüz A (1998) Anatomy of the cortex. Statistics and geometry. Berlin: Springer.

Brown WS, Lehmann D (1979) Verb and noun meaning of homophone words activate different cortical generators: a topographic study of evoked potential fields. Exp Brain Res 2:S159–168.

Brunia CHM, Vingerhoets AJJ (1980) CNV and EMG proceding a plantar flexion of the foot. Biol Psychol 11:181–191.

Cacioppo JT, Tassinary LG, Fridlund AJ (1990) The skeletomotor system. In: Principles of psychophysiology. Physical, social, and inferential elements. (Cacioppo JT, Tassinary LG, eds), pp. 325–384. Cambridge: Cambridge University Press.

Coles MGH (1989) Modern mind-brain reading: psychophysiology, physiology, and cognition. Psychophysiology 26:251–269.

Damasio AR, Damasio H (1992) Brain and language. Scient Am 267(3):89–95.

Damasio AR, Tranel D (1993) Nouns and verbs are retrieved with differently distributed neural systems. Proc Natl Acad Sci USA 90:4957–4960.

Daniele A, Giustolisi L, Silveri MC, Colosimo C, Gainotti G (1994) Evidence for a possible neuroanatomical basis for lexical processing of nouns and verbs. Neuropsychologia 32:1325–1341.

Dehaene S (1995) Electrophysiological evidence for category-specific word processing in the normal human brain. NeuroReport 6:2153–2157.

Fiez JA, Raichle ME, Balota DA, Tallal P, Petersen SE (1996) PET activation of posterior temporal regions during auditory word presentation and verb generation. Cereb Cortex 6:1–10.

Fuster JM (1995) Memory in the cerebral cortex. An empirical approach to neural networks in the human and nonhuman primate. Cambridge, MA: MIT Press.

Gerstein GL, Bedenbaugh P, Aertsen AMHJ (1989) Neuronal assemblies. IEEE Trans Biomed Engng 36:4–14.

Goodglass H, Klein B, Carey P, Jones K (1966) Specific semantic word categories in aphasia. Cortex 2:74–89.

Gratton G, Coles MG, Donchin E (1983) A new method for off-line removal of ocular artifact. Electroenceph Clin Neurophysiol 55:468–484.

Hebb DO (1949) The organization of behavior. A neuropsychological theory. New York: John Wiley.

Hillis AE, Caramazza A (1995) Representation of grammatical categories of words in the brain. J Cogn Neurosci 7:396–407.

Hjorth B (1975) An on-line information of EEG scalp potentials into orthogonal source derivations. Electroenceph Clin Neurophysiol 39:526–530.

Jasper H (1958) The 10–20 electrode system of the international federation. Electroenceph Clin Neurophysiol 10:371–375.

Kounios J, Holcomb PJ (1994) Concreteness effects in semantic priming: ERP evidence supporting dual-coding theory. J Exp Psychol Learn Mem Cogn 20:804–823.

Lagerlund TD, Sharbrough FW, Jack CR Jr., Erickson BJ, Strelow DC, Cicora KM, Busacker NE (1994) Determination of 10–20 system electrode locations using magnetic resonance scanning with markers. Electroenceph Clin Neurophysiol 86:7–14.

Law SK, Rohrbaugh JW, Adams CM, Eckhardt MJ (1993) Improving spatial and temporal resolution in evoked EEG responses using surface Laplacians. Electroenceph Clin Neurophysiol 88:309–322.

Lopes da Silva F (1991) Neural mechanisms underlying brain waves: from neural membranes to networks. Electroenceph Clin Neurophysiol 79:81–93.

Lutzenberger W, Birbaumer N, Preissl H, Pulvermüller F (1997) High-frequency cortical responses: do they not exist if they are small? Electroenceph Clin Neurophysiol 102:64–66.

Lutzenberger W, Pulvermüller F, Birbaumer N (1994) Words and pseudowords elicit distinct patterns of 30-Hz activity in humans. Neurosci Lett 176:115–118.

Lutzenberger W, Pulvermüller F, Elbert T, Birbaumer N (1995) Local 40-Hz activity in human cortex induced by visual stimulation. Neurosci Lett 183:39–42.

Martin A, Haxby JV, Lalonde FM, Wiggs CL, Ungerleider LG (1995) Discrete cortical regions associated with knowledge of color and knowledge of action. Science 270:102–105.

Martin A, Wiggs CL, Ungerleider LG, Haxby JV (1996) Neural correlates of category-specific knowledge. Nature 379:649–652.

Miceli G, Silveri C, Nocentini U, Caramazza A (1988) Patterns of dissociation in comprehension and production of nouns and verbs. Aphasiology 2:351–358.

Miceli G, Silveri M, Villa G, Caramazza A (1984) On the basis of agrammatics' difficulty in producing main verbs. Cortex 20:207–220.

Murthy VN, Fetz EE (1992) Coherent 25- to 35-Hz oscillations in the sensorimotor cortex of awake behaving monkeys. Proc Natl Acad Sci USA 89:5670–5674.

Murthy VN, Fetz EE (1996) Synchronization of neurons during local field potential oscillations in sensorimotor cortex of awake monkeys. J Neurophysiol 76:3968–3982.

Neville HJ, Mills DL, Lawson DS (1992) Fractionating language: different neural subsystems with different sensitive periods. Cereb Cortex 2:244–258.

