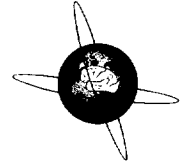




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High-frequency cortical responses reflect lexical processing: an MEG study

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Abstract

Meaningful words and matched pseudowords, such as *moon* vs. *noom*, are of equal perceptual complexity, but invoke different cognitive processes. To investigate high-frequency cortical responses to these stimuli, biomagnetic signals were recorded simultaneously over both hemispheres of right-handed individuals listening to words and pseudowords. Consistent with earlier EEG studies, evoked spectral responses recorded from the left hemisphere revealed depression of spectral power in the low gamma band (around 30 Hz) after pseudowords but not after words. Similar differences between stimulus categories were present in the beta range. These results indicate that distinct patterns of high-frequency cortical responses correspond to the different cognitive processes invoked by words and pseudowords. It is hypothesized that differential high-frequency cortical responses signal the activation or activation failure of distributed Hebbian cell assemblies representing words and other elements of cognitive processing.

Keywords: Cell assembly; Beta; Cognitive; Evoked spectral responses; Gamma; Language; Magnetoencephalography; 30 Hz

1. Introduction

Fast repetitive and coherent activity of large neuronal populations has recently become a focus of neurophysiological research. Single cell, multi-unit and field potential studies indicate that coherent periodic neural activity in the gamma band (20 Hz and up) plays a key role for understanding information processing in the cortex and in other brain structures of higher vertebrates (Von der Malsburg, 1986; Eckhorn et al., 1988; Engel et al., 1992; Aertsen and Arndt, 1993; Singer, 1994). Even in man, differential gamma band activity has been demonstrated by electroencephalography (EEG) (Berger, 1929; Rougeul et al., 1979; Spydel et al., 1979; Madler and Pöppel, 1987) and magnetoencephalography (MEG) (Galambos et al., 1981; Pantev et al., 1991, 1993; Kristeva-Feige et al., 1993; Llinás and Ribary, 1993). While most researchers agree on the impor-

tance of high-frequency phenomena, opinions diverge regarding their specific function. Gamma band activity has been considered an indicator of early processing of stimulus information (Galambos et al., 1981; Pantev et al., 1991, 1993), feature linking and formation of temporary assemblies that represent perceived objects (Eckhorn et al., 1988; Gray et al., 1989; Engel et al., 1991a,b), focussing of attention (Spydel et al., 1979; Murthy and Fetz, 1992; Tiitinen et al., 1993), arousal and motivation (Kristeva-Feige et al., 1993), alertness (Rougeul et al., 1979) or cognition in general (Berger, 1929; Llinás and Ribary, 1993).

Berger's early hypothesis that high-frequency oscillations are an indicator of "mental processes" (Berger, 1929) has so far hardly been tested. Reduced gamma band responses observed in humans during anesthesia (Madler and Pöppel, 1987) or during delta sleep (Llinás and Ribary, 1993) may be caused by a variety of variables (low arousal level, reduced cognitive activity, reduced general brain activity, etc.). Enhancement of cortical gamma band activity during preparation and/or execution of move-

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ments (Murthy and Fetz, 1992; Pfurtscheller and Neuper, 1992; Kristeva-Feige et al., 1993; Pfurtscheller et al., 1994) may be related either to cognitive processes (e.g., planning) or to the activation of motor programs. Investigations of responses to moving bars (Eckhorn et al., 1988; Gray and Singer, 1989; Gray et al., 1989; Eckhorn et al., 1990; Engel et al., 1990, 1991a,b; Kreiter and Singer, 1992; Eckhorn and Obermueller, 1993; Frien et al., 1994; Lutzenberger et al., 1995) or to clicks and tones (Galambos et al., 1981; Pantev et al., 1991, 1993) do not allow firm conclusions about the correspondence between neuronal rhythms and specific cognitive processes either. Such stimulus-elicited activity in the gamma band could result from the fact that excitation of afferent fibers leads to enhanced activity in the brain which is, as a consequence, regulated towards a target value. Such a regulation process must be assumed in order to explain why the cortical level of activity is maintained even if sensory stimulation drastically changes (Braitenberg, 1978; Braitenberg and Schüz, 1991). Periodic high-frequency activity could be a by-product of such a regulation process.

In a recent EEG study, Tiitinen et al. (1993) found stronger 40 Hz responses to attended tones compared to unattended ones. This suggests that gamma band responses can be indicators of selective attention. One may, however, ask whether even attended stimuli invoking distinct cognitive processes lead to different patterns of gamma band activity. The process of selective attention can be related to a thalamo-cortical gating process not specific to particular stimuli (Scheibel, 1981; Lopes da Silva, 1991). It could well be that the activation of the cortical network underlying the cognitive processing of an attended stimulus leads to additional specific changes in high-frequency responses. In this case, attended stimuli that invoke different cognitive processes should induce different patterns of high-frequency cortical responses.

