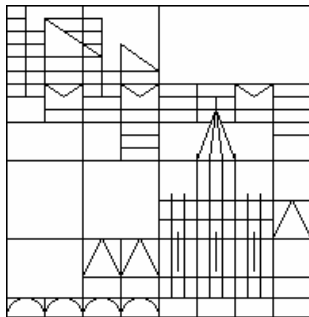Psychophysiologische
Korrelate der Sprach-
verarbeitung im
menschlichen Gehirn

Dissertation zur Erlangung des
akademischen Grades des

Doktors der Naturwissenschaften

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Für Christa & Hassan

## Thank you. Danke schön. Cheli mamnun.

Zusammenfassung:

"Nervenzellen, die gleichzeitig aktiv sind, verbinden sich." Donald Hebb führte diese Lernregel 1949 (Hebb, 1949) ein und benannte Ensembles von Neuronen, die durch dieses Prinzip verbunden sind „Cell Assemblies".

Die vorliegende Arbeit untersuchte linguistische Aspekte von einzelnen Wörtern psychophysiologisch mit dem Magnetoenzephalogramm (MEG). Untersuchte Eigenschaften waren die orthographische Länge von Wörtern, ihre Häufigkeit, ihre Bedeutung, einige ihrer syntaktischen Eigenschaften und ihre phonetische Transkription.

Mit Hilfe der Topographie und der zeitlichen Abfolge wortevozierter Hirnantworten kann nun über eine Abfolge der Wortverarbeitung spekuliert werden: Zunächst werden ab 60ms nach dem Stimulus-Onset visuelle Eigenschaften eines Wortes analysiert. Einflüsse von semantischen Prozessen können ab 80ms gemessen werden, wohingegen die Worthäufigkeit ab 120ms die Hirnantwort beeinflusst. Und zuletzt, ab 140ms, werden syntaktische Eigenschaften eines Wortes evident. Die vorgestellte Verarbeitungskaskade macht den Eindruck, dass das menschliche Gehirn bereits sehr früh nach dem Stimulus-Onset ein Wort zu verarbeiten beginnt.

Basierend auf diesen Befunden werden in der (bewusst hochspekulativen) Einleitung architektonische Implikationen und Anwendungen auf andere linguistische Aspekte vorgeschlagen.

Als experimentelle Paradigmen wurden ein active memory task, ein passive reading task und die Mismatch Negativity (MMN, bzw. ihr magnetisches Äquivalent MMNm) benutzt.

Die in dieser Arbeit angewandten Datenanalysemethoden umfassten die Analyse der gemittelten Rohdaten, ihre Minimum Norm Schätzung (MNE) sowie die Wavelet Konvolution der kontinuierlichen MNE. Statistische Analysen basierten auf der Global Field Power (GFP) oder Regions of Interest (ROI) von Kanälen oder angenommenen Dipolen (MNE).

Summary:

"Cells that fire together, wire together." Donald Hebb introduced this learning principle in 1949 (Hebb, 1949). He named ensembles of neurons connected by this principle "Cell Assemblies".

Using the psychophysiological method of magnetoencephalography (MEG), the present work scrutinised linguistic aspects of single words on the background of Hebb's principle. Features under investigation were the orthographic word length, the familiarity of a word, its meaning, some of its syntactic features and its phonetic transcription.

With the help of topography and timing of the word evoked brain responses it can be speculated about a time-line of word-processing: First, from 60ms after stimulus-onset on visual features of words are analyzed. Signatures of semantic processes can be measured from 80ms on whereas word frequency gains influence on the brain response from 120ms. Finally, syntactic processes become evident from 140ms. The reported processing cascade indicates that the brain can work on words very early after stimulus onset.

Based on these findings, architectural implications and applications on other linguistic aspects are proposed in the (intentionally highly speculative) introduction.

As experimental paradigms we used a active memory task, a passive reading task and a Mismatch Negativity (MMN, or, more precisely, its magnetic equivalent MMNm).

Data analysis methods used in this work comprised the analysis of averaged raw data, its Minimum Norm Estimate (MNE) and the wavelet convolution of the continuous MNE. Statistical analysis was performed either on the global field power (GFP) or on regions of interest (ROI) of channels (raw data) or assumed dipoles (MNE).

# I   INTRODUCTION

In this dissertation I will introduce and discuss linguistic topics concerning the mental lexicon from a psychophysiological and neurobiological point of view. The questions, insights and conclusions from the experiments my colleagues and I performed are all based on a neurobiological framework in which the so-called cell assemblies play a central role. Introduced by Donald Hebb in 1949, cell assemblies describe the idea how associative learning and some resulting mental structures might be implemented neuronally. Applied to the field of linguistics, this 'bottom-up' approach (derive linguistic models from neuronal principles) is somewhat in contrast to the traditional 'top-down' approach (find brain structures that correspond to linguistic models) and hence leads to different questions.

In this chapter, I will briefly introduce the biological framework, sketch some questions that arise from this framework when confronted modeling the mental lexicon and finally give a summary over the five experiments (see Appenices I-V) performed.

The next chapter "Architecture" will discuss issues concerning cell assemblies on a level that is free from biology but looks at neurons as processing units, their connections and topography. This chapter will be highly speculative and hopefully will lead to many further discussions. Optimally, the resulting insights should become mental tools for constructing large scale cell assembly theories of language. These architectural insights are entirely based on the experiments we performed over the last three years and will also be discussed on the basis of their results.

As the next chapter "Applications" will try to apply these architectural insights to linguistics, it will be even more speculative! It might broaden our understanding of cell assemblies reflecting linguistic processes and surely has to be evaluated in forthcoming experiments.

The final chapter will synthesize all the applications into an extension of Pulvermüller's framework (Pulvermüller, 1999).

## I.1 Biological Fundamentals

In order to understand the implications for the mental lexicon I will give a brief account for Hebb's model and its modern interpretation. Hebb's original idea on the emergence of cell assemblies (1949) was based on *coincidence* learning. Learning is usually defined as an adjustment of the weight between two neurons; the weight defines the 'importance' of a neuron's input to another. The coincidence learning rule postulates that weights between two neurons are increased every time both are active at the same time. Biologically however, it is not plausible to increase the weights between neurons infinitely. Moreover, it might be useful to model the information that the two neurons are *not* active at a given point in time. This led to the modern view of the *correlation* rule forming cell assemblies: the connection between two neurons is weakened when only one of them is active at one time but strengthened when they are both active.

## I.2 Investigating Aspects of the Mental Lexicon

Words may be understood as small linguistic units conveying information used by the speaker to establish a mental structure in the listener's mind. Words have different linguistic functions in the processing of the larger context, i.e. the sentence or the utterance. Linguists often think of the mental lexicon where such information is stored and retrieved during the transformation of a concept into a sentence (production) or a sentence into a concept (perception). What kind of information is included, how and when it is accessed are questions currently under debate.

In the context of this dissertation I will discuss some of the relevant bits: The orthographic word length, the familiarity of a word, its meaning, some of its syntactic features and its phonetic transcription.

For reading aloud words it is necessary to process their orthographic and phonetic representations. Certainly, the semantic information must be available to understand a word in a sentence and some syntactic information must be available to form syntactically correct strings of words. One could interpret word length and frequency as epiphenomena of a word's internal organization, but research has shown that they still contain linguistic information and therefore we chose to investigate them as well. We asked how all this information is reflected in the neuromagnetic brain response. Our specific questions were:

1. Do long words induce a stronger brain response than short words?
2. Is the brain response stronger to rare words compared to frequent words?
3. Do these two factors interact?
4. Is the modality the meaning of a word is referring to, reflected in the brain response, e.g. its topography?
5. Can we spot basic syntactic processes?
6. What is the timing of all these reflections?

## I.3 Summary of the Experiments Performed

We performed five experiments to investigate timing and topography of word related neuromagnetic brain responses. Hypotheses underlying these experiments were derived from the Neurobiological Theory of Language Pulvermüller, 1999 and were employed in the following experiments:

1. Length and Frequency (single case study)
2. Length and Frequency (group study)
3. Broad Word Classes (single case study)
4. Action verbs (group study)
5. Syntactic Features (group study)

In the first two experiments, we wanted to know whether and how influences from word length interacted with influences from word frequency. We varied words in two of their features orthogonally (long|short words x high|low frequency words) while keeping others constant. First, we performed this experiment with a single subject to exclude between-subject variance, we then repeated the experiment on a larger population whether the results would hold.

1. Length/Frequency, single case (appendix one):
   - 90ms-120ms, length effect: long words led to stronger neuromagnetic brain responses very early on.
   - 120ms-160ms, frequency effect for short words only: rare short words led to stronger brain responses than common short words.
   - 370ms-470ms, frequency effect for long words only: rare long words induced stronger brain activity than common long words.

We concluded, that word length had an earlier impact on the brain response than word frequency and moreover, the psychophysiological influence of word frequency depended on the word length.

2. Length/Frequency, group (appendix two):

The results of the single case study indicated that changes in the brain response due to word frequency can occur much earlier than previously reported (e.g. Osterhout, Bersick, & McKinnon, 1997: ~200ms). The brain responses could have been speeded up by the repetition in the single case study. Therefore, we repeated the experiment a group of 15 subjects. In the single case study, we analyzed regions of interest, a strategy sometimes criticized as arbitrary. The root-mean-square (RMS) of all dipoles of the minimum norm estimate is a more robust measure of the neuromagnetic brain responses and revealed the following differential effects in the group study:

- 60-120ms, length effect: stronger brain responses to long words compared to short words.

- 120-170ms, frequency effect for short words only: rare short items led to stronger amplitudes than common short items.

- 175-185ms, frequency effect for short and long words: stronger neurophysiological responses to rare words than to common ones.

- 225-250ms, frequency effect for long words only: long rare words led to stronger neuromagnetic fields than common ones.

To our surprise, the length effect was observable *even earlier* in the group study than in the single case study. The order of the frequency effect was similar, albeit somewhat compressed in time.

With this study we replicated the finding that word length first has the earliest impact on the brain response while the impact of word frequency depends on the length and appears later.


3.  Broad Word Classes, single case (appendix three):

We investigated four word classes in this design: function words, action verbs, visual nouns and multimodal nouns (strong visual and action associations):

- 90-120ms: Nouns with multimodal associations evoked stronger magnetic fields than other words, regardless of whether they belonged to the same (nouns) or different lexical categories (verbs, function words). Semantic associations obtained by a questionnaire correlated with the magnitude of neuromagnetic responses.

- 120-160ms: brain responses revealed additional distinctions of the word categories.

- 120-160ms: only brain responses to function words were lateralised to the left hemisphere.

These results indicate that semantic factors can become relevant in cortical processing before grammatical information about a word is reflected in

neuromagnetic brain responses. Moreover, results show that lexical access can be observed as early as 100ms after visual presentation.

4. Action verbs, group:

The class of action verbs already employed on the last experiment was subdivided and expanded to 30 members of each verb class: Face- (e.g. "to grin"), arm- ("to grab") and leg-related verbs ("to kick") were presented visually in the MEG. Our main findings were:

- In a very early time frame, 80-120ms, we found the topographies of brain responses to action related verbs to be determined by the brain areas that are responsible for carrying out the actions the verbs refer to.

- This differential topography was found in the frequency range from 32-40Hz (gamma-band) but not in lower frequencies.

- Gamma-band responses to verbs related to hand- and arm-movements were stronger in the left hemisphere than in the right. In contrast, brain responses to leg- and face-verbs did not differ in their laterality.

The gamma band responses showed at a very early point in time that verbs differentially activate areas in the motor-cortex that relate to their meaning: leg-related words lead to a peak in the gamma band response of the motor-cortex representing the leg.

The study corroborated the finding that lexical access can be observed very early after presentation.

Moreover, the study revealed for the first time that only arm-related words led to a brain response that is lateralised the dominant hemisphere.

5. Syntax, group:

In an MEG analogue of the Mismatch Negativity design we investigated the agreement or disagreement of syntactic features (e.g. feature gender: male vs female) in a determiner phrase, e.g. "the rage". Like in experi-

ments 1-3, we employed an orthogonal design ("der"[m]|"die"[f] x "Mut"[m]|"Wut"[f]). Moreover, the phrases had different sequential probabilities of determiners ("der","die") and nouns ("Mut", "Wut"). Our findings:

- 140-180ms: enhanced Mismatch Negativity to an agreement violation in the determiner phrase" *die [f] Mut [m]".

- We did not observe a brain response that reflected the sequential probability of the words constituting a grammatical phrase.

We concluded that an enhanced brain activity is elicited only when there is an agreement violation and the sequential probability is zero.

In general, experiments revealed that word induced brain activity can differentiate between:

- visual features of words (>60ms)

- semantic processes (>80ms)

- word frequency (>120ms)

- syntactic processes (>140ms).

It thus seems, that different parts of a lexical entry elicit their psychophysiological reflections at different points in time. At present, it can only be speculated about the reasons for this cascaded access. In the following chapters I will try to extract architectural principles from these data, apply these principles to linguistic problems not yet addressed and finally try to extend the current theoretical framework.

# II   ARCHITECTURE

## II.1 Topography predicting Frequency

It is still unclear how high frequency activation in cell assemblies can be measured. Since EEG and MEG only detect the summed action potentials of ten- to hundred-thousands of neurons, the single neurons must fire in synchrony to generate an oscillation. However, if cells are in close cortical vicinity, the various traveling distances between cells would smear the frequency response of a cell assembly. Therefore only a rise in activation would be measurable that is composed of the summed activation of the cells. Because of the short distances, the frequencies by which the cell assembly would reverberate would be extremely high (> 250Hz, Pulvermüller, 2000). To explain gamma band frequency, one could envisage two or more sub-structures that are connected over longer distances leading to lower response frequencies. Pfurtscheller and Lopez da Silva (Pfurtscheller & Lopes da Silva, 1999) for example, report a possibility to model an oscillation that is conveyed by a sub-cortical loop:

As pointed out by Sporns et al (Sporns, Gally, Reeke, & Edelman, 1989),
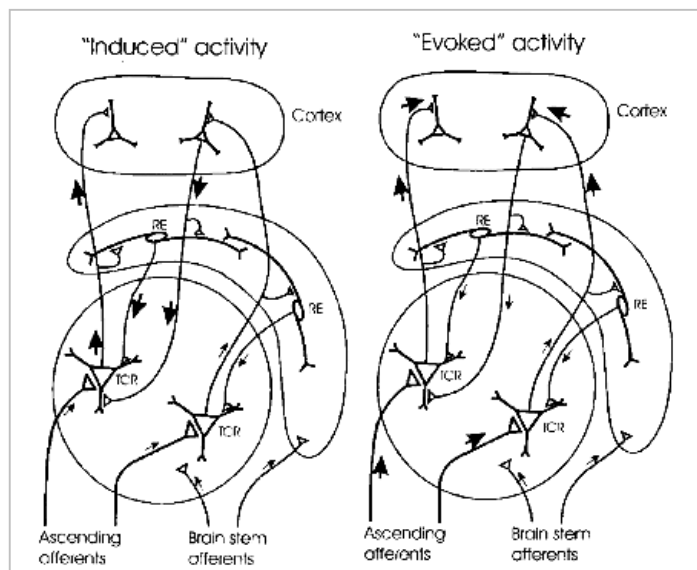


**Figure II.1.1.**
**Schema for the generation of induced and evoked activity. TCR thalamic relay cells, RE reticular thalamic nucleus. (From Pfurtscheller & Lopez da Silva 1999)**

signaling between cell assemblies occurs via excitatory connections that link cortical areas, usually in a reciprocal fashion within or between different levels of the nervous systems. Therefore, oscillations including the frequency range of the gamma band can be generated from two or more cortical areas (Llinás, Grace, & Yarom, 1991, Silva, Amitai, & Connors, 2002) and without the need of sub-cortical structures. Cell assemblies that comprise two or more areas sub-assemblies can be modeled as illustrated in figure II.1.2:
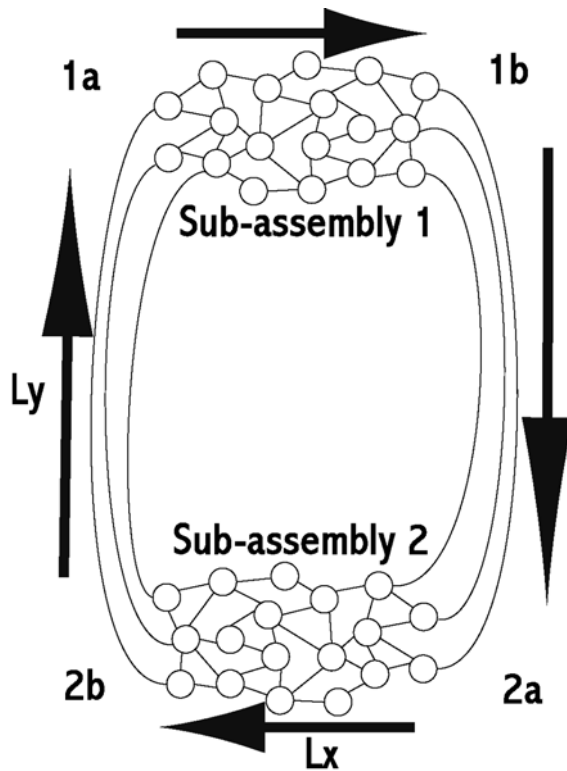


**Figure II.1.2.**
**A cell assembly consisting of two sub-assemblies that are interconnected via long distance projections. Incoming activation progresses from 1a to 1b, 2a and 2b. Travelling times are determined within assemblies by number of connections (Lx) and between assemblies by the length of projections (Ly).**

The initial activation would stem from a distant site, e.g. some sensory area. The activation would then start at 1a of sub-assembly 1, progress through this assembly towards 1b. The long projections to 2a would cause a measurable time lag between the activation of the two sub-assemblies. While activation progresses from 2a to 2b the activation of sub-assembly 1 would slowly decay and would be re-activated again by the long projection of sub-assembly 2 to sub-assembly 1. The frequency by which the whole cell assembly oscillates would crucially depend on Ly, the length of these projections but also on Lx the area of a sub-assembly. Both lengths

Lx and Ly have different influences on the cell assemblies oscillation. While the influence of Ly is predominantly defined by the axonal conduction time (~10m/s Aboitiz, Scheibel, & Zaidel, 1992), the axonal conduction time plays a minor role in Lx. Here, the synaptic transmission time between to neurons is more important (2ms, Pulvermüller, 2000). The number of neurons, the sub-assembly's size, may therefore define the impact of Lx. Given that both sub-assemblies are of the same size and projections Ly are equally long, the signal produced by the whole assembly would be quasi-periodic.

One evidence for such a variable frequency might be found in the fourth study concerning cell-assembly representation of action-verbs reported in Appendix 4 of the present thesis. Cell assemblies consisting of sub-assemblies in the motor cortex and the perisylvian cortex might produce such variable frequencies as illustrated in figure II.1.3.
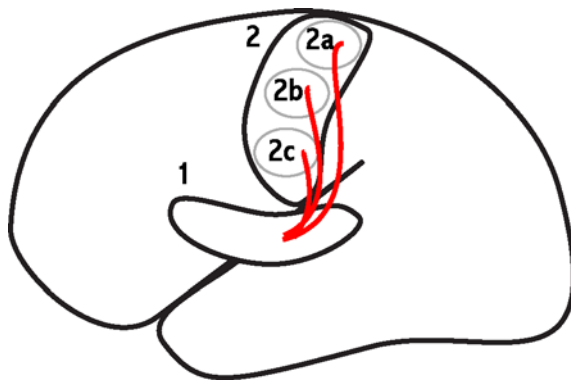


**Figure II.1.3.**
**Illustration of a topography that may predict the frequency of the cell assembly: Leg related words include sub-assemblies in the led area (2a) of the motor cortex and in the Auditory Word Form Area (1). Arm related words include sub-assemblies over arm areas (2b) The connection is short between both areas compared to the topography of the leg word. Frequencies to face related of highest (2c).**

Indeed, we found such a frequency response in the data around 300ms (figure II.1.4). Leg-related verbs lead to strongest activation and a peak frequency of 50Hz at leg areas, whereas arm-related verbs lead to peak activity over arm areas at 56Hz while the face-cell assembly oscillated with at 66Hz. However, the corresponding statistics only approached significance. A more dedicated study might be able to better scrutinize topography dependent frequency effects. A dedicated design could for ex-

ample present the words in a visual steady state paradigm. The three verb-classes could be presented in differeent frequencies that are varied orthogonally: (leg | arm | face) x (50Hz | 56Hz | 66Hz). These frequencies are empirically found, one could however try to compute morphologically motivated frequencies. The prediction would be that a network representing a verb-class has a dominant resonance frequency leading to more prominent amplitudes as opposed to other frequencies.
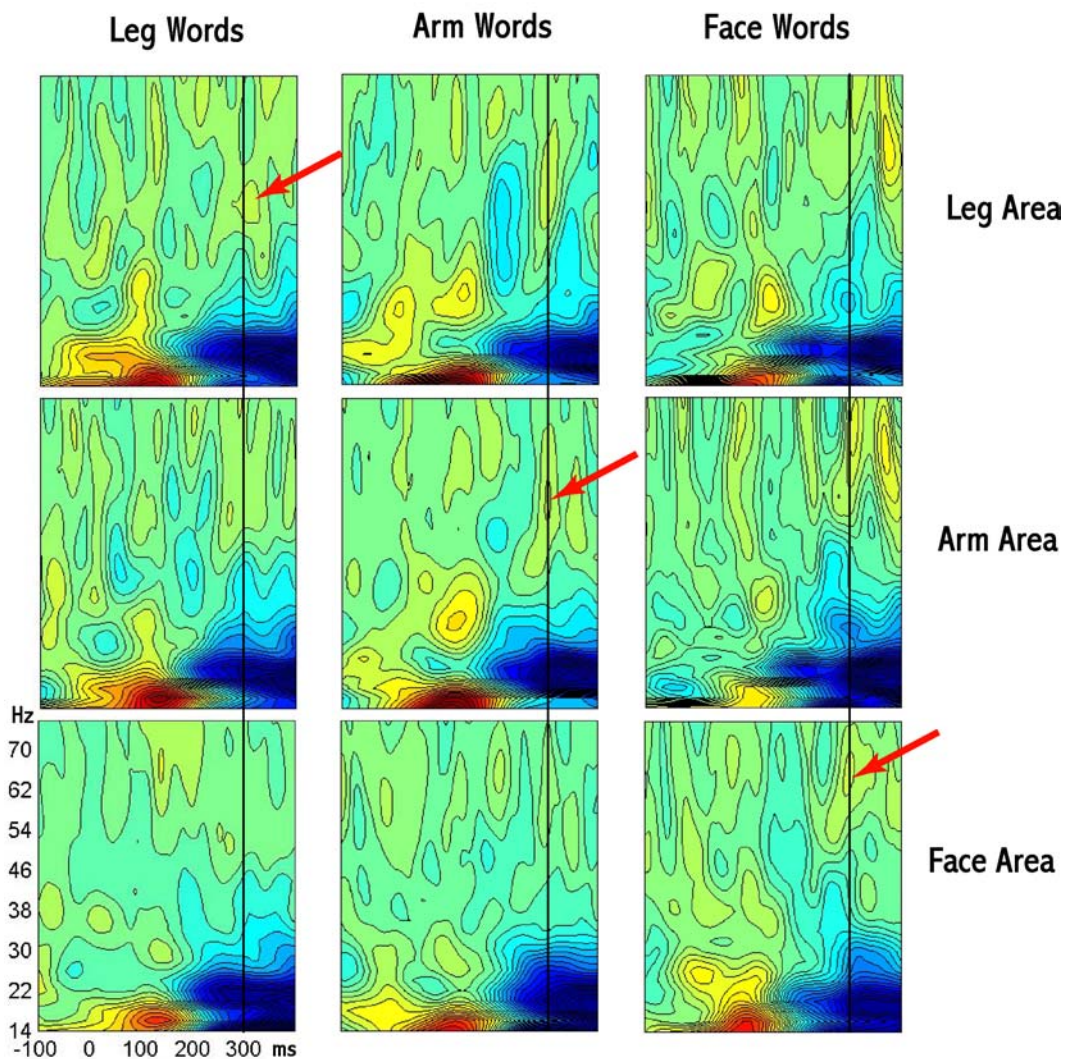


**Figure II.1.4.**
**Columns depict verb classes, rows areas over the motor cortex. The red arrows indicate the peak frequencies in the gamma band around 300ms: 50 Hz for leg verbs, 56 Hz for arm verbs and 66 Hz for face verbs.**

In the present context it might be interesting to note that Hashimoto and colleagues attribute very late gamma-band components with latencies of about 300 ms to the conscious detection of stimuli (Hashimoto, 2000). This could imply that our reported finding of differential word evoked gamma activity around 80-120ms is pre-conscious. Since these differences reflect aspects of verb semantics, the semantic access would be pre-conscious.

When neuronal populations oscillate, they tend to recruit neurons in larger cortical areas in the case of low frequencies, and to be more spatially restricted in the case of higher frequencies, as for beta/gamma rhythms (Pfurtscheller & Lopes da Silva, 1999). In the latter case, the cortex appears to be functionally organized as a mosaic of neuronal assemblies characterized by high frequency synchronous oscillations that may vary considerably in their frequencies. Where does this variability come from?