Nobre AC, Allison T, McCarthy G (1994) Word recognition in the human inferior temporal lobe. Nature 372:260–263.

Nobre AC, McCarthy G (1994) Language-related EPRs: scalp distributions and modulation by word type and semantic priming. J Cogn Neurosci 6:233–255.

Nobre AC, McCarthy G (1995) Language-related field potentials in the anterior-medial temporal lobe: II. Effects of word type and semantic priming. J Neurosci 15:1090–1098.

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 9:97–113.

Osterhout L, Bersick M, McKonnon R (1997) Brain potentials elicited by words: word length and frequency predict the latency of an early negativity. Biol Psychol 46:143–168.

Palm G (1982) Neural assemblies. Berlin: Springer.

Perrin F, Bertrand O, Pernier J (1987) Scalp current density mapping: value and estimation from potential data. IEEE Trans Biomed Engng 34:283–288.

Perrin F, Pernier J, Bertrand O, Echallier JF (1989) Spherical splines for scalp potential and current source density mapping. Electroenceph Clin Neurophysiol 72:184–187.

Perrin F (1992) Comments on the article by Biggins *et al.* Electroenceph Clin Neurophysiol 83:171–172.

Petersen S, Fox P, Posner M, Mintun M, Raichle M (1989) Positron emission tomography studies of the processing of single words. J Cogn Neurosci 1:153–170.

Pfurtscheller G, Klimesch W (1991) Event-related desynchronization during motor behavior and visual information processing. Electroenceph Clin Neurophysiol Suppl 42:58–65.

Picton TW, Lins OG, Scherg M (1995) The recording and analysis of event-related potentials. In: Handbook of neuropsychology, Vol. 10 (Boller F, Grafman J, Johnson R Jr, eds), pp. 429–499. New York: Elsevier.

Preissl H, Pulvermüller F, Lutzenberger W, Birbaumer N (1995) Evoked potentials distinguish nouns from verbs. Neurosci Lett 197:81–83.

Pulvermüller F (1992) Constituents of a neurological theory of language. Concepts Neurosci 3:157–200

Pulvermüller F (1996) Hebb's concept of cell assemblies and the psychophysiology of word processing. Psychophysiology 33:317–333

Pulvermüller F (1999) Words in the brain's language. Behav Brain Sci 22:253–336.

Pulvermüller F, Preissl H (1991) A cell assembly model of language. Network: Comput Neural Syst 2:455–468.

Pulvermüller F, Preissl H, Eulitz C, Pantev C, Lutzenberger W, Elbert T, Birbaumer N (1994) Brain rhythms, cell assemblies, and cognition: evidence from the processing of words and pseudowords. Psycoloquy 5 (48):1–30.

Pulvermüller F, Lutzenberger W, Birbaumer N (1995a) Electrocortical distinction of vocabulary types. Electroenceph Clin Neurophysiol 94:357–370.

Pulvermüller F, Preissl H, Lutzenberger W, Birbaumer N (1995b) Spectral responses in the gamma-band: physiological signs of higher cognitive processes? NeuroReport 6:2057–2064.

Pulvermüller F, Eulitz C, Pantev C, Mohr B, Feige B, Lutzenberger W, Elbert T, Birbaumer N (1996a) High-frequency cortical responses reflect lexical processing: an MEG study. Electroenceph Clin Neurophysiol 98:76–85.

Pulvermüller F, Preissl H, Lutzenberger W, Birbaumer N (1996b) Brain rhythms of language: nouns versus verbs. Eur J Neurosci 8:937–941.

Pulvermüller F, Birbaumer N, Lutzenberger W, Mohr B (1997) High-frequency brain activity: its possible role in attention, perception and language processing. Prog Neurobiol 52:427–445.

Pulvermüller F, Ehlert C, Elbert T (1998) Processing of action words is impaired in right-handers with left-sided hemiparesis. Soc Neurosci Abstr 22:15.

Rockstroh B, Elbert T, Canavan A, Lutzenberger W, Birbaumer N (1989) Slow cortical potentials and behaviour. Baltimore: Urban & Schwarzenberg.

Samar VJ, Berent GP (1986) The syntactic priming effect: evoked response evidence for a prelexical locus. Brain Lang 28:250–272.

Singer W, Gray CM (1995) Visual feature integration and the temporal correlation hypothesis. Annu Rev Neurosci 18:555–586.

Tallon C, Bertrand O, Bouchet P, Pernier J (1995) Gamma-range activity evoked by coherent visual stimuli in humans. Eur J Neurosci 7:1285–1291.

Towle VL, Balanos J, Suarez D, Tan K, Grzeszczuk R, Levin DN, Cakmur R, Frank SA, Spire J-P (1993) The spatial location of EEG electrodes: locating the best-fitting sphere relative to cortical anatomy. Electroenceph Clin Neurophysiol 86:1–6.

Warburton E, Wise RJS, Price CJ, Weiller C, Hadar U, Ramsay S, Frackowiak RSJ (1996) Noun and verb retrieval by normal subjects: studies with PET. Brain 119:159–179.

Warrington EK, McCarthy RA (1987) Categories of knowledge: further fractionations and an attempted integration. Brain 110:1273–1296.

Wise R, Chollet F, Hadar U, Fiston K, Hoffner E, Frackowiak R (1991) Distribution of cortical neural networks involved in word comprehension and word retrieval. Brain 114:1803–1817.