A strict proof of the significance of high-frequency activity for cognitive processing can, therefore, be provided if complex stimuli are chosen that induce certain higher cognitive processes. Possibly, complex stimuli will lead to response patterns which are absent when a simple stimulus is being perceived. This response pattern can then be taken as a correlate of cognitive processes invoked by the complex, but not by the simple stimulus. However, simple stimuli, such as bars or tones, and complex stimuli, such as images or words, do not only differ with regard to the cognitive processes they invoke, they also differ in their physical complexity. In order to avoid such confounding factors, stimuli of equal perceptual complexity must be chosen that nevertheless lead to distinct psychological processes. Two groups of stimuli that satisfy this criterion are meaningful words and meaningless but pronounceable phoneme combinations, that is pseudowords such as *noom*, *thyll*, or *fasp*. While matched pseudowords and words include the same letters or phonemes and have, therefore, equal visual and acoustic complexity, they clearly lead to

different cognitive processes. A word will be matched to a brain internal representation, while this process of *lexical access* cannot take place after pseudoword presentation (Coltheart, 1978; Marslen-Wilson and Welsh, 1978).

In an EEG study of spectral responses evoked by visually presented German words and pseudowords, Lutzenberger et al. (1994) found differences between gamma band responses around 30 Hz. In 15 subjects, gamma band power recorded from the left language-dominant hemisphere was consistently reduced after pseudoword presentation. This result contrasts to the well-known fact that pseudowords elicit larger conventionally averaged evoked potentials (N400) compared to words (Holcomb and Neville, 1990; Pulvermüller et al., 1995a). Thus, while causing *stronger* evoked potentials, pseudowords led to *reduced* power in the gamma band. The power reduction has tentatively been explained by the following hypothesis: depression of gamma band activity reflects a sudden breakdown of cognitive processing induced by an uncommon stimulus for which no cortical representation is available.

The purpose of this study was to confirm the results reported by Lutzenberger et al. (1994). If reduction of gamma band activity after pseudowords reflects a failure of lexical access or another aspect of word processing it should take place regardless of the *stimulus modality* and regardless of the *task* the experimental subjects are engaged in. It should also occur regardless of the *language* the stimuli are taken from. Lutzenberger et al. used German words and pseudowords visually presented to native speakers of German who made lexical decisions on these stimuli. In the present study, English words and pseudowords were presented acoustically to English native speakers who had to memorize them. Furthermore, a reliable difference in spectral responses should be visible using different recording techniques. While Lutzenberger et al. used EEG recordings, this study reports on spectral responses recorded with a biomagnetometer. The MEG has the additional advantage that reference-free data can be obtained without using highly complex evaluation procedures, such as current source density analysis. Thus, it appears worthwhile to investigate evoked spectral MEG responses recorded from both hemispheres while subjects hear and memorize English words and pseudowords.

2. Methods

2.1. Subjects

Five right-handed monolingual native speakers of English volunteered for the experiment. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). None of the subjects had left-handed family members. Their ages ranged between 26 and 38 years (mean = 31). None of the subjects had a history of neurological illness or drug abuse.

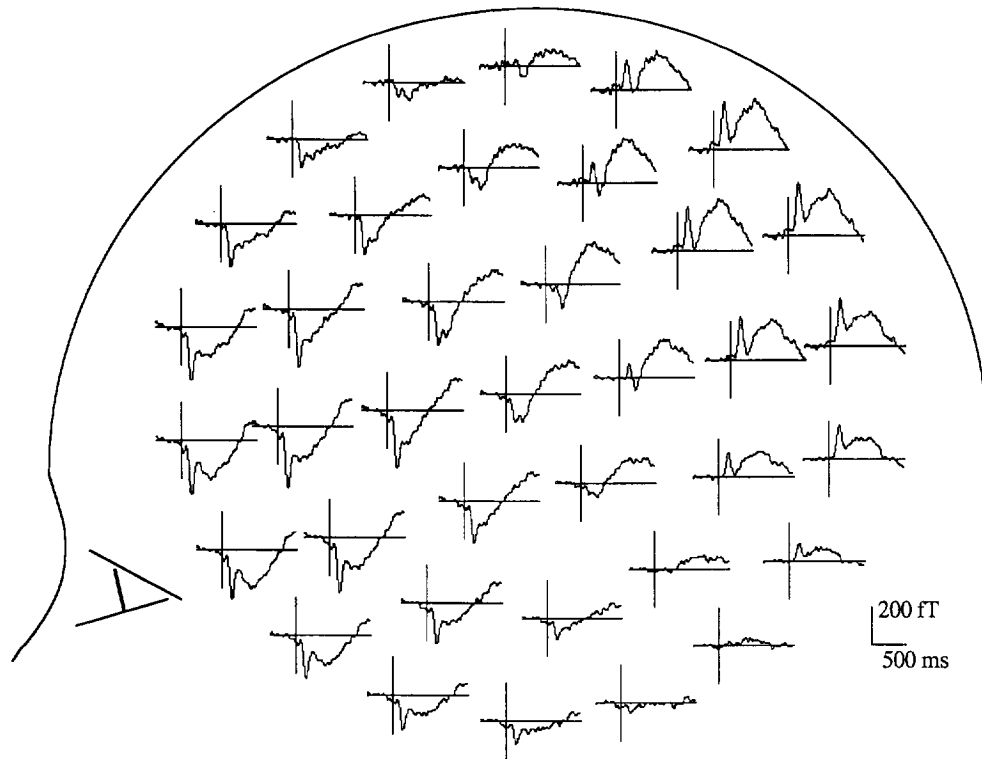


Fig. 1. Evoked magnetic fields recorded from the left hemisphere of subject 1. A dipolar early component, the N1m, occurs 0.1 sec after stimulus onset. 400–500 msec past stimulus onset, there is a late dipolar response, the possible magnetic correlate of the N400 (N4m).