Maybe the neurons that are in one or the other subassembly comprise a considerable area of brain tissue. The traveling time from one end to another of a sub-assembly (e.g. 1a to 1b, figure II.1.2.) would vary and therefore the frequency with which the whole assembly. This would moreover lead to an extended area used by the oscillating neural population. A functional relevance of such a large scale neuronal behavior will be discussed in the next section.

## II.2 Genesis, Coherence and Amplitude

How are the different attributes of an object brought together in a unified representation given that its various features are treated separately in specific cortical areas?

The neurobiological solution to this so-called binding problem has been proposed by Crick and Koch (Crick & Koch, 1990): Coherent oscillation of Cell Assemblies. It is therefore of outstanding importance to understand the specificities of CAs and their implications for modeling as well as for psychophysiological confirmation.

In this section I want to address two questions:

1. How do Cell Assemblies evolve?
2. What is the relationship between coherence and amplitude in their reverberating activity?

As alluded in the introduction, synchronous firing of neuronal elements increases their weights and if this happens often enough leads to an assembly of these elements. Such neuronal elements may be single neurons, but also cell assemblies. The connection between cell assemblies forming a 'super cell assembly' leads to the ability to model hierarchies of assemblies which will be addressed in the next section. If we think of sub-assemblies forming an assembly in a way sketched in the previous section then Singer's (Singer, 1994) proposition of coherence detectors might be useful: In the visual cortex, cells located in V5 are strongly activated when coherence in V1 is high and also project back to V1 leading its neurons into even stronger coherent firing.

Ad 1) A model for the genesis of cell assemblies could take Singer's proposal into account. Prior to the existence of a cell assembly, two feature detectors are uncoupled. Through synchronous activation a coherence detector may detect initially the coherent activity of the two feature detectors and spur a connection between the two by giving additional (back-projecting) activation. Coherence detectors may therefore play an supportive role in the genesis of cell assemblies.

Ad 2) We can use coherence detectors for more modeling on a higher level: The brain often has to detect matches of two stimuli. However, it can be the case that the correlation of the two stimuli and, by extension, their representing cell assemblies is not strong enough to lead to a representing super cell assembly. Then, the detection of their coherent activation might be useful to decide whether they match or not. A case where two cell as-

semblies will not form a super assembly will be discussed in the next chapter, an application of the coherence detection will be introduced in chapter III, section 4.

In the previous section I made the claim, that the specific frequency at which a cell assembly is oscillating is critically defined by the topographic distance (Ly, figure II.1.2.) and the extension (Lx) of the sub-assemblies. Therefore, if two cell assemblies (representing two different concepts and consisting of two sub-assemblies each) are to oscillate coherently (match of the concepts), it is necessary that they oscillate in the same frequency range. If, however their topography (Ly) is different, it is apparently not possible to generate the same frequency. But there is a solution to this problem: The active areas of the sub-assemblies might be extended towards the outer bounds of the sub-assemblies such that Lx becomes larger. This will also lead to a modulation of the response, extending it to a broader frequency band at which the cell assembly oscillates. If there is an overlap of the frequency bands the two cell assemblies oscillate at then there is a better chance for the coherence detector to become activated.

This concept has the important implication that the amplitude of the brain response will be increased if there is not an instant match between the two concepts as more cortical area is activated: The amplitude of oscillations is proportional to the number of synchronously active neural elements (Elul, 1972), slowly oscillating cell assemblies comprise more neurons than fast oscillating cells (Singer, 1993). Thus, if it takes longer to establish coherence, the amplitude will rise.

Well known components in the EEG such as the N400 can be re-interpreted in the light of this concept. The N400 is commonly interpreted as the effort to integrate semantic data (Kutas & Hillyard, 1980). The findings imply paradigms where sentences or phrases are shown to subjects. The component is elicited after a critical word in the sentence. For dynamic structures like sentences it may not be possible to establish cell as-

semblies. Rather it might suffice to detect coherent firing between the elements, i.e. the representation of the words. We will explore this idea in more detail in chapter IV. But still, the effort to integrate semantic data is reflected in the amplitude of the N400 component, whose topography covers large parts of the parietal cortex, although the initial focus of the N400 however can vary considerably.

The prediction that the activated area will extend when there is no instant match thus seems plausible.

An early simulation study related to this idea (Lopes da Silva, Van Rotterdam, Barts, van Heusden, & Burr, 1976) has shown the relationship between amplitude and frequency of brain oscillations. With an increasing number of interconnected neurons and therewith an increasing number of coherently activated neurons, the amplitude increases and the frequency decreases.

## II.3 Cascades and Hierarchies

In neuroscience there are often discussions about serial versus parallel order of processing. Only one computational module would be active at a time and modules would be activated one after another in serial processing while multiple modules can work in parallel and feed their results to multiple other modules in parallel processing. An intermediate architecture is the cascade where the start of a processing module in not exactly determined to be at the end of the preceding processing module so that the processes can overlap. Hierarchies define the topography of the modules, their linking and the flow of information.

In the present context we can understand such modules as cell assemblies or sub-assemblies and this section will try to shed light on the emergence of topographies and the flow of activation between cell assemblies.

If a neuron is frequently co-activated with an other then by correlation rule the two will be connected. But if one neuron is more often active when the other is *not*, then this rule would predict an inhibition of the

other neuron. Yet inhibition is not the primary subject of this chapter and it is important to keep in mind that co-activation at the same time might not always lead to a connection between two neurons (namely if co-activation with other neurons is more frequent).

If a certain concept has just one context and both are presented shortly after another then these two concepts will be linked by the correlation rule. The weight between the two representing sub-assemblies will be 1 reflecting that *if and only if* one concept is activated then the other will be activated, too. If however, a concept has two contexts that occur with the same frequency then because of the inhibition part of the correlation rule the weights between them will be 0.5. While such a connection might suffice to activate the other sub-assembly, it is imaginable that more contexts will further lower the weights between the concept and all of its contexts, which will in turn lower the probability that the activation of one context will not necessarily co-activate the concept.

The ideas formulated here are a prerequisite for building hierarchies of cell assemblies. Another prerequisite might be the distinction between *wide-scope* and *narrow-scope* neurons.

In early visual processing stages one could imagine narrow-scope neurons that focus on local details of the image presented whereas wide-scope neurons 'look' at the more global shape of the visual image. Several stages of narrow-scope neurons would be able to recognize the global shape, maybe even more accurately than wide-scope neurons. However, the recognition would take more time than the more global (one-stage) recognition performed by wide-scope neurons. Architecturally, processes employing narrow-scope neurons would tend to organize serially, whereas wide-scope neurons are suitable for one-stop parallel processing.

For narrow-scope neurons larger structures are too variable to detect contingencies, but the general shape of a structure without the variable details might be more 'interesting' for wide-scope neurons. Thus, high local con-

tingencies would lead to high weights in narrow-scope neurons, whereas high global contingencies lead to high weights in wide-scope neurons.

It might even be useful to employ both processing concepts in parallel as we will see in the first section of the following chapter which introduces a dual route model for visual word form processing.

# III APPLICATIONS

## III.1 Visual Word Form Area: A Dual Route Model

Neurologically motivated dual route models of word processing (Coltheart, Patterson, & Marshall, 1980, Morton & Patterson, 1980, Bub, Black, & Howell, 1989) propose that words can be read either by a phonological route, using grapheme to phoneme correspondence rules, or a direct route, in which there is direct access to the lexicon.

A similar model is moreover supported from psycholinguistic research. Following Fodor's (Fodor, 1983) idea of parallel input systems, Allen & Madden (Allen & Madden, 1990) proposed that a letter processing module and a word processing module are running in parallel and are informationally encapsulated. One module would analyze an incoming word on the letter-level whereas the other is responsible for processing the same word as a whole.

I will give a brief cell assembly approach for this thinking, motivate it from the brain morphology and will then pave its way for the integration into Pulvermüller's frame work (Pulvermüller, 1999).

Two studies summarized in the introduction of this work have shown that a word frequency effect can be observed from 120ms (Appendices I & II). Two other studies have shown that despite matching for word length and frequency there can be differences in the topography of the brain response that are attributed to the word's meaning (Appendices III & IV). These differences are observable from 80ms on.

Thus, the results of the present work suggest that semantic features can be relatively distinctly extracted from other linguistic features in an entry of the mental lexicon. These other variables might be word-form (visual/orthographic, auditory/phonetic), word-stem, word-frequency and syntactic features such as case, gender and number.

In this section I will advocate a dual route model that consists of two routes:

1. The syntactic route or pathway, working serially on the incoming visual word features
2. The semantic route or pathway, working in parallel on the incoming visual word features

The distinction between wide and narrow-scope neurons made in the last section of the previous chapter will motivate the dual route model discussed here.


The serial pathway:

Narrow scope neurons that would react on more detailed information may on a more restricted area of the incoming information from the retina. Such narrow scope neurons could act as letter detectors.

The next stage might integrate letters to syllables or morphemes. These higher representations (or corresponding trains of their representations) could be processed by synfire chains (Abeles, 1991) to verify whether the string is plausible or not. Letter detection tasks would thus crucially depend on this processing area. The structures proposed up to this point would correspond to the letter-processing module in the model of Allen and Madden (Allen & Madden, 1990).

The orthographic representation would then be translated to an phonetic representation in the perisylvian cortex ("Auditory Word Form Area"). In the published papers (Appendix I & II) we argued, that the length dependent frequency effect is mediated by synfire chains that represent the phonetic translation. However, it might be the case that the synfire chains represent the orthographic representation as the effect may be attributed to the posterior part of the brain.

In the perisylvian cortex, series of words may be analyzed using so-called sequence detectors. The sequence detectors proposed by Pulvermüller

(Pulvermüller, 2002) react on simple but specific word orderings such as "A follows B", but not "B follows A". The sequence information is used for syntactic processing and will be discussed in more detail in the next chapter.

The sequential information in representations of various levels is highly important in this pathway that ends up with a syntactic representation of word streams. One could also name this pathway the "syntactic pathway" in contrast to the parallel "semantic pathway".


The parallel pathway:

As pointed out in section 3 of chapter II (hierarchy and cascades), there may be neurons that 'oversee' a larger area of (lower level, feature detecting) neurons and can thus react on a more global pattern. These neurons would react on the word form as a whole rather than on the letters it consists of. Such a recognizer is plausible as the visual recognition system naturally is capable of processing objects as a whole and not by serially analyzing its parts and incrementally building up a representation of the object. The main (evolutionary) advantage of this parallel type of object recognition: it is faster.

This parallel access to the word's meaning would correspond to the word-processing module in the model of Allen and Madden (Allen & Madden, 1990).

It is noteworthy, that the connections made on this parallel pathway can potentially comprise the whole cortex. Following Pulvermüller's view on biological semantics (Pulvermüller, 1999), neurons representing the (referential) meaning of words are located in cortical areas that are responsible for processing the function the meaning of the word refers to (e.g. the representation of "to kick" includes neurons from motor and pre-motor cortices).

This interestingly includes areas that are also used by the serial pathway: the ventral 'what-stream' is an area that contains the referential meaning of words with visual associations (e.g. "the sun"). The explanation is that the areas work on complex visual features (Malach, Levy, & Hasson, 2002) that may comprise letters or faces, for example.

In the next paragraphs I will discuss the underlying brain morphology of these two routes and the flow of activation.

Brain Morphology:

The biological fundament of the syntactic route may be established as follows: As pointed out by Bookheimer et al (Bookheimer, Zeffiro, Blaxton, Gaillard, & Theodore, 1995) the inferior temporal / fusiform gyrus has strong connections to Wernicke's area (cf. figure III.1.1. area 4). Wernicke' and Broca's area (5) are bi-directionally connected via the arcuate fascicle which is intermitted by the angular gyrus (Dronkers, Pinker, & Damasio, 1991, figure III.1.1. area 3). Adjacent to Heschl's gyrus, Wernicke's area is considered to be an auditory association area. An auditorily perceived word is entering the language system here.



1 early visual cortex
2 fusiform gyrus
3 gyrus angularis
4 Wernicke's area
5 Broca's area
6 motor cortex
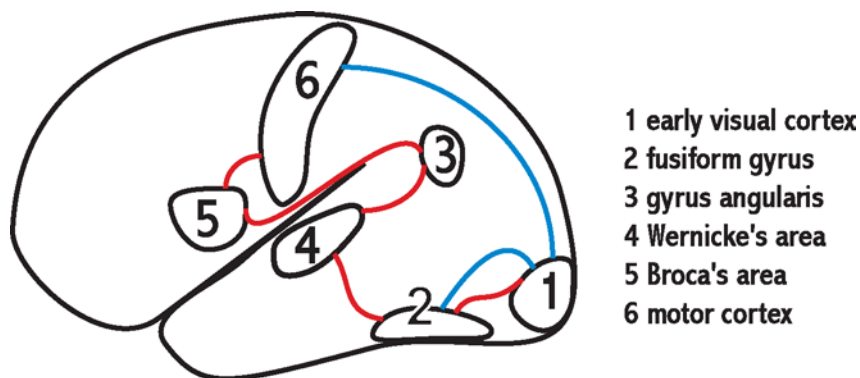
**Figure III.1.1. Brain areas involved in the dual route model. The red path depicts the serial path, the blue path depicts the parallel path.**

Flow of activation:

The serial or cascaded stages of visual word form processing are activated along the red path in Figure III.1.1.. The **left ventral occipital area** is acti-

vated by both, **real words** and **pseudo-words** but not by non-words (Petersen, Fox, Posner, Mintun, & Raichle, 1989, Petersen, Fox, Snyder, & Raichle, 1990). The timing was delivered by Compton et al (Compton, Grossenbacher, Posner, & Tucker, 1991): after 50ms EEG amplitudes distinguished between real words and non-words in the left occipital and parietal temporal sites. This area thus seems to be responsible the discrimination of orthographically plausible word-like material from non-plausible strings.

An fMRI study by Polk et al (Polk et al., 2002) revealed that "an area on or near the left fusiform gyrus was found that responded significantly more to letters than digits."

The group study presented in this work (see Appendix II) undermines the claim that complex visual processing of letter features and their connections might be performed in this area (figure III.1.1.). The orthographic representation of the word might be reflected in the posterior lateral part of the left hemisphere. Figure III.1.2. shows difference maps for short and long words, where activations from high and low frequency words were subtracted. The frequency effect changes with the word length in this area. Thus, if the processing of visual features is completed the word frequency effect is apparent.
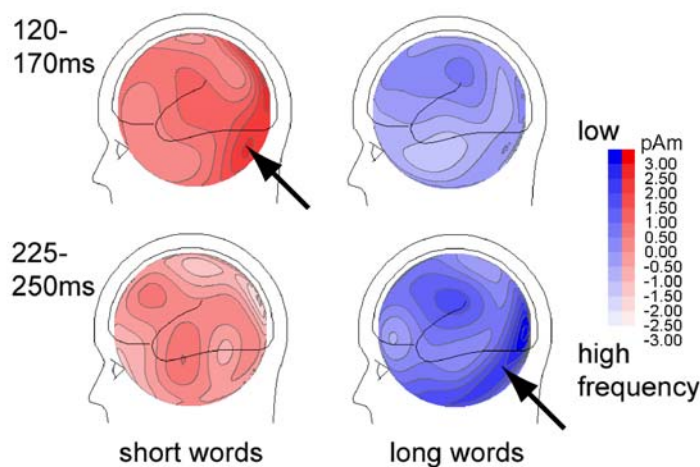


**Figure III.1.2. Word frequency difference (dark colours = low, light colours = high frequency) at different onsets for short (red) and long (blue) words. The most prominent activity is left ventral as indicated by the arrows.**

The next processing step was reported by Horrwitz and colleagues (1998) who have shown that during reading aloud the **angular gyrus** is more strongly activated after single **real words** than after pseudo words. In contrast to healthy controls, activation in dyslectic patients was diminished in both conditions. This processing step might therefore distinguish real words from pseudo-words.

The angular gyrus in turn lies on the pathway (arcuate fascicle) that bi-directionally connects Wernicke and Broca. Wernicke is generally associated with the acoustic word form and is seen to play an important role in the mental lexicon. Thus, the angular gyrus might be a candidate for the generation of 'pre-phonetic' representations that can be derived from the visual word form area. These representations then are translated to **an acoustic word form** in **Wernicke** while the **motor program** for acoustic word production is mediated (and pre-activated?) in **Broca**.

This whole chain would therefore act as a cascaded translator from the orthographic to the phonetic representation.

The perisylvian cortex might moreover house so-called sequence detectors that work on multiple serially activated word representations (Pulvermüller, 2002).

Parallel to this stream the low-level visual word features are accessed by the "semantic"-stream (given in blue, Figure III.1.1.) that immediately activates the sub-assembly representing the meaning of the words. Thus, in contrast to other dual-route models, in this model it is necessary to employ both routes at the same time to process and understand a sentence.

## III.2 Context Dependence

**"turkey** – a mediterranean country OR a large bird."

How are homonyms processed in the human brain, can this processing be spelled out in cell assembly terms? Are concepts that are ambiguous stored in single cell assemblies or multiple?

I want to discuss a model that can achieve context dependent disambiguation of a concept while being compatible with the cell assembly approach to date.

Homonyms are often preceded by other words that disambiguate their meaning and sometimes a non-linguistic context can be used to achieve the appropriate meaning. Moreover, the disambiguating context can be delivered after the homonyms. Therefore a model that is able to disambiguate a homonym must comprise both context types.

One can strongly assume that cell assemblies representing words are active over a relatively long period of time (>1 sec) when used for sentence processing. This implies that the activity of cell assemblies overlaps in time. This will lead to connections between two cell assemblies meaning that word representations are connected to some degree irrespective of their serial order. However, the connections may not be strong enough to activate the other cell assemblies. Additionally, for cell assemblies it can be assumed that within-connections are more strongly weighted than between-connections.

A model as illustrated in figure III.2.1. can help to solve the disambiguation problem.
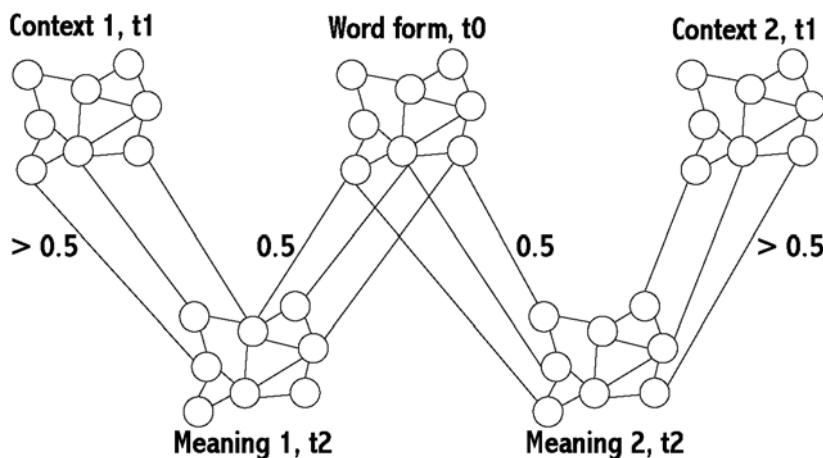


**Figure III.2.1. Illustration of a network of cell assemblies for modelling context disambiguation. T-values denote a point in time, where the corresponding sub-assembly is active. The weights in the middle row indicate that no single sub-assembly is able to activate one of the assemblies that represent the meaning.**

The presentation of the homonymous word form will activate the word-form sub-assemblies, but because of the low weighting (0.5) of the connections to the two sub-assemblies representing the meanings, these will not be activated fully. However, when additional activity of the cell assemblies representing one of the contexts comes in, the corresponding meaning of the homonym will be activated. Notably, this model is not depending on the serial order of the words, i.e. the times given at context one and two could also be –1.

The connections between the two different sub-assemblies related to the meanings do not have full weights because the meanings only co-occur exclusively with the word-form. As we have seen in chapter II.3 the correlation rule therefore weakens the connection strength to the other meaning.

The correlation learning will therefore rule out the possibility that a word-form activates both meanings which could be the other alternative to this model.


## III.3 Variables

It is important to have a neuronal account for variables as they are a vital part of the human brain's cognitive abilities. Variables give us the power to apply a concept acquired in a certain domain to a situation in a different domain. Consider the following examples:

1. $x = 5$ (mathematical variable)
2. He is Peter. (pronoun referring to a certain person)
3. The gentleman over there is Peter. (noun phrase referring to a certain person)
4. I need something to open this. (function word referring to a class of objects)

We can paraphrase a variable's function in a more abstract way which might be more useful for modeling: A variable is a label for a class of structures. Using a variable is to replace this label by a member of this class of structures in a given context.

In chapter II.3. we have seen that in some cases neuronal elements can be connected but do not have a strong connection. There might be a one-to-any architecture between the label and possible objects that it can refer to. In this chapter we have to find ways to:

1. generate classes a label can stand for
2. implement contexts in which variables are used
3. assign members of a class to the label

Ad 1) In neuronal network theories it is often discussed how a class can be formed. One first approach is that members of a particular class share certain features. This idea is further refined through the postulation that not all members must have all features. With this postulation there can be members that do not share features at all as long as there are other members that have some features of both (member 1: features a & b, member 2: features c & d, member 3: features a & c). Although research in this field is ongoing, we can define a class by the set of features its members posses. Further, in the chapter IV. a mechanism for extracting complex linguistic (word classes) and semantic features (animate) from serial word order will be presented.

Ad 2) "Peter$_1$ is in the kitchen. He$_1$ is hungry." Logically speaking, the variable "he" is set to the value "Peter". Thus the word "Peter" activated some features, for example [human being, singular etc.]. These features are shared with some features of the word "he". The context, which is the preceding sentence reduces the search space to what word the pronoun "he" could refer to. Note, that such a context does not have to be introduced

linguistically. There might also be a situation where Peter is present and the word "he" is a deictic reference to the person.

Ad 3) The words that can co-occur with the pronoun "he" are virtually infinite, they cover all male, singular nouns, proper names and more. Therefore, it is rather improbable that a cell assembly consisting of a sub-assembly representing "he" and a second sub-assembly representing "Peter" might exist. Theoretically however, such a solution might be modeled by the architecture discussed in the previous section.

Alternatively, with the coherence detection mechanism reported by Singer (Singer, 1993) and introduced here in chapter II.3., it might be possible to detect the coherent oscillation of the words' sub-assemblies representing grammatical features that both representing word-level cell assemblies share. This coherence detection could be used for the detection of a match *per se*, not for the connection of sub-assemblies.

The connection-based solution proposed in the previous section might therefore work as a one-to-some modeling problem, whereas the coherence-based solution in the present section might serve as a solution to a one-to-many problem. As the coherence detection is potentially capable of strengthening the connections between sub-assemblies, the architecture can be changed from "some" to "many".

## III.4 Verb Valence

As we have gathered some ideas about how variables might be implemented neuronally, we can apply the concepts to the class of verbs.

In modern syntax theories verbs often play a prominent role (Pollard & Sag, 1994) for the coordination of the other constituents. They define how many 'players' (so-called theta-roles) are needed to make the sentence complete and they exhibit the 'grammatical interface' (so-called agreement) to these players or phrases that describe them. On the semantic side, verbs provide a rough interpretation of the sentence's meaning which is

further refined by the nouns that denote the players. The term subcategorisation describes the verb's 'need' for nouns (or their relatives such as proper names or pro-nouns in the simplest case) to form a *semantically* correct phrase. Additional word material (function words) may be required to form a *syntactically* correct phrase:

1. **Peter sang**.
2. **Peter married** a **woman**.
3. **Peter gave** the **man** a **book**.

If one only reads the words given in bold face, the sentences are still understandable (i.e. semantically correct). These words are called *content words* as opposed to the *function words* given in normal face rendering the sentence syntactically correct.

Sentences 1-3 moreover demonstrate the so-called valence of verbs. Valence defines how many 'open positions' a verb has that have to be filled by (adequate) nouns to form a semantically correct phrase. Open positions can be filled backwards in time: In German, the subject often precedes the verbs.

For understanding how the brain processes sentences it is necessary to understand two crucial aspects of verb valence:

- How are verb-valences implemented neuronally?
- How does the brain know when these open positions are filled?

There are strong similarities between verbs and variables. A variable is a structure that has one open position that has to be filled. An intransitive verb like 'breathe' in 'he breathes' has only one open position as well. The difference between variables and verbs is mainly that verbs have at least one certain meaning whereas variables denote a class of structures that

have a certain meaning. In this respect variables are more comparable to nouns that can denote one special object or a class of objects ('house').

The similarity between verbs and variables leads to the impression that verbs are similarly realized in the brain, i.e. the variable and its value share features that oscillate coherently. In the case of verbs, such features should be syntactic such as Number, Case, etc. but also semantic features such as Animate. In contrast to variables, neuronal representations of verbs must also comprise a sub-assembly that reflects their meaning.

Still, it is difficult to model the number of theta-roles, i.e. the verb valence. One possible solution is the measurement of the degree of coherent activation, that is necessary to judge the sentence as acceptable. The level of coherence might be higher, the more positions are filled.

# IV  EXTENDING THE FRAMEWORK

This chapter will synthesize the insights won in the previous chapters and try to sketch an extended and differentiated model of that proposed by Pulvermüller (Pulvermüller, 1999) so far.

I will briefly summarize the key points of the current theory:

- the acoustic word form for a single word is stored in the perisylvian cortex of the language-dominant hemisphere that includes Wernicke's and Broca's area.

- time-series of phonetic representations (i.e. the series of phonemes making up the acoustic word form)  might be realized by synfire chains.

- neuronal representations of content words (referring to e.g. objects (visual nouns) or actions (action verbs)) include neurons from areas where the corresponding modality is processed (e.g. motor and pre-motor areas for action verbs).

- neuronal representations of words with mere syntactic relevance (function words) are restricted to the perisylvian cortex as they do not have any cognitive associations.

- cell assemblies representing function words are more strongly lateralised to the left than to the right hemisphere as content words are transcortically represented.

Currently, detailed modeling is missing in:

1. visual word processing
2. timing of lexical access
3. sentence level processing

Ad 1&2) Section 1 of chapter II (dual route model) made a biologically motivated proposal for a dual route processing of visually perceived words. One route activates the semantic representation of the word while the other extracts linguistic features through an in-depth analysis of the word form and its contexts. The semantic route may be fast and access low level visual word features in parallel while the syntactic route may work in a slow, serial manner. Thus, Pulvermüller's framework might be extended by this piece. It interfaces at the semantics (accessed by the parallel path) and provides an entry point to the existent phonological representation in the perisylvian cortex.

Ad 3) To this point, the model is not spelled out in detail how to understand a whole sentence. Recent work of Pulvermüller (Pulvermüller, 2002) has provided some ideas how sequence detectors might help to achieve this goal. I will give a brief account of the current sequence detector model.

Sequence detectors allow the detection of the serial occurrence of activations. These activations might reflect two cell assemblies representing words. Specifically, they can react on an order of say "first A, then B" but not "first B then A". If such a serial order is also possible it will be encoded by a different sequence detector. During parsing a sentence like "John walks the dog.", all sequence detectors that encode grammatical serial order of words will be activated: "John → walks", "walks → the", "the → dog", but also "John → the", "John → dog" and "walks → dog". The sequence detector model explicitly allows intermittent words between the two words that must follow each other.

However, it is not yet specified how such a model could detect grammatical or ungrammatical series of words. There might be various strategies to check the grammaticality of sentences, for example, the summed activity of all sequence detectors must be over a certain threshold. How such a mechanism would work for different sentence lengths surely has to be

discussed. Moreover, it is not clear, how physiological signatures of sequence detectors could look like. In the proposal above, the activity of sequence detectors might be measurable, but only when biological structures of single sequence detectors comprise enough cells to generate a measurable summed activity. Further, it is not clear, how the sequence detection model can explain the enhanced amplitudes following syntactic mismatches (e.g. Neville, Nicol, Barss, Forster, & Garrett, 1991).

Verb Valence Chapter may contribute to this subject. Clearly, syntactic processing must involve serial processing, the analysis and generation of serial orders of words. In contrast, semantics does not necessarily involve a serial order of the concepts. Consider the following examples:

1. **Jim built** the **house**.
2. The **house** was **built** by **Jim**.

Looking at the bold face content words only, we have the sequences "Jim built house" and "house built Jim". As usually houses are built by human beings and not the other way around, it is clear what the meanings of the sentences are. If we follow this solution we would have stored semantic features in the lexicon such as "human being" for "Jim", "performed by human beings" for "to build" as well as maybe "generates an inanimate object" and "inanimate object" for "house". These features would assure that both sentences convey the same meaning without the explicit serial order of the sentence. Concluding from chapter II.2 (Genesis, Coherence and Amplitude) the brain response to such a sentence would cause high coherence and low amplitude. This in turn is in accordance with the general finding that lower amplitudes are observed for (syntactically and/or semantically) correct strings.

However, coherence caused by semantic congruence cannot explain phenomena modeled by the sequence detectors or address their lack of  psy-

chophysiological predictions. Moreover, also sequence detectors could parse the sentences given above. Consider a sentence like "Jim hit John". The lexical entries for "Jim" and "John" could both have the feature "human being" and one meaning of "hit" might be that one human being hits another. Therefore, the meaning of the sentence can only be extracted when the serial order is taken into account. Linguistically speaking, the question "who hit who?" can only be answered properly if the so-called theta-roles of the proper names are known. The theta-role of "Jim" is the one of "agens" while poor "John" is taking the role of the "patiens". Note that theta-roles cannot be included in the lexical entry of the names as the sentence "John hit Jim." is also syntactically and semantically correct but with theta-roles reversed. Theta-role assignment is usually performed during the syntactic analysis as often the order of the words, their gender, number and case stand for certain classes of theta-roles. In German for example, the nominative case of a noun is often assigned to the "agens" theta-role, whereas dative or accusative stand for the "patiens". Here, clearly sentence-level semantics and syntax must interact as the serial order can provide information about the theta-roles.

Based on theoretical works by Frazier (Frazier, 1987), Friederici and co-workers (Friederici, Hahne, & Mecklinger, 1996) have proposed a two stage model of parsing, including a first stage, during which an initial phrase structure is built and a second stage, during which thematic role assignment and, if necessary, reanalysis takes place. The authors map staged model to the two ERP-components, the left anterior negativity (LAN) for the first stage and the P600 for the second. However, it might not be necessary to attribute the theta-role assignment to a second stage. It might be possible to extract this information earlier. Ritter and Kohonen (Ritter & Kohonen, 1989) have shown, that a preceding context of one single word can generate considerable semantic information:

```
sells visits  ·  walks  · phones ·      ·  Mary  ·
   ·     ·     ·     ·     ·    ·      ·   ·    ·    ·
 buys  ·     · speaks ·        ·    ·     ·    Jim
   ·     ·  eats  ·      ·      ·  cat   ·   ·    ·
   ·     ·     ·     ·     ·      ·    ·   ·    Bob
 runs  ·     ·     ·     ·      ·  dog  ·    ·
   ·     · drinks ·      · horse  ·    ·   ·    ·
walks ·     ·     ·     ·      ·    ·     · bread
   ·  likes  ·     ·     ·      ·    ·   ·    ·
   ·     ·     ·     · water   ·    ·   ·    ·
   ·  hates  ·     ·     ·    beer  ·   ·  meat
   ·     ·     ·     ·      ·    ·     ·   ·    ·
   ·     ·     · much   ·      ·    ·   ·    ·
poorly ·     ·    little  ·     · often  ·  fast
   ·  well   ·     ·     · seldom ·    · slowly ·
```
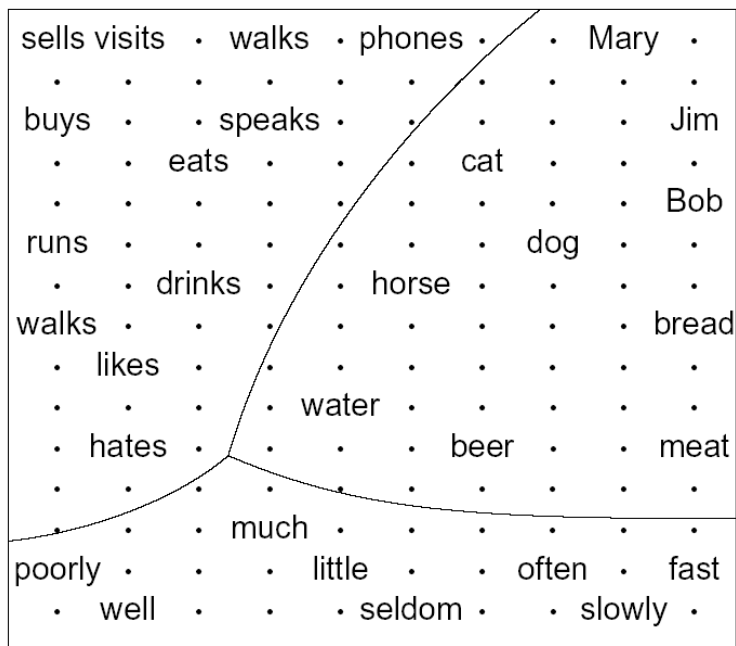
**Figure IV.1. Kohonen maps generated for single words in a context of one word within a sentence. Not only syntactic word classes cluster together but also semantic features (e.g. Animate).**

As illustrated in figure IV.1., words with certain features cluster together. These features not only include syntactic classes (e.g. Nouns) but also semantic classes (e.g. Animate). Thus it seems possible to extract semantic features and a class information from the serial order. This information in turn can be used for theta-role assignment. As these features arise from the context preceding the word, they might be available very early (~140ms after onset of visual word presentation) such that a theta-role could be assigned much earlier than 600ms.

Note that these features were extracted solely on the words' orders, not on any other information. This indicates that the pure serial order of words can convey semantic information of a word realized in features (so to speak the position on the map).


The model:

The extended model proposed here will describe the process of understanding a sentence rather than a single word. The issues discussed above will also be addressed.
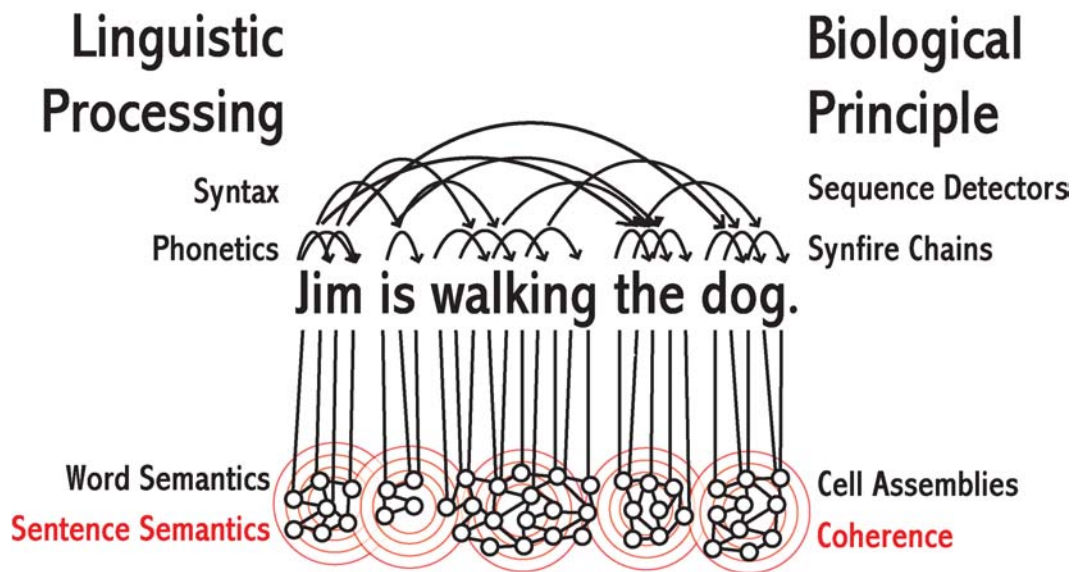
**Figure IV.1. The extended model. The language system might be divided in a serial (phonetics, syntax) and a parallel part (word/sentence semantics). For detailed explanations see text.**

- During reading, words activate the occipital lobe in a serial fashion.

- Following the dual route model the low level features of an incoming word are processed in a serial path and a parallel path.

- Processing results of the serial path are syntactic features, theta-roles and phonetic translation and information on the serial order of the words.

- The parallel path generates a biological representation of the semantics of the word in the conventional way.

- The semantic representation of a verb might include subcategorisation information (i.e. its open positions).

- The detection of the filling of an open position might be conveyed by coherence detectors leading to a theta-role assignment.

- Further incoming words might fill open positions of the verb and will allow for checking the semantic acceptability.

- Serial detectors might compute the acceptability of the sentence on the syntactic level.

This extended model accounts for the visual processing of single words, for the processing of words in context and the construction of a sentence-level meaning out of the verb's meaning, its sub-categorized nouns and their theta-roles. Further, through the division into a serial and a parallel path, the timing of the processing cascades may be predicted. The computation of the latencies will depend on number of neurons in a chain, their interconnections and the distances between the areas. The timing-predictions together with the hypothesized areas (illustrated in chapter III.1.) allow the construction of several experiments to confirm or falsify the model or to determine further specifics:

1. Verbs could be presented visually, matched for length and frequency, but varied in their valence. Here, the prediction would be that amplitudes of the brain response would vary with the valence (high valence leading to larger amplitudes).

2. Pairs of words consisting of one noun and one verb (used in the prior experiment) could be presented to check the coherence prediction (lower amplitude, higher degree of coherence) with one-place verbs (e.g. to breathe) generating lowest amplitudes and largest coherence.

3. Dedicated experimental series might map the stages of the serial path. Other experimental work has often focused on single stages eliding others.

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# VI APPENDIX ONE

# Neuromagnetic Evidence For Early Access To Cognitive Representations[1]

## VI.1 Abstract

How do physical and cognitive properties of stimulus words influence the neuromagnetic response of the human brain? Are the physiological correlates of these properties dissociable and at which latencies can they be observed? Short and long words, as well as rare and common words, were repeatedly presented in a memory task while neuromagnetic brain responses were recorded using magnetoencephalography (MEG). Word length and frequency were reflected by brain responses at overlapping but distinct intervals. The influence of the physical factor, length, started at ~ 100 ms after onset of written words, immediately followed by a physiological manifestation of the non-physical cognitive stimulus property, word frequency, which was first apparent 120 – 160 ms. Further, there was a differential frequency effect: neurophysiological correlates of short words showed the frequency influence much earlier than did longer words. These data indicate (I) that non-physical cognitive aspects of word stimuli can be reflected in early neuromagnetic responses, and (II) that the latency of these physiological correlates of cognitive stimulus properties may depend on the physical stimulus make-up.

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## VI.2 Introduction

How do afferent and central processes interact in cognitive processing? An incoming stimulus causes a wave of activity which progresses toward the brain and finally reaches the cortex. Distinct from such afferent activation are central processes related to neuronal feedback- and feedforward-loops within the higher brain structures, in particular the cortex. For investigating the time course of afferent and central activation processes and their relation and interaction, it is necessary to vary different types of stimulus properties. Variation of physical stimulus properties, such as the size or luminance of visual stimuli, primarily alters the amount of afferent activation. Psychological or cognitive stimulus properties, such as their familiarity or meaning, are organized in the central wiring, likely in cortico-cortical connections. The physical / afferent and cognitive / central effects may be dissociable.

We chose to alter the length and the familiarity of words and investigated neuromagnetic responses of the human brain to these stimuli. Changes in the length of words can be expected to alter an early brain response related to afferent processing, while changes in the familiarity of words would reveal their influence at a later point in time. We asked (i) when the physiological manifestation of word frequency would first become apparent, and (ii) whether physical properties of words change the point in time when neurophysiological correlates of word frequency appear.

Two experimental strategies have been employed to scrutinize the physiological side of word length, which is usually counted in letters, and word familiarity, which is objectified in the normative lexical frequency calculated from large text corpora. Recent studies examined brain responses to words exhibiting the normal distributions of lengths and frequencies. Osterhout *et al.* [1] reported latency as well as amplitude differences between high- and low-frequency words which varied between 350 ms to 450 ms post onset of visually presented words. In a later study, King and

Kutas [2] found that high frequency words elicited a negative component about 285ms after onset of visually presented stimuli. Words with lower frequency evoked a brain response with a somewhat greater latency, up to 335ms. In this study, no amplitude effects were recorded, neither related to word frequency nor to word length. A methodological problem in both of these studies was that word frequency and length were mutually confounded: It is well-known that there is a strong inverse correlation of word length and frequency (e.g. [3]). Thus, if stimuli are arbitrarily selected, any correlation of a brain measure with one of these variables implies its inverse correlation with the other. Therefore, it cannot finally be decided whether the relevant variable is physical (length) or cognitive (familiarity) (see [4] for discussion).

One way to solve this problem would be to carefully match stimuli for one of the variables and investigate the influence of the other on this preselected material. This strategy was amply used in neurocognitive research (for example, [5, 6, 7]). Rugg [6] compared event-related potentials elicited by words carefully matched for length that only varied in their frequency and found that low frequency words elicited higher ERP amplitudes than high frequency words in the time range from 300 ms to 500 ms. No latency difference was observed in this study. In a later time frame (500 - 800 ms) a different frequency-amplitude relation was observed, high frequency words led to greater P300 amplitudes. Polich and Donchin [5] also found that the P300 component was related to word frequency. Presentation of high frequency words produced an earlier peak of the P300 (565ms vs. 585ms) as well as a greater amplitude compared to low frequency words. It thus appears that a change in word frequency can co-occur with a variety of physiological phenomena, a change in evoked potential-latencies in different time windows (~300 ms: King and Kutas [2]; ~400 ms: Osterhout et al. [1]; ~570 ms: Polich and Donchin [5]) and an amplitude difference (400 and >500 ms: Rugg [6]; >500 ms: Polich and Don-

chin [5]; >200 ms: Osterhout et al. [1]). Table 1 summarizes effects of word length and frequency on physiological brain responses as reported in the literature.

| | Time after stimulus onset | | | |
| --- | --- | --- | --- | --- |
| | ~200 | ~300 | ~400 | >500 |
| Polich & Donchin 1988 [5] | | | | A + L |
| Rugg 1990 [6] | | | A | A |
| Osterhout et al. 1997 [1] | A | A | A + L | A |
| King & Kutas 1998 [2] | | L | | |

**Table 1: Summary of 4 studies of word frequency effects. In two of these, by Rugg [10] and Polich and Donchin [6], the groups of words varying in their frequency of occurrence were matched for length. In the two other studies, by Osterhout et al. [5] and King and Kutas [3], words varying in both frequency and length (with longer words exhibiting lower frequencies) were compared. The table shows at which time after onset of visual word stimuli a frequency (or frequency-length) difference was found. Differences were either found in amplitude (A) or in latency (L) of evoked potentials, or in both. Note the variability of the results.**

In summary, only the late amplitude differences could be replicated. Latency differences were not consistent over studies. Differences may be due to variations between tasks, stimulus sets and subjects. Overall, the earlier results suggest a late onset of the influence of the frequency factor on word-evoked brain activity. Accordingly, the non-physical and thus cognitive variable word frequency is reflected in brain activity substantially after sensory activation had been elicited by the stimuli.

The present experiment was designed to re-investigate the issue with a different method (MEG) and to resolve the partial incompatibilities between the earlier results. We used stimuli controlled for word frequency and length. To unconfound the influence of each of these variables, these parameters were varied orthogonally: long and short words, as well as common and rare words were selected so that four categories were obtained (one-syllable low-frequency words, one-syllable high-frequency

words, two-syllable low-frequency words and finally two-syllable high-frequency words).

Our predictions for this experiment were based on the following assumptions [8]:

- Afferent activation precedes cortico-cortical feedback.

- Words are organized as ensembles of cortical neurons that instantaneously ignite after adequate stimulation.

- Repeated activation of neuron ensembles produces more strongly connected assemblies. The amount of cortico-cortical activation following word presentation should therefore depend on word frequency.

Based on these assumptions, we expected the earliest brain response to reflect word length only. The physiological differentiation of word frequency – which we take as an index of differential connectedness of cortical neuron ensembles – was expected to immediately follow afferent activation. Finally, we predicted that the physical word property, length, has a modulating effect on the point in time when the word frequency factor manifests itself in the neuromagnetic response.

The earlier studies compared evoked potentials elicited by large groups of different words in different subjects. This implies many possible sources of variance related to inter-word and inter-subject differences. This variance may mask fine-grained differences related to the variables under investigation. We aimed at minimizing this variance, first by choosing only a small set of well-matched words, and second by investigating brain responses in a single subject. The experiment was performed with one right-handed monolingual individual who participated in 11 recording sessions. A single subject-study was preferred to a group study for the following reasons: (1) The latency of evoked brain responses related to cognitive

processing has been reported to vary as a function of stimulus familiarity. Consequently, variation can also be expected between experiment participants (cf table 1). (2) Structural and functional brain organisation differ considerably between individuals [9], thus causing devastating between-subject variance in both topography and timing of evoked fields. If one expects the brain correlates of words to differ at an early processing step, the between-subject differences in latencies and topographies of, for example, the P70m or N100m components imply that the correlates of word processing become visible at different latencies and at different loci in different individuals. They will therefore be masked in the group average. In order to demonstrate such differences in brain responses, it is therefore necessary to thoroughly investigate neurocognitive processes with physiological means in individual subjects. Although, at present, most imaging studies concentrate on group averages, rather than thoroughly investigating the reproducibility of results in individual subjects, the single case-strategy appears to us to be as important in cognitive neuroimaging as it undoubtedly is in the study of single patients in cognitive neuropsychology [10].

To examine a possible relation between frequency and length, averaged event-related neuromagnetic responses to the four word groups mentioned above were analysed. The magnetic brain responses were recorded using a 148 channel Biomagnetometer.

## VI.3 Material and Methods

### Subjects

The participant was a 21 year old right handed monolingual female student with 15 years of formal education. The subject had normal eyesight and no history of neurological disease or drug abuse. She was paid for her participation.

Stimuli

The stimulus set consisted of 16 words (recurrent words) halved into one- and two-syllable words, with 4-5 and 6-7 letters, respectively. Half of the words in each subgroup had high (range: 123-329/mio.; average: 210.4) and low (range: 10-15/mio.; average: 12.9) frequency. This resulted in 4 syllable/frequency combinations with 4 words in each of them. Stimulus groups comprised equal proportions of content and function words in order to minimise word class effects [11]. Additional words were only presented once or twice (new words). These were generated by exchanging one letter of one of the 16 recurrent words forming a correct word.

Procedure

In each block, the 16 recurrent words and two new words were presented in random order. Before the experiment, the subject was familiarised with the recurrent stimuli and she was told to memorise these words. She was instructed to respond to those stimuli that were not in the memorised set (new words) by pressing a button with her left index finger. No response was required after the recurrent words. The task was applied to assure sustained attention to the stimuli, and to force the participant to keep the set of recurrent words in active memory. One run consisted of 20 such blocks and 3 runs made one session. Thus, each of the repeated words was presented 60 times in each session resulting in 240 presentations per syllable/frequency pair. The subject was allowed to pause freely between blocks and between runs. 11 sessions took place within 4 weeks, with a minimum pause of 2 days between subsequent sessions.

All stimuli were presented for 100 ms in white upper case letters (maximum word size 7x3 cm) on a black background 1.4m away from the participant's eyes. A fixation cross appeared in the middle of the screen whenever no word was visible. The asynchrony of stimulus onset was var-

ied randomly between 1.4 and 2.0 sec. An LCD-projector outside the MEG chamber was used to project the stimuli onto the screen inside.

MEG Recordings

Neuromagnetic signals were recorded continuously with a 148 channel whole head magnetometer (BTI WH2500, Biomedical Technology Inc., San Diego) using a 0.1-100 Hz band-pass filter and sampled at a rate of 508 Hz. Along with the magnetic signals the vertical and the horizontal EOG together with the ECG were recorded. The data was stored on optical disc for off-line analysis.

Data Analysis

MEG data were submitted to a global noise filter subtracting the external, non-biological noise obtained by the MEG reference channels. The data was then split into epochs while discarding all epochs where the button had been pushed by the subject. Epochs with an EOG level > 100 μV or MEG level > 5 pT between minimum and maximum on one or more MEG channels were automatically excluded from further analysis. In the 11 sessions a maximum of 2640 MEG-traces were obtained for each of the 4 syllable/frequency combinations in total and 240 MEG-traces were recorded per session. For each recording session and for each of the four syllable/frequency pairs, stimulus-triggered evoked magnetic fields were calculated relative to a 100 ms baseline. Grand averages were obtained for all syllable-frequency combinations.

Statistical Analysis

For statistical analyses, average values were calculated in pre-selected time windows. These windows were defined around the maxima of the difference in global field power between pairs of stimulus groups. The entire set of 148 recordings was divided into subsets of 5 channels. This

resulted in less noisy data at the cost of a reduction of spatial resolution. Mean RMS values obtained for pre-defined time windows were entered into statistical analysis. Only foci of interest with large signals in a particular time window therefore resulting in high signal-to-noise-ratios, were chosen  (arbitrary criterion: average signals > 100 fT).

| | |
|---|---|
| **i1: 90-120 ms** | LPO, RPO, RCP |
| **i2: 120-170 ms** | LPO, RCO |
| **i3: 180-220 ms** | LS, LC, LPO, RS, RC, RPO |
| **i4: 240-290 ms** | C |
| **i5: 320-370 ms** | LC, RC, RPO |
| **i6: 370-470 ms** | LS, LC, LPO, RS, RC, RPO |
| **i7: 500-800 ms** | LA |
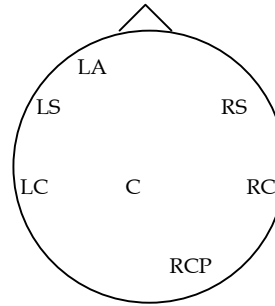
**Table 2: MEG recording sites from which high amplitude signals were obtained and their approximate location on the head surface. Note that the high amplitude loci changed over time. High amplitude channels were chosen for analysis because of their high signal-to-noise ratio (L – left, R – right, A – anterior, C – central, S – Sylvian, P – parietal, O - occipital).**

Analyses of Variance (design: locus (2 or more levels) x syllable (2 levels) x frequency (2 levels)) were calculated to assess significance of between-category differences. The Greenhouse-Geisser correction was applied when appropriate. F-tests were used to further investigate significant main effects or interactions.