2.2. Stimulus material

Thirty words and 30 matched pseudowords were chosen. All stimuli consisted of one syllable. All word stimuli were highly frequent English nouns or verbs (word frequency higher than 100/million according to Francis and Kucera (1982))¹. Pseudowords were constructed from word stimuli by permutating and exchanging phonemes within and between words. All pseudowords were in agreement with the phonological rules of English. Each stimulus was presented 4 times resulting in a total of 120 stimulus presentations per category.

2.3. Procedure

Subjects lay on their right side in a magnetically shielded room. They heard words and pseudowords presented in pseudo-random order. Not more than 4 stimuli of one of the two classes were allowed in direct succession. Stimuli were spoken by a professional female speaker, recorded on a DAT recorder and presented via a non-magnetic and echo-free stimulus delivery system to both ears. Mean word length was 380 msec. Stimulus onset asynchrony varied randomly between 1.5 and 2.5 sec. The list of 60

stimuli was presented 4 times in 4 experimental blocks, with short breaks between any 2 blocks. For each block, a new pseudo-random order of stimuli was made up. Subjects were instructed to listen carefully to the stimuli and to memorize them. After blocks 2 and 4, subjects were presented with a recognition task. In this task, they heard words and pseudowords for each of which they were asked to indicate whether the item had previously occurred in the experiment. In the recognition task, all subjects performed above chance and equally well on both stimulus categories, indicating that stimuli were perceived and memorized equally well.

2.4. MEG recordings

Biomagnetic responses were recorded over both hemispheres using a 2×37 -channel biomagnetometer (Biomagnetic Technologies, San Diego, CA). The two sensor arrays were centered over the perisylvian cortices, respectively. A sensor position indicator system determined the locations of the sensors relative to the head and insured that no head movement occurred during the measurement. The voltage signals obtained from SQUIDS were 0.1–149 Hz bandpass filtered and recorded with a sampling rate of 297.6 Hz. In order to minimize muscle artifacts in the recordings, trials deviating more than 3 pT from the baseline were rejected.

¹ The word stimuli were taken from the one-syllable words listed in Mohr et al. (1994).

2.5. Calculation of evoked spectral responses

In order to obtain information about the temporal dynamics of activity in various frequency bands, spectral power values were calculated for time frequency windows. All time intervals were 0.3 sec (more exactly 310 msec) wide, the first interval starting 0.6 sec before stimulus onset and the last terminating 1.2 sec past stimulus onset. Two adjacent time intervals overlapped by 0.2 sec (first interval -0.6 to -0.3 sec, second interval -0.5 to -0.2 sec, etc.). Power spectra were calculated for each of the following frequency bands: 0.1–4.7 Hz, 4.7–14.0 Hz, 14.0–23.3 Hz, 23.3–32.6 Hz, 32.6–41.9 Hz, 41.9–51.2 Hz (bands I–VI). So for each individual trial, one power value was calculated for each of 96 time frequency windows, respectively. For each individual, recording channel and condition, power values were averaged over trials (120 trials (minus artifact trials) per average). Note that this procedure makes it possible to calculate spectral power which is not phase-locked to the stimulus (Makeig, 1993; Makeig and Inlow, 1993). After traditional averaging, non-phase-locked activity would be cancelled. For further evaluation, these averaged spectral power values were normalized, that is, divided by the baseline power value

for the respective frequency band (baseline -0.6 sec to stimulus onset). Preliminary comparisons of absolute baseline values between conditions failed to reveal any differences. Therefore, it appeared justified to use normalized values instead of absolute values for further evaluation. Note that absolute spectral power of the MEG signal is relatively small for high-frequency bands (Pantev et al., 1991). Normalized data make it easier to compare power changes across frequencies and individuals.

2.6. Statistical evaluation

For each individual, data from 3 channels entered the analysis. These *critical channels* satisfied the following criteria: (1) they were located at anterior sites, and (2) the intensity of the late evoked magnetic field (what is called “N4m,” see Fig. 1) was larger than at all other channels (largest signal-to-noise ratios). Evoked magnetic fields were calculated for each individual separately. Maximal amplitudes of evoked magnetic fields at the critical channels in the time interval between 300 and 600 msec after stimulus onset were compared between subjects and hemispheres. Analyses of variance were used for statistical