## VI.4 Results

In the first time window, already 90 – 120 ms after stimulus onset, the analysis revealed a significant main effect for the one/two-syllable contrast ($F_{(1,10)} = 39.4$, $p = 0.0001$) with higher mean RMS values for two-syllable words (127 fT) than for one-syllable words (79 fT). Notably, the high/low-frequency contrast was not significant at this point. The high-

amplitude channels that delivered these data were at left and right parietal as well as right centro-occipital sites.

Some 30 milliseconds later (second time window, 120-170 ms), the word induced brain activity became more prominent and now the effect of word frequency kicked in: The main effect of the factor syllable remained stable in this time frame ($F (1,10) = 388.7$, $p = 0.0001$), but, in addition, there was a significant main effect of frequency ($F( 1,10) = 29.6$, $p = 0.0003$) and a significant interaction of both factors ($F (1,10) = 20.4$, $p = 0.001$, see figure 1a):
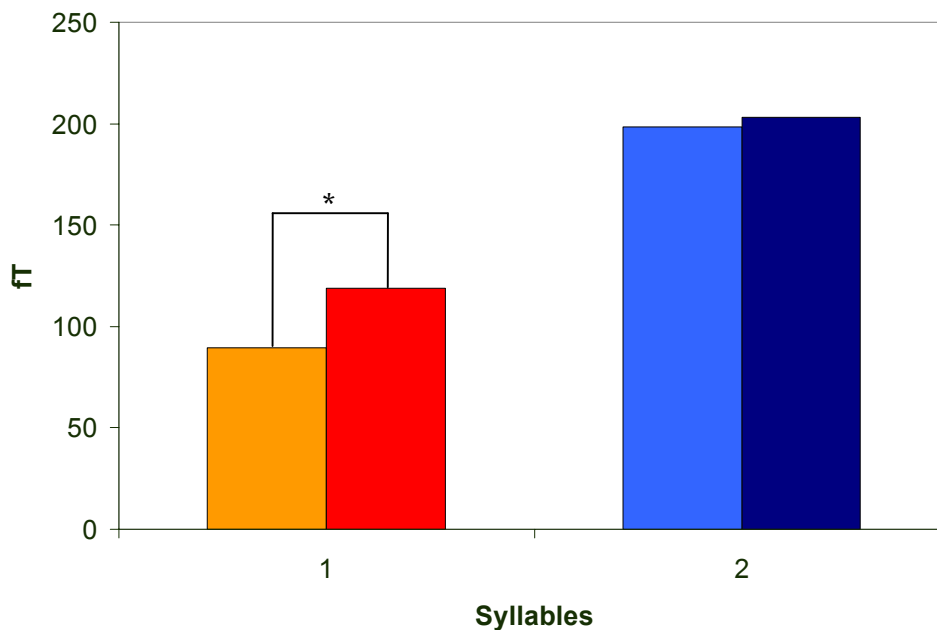


**Figure 1a:**
**An early time window, between 120 ms and 170 ms, revealed a significant difference of neuromagnetic responses as a function of word length and word frequency. A significant interaction indicated a frequency contrast for one syllable words, but not for two syllable words (high frequency items in light colours, low frequency items in dark colours, monosyllabic items in red, bisyllabic items in blue).**

Again the presentation of two syllable words led to higher mean RMS values than one syllable words (one-high: 90 fT, one-low: 119 fT, two-high: 198 fT, two-low: 202 fT). Low frequency words tended to produce higher amplitudes (161 fT) than high frequency words (144 fT). However, post-hoc tests on the syllable-frequency interaction revealed a significant difference between all syllable-frequency combinations ($F (1,10) > 46.1$, $p <$

0.00004) except for the high/low contrast for two syllable words. In other words: In this time window, the brain responses of one syllable words reflected word frequency, but those of two syllable words did not (see figure 1a).

The main effect of the syllable factor persisted in the time window between 180 ms and 220 ms (F (1,10) = 16.7, p = 0.002) and between 240 ms and 290 ms (one: 95 fT, two: 139 fT, F(1,10) = 33.4, p < 0.0002). In addition there was a main effect of frequency (F (1,10) = 4.7, p = 0.05). Contrary to the finding in the window around 150 ms, high frequency items now elicited significantly stronger neuromagnetic responses (high: 127 fT, low: 107 fT) at 240-290 ms. No significant interactions were found here.

The fifth time frame (320 ms to 370 ms) did not reveal significant differences between stimulus categories.

In the sixth time frame (370-470 ms) there was a significant interaction of the factors syllable and frequency (F (1,10) = 7.7, p < 0.02). All post hoc tests were significant (all F values > 7.5, all p values < 0.02) except for two: The frequency contrast for one syllable words and the syllable contrast for high frequency words. Thus, in contrast to the interaction obtained for the second time frame, there was now a significant word frequency contrast in the brain responses to two syllable words (F (1,10) = 7.5, p < 0.02), but no such effect for one syllable words (see figure 1b).
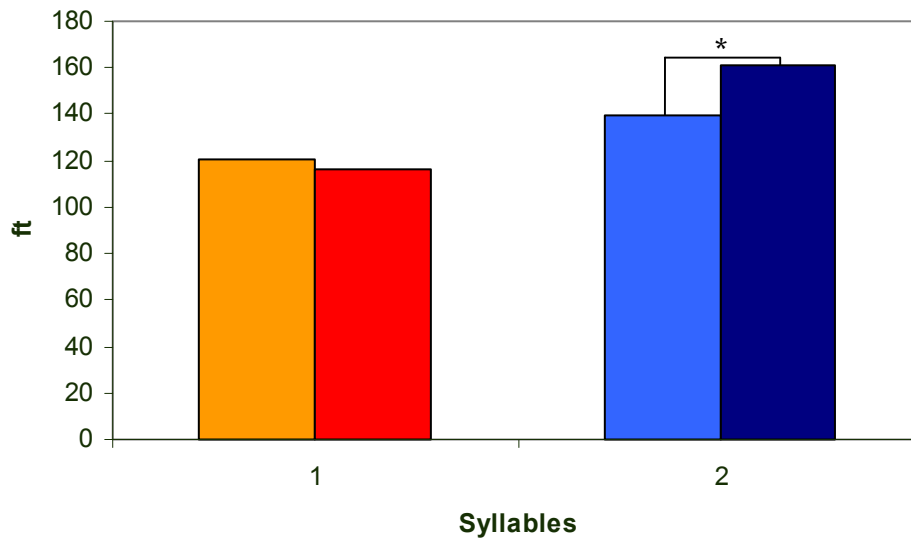
**Figure 1b:**
**The time window between 370 ms and 470 ms revealed another significant interaction of the factors word length and frequency. In this case, the frequency contrast was significant for bisyllablic words only.**

The last time frame of our analysis, 500-800 ms, showed a significant main effect for the frequency factor (F (1,10) = 15.6, p = 0.003) and also again the significant interaction of frequency and length (F (1,10) = 17.9, p = 0.002, see figure 1c). In this case, post hoc tests showed a significant frequency contrast for one (but not two) syllable words (F(1,10) = 25.4, p = 0.0005, high: 83 fT, low: 130 fT) as well as a significant syllable contrast for low (but not high) frequency words (F (1,10) = 35.5, p = 0.0001) (see figure 1c).
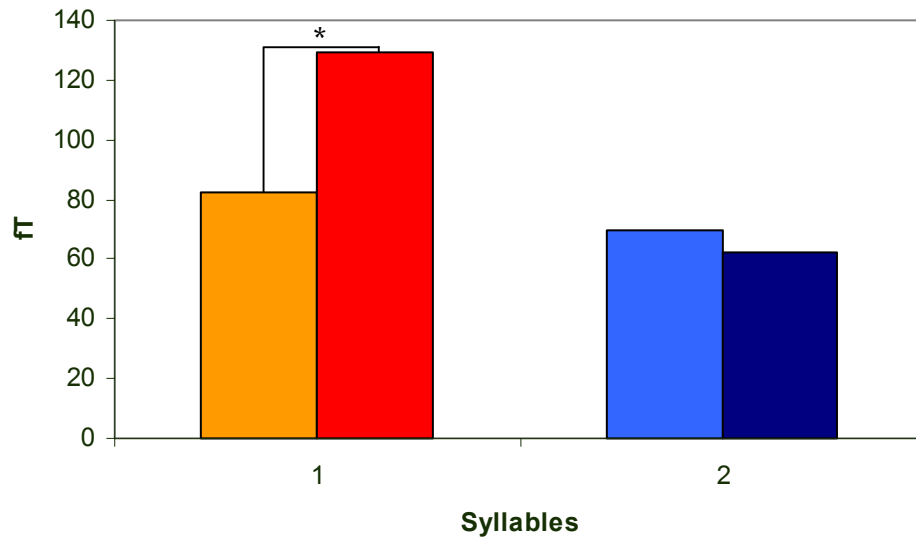
**Figure 1c:**
**Another significant interaction of the factors word length and frequency was present in the time slice between 500 ms and 800 ms. As in the early time window (cf. Figure 1a), the frequency contrast was again significant for monosyllablic words only.**

All results are summarized in table 2.

| | Main effect Word length | | Main effect Frequency | | Interaction Length x Frequency | |
|---|---|---|---|---|---|---|
| | F | p | F | p | F | p |
| i1: 90-120 ms | 39.4 | 0.0001 | | n.s. | | n.s. |
| i2: 120-170 ms | 388.7 | 0.0001 | 29.6 | 0.0003 | 20.4 | 0.001 |
| i3: 180-220 ms | 16.7 | 0.002 | | n.s. | | n.s. |
| i4: 240-290 ms | 33.4 | 0.0002 | 4.7 | 0.05 | | n.s. |
| i5: 320-370 ms | | n.s. | | n.s. | | n.s. |
| i6: 370-470 ms | 15.5 | 0.003 | | n.s. | 7.6 | 0.019 |
| i7: 500-800 ms | 17.5 | 0.002 | 15.6 | 0.003 | 17.9 | 0.002 |

**Table 3:**
**Summary of statistical results obtained in the present study. Neuromagnetic brain responses showed clear effects of word length almost over the entire interval analysed, up to 800 ms. The word frequency effect only appeared in specific time windows. Frequency effects for short (1-syllable) and long (2-syllable) words appeared in distinct time intervals (cf. Figures).**

The significant interactions of word length and frequency in 2 distinct time intervals are illustrated in figure 2. The earliest divergence of neuromagnetic traces is between one and two syllabic items at 90-120 ms. In the subsequent window between 120 and 170 ms, the traces for high and low frequency items of the 1 syllable items diverge: out-going fields are stronger for low frequency items than for high frequency items. Substantially later, in the window between 370 and 470 ms, the 2 syllable items show a similar effect in in-going fields: again, stronger neuromagnetic responses are elicited by low frequency items. The frequency effects are, thus, separated in time for one and two syllable items. This figure also suggests an additional late frequency effect for the 1 syllable items, which was confirmed by our above analysis of the late (500-800 ms) time window.
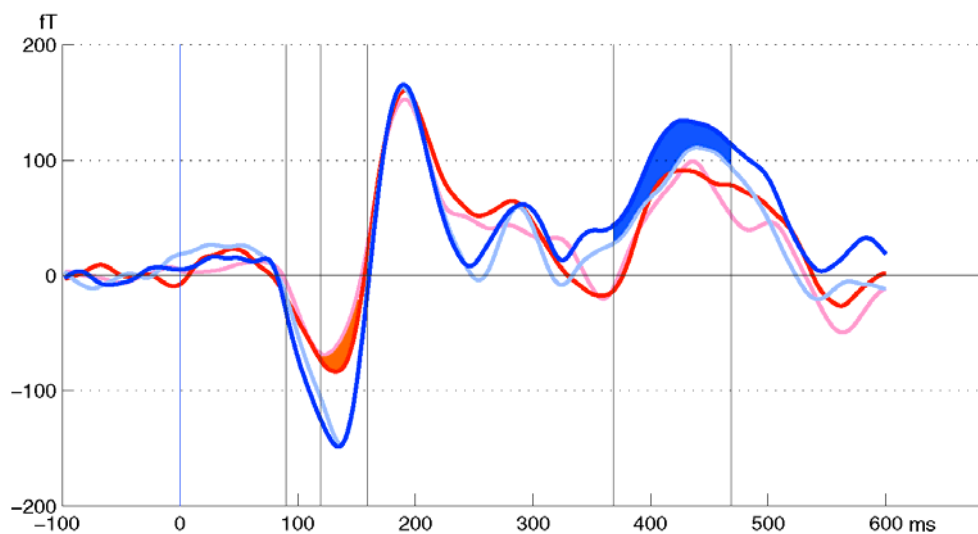


**Figure 2:**
**Time course of neuromagnetic signals of one channel (#99 over left parieto-occipital areas) illustrating influences of word length (1 syllabic items in red, 2 syllabic items in blue) and frequency (light colors for high frequency items, dark colours for low frequency items). Already around 100 ms after stimulus onset, long and short words were distinguishable neuromagnetically. The frequency effect for short words was present subsequently (120-170 ms, orange area), and the frequency effect for longer words only appeared after a substantial delay (~400 ms, light blue area). Note that statistical analysis was performed on the RMS of five channels per focus and revealed reliable effects.**

## VI.5 Discussion

This experiment revealed the following differences in MEG responses to words with varying length and frequency:

- variation in word length modulated neuromagnetic brain responses at 90 – 120 ms after presentation onset, and this difference persisted almost throughout the recording interval.
- slightly later, at 120 – 160 ms, brain waves changed with word frequency; this was found for short mono-syllabic words only.
- another ~100 ms later, at 240-270 ms, there was a frequency effect irrespective of the length of words.
- ~ 400 ms (370-470 ms) after stimulation onset, neuromagnetic fields evoked by bi-syllabic words were modified by word frequency. Such modification was not observed for the mono-syllabic words.
- there was a late effect (500-800 ms) of word frequency for one syllable items only.

As expected and consistent with earlier findings, we saw an early modulation of event-related brain responses to words of different lengths (for review, see [8]). On the background of earlier reports, however, the finding of an onset of the word frequency influence already at 120 ms post stimulus onset was highly unexpected. The earliest word frequency differences have so far been reported by Osterhout *et al.* [1] where it was seen between 150 ms and 250 ms after stimulus onset (cf. Table 1). The early occurrence of differential brain responses found in the present study may be due to a number of methodological factors. First, the major cortical sources underlying the early word frequency effect may be easier to record with MEG than with EEG. Second the careful matching of word length and frequency between stimulus subgroups may have played a role. Third, compared to earlier studies, our stimuli exhibit less variance with regard to both of

these parameters. As mentioned above, a greater variation in word length and frequency may result in a greater variation of amplitudes and/or latencies of physiological brain responses. It may therefore be that precise matching of these parameters between stimulus categories and, in addition, small variances of these parameters, are necessary conditions for obtaining these early effects.

As a further possibility, the early occurrence of the effects in the present study could be a result of speeded neurophysiological response due to learning. Note that the single subject was trained over several sessions with the same words being repeated more than 50 times in each session. This may have led to learning in neuronal pathways and therefore to faster processing. Finally, studying a single subject may have reduced the variance in early brain responses normally found in group studies where fine grained differences may have been masked through, for example, inter-individual variations in neuroanatomy and localization of functions (see introduction). Naturally, this inter-subject variation would affect the early focal physiological brain responses much more than the late more widespread potentials or fields. We conclude that a MEG single case study using well-matched stimulus groups with small variance of the relevant parameters can reveal early physiological effects of the length and frequency of words.

The length of a word modulated the brain response before its frequency was taking any effect. Apparently the time by which word frequency influenced the neuromagnetic response was determined by word length: Short words with low frequency evoked larger brain responses than short high-frequency words, although, again, at an earlier point in time than in other work (e.g. Rugg [6]: >300 ms).

Word length had a strong and long-lasting impact on the amplitudes of the word evoked fields as it was present almost throughout the intervals analyzed. Long words elicited higher amplitudes and short words lower

amplitudes. This difference likely relates to the physical stimulus proper-
ties and to the amount of cortical activation caused  by afferent input
(longer words - more cortical input).

The window from 240 ms to 290 ms is comparable to previous studies re-
porting findings in the present context: Neville *et al*. 1992 [12] found the
first distinction of function and content words (which were distinguished
by word frequencies) in this latency range. The earliest word frequency
influences on ERPs (latency effects) found by King and Kutas in 1998 [2]
began at ~280 ms. In our study, all words showed the frequency influence
on physiological brain responses in the corresponding time window (240-
280 ms). Here, the main effect of word frequency coexisted with a main
effect of word length. The present single-case study thoroughly investigat-
ing a small number of repeated words could thus replicate some of the
length and frequency results from earlier group studies using large num-
bers of single words presented only once. This suggests that the physio-
logical side of similar cognitive processes were documented.

In contrast to earlier studies, we could not replicate the finding that the
latency of brain responses directly depended on word frequency [1, 2, 5].
The specific frequency effect for short words appeared some 200 ms before
that of long words (120-170 ms vs. 370-470 ms). Therefore, *word length
caused the frequency effect to shift*, but not the latency of a specific compo-
nent.

It may be that in earlier studies in which length and frequency acted as
mutual confounds, the present result masqueraded as a latency shift. With
this in mind, it is worth taking another look at figure 2. Around 250 ms,
very close to the point in time where King and Kutas [2] found their early
maxima for high frequency short words, the light red trace (representing
high frequency short words) is above the dark blue line (representing low
frequency longer words). At around 350 ms, however, the opposite is the
case, that is, the dark blue line is above the red lines. The earlier (250 ms)

wave seems to be more pronounced for the short and highly frequent words whilst the late (400 ms) wave is clearly most pronounced for the long and rare words. This is essentially the same result as the one reported by King and Kutas, but in the present data set, where frequency and length effects can easily be distinguished, it becomes clear that it is the length factor that has the stronger effect in modulating amplitudes.

Again, consistent with earlier work, our study revealed that the frequency of a word is related to the amplitude of an evoked brain response [1, 6]: Rare words led to higher amplitudes than common ones in three time windows 120 to 170 ms, 240 to 290 ms and 300 to 500 ms. However, in the late time frame between 500 and 800 ms the presentation of high frequency words in our study led to *smaller* amplitudes, a finding somewhat in contrast with Polich & Donchin [5] and Rugg [6] who found *larger* P300s for high frequency words.

As mentioned, a plausible explanation of the early-onset long-lasting word length effect can be based on the amount of afferent input to the cortex. A larger stimulus causes a stronger neuromagnetic brain response because it activates a larger number of cells in the retina and thus at higher processing stages.

As mentioned in the discussion (assumptions (a) to (c)), we assume that words are cortically represented by Hebbian cell assemblies [8, 13]. The frequency effect itself can be explained by the strength of connections within a cell assembly. Hebb's rule implies that the higher the frequency with which a set of neurons is activated together, the tighter the assembly-internal connections become. This implies more strongly coupled cell assemblies for high frequency words compared to low frequency words. The stronger the coupling between neurons of a cell assembly the more easily the word's cell assembly will ignite. For explaining the physiological difference between rare and common words, the following consideration is also relevant: It is evident that there is background activity in the brain

which leads to baseline activity in all assemblies. The baseline activity level will be higher in the more strongly connected assemblies, and thus the remaining amount of activity necessary for fully activating the assembly will be smaller. In summary,

$$\Delta A_{\text{high freq. words}} \quad < \quad \Delta A_{\text{low freq. words}},$$

where $\Delta A$ is the activity increase produced by an assembly when it ignites. This idea explains the smaller evoked fields to the more common items found in this study. These items have the tighter cortical representations and therefore their corresponding networks exhibit the higher baseline activity levels, that is, smaller differences between baseline and ignition.

The early manifestation of the frequency effect in MEG responses to words is consistent with and provides support for the idea that cell assemblies representing words ignite immediately after their adequate stimulation by afferent activation [8, 14]. However, the explanation of different latencies of frequency effects of short and long words – which is reported in this study for the first time – requires a modification of the cell assembly approach to language proposed so far. Consistent with earlier proposals, it can be assumed that the cell assemblies of short monosyllabic words ignite instantaneously and as a single neuronal unit. However, we propose that those of bisyllabic longer items include a subgroup of neurons that are recruited later in the activation process. This later subgroup may be related to the activation of the *phonological program* of the second syllable implemented as a synfire chain of cortical neurons [15]. In contrast, the phonological program (synfire chains) organizing the first syllable is activated together with the initial ignition of the assembly representing the word. This would account for the fact that frequency effects were seen earlier for monosyllabic items than for bisyllabic items. While one may doubt that the physiological effect of word frequency is related to phonological word properties, it appears clear that it must be related to cognitive,

namely lexical, properties of the stimulus words, rather than to their physical makeup. As this study clearly demonstrates, brain correlates of these cognitive factors based on cortico-cortical loops can immediately follow afferent activation processes.

## VI.6 Conclusion

In a single case study of neuromagnetic correlates of visual word processing, we found differential activation for long and short words starting 90 ms after stimulus onset. Only slightly later, starting already at 120 ms, word frequency showed an additional influence on the amplitude of neuromagnetic signals. Frequency effects appeared at different points in time for longer and shorter words. Our data are consistent with the view that processing of language-related information is, in part, cascaded: processing of visual stimulus features precedes the word frequency effect related to the activation of lexical word representations in the brain. Early cortico-cortical activation processes related to lexical access appear to immediately follow afferent activation. Physical properties of words can modulate the point in time when processes differentiating between rare and common items become manifest in the neuromagnetic response of the human brain.

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# VII APPENDIX TWO

## Interacting Perceptual And Cognitive Processes In Early Lexical Access: A Group Study Using MEG[1]

## VII.1 Abstract

At which latencies are physical word properties (e.g., length) and cognitive properties (e.g., frequency) reflected in the neurophysiological brain response? Long and short, as well as highly frequent and rare words were presented repeatedly during a memory task. Neuromagnetic brain responses of 15 subjects were recorded using 148 channel MEG. Shortly after presentation onset (60ms), long words led to significantly stronger activation than short words, as revealed by the global field power (GFP) of neuromagnetic responses. Slightly later, 120-170ms after stimulus onset, there was a frequency effect for short words only, and at 225-250ms, only the frequency of long words was reflected in the brain response. The early difference between long and short words may indicate the onset of visual feature analysis, whereas the later differences reflecting word frequency may indicate access to cortical memory traces for words of different kinds. The present data indicate that the exact timing of the latter cognitive process, lexical access, depends on word length. A neurobiological model of word processing is used to tentatively explain the present pattern of results.

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## VII.2 Introduction

Psycholinguistic research on word properties has shown that frequency and length of words exert a strong influence on how the words are being processed. Word length is counted in the number of letters of a written word stimulus. Word frequency is objectively defined as the normative lexical frequency calculated from large text corpora (how frequently does the word form occur in a text of, say, one million words?). Rare, low frequency words are generally recognized more accurately than high frequency words (e.g. Gorman, 1961; Kinsbourne & George, 1974), and also words are better remembered when they have been shown before (repetition priming, e.g. Paller & Gross, 1998). A general finding is that low-frequency words benefit from repetition to a greater degree than high frequency words (e.g. Forster & Davis, 1984; Norris, 1984). As most studies controlled for word length, isolated behavioral findings on word length are more sparse, although they have been documented. Compton *et al.* (1991), for example, varied their stimuli in two steps (4 letter vs. 6 letter words) and found reaction times to long words to be longer than to short words. Because word length and frequency affect the behavioral response, it appears likely that these stimulus properties affect the way words are processed in the brain.

Most neurophysiological studies of word processing investigate the waveforms of the word induced brain activity as provided by high-resolution EEG or MEG recordings. Such studies can reveal THAT the brain treats word types differently, and they can also show WHEN differences occur. The high temporal precision of the large-scale neurophysiological techniques, EEG and MEG, makes this possible. In order to uncover WHERE in the brain particular differences appear, it is also possible to apply modern source localization techniques to multi-channel EEG/MEG data. Recently developed advanced mathematical procedures, such as the Minimum Current Estimate (Ilmoniemi, 1993; Hämäläinen & Ilmoniemi, 1994;

Hämäläinen *et al.*, 1993), allow for educated guesses on where the relevant sources are localized in the brain.

Neurophysiological generators of early visual word processing have been localized in the occipital lobe. Later on, 100-200 ms after a visual word form has been flashed on the screen and later, differences seem to be more broadly distributed including anterior parts of the brain (Rugg, 1990; Compton, *et al.*; 1991). Sereno *et al.* (1998) contrasted real-words with random consonant strings, called non-words, and phonologically and orthographically regular pseudo-words and varied words of the same length with regard to their frequency. There was a difference between real words and non-words from 100-132ms, whereas word frequency had an impact on the brain response slightly later, from 132-164ms. Also, Rugg (1990) varied the frequency of words matched for length. Low frequency words elicited higher ERP amplitudes than high frequency words between 300 and 500ms after stimulus onset. Later-on, the frequency-amplitude relation reversed: high frequency words led to greater amplitudes of the P300 ERP-component (500-800ms). No latency differences between the brain responses to rare and common words were observed in this study or any of the other studies mentioned above. Further, the brain response to repeated items did depend on their word frequency. The frequency effects in the brain response were more strongly diminished for repeated low frequency words than for repeated high frequency words. Polich and Donchin (1988) also found a relation between the P300 component and word frequency in the EEG. Presentation of high frequency words led to a greater amplitude and to an earlier peak of the P300 (565ms vs. 585ms) compared to low frequency words. Preliminary data from an earlier MEG study performed with a single subject (Assadollahi & Pulvermüller, 2001) indicated that variation in word length can modulate neuromagnetic brain responses as early as 90–120ms ms after the stimulus onset. Table 1 summarizes effects of word length and frequency on physiological brain

responses as reported in these earlier publications. Although these results diverge, it is noteworthy that brain indicators of word frequency were present in all studies. An important question therefore is which factors determine the exact latency, and possibly location, where different brain processes are elicited by short and long, and rare and common, words.

| | Time after stimulus onset | | | | |
| --- | --- | --- | --- | --- | --- |
| | ~100 | ~200 | ~300 | ~400 | >500 |
| Polich & Donchin 1988, EEG | | | | | A + L |
| Rugg 1990, EEG | | | | A | A |
| Sereno et al. 1998, EEG | | A | | | |
| Assadollahi & Pulvermüller 2001, MEG | A | A | | A | A |

Table 1: **Summary of three studies on word frequency effects where word stimuli were matched for length. The table shows at what time after onset of visual word stimuli a frequency difference was observed. Differences were either found in amplitude (A) or in latency (L) of evoked brain response, or in both.**

The present group study used magnetoencephalography (MEG) to investigate neurophysiological reflections of perceptual and central cognitive (linguistic) processes and their interaction.

The physical stimulus property word length and the cognitive factor word frequency were investigated. The study aimed at answering the questions: (i) when do the neurophysiological correlates of word length and frequency first become apparent, and (ii) do these factors interact, that is, do physical properties of words modulate the point in time when the physiological manifestation of word frequency appears?

In natural texts word length and frequency are inversely correlated: short words tend to exhibit high frequencies, whereas long words have low frequencies (Zipf, 1935). Therefore, high and low frequency words not equated for length would normally differ in their length, the low frequency items being longer in the average. Earlier studies compared word

samples varying in both frequency and length (Osterhout *et al.*, 1997a; King & Kutas, 1998), but in these studies, it is difficult to assess which of the mutually confounding factors was relevant for yielding differential brain responses. To avoid this problem, the present study for the varied the factors word frequency (high/low) and word length (one/two syllable) orthogonally. This led to four stimulus categories: short rare, short common, long rare, and long common words.

We expected that a variation in word length as a physical stimulus property would alter an early brain response and that the influence of word frequency as a cognitive factor would follow immediately. We also speculated that the word length factor may affect the latency at which word frequency effects appear.

## VII.3 Materials and Methods

### Subjects

15 subjects (mean 24.6 years) right handed monolingual students (9 female) with at least 13 years of formal education. The subjects had normal or corrected to normal eyesight and no history of neurological disease or drug abuse. They were paid for their participation.

### Stimuli

The stimulus set consisted of 16 words (*recurrent words*) halved into one- (range: 3-4 letters; average: 3.9) and two-syllable (range: 5-7 letters; average: 6.1) words. Half of the words in each subgroup had high (range: 123-329/mio.; average: 210.4) and low (range: 10-15/mio.; average: 12.9) frequency. This resulted in 4 syllable/frequency combinations with 4 words in each of them. Only a small number of well-matched words was chosen to keep the variance of physical and cognitive properties of the stimuli small. Apart from the frequently repeated recurrent words, additional words were only presented once or twice during the experiment (*rare*

*words*). These were generated by exchanging one letter of one of the 16 recurrent words forming a correct word.


Procedure

Before the experiment, the subjects were familiarised with the recurrent stimuli and they were told to memorise these words. They were instructed to respond only to stimuli that were not part of the memorised set (that is, to the rare words) by pressing a button with their left index finger. No response to the recurrent words was required. Behavioural responses to recurrent words were not collected to avoid contamination of the brain response by physiological signs of motor preparation. A motor response would necessarily lead to a readiness-potential and -field visible in the MEG (see Rockstroh et al., 1989).

In each block, the 16 recurrent words and two rare words were presented in random order. One run consisted of 20 such blocks and 3 runs made one session. Thus, each of the repeated words was presented 60 times for each subject resulting in 240 presentations per syllable/frequency group. The subjects were allowed to pause freely between blocks and between runs.

All stimuli were presented for 100 ms in white upper case letters (maximum word size 7x3 cm) on a black background 1.4m away from the participant's eyes. A fixation cross appeared in the middle of the screen whenever no word was visible. The asynchrony of stimulus onsets was varied randomly between 1.4 and 2.0 sec. An LCD-projector outside the MEG chamber was used to project the stimuli onto the screen inside.


MEG Recordings

Neuromagnetic signals were recorded continuously with a 148 channel whole head magnetometer (Magnes 2500 WH, 4D NeuroImaging Inc., San Diego) using a 0.1-100 Hz band-pass filter and sampled at a rate of 508 Hz.

Along with the magnetic signals the vertical and the horizontal EOG and the ECG were recorded.

Data Analysis

MEG data were submitted to a global noise filter subtracting the external, non-biological noise obtained by the 11 MEG reference channels. The data was then split into epochs discarding all epochs where a button press occurred. Epochs with an EOG level > 100 μV or MEG level > 5 pT between minimum and maximum on one or more MEG channels were automatically excluded from further analysis. Thus, a maximum of 240 MEG-traces were obtained for each of the 4 syllable/frequency groups per subject. For each subject and for each of the four syllable/frequency groups, stimulus-triggered evoked magnetic fields were calculated relative to a 100 ms baseline. For all three runs per subject grand averages were obtained for all syllable-frequency groups.

Cortical sources of these averages were estimated using the minimum norm estimate (MNE, Ilmoniemi, 1993; Hämäläinen & Ilmoniemi, 1994; Hämäläinen *et al.*, 1993). The MNE is an inverse method to reconstruct the topography of the primary current underlying a magnetic field distribution (cf. Grave de Peralta Menendez *et al.*, 1997) with an acceptable accuracy (here: <5%). During pseudo-inversion matrices were regularized (Tikhonov-Phillips, $\lambda = 0.01$). Following Hauk and co-workers (1999) we approximated cortical activity in a three-dimensional source space consisting of four concentric spheres. The outer shell is individually fitted to the head-shape of the subjects (4-D Neuroimaging software). Sarvas (1987) proved that the head radius is not relevant for the computation of the magnetic field generated by primary currents in a spherically symmetric volume conductor. We assumed the head radius to be 10cm and will report the MNE for the shell at 80% radius which roughly corresponds to the cortex in the brain. On this shell 197 equidistant dipoles were assumed

of which the upper 121 locations on this shell were selected (to exclude the neck, jaw etc.) and the respective MNE amplitudes at these sites were submitted to global field power (GFP) computation.

There are several important features of the MNE:

- activation of multiple cortical dipoles can be objectively estimated without a priori information about the number or location of cortical sources.
- sources that do not contribute to the measured scalp topography, in particular radial sources in the case of MEG data, are omitted.
- head-position and -size of all subjects are standardised.

Difference maps of the minimum norm estimates were calculated to illustrate the distribution of the difference between to conditions.

For statistical analyses, average values of the GFP over time were calculated in pre-selected time windows. The time windows were placed so that they included definable parts of the GFP curve, such as local maxima and minima or rise and fall intervals. Two-way repeated measures Analyses of Variance (design: syllable (2 levels) x frequency (2 levels)) were calculated to assess significance of between-category differences. F-tests were used to further investigate significant main effects or interactions.

## VII.4 Results

Figure 1 depicts the global field power over all 15 subjects. It can be seen that, between 60 and 200 ms, the blue lines representing the long words (two syllable items) are above the red lines representing the shorter ones (one syllables). This indicates stronger brain responses to long words than to short words. Word frequency influenced brain responses where lines in

light and dark colour diverge. Statistically significant differences were found as summarised in table 2. The time frames are indicated in figure 1.
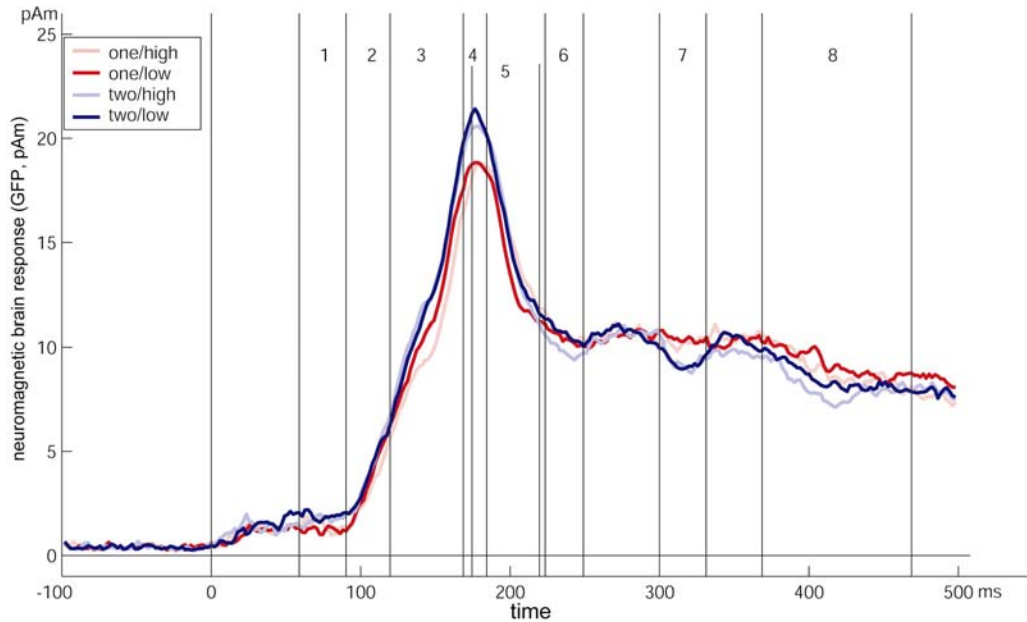


**Figure 1:**
**Time course of the global field power (grand mean over 15 subjects) of word-evoked neuromagnetic activity. The four curves show responses to words of different length (one syllabic items in red, two syllabic items in blue) and frequency (light colours for common items, dark colours for rare items). Already from 60 ms after stimulus onset on, differences between long and short words became manifest neuromagnetically (time window 1). A frequency effect specific for short words was present subsequently (time window 3: 120-170 ms), and a frequency effect only for longer words appeared after an additional delay (time window 5: 225-250 ms). Frequency modulation of brain responses irrespective of word length was present around 180 ms (time window 4).**

In the first two time frames, 60-90ms and 90-120ms, the GFP measure revealed significant main effects of the factor word length ($F(1,14) = 6.3$, $p = 0.024$, $F(1,14) = 5.3$, $p = 0.036$) with long words showing a stronger brain response (one: 2.2 pAm, two: 2.7 pAm, one: 4.5 pAm, two: 5.1 pAm). Difference maps of the MNE in figure 2a reveal that long words elicit a stronger brain response than short words centrally in the occipital lobe.
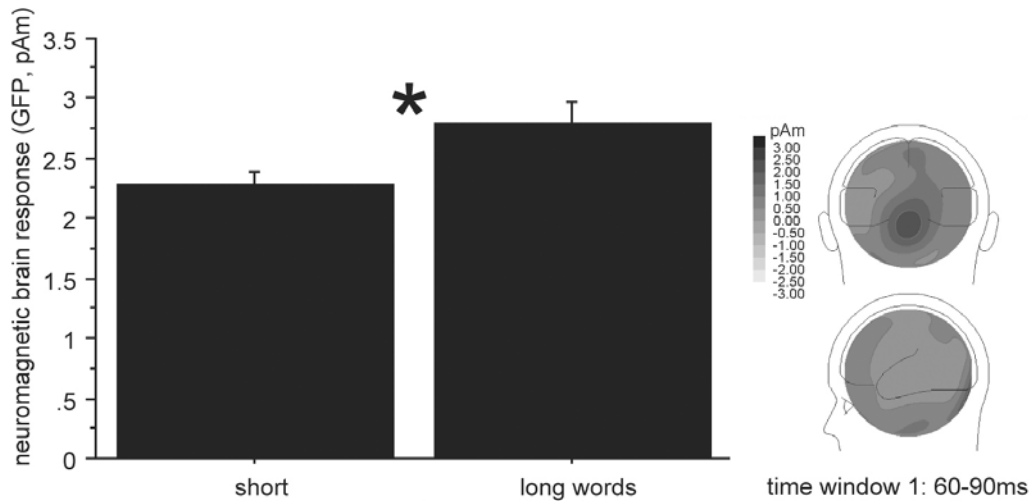
**Figure 2a:**
**Visually presented long words led to a significantly stronger global field power than short words already 60-90ms after presentation onset. The difference map of the minimum norm estimate reveals that brain response to long and short words differs mainly over the occipital lobe, where the dark colour indicates stronger activity for long words.**

The third time window from 120 to 170ms revealed a significant main effect of the word length factor again ($F(1,14) = 8.9$, $p = 0.009$; one: 11 pAm, two: 13 pAm) but in addition a significant interaction between the factors length and frequency ($F(1,14) = 14.7$, $p = 0.001$), see figure 2b). Post-hoc tests documented a significant frequency effect of the one syllable items ($F(1,14) = 9.5$, $p = 0.008$), with low frequency items leading to stronger brain responses (high: 11 pAm, low: 12 pAm). The corresponding difference maps (fig. 2b) reveal that only for short words, there was a strong amplitude difference between high and low frequency words mainly over posterior regions but also over the left perisylvian cortex. In the post-hoc tests there was also a significant contrast between long and short words for high frequency items ($F(1,14) = 16.1$, $p = 0.001$). Notably, the frequency contrast for two syllable items was not significant at this time.

time window 3: 120-170ms
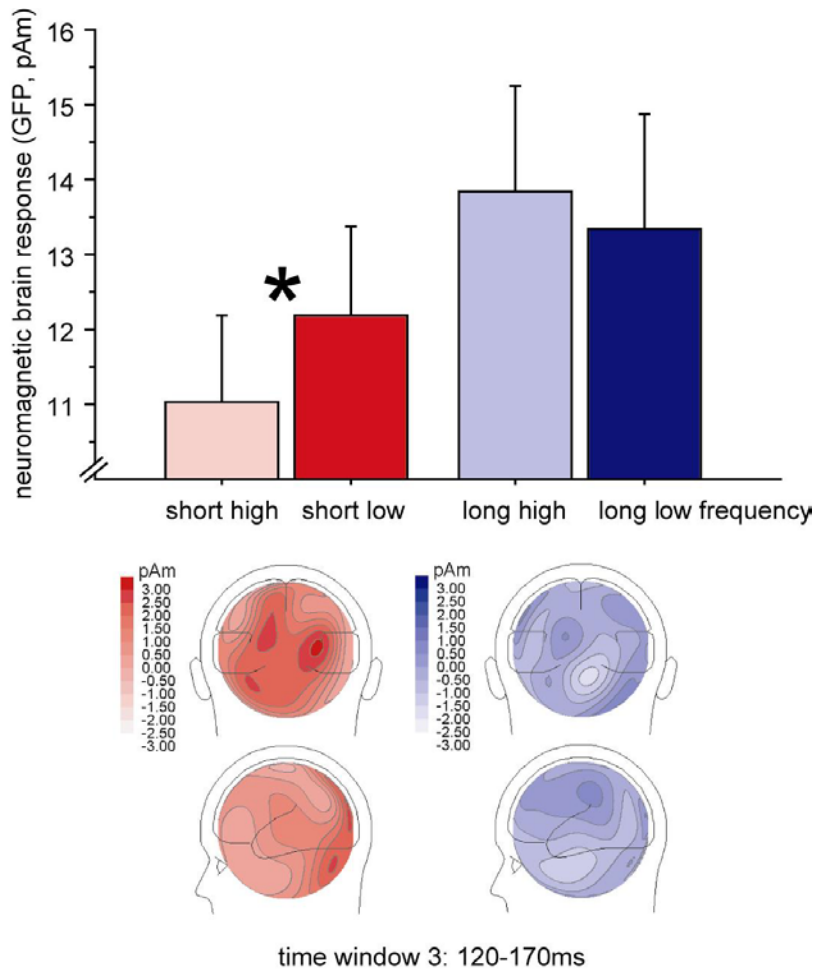
**Figure 2b:**
**Between 120ms and 170ms cognitive and physical word properties interacted in their influence on the global field power. The significant interaction indicated a frequency contrast for short words, but not for long words (high frequency items in light colours, low frequency items in dark colours, short words in red, long words in blue). Difference maps of the minimum norm estimate show that for short there is a strong difference between high and low frequency items (red) over posterior areas and to some degree over left language areas. This difference is absent for long words (blue).**

Two main effects were observed from 175-185ms in window 4: factor length ($F(1,14) = 12.2$, $p = 0.003$, one = 19 pAm, two = 22 pAm) and frequency ($F(1,14) = 5.0$, $p = 0.04$, high = 20 pAm, low = 21 pAm) Figure 2c reveals that generators in left ventro-occipital areas were stronger for low frequency items than for high frequency items.
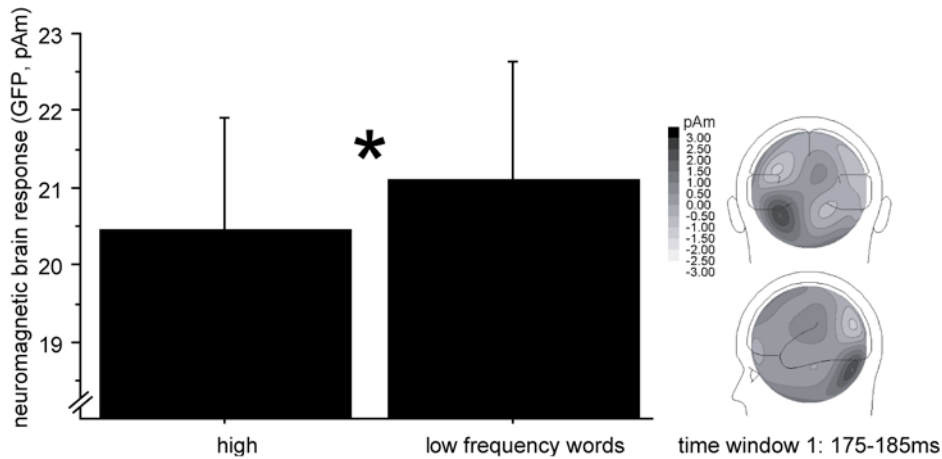
**Figure 2c:**
**From 175ms to 185ms low frequency word induced a significantly stronger global field power than high frequency words. This difference becomes apparent mainly over the left ventro-occipital lobe as revealed by the difference map of the minimum norm estimate.**

There was a main effect of the factor word length in time frame five from 180 to 220ms: $F(1,14) = 5.5$, $p = 0.03$ (one = 17 pAm, two 18 pAm).

The sixth time window, 225-250ms, revealed another significant interaction between the two factors ($F(1,14) = 4.8$, $p = 0.04$, see figure 2d): At this latency the contrast on word frequency was not significant for one syllable items, but for two syllable items instead ($F(1,14) = 4.6$, $p = 0.047$). Again low frequency words lead to stronger brain responses (high: 11 nAm, low: 12 pAm) as illustrated in the corresponding map where the main cortical generators were located left occipitally, right parietally and in the left perisylvian cortex. All other post-hoc test were not significant.

time window 6: 225-250ms
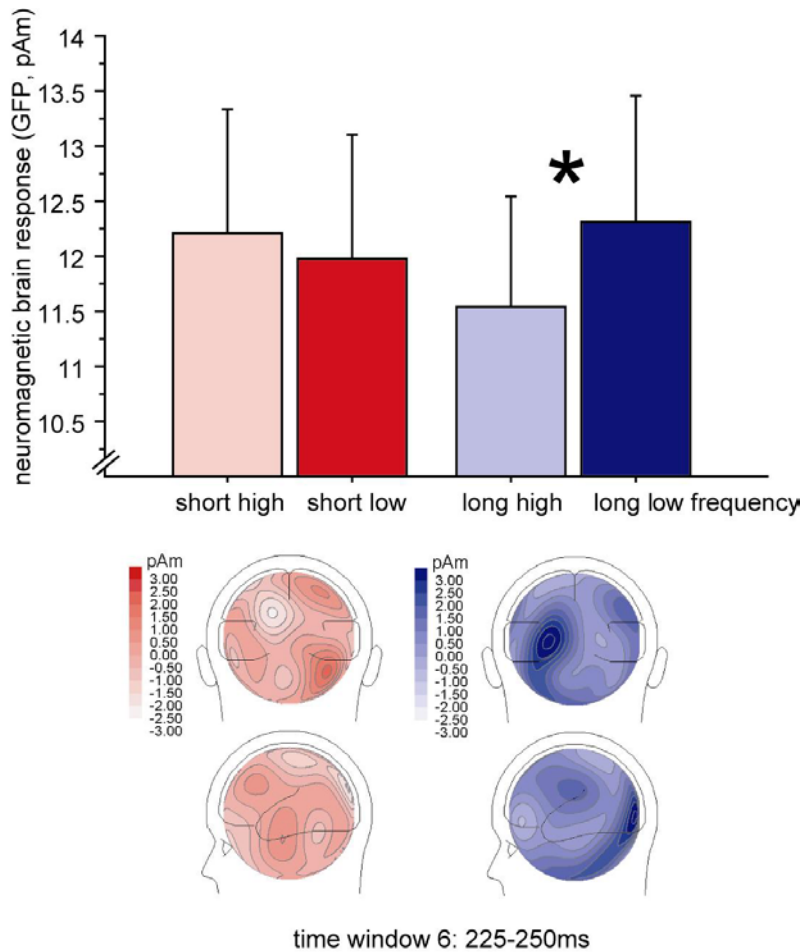
**Figure 2d:**
**The interaction of word length and frequency from figure 2b was reversed in the time window from 225ms to 250ms: the global field power to long words (blue) differentiated between high and low frequency items but did not for short words (red). This difference is mainly over the left occipital lobe and over left language areas, where dark blue indicates stronger activity for low frequency items.**

The time range from 300-340ms, the seventh window, failed to reveal significant effects, only a tendency towards a main effect of length (p = 0.08) emerged.

There was a main effect of the factor word length (F(1,14) = 5.5, p = 0.03) in the eighth window from 370-470ms, with one syllable items leading to stronger brain responses from now on (one = 8 pAm, two = 7 pAm).

The ninth time window (500-800ms) revealed another significant main effect on the factor word length (F(1,14) = 5.6, p = 0.03, one = 8 pAm, two = 7 pAm).

| | main effect length F(1,14), p | main effect frequency F(1,14), p | interaction length x frequency F(1,14), p |
|---|---|---|---|
| 1:    60-90ms | 6.3,  0.024 | - | - |
| 2:   90-120ms | 5.3,  0.036 | - | - |
| 3: 120-170ms | 8.9,  0.009 | - | 14.7,  0.001 |
| 4: 175-185ms | 12.2,  0.003 | 5.0,  0.04 | - |
| 5: 180-220ms | 5.5,  0.03 | - | - |
| 6: 225-250ms | - | - | 4.8,  0.04 |
| 7: 300-340ms | (p = 0.08) | - | - |
| 8: 370-470ms | 5.5,  0.03 | - | - |
| 9: 500-800ms | 5.6,  0.03 | - | - |

**Table 2:**
**Summary of statistical results obtained in the present group study. Neuromagnetic brain responses showed clear effects of word length almost over the entire interval analysed, up to 800 ms. The word frequency effect only appeared in specific time windows. Frequency effects for short (1-syllable) and long (2-syllable) words appeared in distinct time intervals (cf. Figure 2b and 2c).**

## VII.5 Discussion

The GFP of MEG brain responses to words, whose length and normalised lexical frequency were varied orthogonally, revealed the following differential effects:

- 60-120ms, length effect: stronger brain responses to long words compared to short words.
- 120-170ms, frequency effect for short words only: low frequency items led to stronger amplitudes than short high frequency items.
- 175-185ms word frequency effect: stronger neurophysiological responses to rare words than to common ones.

- 225-250ms, frequency effect for long words only: long words with low word frequency led to stronger neuromagnetic fields than high frequency ones.
- >370ms: in contrast to the earlier time frames, short words now led to stronger neurophysiological responses than long words. There was no effect of word frequency in the late intervals.

We will first discuss these findings about the time course of length and frequency effects on the background of earlier work and relate them to attempts at localizing relevant effects using MNEs. Finally, we will give a tentative explanation for aspects of the results on the basis of a neurobiological model of word processing.