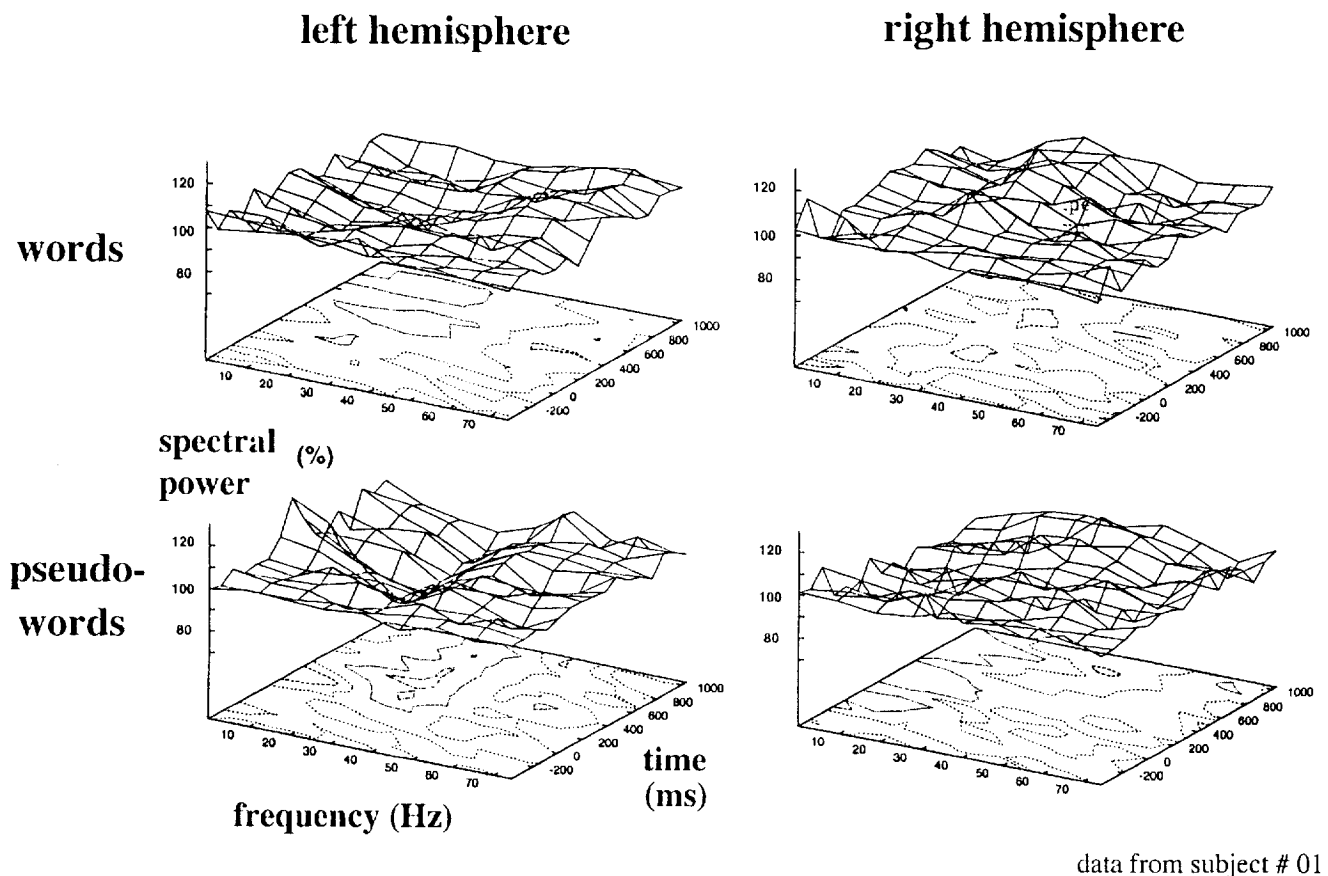


Fig. 2. Normalized power as a function of frequency and time (subject 1). For clarity, information contained in 3-dimensional graphs is repeated in contour plots. The channel with the largest late evoked magnetic response was selected for each hemisphere, respectively. Illustrated are responses to words (upper diagrams) and pseudowords (lower diagrams) recorded over the left hemisphere (left side) and over the right (right side). Note the “30 Hz valley” in the lower diagram on the left.

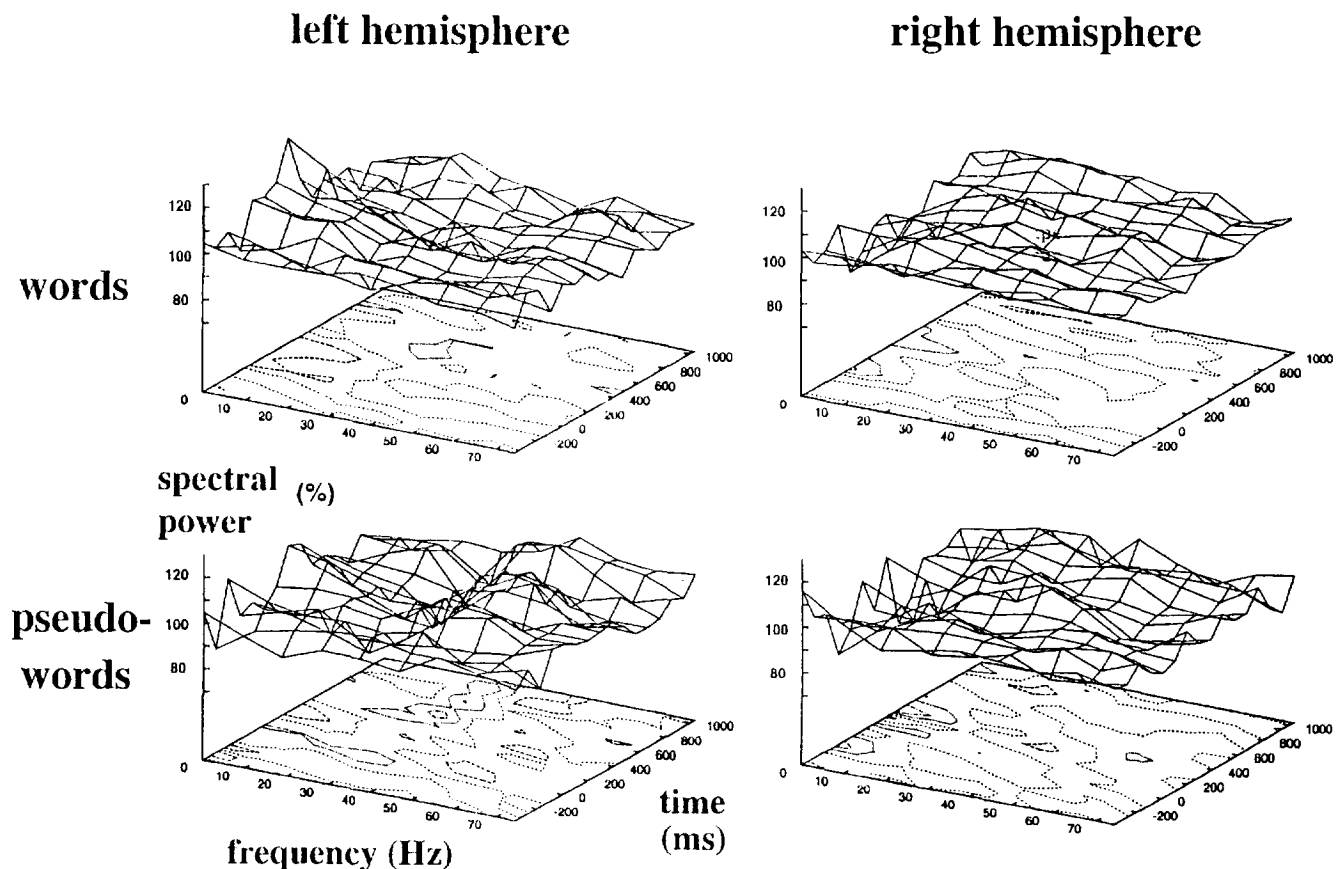
analysis (design: Channels (3 levels) \times Hemisphere (2 levels) \times Wordness (2 levels) \times Frequency (6 levels) for analysis of spectral responses, and Channels (3 levels) \times Hemisphere (2 levels) \times Wordness (2 levels) for analysis of evoked fields). Greenhouse-Geisser correction was applied to correct for degrees of freedom when appropriate (*GG* values), *t* tests were used for planned comparisons. Bonferroni correction for multiple *t* tests was used throughout.

3. Results

Averaged evoked magnetic fields recorded from one hemisphere of one of the individuals are shown in Fig. 1. Two dipolar components can be distinguished, an early component peaking around 100 msec after stimulus onset (N1m) and a late evoked field which may be considered the biomagnetic equivalent of the evoked potential called the N400. We call this second wave the N4m. Recall that the 3 anterior channels with the largest amplitudes were used for analysis of spectral responses (critical channels). At the critical channels over the left hemisphere, maxima of this late biomagnetic component (N4m) evoked by pseudowords tended to be stronger compared to the N4m

evoked by words (means (S.D.s): 170 fT (28.4 fT) vs. 203 fT (21.9 fT)). Over the right, a similar tendency was less apparent (136 fT (25.9 fT) vs. 150 fT (21.2 fT)). However, there were no statistically significant differences of evoked fields between words and pseudowords or between the hemispheres, and the interaction of the factors Wordness and Hemisphere was also not significant ($F(1, 4) = 1.5$, $P > 0.2$).

Figs. 2 and 3 present normalized evoked spectral responses after word and pseudoword presentations recorded from one channel over the left and right hemisphere of two individuals, respectively. In both cases the anterior channel with the largest intensities of evoked magnetic fields was selected. Note that every diagram presents spectral power averaged over 120 trials (minus a small number of artifact trials). While no pronounced changes of spectral power were apparent after word presentation, pseudowords led to a deflection of spectral power around 30 Hz in the recordings from left anterior channels. This deflection shows up as a valley in the contour plots on the lower left of Figs. 2 and 3, respectively. In order to investigate whether this valley was consistently deepest after pseudoword presentation, minima of normalized power values for all critical channels, frequency bands and subjects were calculated in the time interval 0.1–0.7 msec post stimulus onset. When



data from subject # 02

Fig. 3. Normalized power as a function of frequency and time (subject 2). For explanation, see Fig. 2.