Brain responses reflecting word length

The study revealed a very early reflection of word length by the evoked fields. Longer words led to stronger brain responses. This effect was already significant starting at 60ms after the onset of word presentation. Its main cortical locus was found in occipital areas. It is well-known that visually-evoked neurophysiological activity can be seen as early as 60 ms after onset of visual stimulation in the visual cortex (e.g. Ducati *et al.*, 1988: ~50ms, V1). The present data show that early activation can be recorded non-invasively using the MEG, and that its approximate cortical locus can be appropriately determined using MNEs. The stronger MEG responses to long words compared to short ones may be due to stronger neuronal activation, or activation of a larger area of visual cortex, by the more extended visual stimuli.The bigger stimuli activate more receptor cells in the retina and may therefore lead to stronger neural activation in the visual cortical systems.

The point in time and locus at which our earliest word evoked brain activity appeared resembles that reported by Compton *et al.* (1991) who found

word-evoked EEG activity around 70 ms after stimulus onset at posterior sites. Sereno and colleagues (1998) found a word-evoked potential at parietal posterior sites starting around 115 ms. The time difference may be due to differences in the signal-to-noise-ratio. Compton *et al.* also reported that EEG responses to words and orthographically illegal letter strings differed early-on, at 70-110 ms. This indicates that visual stimulus properties such as the frequency with which letter combination occur (e.g., so-called bi- and tri-gram frequencies) can be reflected in the brain response at short latencies. Therefore, it is possible that the early effect of word length reported here is not solely related to physical word properties but also to the processing of other aspects of the word form (for discussion, see Shallice, 1988; Petersen *et al.*, 1990).

Global word frequency effects

We found a global influence of word frequency, irrespective of word length, between 175 and 185ms. This is only slightly later than the earliest neurophysiological word frequency effect reported so far, the difference between high and low frequency words at 132 to 164 ms in the event-related potential reported by Sereno *et al.* (1998). Investigating content and function words, Osterhout *et al.* (1997a) found event-related potentials to content words (mostly low frequency) to be more negative going than to function words (mostly high frequency) from 150-250ms. Also, Neville *et al.* (1992) found the earliest distinction between highly frequent function and moderately frequent content words in the latency range between 240ms and 290ms. The earliest word frequency influences on ERPs (latency effects) found by King and Kutas (1998) started at ~280ms, and Rugg (1990) found low frequency items to lead to more negative-going ERPs than high frequency items at 300ms. In summary, there is ample evidence for an early (< 300 ms) manifestation of word frequency in the word-

evoked potential and field. One may still ask why different investigators found their respective effects at variable delays.

The late frequency (500-800ms) effect revealed by some earlier investigations (Polich & Donchin, 1988; Rugg, 1990; Assadollahi & Pulvermüller, 2001) was not present in the group study. Stimulus words were presented only once in most studies, but were frequently repeated in the present study. Also the memory paradigm used in the present study contrasts with the lexical decision task applied in many earlier studies. These differences may explain the absence of late word frequency effects. For example, the late word frequency effects appear to be reduced by repetition of words (Rugg, 1990), so that the late frequency differences found earlier might have disappeared here due to word repetition.

Interactions of word length and frequency

120-160 ms after onset of written words, and thus much earlier than in most other studies (e.g., Rugg, 1990: 300ms; King & Kutas, 1998: >280ms), we found a significant frequency effect for short one-syllable words. It has been proposed earlier (Pulvermüller, 1999) that it might be necessary to keep stimulus variance in length and frequency within narrow limits in order to record early neurophysiological differences between word groups. This can be confirmed for the four subgroups of stimuli we investigated here. The short low frequency, short high frequency, long low frequency, and short low frequency word groups each exhibited a rather small within-group variance in length and frequency. However, there was much early variation between the stimulus groups. The fact that we could now record neurophysiological manifestations of word frequency for the narrowly defined stimulus groups exhibiting only minimal within-group variance is in line with the prediction. Whereas the present data indicate a short and topographically restricted frequency effect, averaging over responses to strongly varying stimuli which may show their effects at

slightly different latencies or loci may blur or erase the early effects. Furthermore, consistent with this, the longer words showed their frequency effect later in the brain response. Thus, the absence of early frequency effects in earlier studies can tentatively be attributed to large stimulus variance. In keeping with an established strategy in psychophysics and psycholinguistics (e.g. Broadbent & Gregory, 1971), we used not only well-matched but also low-variance stimulus groups here.

The main results confirm some of the results of our earlier MEG study of a single experiment participant (Assadollahi & Pulvermüller, 2001). In both studies, a long lasting syllable effect that lasted for over half a second was accompanied by a differential frequency effect with slightly later onset depending on stimulus length. The two studies revealed some differences in the exact timing of cortical activation: Word length modulated neuromagnetic responses starting at 90ms in the single case study, whereas the onset was about 30ms earlier in the present group study. In both studies, a frequency effect specifically for short words appeared after 120ms, at exactly the same point in time. A frequency effect irrespective of length was observed 65ms earlier in the group study. Finally, the specific frequency effect for the longer words started substantially earlier in the present study (difference 145 ms). It seems that the entire processing cascade underlying these brain responses was somewhat compressed in time in the present study, but the general findings were the same.

MNE localization of length and frequency effects

The cortical localization using MNEs led to the following general result. The effects observed globally in the GFP response were primarily visible in posterior occipital areas early-on, whereas they became more global later-on. Before 100 ms, the MNE difference obtained for the significant word length effect was restricted to sources at the back of the brain, certainly in occipital lobes, and most likely in visual areas including pri-

mary visual cortex (Figure 2a). The frequency effect for short words present around 150 ms after stimulus onset was also reflected in the occipital lobes, but the MNEs suggest that the difference in cortical activation was now more global and characterized by a source area in the left hemisphere extending towards the Sylvian fissure (Figure 2b). Also the frequency effect at  around 180 ms appeared not only in occipital lobes, but in left-perisylvian areas as well (Figure 2c). Finally, the frequency effect seen specifically for long words, at around 250 ms, was reflected at occipital and left-perisylvian sites in the MNE difference map (Figure 2d). Although these results must be interpreted with great care, because the MNE is an estimate that can fall victim to localization errors (Ilmoniemi, 1993), the present results suggest a contribution of left-hemispheric perisylvian language areas to the frequency effects observed.

Putative neurobiological explanation of differential word frequency effects
The time by which word frequency influenced the neuromagnetic response was determined by word length. First, short low-frequency words evoked larger brain responses than short high-frequency words, and later-on, the same frequency effect was observed for long words. This finding raises the following questions:

- Why were brain responses to low-frequency words stronger than those to high frequency words?
- Why occurred the frequency effects to long words with a delay?

It has been proposed that words are cortically represented as Hebbian neuronal assemblies (Hebb, 1949; Braitenberg & Pulvermüller, 1992; Pulvermüller, 1999a). Hebb's rule implies a tightening of assembly-internal connections with their frequency of activation, thus implying stronger assembly-internal coupling for the networks organizing high frequency

words compared to those of low frequency words. Background activity in the brain implies baseline activity in all assemblies. In an assembly of neurons with strong internal coupling (high-frequency words), the background activity will lead to a higher baseline activity level than in a less strongly linked assembly (low-frequency words). We assume that the same state of full activation is reached by the strongly and the weakly linked cell assembly if appropriate stimulation is present, that is, when the adequate word is being presented. Therefore, the smaller activation found for high frequency words can be related to the high baseline activity level of these words' assemblies. In contrast, the stronger activation signs recorded to low frequency words may be related to a lower baseline activity of the weakly linked networks of these rarer words. This can be summarized by the inequality

$$\Delta A \text{ high freq. words} \quad < \quad \Delta A \text{low freq. words},$$

where $\Delta A$ is the activity increase produced by an assembly when it ignites. Highly frequent words have the tighter cortical representations, their corresponding networks exhibit the higher baseline activity levels producing *smaller activity differences between baseline and ignition*, as observed in the present study.

The early manifestation of frequency in the MEG response to words is consistent with, and provides support for, the idea that cell assemblies representing words ignite immediately after adequate stimulation by afferent activation (Braitenberg & Pulvermüller, 1992; Pulvermüller, 1999b). However, the explanation of different latencies of neuromagnetic frequency effects of short and long words – which has first been reported by Assadollahi & Pulvermüller (2001) and has been replicated in this study – requires a modification of the cell assembly approach to language proposed so far. We suggest that the cell assemblies of short monosyllabic words ignite instantaneously and as a single neuronal unit. The neuronal

memory traces of bisyllabic longer words might include a subgroup of neurons that are recruited later in the activation process. This later subgroup may be related to the activation of the *phonological program* of the second syllable implemented as a synfire chain of cortical neurons (Abeles & Prut, 1996). In contrast, the phonological program of the first syllable is activated together with the initial ignition of the assembly representing a word. This would account for the fact that frequency effects were seen earlier for monosyllabic items than for bisyllabic items. This tentative account for the delayed frequency effect for longer words to phonological processes following word assembly ignition should be further tested in neurophysiological experiments.

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# VIII  APPENDIX THREE

## Neuromagnetic Evidence For Early Semantic Access In Word Recognition[1]

## VIII.1 Abstract

Magnetic brain responses recorded in the human magnetoencephalogram (MEG) distinguished between words with different semantics but carefully matched for frequency and length. Multiple recordings from a single subject showed that 100 milliseconds following stimulus onset, significantly stronger neuromagnetic responses were elicited by words with strong multimodal semantic associations compared to other word material. At this early processing step, there was a highly significant correlation (0.8) between the magnitude of brain responses to individual words recorded over parieto-occipital areas and their semantic association strengths. Subsequent to this early difference related to word meaning, additional differences in MEG responses emerged for words from different grammatical categories. Together, these results suggest that word meaning can be reflected by early neuromagnetic brain responses and before the grammatical information about the word is encoded.

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## VIII.2 Introduction

One of the most challenging questions in the cognitive neuroscience of language addresses the specific types of information that become available when a word is being comprehended. If a letter string is perceived as a word, does the information about the word's form, grammar and meaning become available at once or in successive steps? Would grammatical information become available before the words' meaning (semantics), or vice versa? We address this question by investigating magnetic brain responses to words belonging to different grammatical and semantic categories and ask whether the earliest physiological distinction would be between grammatical or between semantic word categories.

## VIII.3 Methods

*Subjects:*

The subject was a 21-year-old right-handed monolingual female student with 15 years of formal education. She had normal eyesight and no history of neurological disease or drug abuse. She was paid for her participation. A single subject-study was preferred to a group study for the following reasons: (1) The latency of evoked brain responses related to cognitive processing varies substantially as a function of stimulus familiarity and, consequently, between experiment participants (Osterhout et al.1997). (2) Structural and functional brain organization differ considerably between individuals (Damasio, 1995), thus causing devastating between-subject variance in both topography and timing of evoked fields. Although, at present, most imaging studies concentrate on group averages, rather than thoroughly investigating the reproducibility of results in individual subjects, the single case-strategy appears to us to be as important in cognitive

neuroimaging as it undoubtedly is in the study of single patients in cognitive neuropsychology (Caramazza, 1986).

*Stimuli*

All words were short and common (4-7 letters, 1-2 syllables, word frequency 12 and 329.mio). There were 2 types of words, frequently repeated *recurrent words* and *new words*. The *new words* were obtained from recurrent words by replacing one letter. The 16 *recurrent words* were from 4 categories: (1) grammatical function words, (2) action verbs, (3) nouns with strong visual associations and (4) nouns eliciting both visual and action associations. As Table 1 illustrates, categories (1) to (3) differed regarding their grammatical category. Category (4) was also grammatically distinct from (1) and (2), but differed from (3) only with respect to semantic features. Word length and frequency was exactly matched between the 4 word categories. A pre-experiment carried out with 10 native speakers of German confirmed the classification of these words into the 4 categories. A significant interaction of the factors word category and association modality (visual vs. action), $F(3,27) = 45.54$, $p < 0.00001$, showed that strong associations of actions were only reported for the stimuli in categories (2) and (4) and strong visual associations were reported for (3) and (4) (Figure 1). Thus, category (1) showed no associations *(amodal)*, (2) and (3) elicited associations in one modality *(unimodal)*, and (4) in more than one *(multimodal)*. Overall semantic association scores were computed as the sum of action and visual ratings.

| | | MEANING | | |
|---|---|---|---|---|
| | | amodal | unimodal | multimodal |
| LEXICAL CATEGORY | function word | (1) | - | - |
| | verb | - | (2) | |
| | noun | - | (3) | (4) |

**Table 1. The four word groups used in the experiment differed in their lexical categories and meaning. Whereas lexical distinctions are along the horizontal lines, meaning-related differences predict major differences along vertical lines.**
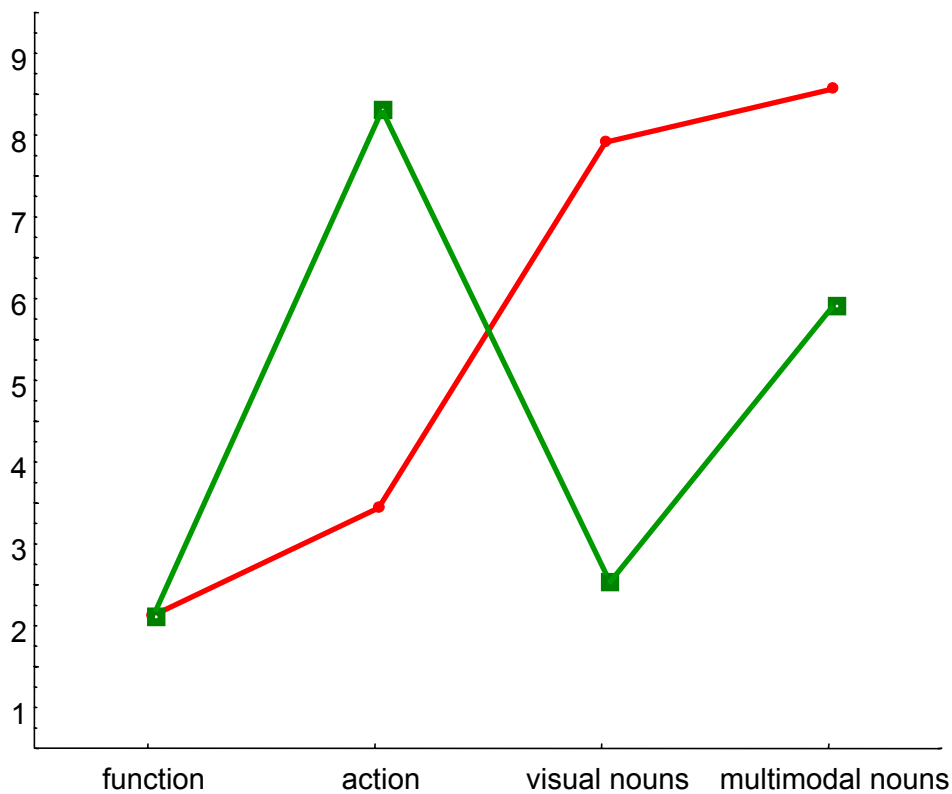


**Figure 1. Semantic association ratings for the four word categories: Only minor semantic associations were reported for function words. Only strong action associations (green) were reported for our verbs, and strong visual associations (red) only for the visual nouns. The multimodal noun category received strong visual association ratings and also substantial scores for action associations.**

*Procedure:*

Within 4 weeks, there were 12 recording sessions, each including 3 "runs" which, in turn, included 20 blocks. In each block, 16 recurrent words and 2

new words were shown in randomized sequences. Prior to the investigation, the participant was familiarized with the recurrent stimuli. She was told to memorize them and to respond by button press (left index finger) only to stimuli not in the memorized set. The task was applied to force the subject to keep the recurrent word set in active memory, and to assure sustained attention to the stimuli. The subject reported that, after reading the short word list a few times, she easily remembered the words without applying mnemonic strategies. Free recall was error-free before each session. All words were presented tachistoscopically (for 100 ms) written in white uppercase letters (maximum word size 7x3 cm) on a gray screen 1.4 m away from the eyes. Stimulus onset asynchronies randomly varied between 1.4 and 2.0 s. A fixation cross appeared in the middle of the screen whenever no word was visible. A Sharp LCD-projector outside the MEG chamber was used to project the stimuli onto the screen inside.

*MEG Recording:*

Neuromagnetic signals were recorded (0.1-100Hz bandpass, 508Hz sampling rate) using a 148 channel whole head magnetometer (MAGNES 2500, Biomagnetic Technologies Inc.). Vertical and the horizontal electro-oculograms (EOG) were also recorded. The sensor array was always positioned over the same landmarks of the subject's head.

*Data Analysis:*

Raw MEG data were submitted to a global noise filter, split into epochs, and artifacts were rejected (thresholds: EOG > 100µV, MEG > 5pT). Data from one session were excluded from analysis because of high rejection rates (30%). For each recording session and word category, stimulus-triggered evoked magnetic fields (evoked fields, EF) were calculated relative to a 100 ms baseline. For statistical analysis, data from channels with high signal-to-noise ratios and, hence, strong EFs (>100fT) were selected.

The loci from which data were analyzed were over left and right parieto-occipital cortex and at the parieto-occipital midline (Figure 2). Each locus included five adjacent coils from which root mean square values were calculated. Greenhouse-Geisser-corrected Analyses of Variance (3 loci x 4 word categories) were calculated to assess significance of between-category differences. For correlation analysis, averaged neuromagnetic signals obtained for each of the 16 words was z-transformed to normalize for any difference related to word length or frequency (Osterhout et al. 1997). The normalized values were correlated with the semantic ratings obtained in the pre-experiment.

## VIII.4 Results

*Behavioral data:*

95-98 % correct responses were made in the individual sessions. The extremely rare false positives were equally distributed over the recurrent words indicating that all words were remembered equally well.

*Physiological data:*

Figure 2A shows the distribution of word-evoked fields over the head. Figure 2B presents recordings from the left parieto-occipital area for all 4 word categories. The grand average indicates between-category differences, already around 100 ms after stimulus onset. Statistical analyses were based on an early component, presumably an N1m. Average values from the time window 90-120 ms revealed a significant main effect of word category, $F_{(3,30)} = 5.51$, $\varepsilon = 0.93$, $p = 0.005$ (Figure 4A). Planned comparisons showed significant differences between multimodal nouns (word category (4)) and all other word groups ((4) vs. (1): $F_{(1,10)} = 6.2$, $p = 0.03$; (4) vs. (2): $F_{(1,10)} = 15.3$, $p = 0.002$; (4) vs. (3): $F_{(1,10)} = 6.8$, $p = 0.02$). There was no significant difference between any two of the other three categories. Thus, there was a physiological distinction exactly along

the boundary of one semantic category. Words with strong multimodal associations were isolated neuromagnetically from other words, regardless of whether they belonged to the same lexical category or not.

A



B



multimodal words ——
function words  ......
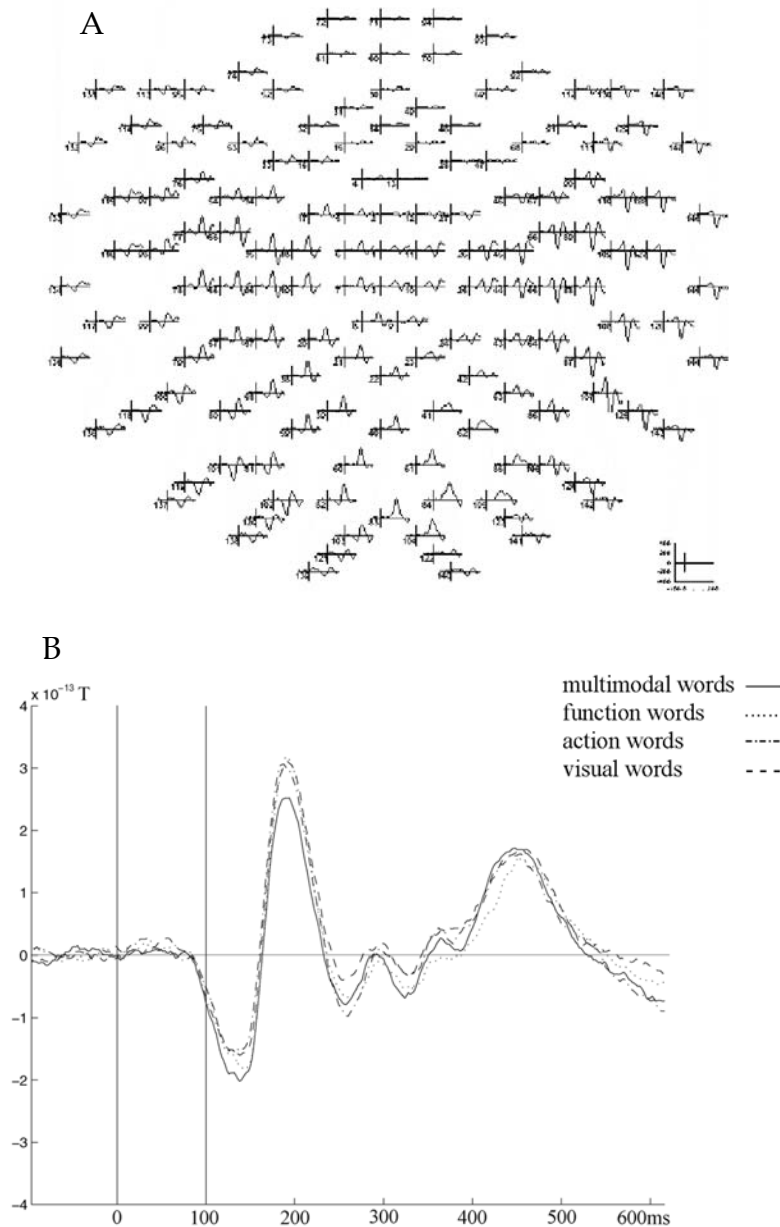action words  —·—·
visual words  - - -

**Figure 2. (A) Neuromagnetic responses evoked by words recorded at 148 MEG channels. The nose is up and left is left. (B) The single subject study showed that, already around 100 ms after stimulus onset, neuromagnetic responses differed between word categories.**
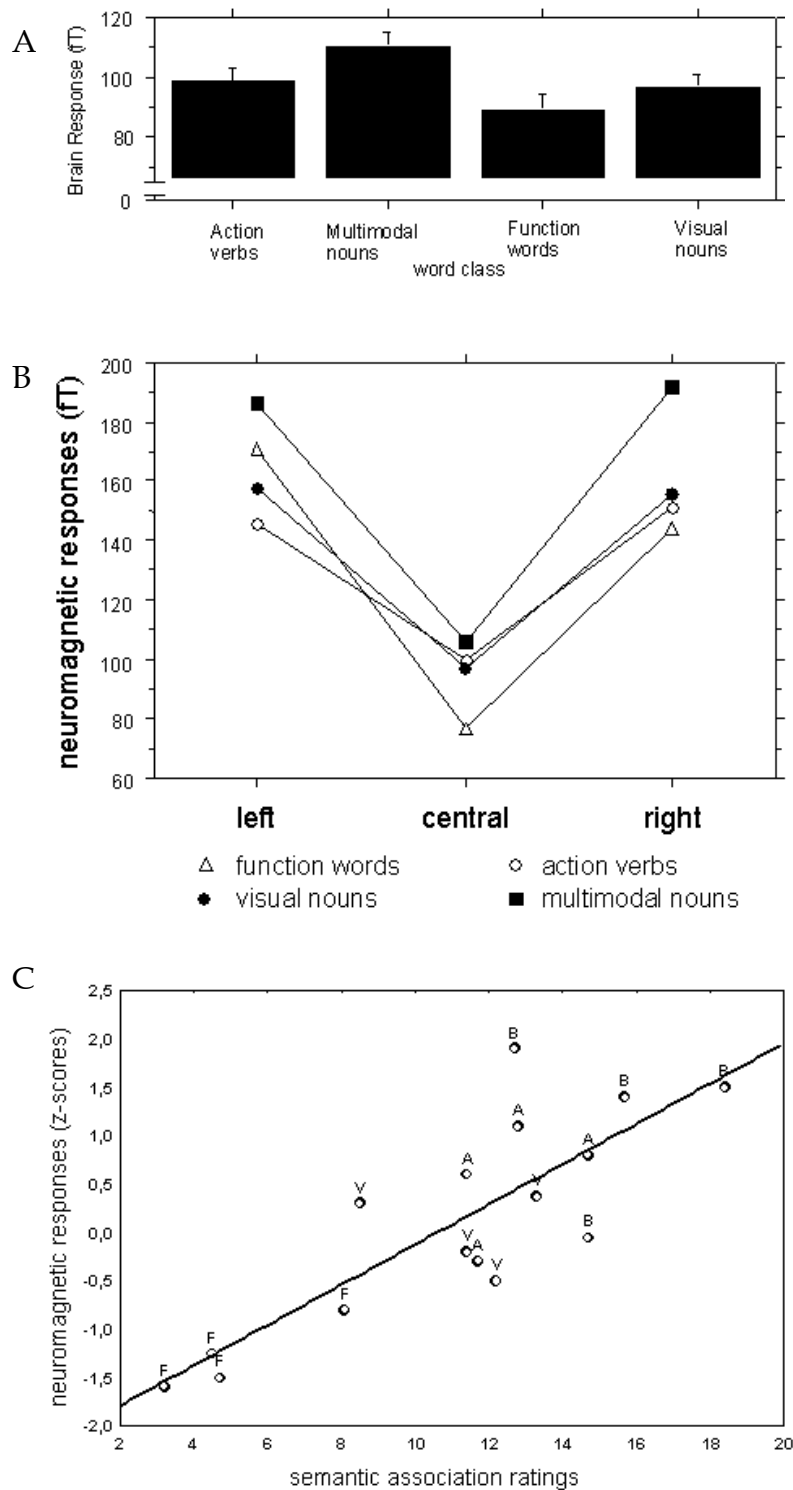
**Figure 3. Statistical analyses of neuromagnetic responses revealed early meaning-related differences between words. (A) Significant main effect of word category in the 90-120 ms time window. (B) Significant correlation (r = 0.796) of semantic association strength and magnitude of neuromagnetic responses in the 90-120 ms window. Each dot represents one word. (C) Significant interaction of word category and locus (left hemisphere, midline, right hemisphere) in the 120-160 ms time window.**

Correlation analyses further confirmed that semantic associations were reflected in neuromagnetic signals. For the early time window around 100 ms, normalized average physiological values obtained for each individual word were plotted against the strength of semantic associations, as revealed by the pre-experiment. This yielded a highly significant correlation between semantic association strength and amplitude of neuromagnetic responses ($r = 0.796$, $t = 4.93$, $p = 0.0002$). In the regression plot in Figure 4B, the four dots representing the amodal function words are on the lower left, and those representing multimodal nouns cluster on the upper right. Dots corresponding to unimodal nouns and verbs amalgamate in the middle. This strong correlation leaves little doubt that semantic aspects of the words became manifest in the neuromagnetic activity already early after stimulus onset.