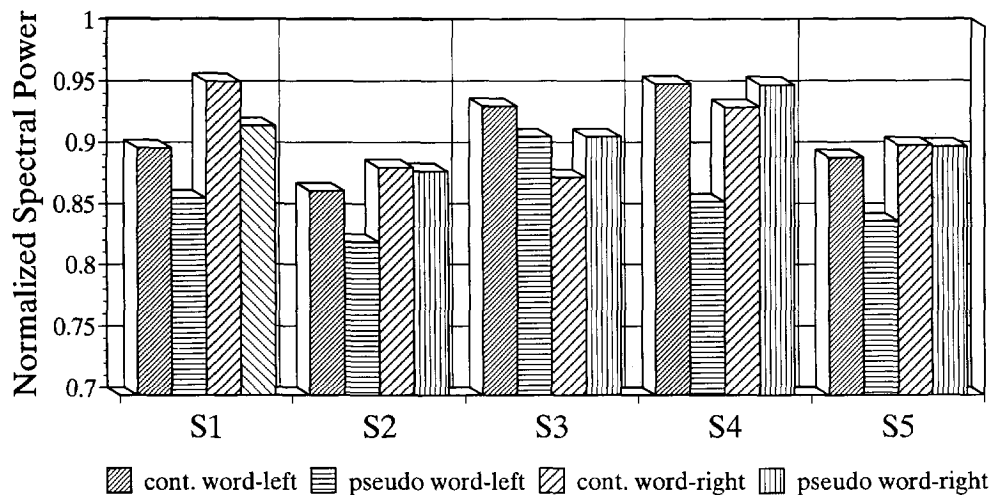


Fig. 4. Minimal normalized power values (14–33 Hz) in the time interval 100–700 msec after stimulus onset for all subjects. Pseudoword depression can consistently be observed over the left hemisphere.

minimal normalized power values from this interval were compared using an analysis of variance, reliable main effects were obtained for the factors Frequency, Wordness and Hemisphere (all F values > 5 ; all P values < 0.01). The main effect of Frequency was due to reduced spectral power in lower frequencies (bands I–IV) compared to the higher bands (V and VI). While all other interactions did not reach significance, there was a significant 3-way interaction of the factors Frequency \times Wordness \times Hemisphere, $F(5, 20) = 5.09$, $GG = 0.49$, $P = 0.02$. Planned comparisons revealed no reliable differences between words and pseudowords over either the right or the left hemisphere in frequency bands I, II, V or VI. However, in frequency bands III (14.0–23.3 Hz) and IV (23.3–32.6 Hz) significant differences between stimulus classes were obtained. Therefore, a second analysis of variance was performed comparing activity in these critical bands. In this analysis, there was a significant main effect of the factor Hemisphere, $F(1, 4) = 12.3$, $P = 0.02$, and the factors Wordness and Hemisphere interacted significantly, $F(1, 4) = 11.2$, $P = 0.02$. Planned comparisons revealed a reliable difference between pseudowords and words over the left hemisphere, $t(4) = 4.32$, $P = 0.01$, and a left to right difference for pseudowords, $t(4) = 3.81$, $P = 0.01$ ². Fig. 4 displays minimal normalized power between 14 and 33 Hz averaged over the 3 critical channels (indicating the depth of the valley) for all 5 subjects tested.

4. Discussion

The most striking difference of MEG spectral responses to words and pseudowords was the pronounced power reduction in the beta and lower gamma bands (14–33 Hz)

over the left hemisphere following pseudoword presentation. In contrast, words did not cause such pronounced power reduction in the beta or gamma bands. Over the right hemisphere, there were no consistent differences in spectral power elicited by words and pseudowords.

These results are in agreement with those reported by Lutzenberger et al. (1994) who also found reduced spectral power in the low gamma band after pseudowords. While Lutzenberger et al. found significant differences around 30 Hz, the present results suggest that similar changes are sometimes present in the beta range. The earliest latencies after which differential spectral responses could be observed was similar in both studies. Lutzenberger et al. reported significant differences 320–520 msec post onset of visually presented words and pseudowords. In this study, reduced spectral power after pseudowords could be observed in time windows starting as early as 0.3 sec post stimulus onset and ending some 0.6 sec afterwards. However, in some of the individuals participating in the MEG study word/pseudoword differences could still be observed up to time windows starting around 0.7 sec post stimulus onset (see Figs. 2 and 3). It is not surprising that the effect lasted longer in the study using auditory stimuli. Visual stimuli are fully visible at the time of stimulus onset, while auditory stimuli were 380 msec long on the average. In many cases, the time point where words are being recognized is substantially before the end of the word (Marslen-Wilson and Tyler, 1980), but several stimuli used in the present experiment were longer than 400 msec and this can possibly account for the prolonged effect sometimes still visible after 700 msec post onset. Most pronounced deflection was usually seen in the time windows starting around 300–500 msec. It should be noted that this latency makes it clear that the dynamics of gamma and beta activity reported here are distinct from the transient gamma response which occurs 100–150 msec after the onset of acoustic stimuli (Pantev et al., 1993).

Another difference between this and the EEG study by

² These differences were still significant after Bonferroni correction (adjusted $P = 0.01$).

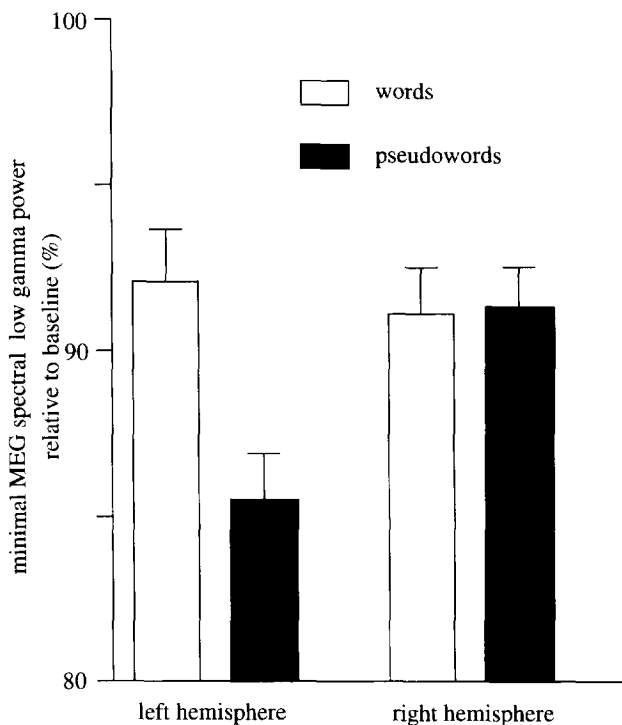


Fig. 5. Averages and standard errors of minimal normalized power in the low gamma range (23–33 Hz) in the time interval 100–700 msec after stimulus onset.

Lutzenberger et al. is the magnitude of power changes in the gamma range. While these authors reported a power reduction of a few percent of the baseline, the present data revealed a reduction of spectral power of 25% and more in some of the individuals (see Figs. 2 and 3). It appears that changes in high-frequency bands are easier to detect in MEG recordings. Fast changes in the electrical field are attenuated by the skull and skin while magnetic field changes are not subject to such attenuation. This may be the reason why differences in high-frequency spectral responses were more pronounced in MEG recordings. It is important, however, to note that the main finding of the EEG study, different spectral responses in the gamma band to words and pseudowords, could be replicated in this MEG experiment. Furthermore, in both studies, the reduction of high-frequency spectral activity was visible after pseudowords over the left language-dominant hemisphere, exclusively. This was the case regardless of the differences in the experimental paradigms applied in the two studies. The difference in high-frequency activity was similar in responses evoked by visual and auditory presentations of words vs. pseudowords obtained from English- and German-speaking subjects engaged in lexical decisions and memory tasks. This consistency of results makes it likely that the dynamics of spectral power in the low gamma band reflect a general processing difference between words and pseudowords. Fig. 5 summarizes the present data obtained in the 30 Hz range.

No significant changes could be observed in average

magnetic fields evoked by words and pseudowords, although pseudowords tended to elicit larger amplitudes of a late component of the evoked field (N4m). The lack of significant differences may be due to the small number of subjects tested. Because EEG studies consistently show larger late negative-going evoked potentials after pronounceable pseudowords compared to words (Holcomb and Neville, 1990; Pulvermüller et al., 1995a), it appears likely that what is suggested by a tendency in the present data will be confirmed by a study of a larger subject sample. In the context of the analysis of spectral responses, the data on evoked magnetic fields exclude the possibility that differences in spectral power are related to differences in the strength of the biomagnetic field. While pseudowords were followed by a *reduction* in high-frequency spectral responses, their evoked fields tended to be *stronger* compared to words. Again, this is consistent with what has been reported from EEG experiments (see Introduction).

It is unlikely that the differences in spectral responses are caused by artifacts related to muscle activity. Power spectra of the electromyogram (EMG) demonstrate that EMG power monotonously increases with frequency (up to at least 75 Hz) (Cacioppo et al., 1990). If muscle activity differs between conditions and this difference is visible in spectral power around 20–30 Hz, the same difference must, therefore, be present (and must even be more pronounced) in higher-frequency bands. An artifact caused by muscle activity will not lead to an effect specifically visible in the 14–33 Hz band. Thus, muscle artifacts that may have survived the artifact rejection criterion applied cannot be the cause of the observed pattern of spectral responses.

It is also unlikely that variables such as arousal, alertness, attention or motivation confounded the results. Subjects were instructed to attend to all stimuli equally well and the recognition tests indicate that they did so. While it could be argued that pseudoword presentation may diminish or raise the attention and even arousal level, it must be noted that such changes are usually accompanied by a reduction of alpha power (8–14 Hz) (see Rockstroh et al., 1989 for review). In this study, no differences between stimulus categories were visible in the alpha band. Thus, there is no indication that arousal differences were present. While there are data suggesting that selective attention can enhance gamma band responses (see Introduction; Tiitinen et al., 1993), it should be noted that the cognitive process affecting high-frequency cortical responses in the present experiment is, most likely, different from the process of selective attention.

On first view, one may argue that the critical cognitive variable leading to power changes in high-frequency bands is the familiarity of the meaningful words and the exceptionality of the pseudowords which have, most likely, never been perceived by the subjects. Psycholinguistic theories go one step further and postulate that word perception leads to a process called *lexical access*, that is, a

matching of stimulus information to a stored representation of a word. In contrast, pseudowords cannot be matched to a stored representation and, therefore, the lexical access process fails to take place. This matching failure may cause reduced spectral power in high frequencies.