In a later time interval 120-160 ms after stimulus onset, there was a significant interaction of the factors word category and locus, $F (6,60) = 4.04$, $\varepsilon = 0.431$, $p = 0.02$ (Figure 3B). At left-hemispheric recordings, all word categories diverged from the multimodal category which again produced the strongest signals. Over the midline, function words produced significantly weaker responses compared to all other groups, while over the right hemisphere only the multimodal words separated from the rest ($21.6 > F > 4.7$, $0.0009 < p < 0.05$). At this later time interval, word category differences in neuromagnetic responses thus varied with recording site. Consistent with earlier findings *(Pulvermüller et al.1995)*, there was a significant left-to-right difference for function words (stronger signals over the left hemisphere than over the right; $F (1,10) = 5.80$, $p = 0.03$), but not for any of the other word groups.

## VIII.5 Discussion

Neuromagnetic responses from a single subject reflected word semantics already 100 ms after onset of visually presented word stimuli. Nouns with multimodal associations evoked stronger magnetic fields than other words, regardless of whether they belonged to the same or different lexical categories. At this early point in time, semantic association strength was correlated with the magnitude of neuromagnetic responses. Some 50 ms later, around 150 ms after stimulus onset, magnetic brain responses revealed additional physiological distinctions of the categories of nouns, verbs, and function words over the left hemisphere. These results show that semantic information about a word under processing can become apparent in neuromagnetic responses before there is evidence for grammatical distinctions.

These results obtained in a memory task replicate aspects of earlier findings about word-category differences revealed by large-scale imaging techniques. Using naming tasks, Damasio et al. (1996) and Martin et al. (1996) found differences in local cerebral blood flow between tool and animal names. The present MEG data from a memory retrieval task confirmed such differences between nouns with unimodal visual associations (including most animal names) and nouns with associations in more than one modality (visual and motor, including most tools). Electrocortical differences between lexical categories, such as function words, verbs and nouns, had been reported in earlier EEG studies (e.g., Neville et al., 1992; Dehaene, 1995; Pulvermüller et al., 1995). These studies detected word category differences at 150 ms or later after stimulus onset.

The present study has, as we believe, a potentially important methodological implication. Our results indicate that the earliest neurophysiological indicators of cognitive brain processes can best be investigated in single subject studies where one subject is examined numerous times. Detailed physiological investigation of healthy individuals can be used to

draw careful conclusions on the organization of the brain-internal lexicon, in the very same way as observation of single neuropsychological patients – who show, for example, category-specific difficulties consistent with grammatical or semantic distinctions – can illuminate the neurobiological basis of cognition.

However, the single subject design may not have been the only reason why early cognition-related brain activity was revealed by this study. In the present recognition task, the relevant memory traces for words were, most likely, already active when the word stimuli were presented (*active memory*; Fuster, 1997), and less time may therefore have been necessary to fully ignite them. Further, Skrandies (1998) reported early physiological differences between semantic word categories obtained from a group of subjects who looked at and memorized new words. Therefore, the single case design appears helpful but not indispensable for obtaining early (~100 ms) physiological correlates of word semantics.

One may claim that not their visual and action associations, but an additional unknown property of the word groups may have been responsible for the early divergence of brain responses. However, we re-emphasize that the words were carefully matched for important psycholinguistic variables (including word length and frequency), which rules them out as possible confounds. In addition, the words' concreteness or imageability cannot account for the difference, because all nouns selected were rated as equally concrete and imageable. Therefore, concreteness/imagery alone would not allow to distinguish the visually-related and the multimodal noun categories. The only variable accounting for the early difference in neuromagnetic responses appears to be the cumulative semantic association strength obtained for different modalities. Further, there was no evidence that different mnemonic strategies were applied for different words, arguing against the possibility that putative mnemonic differences contributed to differential brain responses to words.

The relative timing of syntax and semantic processing has earlier been investigated in numerous studies. Event-related potentials indicated that, in sentence processing, syntactic anomalies can be reflected in a late positive component (P600; Osterhout & Holcomb, 1992), while semantic violations usually elicited an earlier response starting around 300 ms (N400; Kutas & Hillyard, 1983). The earliest grammatically related brain-response was a wave elicited by syntactic anomalies (phrase structure violations) which peaked at 125 ms (Neville et al., 1991). The present results confirm that syntactic distinctions can be reflected in neurophysiological responses around 120-150 ms after stimulus onset. However, the data also show that the earliest linguistically-related brain responses recorded so-far, at ~100 ms after visual stimulus onset, reflected aspects of word semantics.

The early category-specific neuromagnetic difference between multimodal and other words, the early correlation of brain responses with word semantics, and the later physiological distinction of nouns and verbs cannot be explained by models postulating that the processing of the meaning of a word is a late process. Some psycholinguistic models (e.g., Caplan, 1992) postulate that semantic access is actually the last process in word comprehension, following access to the word form in the lexicon – where some of its grammatical properties are stored. The present results provide an existence proof that semantic information can become physiologically apparent before grammatical information characterizing words. They are consistent with models proposing that the processing of syntactic aspects of words follows semantic access (Pulvermüller, 1999; 2000) and add to earlier observations that the neurophysiological signs of aspects of semantics can precede syntactic brain processes (Brown et al., 2000).

Finally, we wish to highlight implications of this study for brain models of cognitive processing. Stimulus-evoked neuronal activity in the primary visual area can be detected about 50 ms after visual stimulation (Ducati et al.1988). Only another ~50 ms later we found a difference between physi-

cally similar words with different meanings. Being of equal length, similar shape and luminance, these stimuli activate the same sensory pathway to a similar degree. To account for the differential cortical activation they elicited, it is necessary to assume that cortico-cortical circuits were effective. It may be that the stronger semantic associations of multimodal words are laid down in the cortex as strong links between numerous widely scattered neurons. This may provide a tentative explanation for the present data. Fast feedforward and feedback activation within distributed word representations may be the cause of the early divergence of word-evoked neuromagnetic fields.

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# IX  APPENDIX FOUR

## Magnetic Mismatch Negativity Indexes

## Grammaticality but not Serial Order Probability[1]

## IX.1 Abstract

What is the influence of grammatical context on the brain response elicited by a word? Research on sentence processing was to date not able to establish a theoretical answer to the question how exactly the formation of words as a phrase is processed neuronally. The Mismatch Negativity was recorded to scrutinise neuromagnetic signatures of basic syntactic processing of spoken noun phrases while subjects were instructed to ignore the language stimuli and watch a silent movie.

The frequent presentation of two determiners was interrupted by eventual presentations of nouns to generate a mismatch negativity. Combinations of determiners and words of varying sequential probabilities were chosen as well as one syntactically incorrect German phrase.

When a noun was preceded by a grammatically impossible determiner, the amplitude of the MMNm was significantly stronger than the MMNm to correct phrases. No comparable effect was seen when the sequential probability of two words was near zero, but the string was grammatically possible. The enhancement of the MMNm reported here thus reflects the processing of grammatical violations rather than a low probability of words to follow each other.

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## IX.2 Introduction

Donald Hebb proposed that neurons frequently active together strengthen their connections thereby increasing their influence on each other and developing into a functional unit or Cell Assembly (Hebb, 1949). On the basis of Hebbian correlation learning, single words were proposed to have their acoustic word form representation in the perisylvian cortex connected to areas that are involved in processing aspects of the word's meaning (e.g. Pulvermüller, 2001).

Neurons processing the meaning of nouns that have strong visual associations (like "sheep") for example would be located in the visual cortex and parts of the inferior temporal lobe. In contrast to this basic linguistic question of the neuron-level representation of words, the biological fundamentals of syntax processing are unclear. Linguistically, the combination of words into syntactic phrases is conducted by rules that define what word classes can be combined in order to form a syntactically correct phrase. Further, words within a phrase have to agree in certain features, such as case, number or gender. Together with the interpretation of words as distributed neuronal ensembles, syntactic sequences of words might be realised biologically by sets of neurons that specifically respond to sequences of words from defined lexical categories. These sequence detectors would be activated by grammatical strings, but not by ungrammatical ones. Importantly, a sequence detector connecting two word-related networks can mediate priming between the two, so that activation of the second is facilitated if the first occurs. The concept of a sequence detector moreover implies that an activation of the second *does not* facilitate the activation of the first, emphasising the importance of the serial order of the two.

Previous work

A common strategy in the sentence processing community is to present sentences that are in a dedicated way malformed and obtain the brain's

electrophysiological response to these violations. In the first work report-ing a left anterior negativity related to syntax processing in the brain, Neville and her colleagues (Neville, Nicol, Barss, Forster, & Garrett, 1991) investigated three different kinds of syntactic violations:

N1) phrase structure violations: *"The man admired Don's *of* sketch the landscape."

N2) specificity constraint violations: *"What$_i$ did the man admire Don's *sketch* of t$_i$?"

N3) subjacency violation: *"What$_i$ was [$_{NP}$ a sketch of t$_i$] *admired* by the man?"

Brain responses after the critical words (given in italic) in phrase structure violations (N1) revealed a left anterior negativity from 50-250ms as well as a sharp left temporal and parietal negativity around 400ms and a late posi-tivity. EEG-responses for specificity constraint violations (N2) lead to a strong ramp-shaped left anterior negativity starting from stimulus onset. Finally, subjacency violations (N3) lead to an enhanced positivity around 200ms and a late positivity over parietal sites, which was smaller com-pared to the positivity after phrase structure violations.

In their EEG study Osterhout & Holcomb (1992) were the first to label the late posititvity "P600" and claimed to have it identified as a biological in-dicator of syntactic error detection/reprocessing.

O1) phrase structure violation: *The broker persuaded *to* sell the stock.

O2) subcategorisation constraint violation: *"The broker hoped to sell the stock *was* sent to jail."

There was a slow positive shift in the ERP, largest over the right anterior scalp to the word "to" in O1, but also an N400 to the last word "stock". This might suggest that the semantic processing is concurrently active and tries to process the sentence although it is not grammatical. There was a more posterior and symmetric positivity to the word "was" in O2, which is a violation of a subcategorisation constraint.

Similar results of syntactic violations generating a late posterior positivity were amply obtained by other researchers (e.g. Hagoort, Brown, & Groothusen, 1993; Friederici, Hahne, & Mecklinger, 1996).

Problems with earlier studies

As pointed out by Coulson and colleagues (Coulson, King, & Kutas, 1998) findings about topography and timing of brain responses to syntactic violations are rather inconsistent in the literature. Some syntactic violations seem to lead to positivities, some to negativities and some to both. The topographies of these components seem to span over the whole cortex, although most studies did not report source localisations but electrodes where largest amplitudes were observed. Timing of brain responses is also distributed from 0 to >500ms after stimulus onset.

There might be multiple reasons for the variability in the findings: Word frequencies, repetition of words, modality of stimulus presentation (auditory, visual), type of presentation (continuous, word by word). But most important might be the different syntactic complexities of the sentences. Moreover, it is often possible to explain the syntactic violation of a sentence in various ways. As pointed out by Osterhout and Holcomb (Osterhout & Holcomb, 1992) themselves, the violation in O1 might be induced by a missing word ("The broker persuaded **the man** to sell the stock." preferred reading) or the elision of a phrase ("The broker persuaded to sell the stock **was sent to jail**.") or the verb might be wrong ("The broker **hoped** to sell the stock."). Different strategies of subjects to

cope with the violations will almost certainly lead to different brain responses.

Previous findings in the light of sequential probabilities

The grammatical violations of some of the sentences cited above can be alternatively explained by sequential probabilities. For example, it is highly unlikely that the genitive of the name "Don" is followed by the word "of" in natural texts (i.e. the sequential probability is zero or near zero), which might simply render the sentence N1 (Neville, Nicol, Barss, Forster, & Garrett, 1991) syntactically incorrect. The same might hold true for sentence N3: the sequence "of admired" is highly unlikely, although not impossible. Although this explanation is not straightforward for the sentences N2, O1 and O2, violations in sentences used many experiments can be explained in this simple manner.

Motivation for using a different paradigm

As stated above, the complexity of the syntactic violations is a general problem with studies looking at whole sentences. The multiple possibilities for the brain to handle the violations make the results difficult to interpret. Therefore we chose the strategy to scrutinise a well defined subset of syntactic material, the gender agreement between determiner and noun in a determiner phrase. The phrases were exactly defined in their linguistic properties leading to a well known context on which the interpretations could be made.

Characteristics of the Mismatch Negativity

Rather than presenting our stimuli in a continuous (acoustic) fashion or a (visual) word by word paradigm, we chose to employ the Mismatch Negativity (MMN, cf. Näätänen, 2001) paradigm. The paradigm consists of two sorts of auditory stimuli: a train of frequently presented stimuli (*standards*)

interspersed with *deviants*, that are discriminable from the standards in a certain defined aspect. A standard does not need to be constant, but can follow a certain pattern, so that there might be several standards that vary in one particular feature. Deviants breaking this pattern by changing a different feature will lead to an MMN. The MMN and its magnetic equivalent, the MMNm, are indicators of change detection that occurs in the absence of directed attention (Näätänen, 2001)

Investigating higher linguistic structures using the MMNm

The MMN has been found to be a sensitive tool in the investigation of language processes. Language sound that correspond to phonemes in the subjects' language lead to an enhanced MMN as do words. Unknown sounds and meaningless pseudowords, in contrast, only elicit a much reduced MMN (Näätänen, 2001; Näätänen, Tervaniemi, Sussman, Paavilainen, & Winkler, 2001; Näätänen et al., 1997; Shtyrov & Pulvermüller, 2002).

In the next step the MMN-paradigm might be employed for investigating syntax in the brain. Analogous to the phoneme traces proposed by Näätänen (2001) there might be evidence for syntax related memory traces. We investigate the sequential probability of words and syntactical correctness in determiner phrases. Determiners varying in their gender and case were chosen as standards. Deviants were nouns whose gender and case does or does not agree with the preceding standard. As all deviants are nouns and all standards are determiners, differences in the MMN-responses can not be attributed to the mere fact that nouns followed determiners, but rather whether their features agreed or not. In contrast to the activation that is expected for existing Sequence Detectors reflecting a "syntactic memory trace". MMN-research to date has not addressed syntactic processes. The previous non-MMN literature reported larger amplitudes to violations of syntactic structures. Brain responses of the latter

case, especially in a later time range (>500ms) are generally interpreted as the activity of the brain during the attempt to repair the ungrammatical sentence. Earlier activations (<300ms) are often interpreted as the detection of a syntactic violation. The MMN-paradigm employed for the first time in topic will hopefully shed more light on this research.

To sum up our hypothesis:

We expected that an early brain response reflects the invokement of a grammatical sequence detector and thus differences between the grammatical strings with high and low probability on the one side and the ungrammatical string on the other.

## IX.3 Material and Methods

Subjects

13 subjects (Ø 25.2a) right handed monolingual students (7 female) with at least 13 years of formal education. The subjects had normal or corrected to normal eyesight and no history of neurological disease or drug abuse. They were paid for their participation.

Stimuli

Standards were the two German determiners "der" (the, gender: male) and "die" (the, gender: female) occurring at 42% each. The deviants were "Wut" (fury) and "Mut" (courage). *Sequential probabilities (sp)* for each word pair were assessed ("der Wut" 1.5*10e-5; "die Wut" 5.9*10e-5; "der Mut" 14.4*10e-5; "*die Mut" 0) using the Mannheim lexicon/corpus 1+2 of the CELEX database (Baayan, Piepenbrock, & van Rijn, 1993). Importantly the phrase "die Mut" is syntactically incorrect and thus has a sequential probability of zero. The acoustic realizations of the words were synthesized using the MBROLA text-to-speech system (Dutoit, Pagel, Pierret,

Bataille, & van der Vrecken, 1996) and then adjusted manually. Stimuli had the same fundamental frequency (F0), and same maximal sound energy, consisted of as many identical parts as possible to keep the variance of physical stimulus properties as low as possible. Standards were 250ms long, deviants were 300ms. The ISI was chosen such that there were 500ms between two stimulus onsets, producing a rhythmic acoustic pattern of standards and deviants.

Procedure

The experiment consisted of two runs each including one of the two deviants ("Wut", "Mut"). The sequence of the runs was counterbalanced. There were at least three standards between two deviants and the first 30 stimuli were standards. The deviant was presented 332 times, 166 times in each context ("der", "die") which resulted in 2080 trials overall. Stimulation loudness was adjusted individually to a comfortable level (70-80 dB) and kept constant over the runs. Subjects were instructed to watch a silent movie and ignore the acoustic stimuli. No response was required. Before each run they were informed about what deviant they were about to hear.

MEG Recordings

Neuromagnetic signals were recorded continuously with a 148 channel whole head magnetometer (Magnes WHS 2500, 4D NeuroImaging Inc., San Diego) using a 0.1-100 Hz band-pass filter and sampled at a rate of 508 Hz. Along with the magnetic signals the vertical and the horizontal EOG and the ECG were recorded.

Data Analysis

MEG data were submitted to a global noise filter subtracting the external, non-biological noise obtained by the 11 MEG reference channels. The data was then split into epochs discarding all epochs where a button press oc-

curred. Epochs with an EOG level > 100 µV or MEG level > 5 pT between minimum and maximum on one or more MEG channels were automatically excluded from further analysis. For each subject and each run, each standard and each deviant in context stimulus-triggered evoked magnetic fields were calculated relative to a 100 ms baseline.

Cortical sources of these averages were estimated using the minimum norm estimate (MNE, Hämäläinen & Ilmoniemi, 1984). The MNE is an inverse method to reconstruct the topography of the primary current underlying a magnetic field distribution (cf. Grave de Peralta Menendez, Hauk, Gonzalez Andino, Vogt, & Michel, 1997) with an acceptable accuracy (here: <5%). During pseudo-inversion matrices were regularized (Tikhonov-Phillips, $\lambda$ = 0.01). Following Hauk and co-workers (Hauk, Keil, Elbert, & Müller, 2002) we approximated cortical activity in a three-dimensional source space consisting of four concentric spheres. The outer shell is individually fitted to the head-shape of the subjects (4-D Neuroimaging software). Sarvas (1987) proved that the head radius is not relevant for the computation of the magnetic field generated by primary currents in a spherically symmetric volume conductor. We assumed the head radius to be 10cm and will report the MNE for the shell at 80% radius which roughly corresponds to the cortex in the brain. On this shell 197 equidistant dipoles were assumed which were used for further analysis. There are several important features of the MNE:

- activation of multiple cortical dipoles can be estimated without a priori information about the number or location of cortical sources.
- sources that do not contribute to the measured scalp topography, in particular radial sources in the case of MEG data, are omitted.
- head-position and -size of all subjects are standardised.

Subtraction of standards from the deviants was performed in source space (i.e. on the minimum norm estimate). two standards ("der", "die") evoked different patterns in the brain response probably because they have different acoustic properties. The patterns were such that the topography of the brain response was similar between the words used as standards, but the timing of the amplitudes were different. Such differences would modify the MMNm where the standard is subtracted from the deviant. However, differences due to the different brain responses to the standards would mask differences related to the different grammatical phrases. We therefore averaged the two standards of each condition and used this average brain response for computing the MMNm-brain response. This strategy was also used by Pulvermüller et al. (2001). Statistical analyses confirmed that the averaged brain response to the standards did not differ between the two deviants ("Mut" and "Wut"). Thus the average of the two standards of each condition was subtracted from the corresponding deviant in order to obtain the MMNm. Standards also did not differ significantly between blocks.

Investigating the MNE-maps of the MMNms we decided to analyse the brain response on different regions of interest as well as the global mean. We defined one fronto-central focus (average of 21 dipoles), foci over left and right auditory cortices (average of 10 dipoles each) and the temporal poles (average of 6 dipoles each).

For statistical analyses, average values were calculated in *a priori* defined, fixed time windows of 40ms length starting from stimulus onset. Moreover, a time frame (140-180ms) was chosen where an obvious effect in the global mean occurred. Repeated measure Analyses of Variance were calculated to assess significance of between-category differences. F-tests were used to further investigate significant main effects or interactions.

## IX.4 Results

The global mean is given in Figure 1. Around 120ms the activity is below zero pAm indicating that responses to standards were stronger than to deviants. The next deflection peaking around 160ms is the neuromagnetic equivalent to the MMN and differentiates well between the non-grammatical (*"die Mut", black) and the other conditions (red, green, blue). The next positive deflection peaks around 270ms followed by another positive deflection starting from 340ms. These two do not seem to differentiate well between conditions.
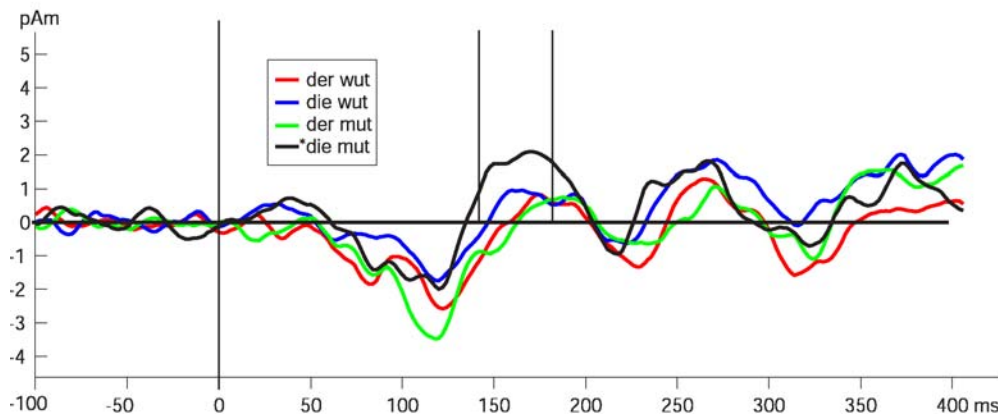


**Figure 1. Global mean over all dipoles of the minimum norm estimate (MNE) of the magnetic equivalent of the mismatch negativity (MMNm). Positive values indicate a stronger activation for the deviants ("Wut", "Mut") whereas negative values denote stronger brain responses to the standards ("der","die"). There is a clear deflection for the ungrammatical condition *"die Mut" (black) in comparison to the grammatical conditions ("der Wut", red; "die Wut", blue; "der Mut", green) in the time range form 140 to 180ms as indicated by the vertical lines. The earlier difference between "der Mut" and the others was not significant.**

Figure 2 depicts the topography of the brain response obtained by the minimum norm estimate. The syntactic violation led to a general enhancement of the brain activity that is most pronounced over fronto-central areas extending to the left anterior part of the brain. The frontal activity to grammatical phrases seems to have its peak somewhat more anterior than the activity induced by the ungrammatical phrase.
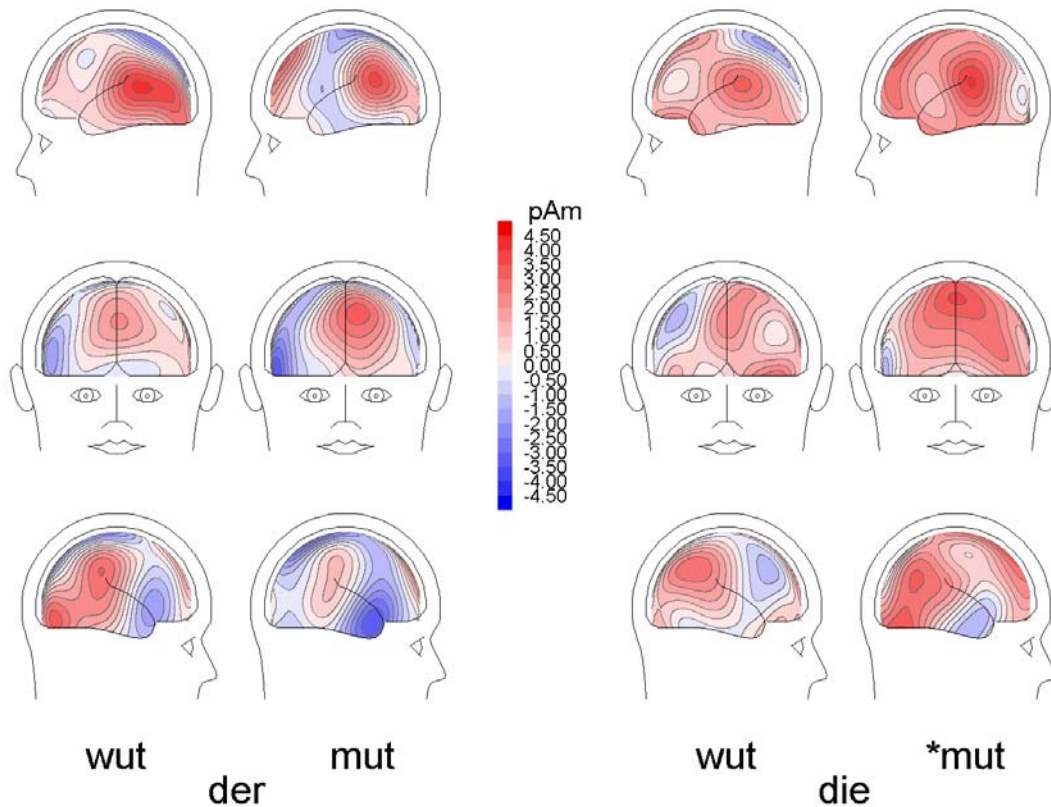
**Figure 2. Topographical maps for the minimum norm estimate (MNE) of the magnetic equivalent of the mismatch negativity (MMNm). Red colors indicate a stronger activation for the deviants ("Wut", "Mut") whereas blue colors denote stronger brain responses to the standards ("der","die"). The upper row shows the right hemisphere, middle row is the front view, lower row depicts the left hemisphere. The ungrammatical condition is given in the rightmost column. There is generally a stronger, widespread brain response especially over the left hemisphere and frontal sites for the ungrammatical condition compared to the grammatical conditions.**

In the time window immediately after onset (0-40ms) there was a main effect on context in the fronto-central focus (F(1,10) = 11.74, p = 0.0065), where the MMNm response was stronger to the determiner "die" than to "der". These findings might reflect the difference in the auditory processing of the stimuli as alluded in the introduction.