A possible brain mechanism underlying the differential spectral responses to words and pseudowords is the following: words but not pseudowords are represented in the brain by Hebbian cell assemblies (Hebb, 1949). Such strongly coupled neuron populations may develop when the child perceives and produces word forms (Braitenberg and Pulvermüller, 1992; Pulvermüller and Schumann, 1994). After presentation of a word, the “ignition” of an assembly leads to repetitive and fast circulation of activity in a distributed cell assembly which is visible in relatively strong evoked spectral responses of high frequencies. After presentation of a pseudoword, no cell assembly ignition takes place but desynchronized activity is present in loosely coupled neurons, or activity circulates asynchronously in several assemblies. This desynchronized neural activity causes less spectral power in high-frequency bands recorded from EEG electrodes and MEG channels.

This tentative explanation raises the question of why spectral power elicited by words did not significantly deviate from the baseline in the present experiment. Why is there a reduction of high-frequency activity after pseudowords instead of an increase after presentation of a meaningful word (which presumably leads to an ignition of a cell assembly)? The answer to this question requires a hypothesis about the psychological processes taking place during the baseline, before words or pseudowords were acoustically perceived. In this experiment, subjects had to memorize the stimuli and it can, therefore, be assumed that word representations remained active throughout the inter-stimulus interval. In this case, the perception of a new word should not significantly change the psychological state during the baseline (word processing), but the perception of an uncommon stimulus should induce a markedly different process, namely the breakdown of lexical access and processing³.

However, it may still be argued that psychological

processes during the baseline are hard to determine, and it is perhaps more conclusive to restrict the interpretation to the *difference* between the two conditions for which cognitive processes can be specified with less difficulty, namely to the processes following presentation of words vs. pseudowords. In one case, lexical access takes place and in the other the lexical access process does not occur. The difference in spectral power can be explained by assuming cell assembly ignition after word presentation only. It is either failure to activate a brain internal representation which may underlie relatively low spectral power observed in the beta and gamma range or, as an alternative, different cortical representations (cell assemblies) may become active simultaneously but asynchronously when a pseudoword is being perceived, so that the asynchronous rhythmic patterns generated cancel each other. If the brain internal representations are conceptualized as Hebbian cell assemblies, it can also be explained why a breakdown of lexical access shows up in relatively high-frequency bands. The activation of a strongly coupled cortical neuron population leads to fast circulation of neural activity, while the failure to activate such a network will cause reduced fast synchronously circulating activity.

Although the present study did not reveal any systematic differences in alpha power between the word and pseudoword conditions, it should be noted that there is recent evidence that certain aspects of cognitive processing are accompanied by power changes in the alpha range (Pfurtscheller and Klimesch, 1991). For example, the duration of the reduction of alpha power during visual memory tasks appears to depend on cognitive processing demands (Schwartz et al., 1989; Michel et al., 1994), picture naming leads to more pronounced and more widespread alpha desynchronization than perception of the same pictures (Salmelin et al., 1994), and complex sequential finger movements are accompanied by more widespread (and bihemispheric) alpha reduction than simple repetitive movements (Pulvermüller et al., 1995b). However, different processes can be assumed to underlie power changes in the alpha and gamma ranges (Lopes da Silva, 1991). Probably the most important difference is that reduction of alpha power is usually seen with activation of a cortical area, while recent studies suggest that transient gamma band activity is relatively strong when certain perceptual and/or cognitive processes take place (Singer and Gray, 1995). It may well be that gamma band responses include information about the ignition of specific cortical assemblies while dynamics of alpha activity indicate the general state of activity of cortical areas.

5. Conclusions

In summary, the present study confirms that the cortex responds differently to words and to uncommon and meaningless items. Word processing is accompanied by stronger

³ An alternative explanation for the power reduction after pseudowords (rather than enhancement after words) can be provided on the basis of power changes taking place in other frequency bands. It has been argued that spectral changes in the low gamma band are sometimes the result of changes in lower frequencies, for example the alpha band (Jürgens et al., 1995). Because in this study general reduction of power was observed after both words and pseudowords in lower frequencies (see Results), it could be that a general power reduction in higher bands (beta and gamma) resulted from power reduction of harmonics of lower frequencies (for example alpha desynchronization). In this case, relatively low spectral power between 14 and 33 Hz, as observed after pseudowords, was to be expected, and the stronger beta and gamma responses to words could be related to an additional periodic high-frequency process (activation of a cell assembly). For further discussion, see Pulvermüller et al. (1995c).

high-frequency MEG activity compared to the perception of pseudowords. The breakdown of beta and low gamma band power after pseudoword presentation possibly indicates a failure of lexical access processes. The different spectral responses are consistent with the view that ignition of large cell assemblies takes place after word presentation, but not after pseudoword presentation. These results indicate that gamma band responses have psychological “meaning”; they can be an indicator of specific cognitive processes, such as successful vs. unsuccessful lexical access.

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