The next two time windows did not reveal any significant differences (40-80ms, 80-120ms).

The fourth time frame from 120-160ms gave rise to a significant main effect (F(1,10) = 4.84, p = 0.05) of context on the global mean indicating that the MMNm in the "die" context was stronger than in the "der" context. Further, the data from auditory areas revealed a main effect (F(1,10) =

10.83, p = 0.008) of laterality. The MMNm was stronger in the left auditory cortex  than in the right. This was also true found in the temporal poles (F(1,10) = 6.07, p = 0.03), where an additional main effect (F(1,10) = 7.55, p = 0.02) of context was observed ("der" > "die").

Statistical analyses of the data-driven window from 140-180ms revealed that there was a significant interaction (F(1,10) = 5.34, p = 0.04) between context ("der", "die") and noun ("Wut", Mut") as given in figure 3. Post-hoc tests revealed that the non-grammatical phrase lead to a significantly stronger brain response than the other, grammatical phrases. The MMNms elicited by the non-grammatical "*die Mut" significantly differed from the grammatical phrases "der Mut" (F(1,10) = 5.14, p = 0.04) and "die Wut" (F(1,10) = 4.7, p = 0.05). Notably, there was no statistically significant difference between the syntactically correct phrases: "der Wut", "die Wut" and "der Mut".
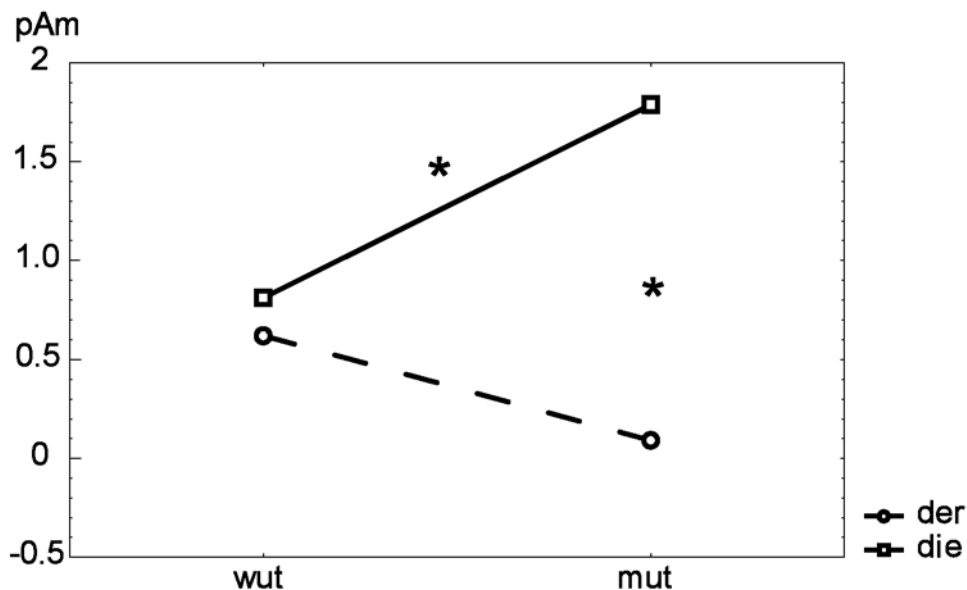


**Figure 3. From 140 to 180ms there was a significant interaction of the factors context ("der", "die") and noun ("Wut", "Mut"). Post-hoc tests revealed that the ungrammatical condition (*"die Mut") lead to the strongest brain response (vertical axis, global mean given in pAm) and that the grammatical conditions did not differ.**

There was a tendency towards the same interaction when the auditory (p = 0.08) and temporal (p = 0.1) sources were analysed separately. The frontal area did not reveal a significant effect or a clear tendency.

The analysis of the time frame from 160-200ms did not reveal any significant effects for the global mean. Instead, the effects that we observed in the time frame from 140 to 180ms seemed to be replicated here by activity over the various areas: There was an interaction of the factors noun and context (F(1,10) = 5.30, p = 0.04) over the auditory cortices that roughly resembled the findings of the global mean analysis of 140-180ms window, although post-hoc tests were weaker in this case, only the difference between "der Mut" and "die Mut" was significant (F(1,10) = 11.1, p = 0.007). The temporal poles revealed a main effect on context (F(1,10) = 4.99, p = 0.04, "der" > "die"), whereas the centro-frontal area revealed a main effect on the factor noun (F(1,10) = 5.84, p = 0.03, "Mut" > "Wut" ).

In the window from 200-240ms there was a main effect on context over temporal (F(1,10) = 7.49, p = 0.02) and auditory cortices (F(1,10) = 5.21, p = 0.04), where the MMNm was larger to "die" than to "der". Over auditory areas only there was an interaction of the factors context and hemisphere (F(1,10) = 6.64, p = 0.02, "der" > "die", left > right, lateralisation of "die" stronger than of "der").

In the time range from 240-280ms (seventh window) and from 280-320 (eighth window) there was a main effect (F(1,10) > 5.49, p < 0.04, "der" > "die") on context only over temporal areas.

There were no statically significant effects in the ninth window (320-360ms).

The analysis of the tenth window (360-400ms) gave rise to a significant interaction (F(1,10) = 5.29, p = 0.04) between hemisphere and context, were the MMNm to the "der" was stronger in the left hemisphere than in the right whereas the reverse was true for the "die" context.

There were no significant effects in the next two time windows (400-440ms, 440-480ms).

A summary of the fixed time windows is given in table 1.

| | 0-40 | 40-80 | 80-120 | 120-160 | 160-200 | 200-240 | 240-280 | 280-320 | 320-360 | 360-400 | 400-440 | 440-480 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Global Mean** | / | / | / | C | / | / | / | / | / | / | / | / |
| **Auditory** | C | / | / | H | CxN | C,CxH | / | / | NxH | / | / | / |
| **Temporal** | NxH | / | / | C,H | C | C | C | C | / | / | / | / |
| **Frontal** | C | / | / | / | N | / | / | / | / | / | / | / |

**Table 1. Summary of the statistical analyses from 0 to 480ms in frames of 40ms. C denotes a main effect of context ("der","die"), N of noun ("Wut", "Mut"), H of hemisphere (left, right). The early effects might be due to differences of the acoustic stimuli, whereas the major effects lie around 120-200ms.**

All findings concerning laterality showed a preponderance of the activity in the left hemisphere, which is well established in the literature (e.g. Giraud & Price, 2001).

## IX.5 Discussion

For the first time, we employed the Mismatch Negativity paradigm to investigate syntactic processes involving agreement violations in determiner phrases. Our main finding is an enhanced brain response from 140-180ms to an agreement violation in a determiner phrase (*"die [f] Mut [m]"). Moreover, we varied the sequential probabilities of the words in the phrase, but did not observe a brain response that reflected the sequential probability of the words constituting a grammatical phrase. In sum, it seems that an enhanced brain activity seems to be elicited only when there is an agreement violation and the sequential probability is zero.

In German, the syntactic agreement between a noun and a determiner forming a determiner-phrase is conducted by the three features number, case and gender. However, in some cases a word form of a specific deter-

miner can be ambiguous in its features. The word form "der" for example can act as a [singular, nominative, male] determiner or as a [plural, genitive, female] determiner. Thus we are here not able to attribute the feature which lead to the agreement violation.

Most effects found due to agreement violations reported in the literature occur late after word onset (*number:* Kutas & Hillyard, 1983: 200-500ms, Hagoort, Brown, & Groothusen, 1993: >500ms, Osterhout & Mobley, 1995: 300-500ms, *case:* Münte & Heinze, 1994: 250-500ms, *gender:* Osterhout & Mobley, 1995: 300-500ms, Brown, van Berkum, & Hagoort, 2000: 500-750ms).

Early effects:

In contrast to these findings our effect of a stronger activation after a syntactic violation was observable very early on (140-180ms). In agreement to our early findings there are also studies that report early syntax-related effects such as Osterhout & Mobley (1995: ~100ms parieto-central negativity) or Neville, Nicol, Barss, Forster, & Garrett (1991: 125ms, left anterior negativity).

There may be several reasons for our early observation:

- Most studies (except Brown, van Berkum, & Hagoort, 2000) used visual stimulation whereas we stimulated auditorily.
- The context in which words were embedded was larger in other experiments ranging from several words to whole paragraphs. Such a variance could affect and mask the modulation of early components in the other experiments. In the present study, we aimed at minimising the contextual variance and thus reducing its impact on the brain response. This may have resulted in a more clearly pronounced early response.

- In contrast to other tasks, here the MMN paradigm was employed to investigate syntactic processes. It is well known that deflections of the mismatch negativity due to experimental manipulations of a variable lie in the latency range from 100-250ms (Näätänen, 2001). Therefore the experimental paradigm (MMN) may be important for imaging early grammar effects as documented here.

- Our subjects were informed about what noun they would hear in the particular experimental run. One could argue, that the representations of these nouns were pre-activated during the experiment and had been fully activated very fast as the actual sensory information came in. However, it has been documented earlier that specific brain correlates of words can be recorded already 100-200ms after word specific information becomes available. The early access to linguistic information thus appears to be independent of details of the task.

Late effects:

In contrast to the literature, we did not observe any late effects. Very late effects (>500ms) may have been masked by the processing of next incoming stimulus. This, however, is a specificity of the paradigm.

Topography:

The topographic findings of all studies cited above were based on EEG-data where no source localisation was performed. Therefore the findings concerning the brain areas have to be handled with care. We rendered a Minimum Norm estimate of our MEG-data in order to obtain an objective localisation of the sources underlying the brain response. There was a frontal focus, that topographically seems to be slightly modified by condition. Activity over auditory areas in both hemispheres was more pronounced than in other studies, which is natural as stimuli were presented

auditorily. As the effect was not lateralised and only approached signifi-
cance, it seems that these areas were more strongly involved with the
processing of the auditory features of the stimuli than their syntactic in-
formation.

In sum, it is necessary to replicate our finding using the MMN-paradigm
in order to investigate the relation between the paradigm and the timing
of the effects.

Automaticity of responses:

One of the most important features of the MMN paradigm is that the sub-
jects attention is drawn away from the stimuli of interest (Näätänen, 1995).
In the present study subjects had to watch silent movies while stimuli
were presented auditorily. Moreover, the paradigm does not include any
overt responses by the subjects and they were asked not to focus attention
on the auditory stimulation. We therefore conclude that the brain response
to the syntactic violation was automatic.

Tentative explanation of the findings:

Earlier results in differences between grammatical and ungrammatical
strings could be interpreted in terms of grammaticality or, as an alterna-
tive, in terms of sequential probabilities. Our findings failed to support an
influence of sequential probability, but underpinned an early effect of
grammaticality.

A Sequence detector may connect the neuronal representations of two
words that follow each other in a grammatical sequence. Thus, the se-
quence detector would mediate priming that could explain the reduced
MMNm to grammatical phrases. The unprimed activation of a word in an
ungrammatical string would elicit an enhanced MMNm. These processes
could also account for the left anterior negativity to syntactic violations
(Neville, Nicol, Barss, Forster, & Garrett, 1991).

We did not observe an effect of sequential probability. This might have several reasons: First, the activation of sequence detectors may be too small compared to the other activity in the brain and thus might be undetectable by the MEG. Second, as determiners are the most frequent words in written language, the differences in the sequential probabilities of the phrases may be too small to produce an effect ($1.5*10^{-5}$ vs $14.4*10^{-5}$). Although complicated to compare, single words must have probability of 10 vs 100 per million words text to lead to differential brain responses. Third, the mere existence of a sequence detector might lead to a stronger and therefore measurable effect than the sequence probability itself.

## IX.6 Conclusion

Using the Mismatch Negativity paradigm we have found a difference in the brain response around 140-180ms that is attributed to a syntactic violation in the agreement between determiners and nouns. However, more studies are needed to corroborate the findings presented here and may even lead to the proof of the existence of sequence detectors.

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# X  APPENDIX FIVE

## From Zero to Action in 100ms:

## Word Induced Gamma-band Activity over the Motor Cortex as

## Revealed by the MEG[1]

## X.1 Abstract

We investigated whether the visual presentation of words from one single linguistic class, verbs, can induce a differential brain response. Moreover, we wanted to know whether such a differential activation might become apparent in the gamma-band. Three classes of action-related verbs were presented to 11 subjects while their brain responses were recorded in the MEG. Brain responses to face-, arm- and leg-related words were Minimum-Norm transformed on a single trial basis and wavelet convoluted afterwards. Already around 100 ms the averaged wavelets to the verb-classes revealed a significant differential activity over motor cortices in the frequency range from 32-40Hz. This gamma-band activity was stronger over the vertex after leg-related words than after face- or arm-related words. Face-related words in turn induced stronger activity over supra-temporal areas than the other two word classes. Activity related to arm-words was in both cases in between. Results are interpreted in the neurobiological theory of language postulating a distributed representation of words in the human cortex. The topography of this neuronal representation depends on the areas  involved processing the specific domains the word's meaning refers to.

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## X.2 Introduction

1949 Donald Hebb (Hebb, 1949) proposed that neurons that are frequently activated together strengthen their connections such that if in future one of the two is activated the probability for the other to be activated is increased. Several neurons involved in such a learning process were termed Cell Assemblies. Hebb's view on learning that is based on coincidence is superseded by the modern view in which cell assemblies are defined as distributed local networks of neurons linked by reciprocal dynamic connections whose strength is modulated based on correlation learning (Pulvermüller, 1999; Varela, Lachaux, Rodriguez, & Martinerie, 2001).

This concept has been applied to the problem of neurobiological representation of linguistic material, especially words. The rationale underlying neurobiological word representations is that the auditory word form memorised in the perisylvian cortex is linked to an area that is involved in processing the structure the words refer to.

For example, visual associations stored in the occipital and parts of the inferior temporal lobe might characterise most nouns ('the sun'). In contrast verbs, especially action verbs, can be characterized by the actions and body movements ('to kick') they refer to. Therefore one might predict, that the frontal lobes and the central sulcus may be involved in representing (action) verbs. This dissociation between cognitive associations of body movements and visual images was indeed reflected in psychophysiological findings in the EEG from 200-230ms (Preissl, Pulvermüller, Lutzenberger, & Birbaumer, 1995).

Penfield and Boldrey (Penfield & Boldrey, 1937) have shown that the peri-central cortex is ordered topographically: areas that are in neighbourhood on the body of a human are represented in neighbourhood in the primary sensor-cortex and the primary motor-cortex. More recently, the somatotopic organisation has been shown for the pre-motory cortices as well (Buccino et al., 2001).

Psychophysiological studies have shown that this topographic ordering of the motor cortex is mappable using the readiness potential that precedes any motor action: Toe-movements at the vertex, but finger movements over hand-areas at the contralateral hemisphere (Boschert, Hink, & Deecke, 1983). Tongue movements (Cheyne, Kristeva, & Deecke, 1991) lead to readiness potential over the face areas.

Therefore the proposal arose to subdivide the class of action-verbs and investigate whether specific activity in the motor cortex can be found that relates to the meaning of the verb. Words that involve movements of the face (like 'to grin') should be represented in cell assemblies that include neurons in the motor-cortex most lateral, in Brodman areas 4 and maybe 6 compared to words that refer to movements that are performed by the feet ('to kick') whose corresponding cell assemblies should comprise parts of the motor cortex near the vertex.

In a lexical decision task (Pulvermüller, Hummel, & Härle, 2001) action words of the verb-classes mentioned above were investigated on a behavioural (reaction time) and psychophysiological (EEG) level. Latencies of lexical decisions were shorter for face-related words compared to leg-words. There were topographical differences in neurophysiological responses between verb types. Currents above the cortical representation of leg movements were most negative going for leg-related verbs, while recordings close to the representation of face and articulators revealed most negative-going signals for face-related verbs. Additionally, there were significant differences over prefrontal and occipital areas. The timing of the neurophysiological responses followed the timing of the behavioural results: activity over face areas distinguished face-related verbs from other words at 250 ms while leg-related word evoked activity was largest around 300 ms. Prior to the psychophysiological experiments, (Pulvermüller, Hummel, & Härle, 2001) performed a rating study for the stimuli which confirmed that subjects associate them with movements of different body parts. One experimental draw back of the Lexical Decision Task design was that an explicit response by the subject was needed. Areas responsible for arm and hand movements may have elicited a potential related to response preparation (see Rockstroh, Elbert, Canavan, Lutzenberger, & Birbaumer, 1989). Therefore the activity evoked by arm-related words may have been masked by this activity. Another caveat is that words of the stimulus classes were matched for their length, but their word form frequency differed. However, word frequency can have a significant impact on the timing of brain responses (e.g. Assadollahi & Pulvermüller, 2001).

In a subsequent study performed by Hauk and Pulvermüller (2002) these two problems were avoided by more exactly matching the stimulus material and eliding the

requirement for an overt response. Around 120 ms after their visual presentation, event-related potentials distinguished between face-, arm- and leg- related action words. There was a systematic shift of the zero line in the difference maps comparing word categories. Later on, around 220 ms after stimulus onset, Minimum Current Estimates showed differential cortical activation in the left and right frontal lobes for different action word-classes. Leg-words specifically activated areas close to the cortical leg-areas, whereas face-words primarily activated left anterior areas. Surprisingly, arm-words prominently activated right frontal areas.

Hauk and Pulvermüller (2002) did not find differences in the Minimum Current Estimate of the brain response in the early time frame and attribute this to the statistical power. An alternative view may be that differences only occurred in the gamma band whose energy is by orders weaker than the energy of lower bands such as the alpha-band (the amplitude of a frequency generally decreases with its square-root). Therefore differences might have been observable by specifically analysing gamma band activity.

Physical data from travelling velocities of action potentials (Aboitiz, Scheibel, & Zaidel, 1992) lead to the theoretical claim that the activity in Cell Assemblies should reverberate in a frequency range that is typically higher than 20Hz (e.g. Pulvermüller, 1999) which is commonly called gamma band. Several studies undermine this claim. Lutzenberger and colleagues (Lutzenberger, Pulvermüller, & Birbaumer, 1994) found gamma band activity in the 30Hz range to be suppressed for pseudo-words, combinations of letters that are phonologically plausible but lack a semantic representation and hence a corresponding Cell Assembly. A difference between nouns and verbs was found in the range of 25-35Hz in a study by Pulvermüller et al. (Pulvermüller, Lutzenberger, & Preissl, 1999). Body representations in the gamma band range were also reported: Using EEG Pfurtscheller and colleagues (Pfurtscheller, Flotzinger, & Neuper, 1994) were able to map the somatotopic organisation of the motor cortex on single trial basis in the gamma band (30-40Hz).

In sum, there is a strong evidence from the literature that the mapping of action verb-representations to the motor cortex in the gamma-band range could be promising.

Inferring from Pulvermüller's neurobiological theory of language (Pulvermüller, 1999) we can formulate four hypotheses in ascending order of specificity:

- **Topographies** of brain responses to different verb-classes **differ** (activity induced by 'to kick' has a different cortical distribution than activity after 'to grin'). This is in contrast to localisationist theories postulating that the mental lexicon is confined to a certain area of the brain.

- More specifically, presentation of a word should lead to a stronger **activity in an area** that is responsible for processing activities that are **related to** the word's **meaning** ('to kick' – leg-related area in the motor cortex near the vertex). This activity should be **stronger than in other areas**.

- Activity induced by a word from a verb-class whose **meaning** is **related** to activity's localisation should be **stronger than** activity induced by words of **other verb-classes** ('to kick' to lead to stronger activity at the vertex than 'to grin').

- Activity induced by **arm-words** might be **lateralised** to the hemisphere that is responsible for controlling the subject's preferred hand. In contrast to this verb-class leg- and face-related words might not lead to differences in the lateralisation. These actions are often performed using both extremities ('to walk', 'to grin') in contrast to arm-words ("to write").

## X.3 Methods & Materials

Subjects:

14 subjects (mean 24.8 years) right handed monolingual students (6 female) with at least 13 years of formal education. The subjects had normal or corrected to normal eyesight and no history of neurological disease or drug abuse. They were paid for their participation.

Stimuli:

We used most of the words previously employed in the study by Pulvermüller et al. (Pulvermüller, Hummel, & Härle, 2001). This ensured, that the ratings of the verb-

classes would still hold. However, we refined the stimulus set by items matching for length (face: 6.83, arm: 6.76, leg: 7.23 letters), word form frequency (face: 1.33, arm: 2.4, leg: 1.87 per million words), lemma frequency (face: 8.73, arm: 9.03, leg: 8.67 per million words) and verb valence, such that there were equal numbers of words with the same valence in each category. Data were assessed on the CELEX database (Baayan, Piepenbrock, & van Rijn, 1993) and analysed statistically. There were no significant differences on any of the measures mentioned.

Procedure:

30 words per verb-class were presented in four blocks interspersed with 30 non-action related words as distracters per block. No overt response was required for reasons discussed in the introduction. All stimuli were presented for 100 ms in white upper case letters (maximum word size 7x3 cm) on a black background 1.4m away from the participant's eyes. A fixation cross appeared in the middle of the screen whenever no word was visible. The asynchrony of stimulus onsets was varied randomly between 1000 and 1200 ms. An LCD-projector outside the MEG chamber was used to project the stimuli onto the screen inside.

MEG-Recording

Neuromagnetic signals were recorded continuously with a 148 channel whole head magnetometer (Magnes 2500 WH, 4D NeuroImaging Inc., San Diego) using a 0.1-100 Hz band-pass filter and sampled at a rate of 508 Hz. Along with the magnetic signals the vertical and the horizontal EOG and the ECG were recorded.

Data Analysis:

Raw MEG data were submitted to a global noise filter subtracting the external, non-biological noise obtained by the 11 MEG reference channels. The continuous data was chunked of into epochs of 512 data points (length 1007ms, 350ms baseline), while discarding epochs contaminated by eye-blinks and other artefacts (>100mV, >5pT between minimum and maximum). This resulted in a maximum of 120 epochs

per word-category or condition. Data from three subjects had to be excluded from further analysis because of excessive eye-blink artefacts.

For source estimation of single trials we chose the minimum norm (MNE, Hauk, Keil, Elbert, & Müller, 2002) method as a linear estimation technique that does not make explicit assumptions about the number of active sources and their approximate locations (Hämäläinen & Ilmoniemi, 1994) and thus objectively models the current sources underlying the magnetic brain response. This approach yields an estimate of the current density distribution inside the head, projected on a the surface of a two-dimensional sphere of 80% of the head-radius. Tikhonov–Philips regularization was used to suppress uncorrelated noise (Bertero, de Mol, & Pike, 1988). Two orthogonally oriented dipoles per location on a sphere with 0.8 of the head radius were used for modelling. The dipoles were positioned tangentially to the surface of the shell consisting of 197 locations. Therefore 2x197 minimum norm estimates were submitted to wavelet convolution.

We used the wavelet convolution to determine the evolutionary spectrum, as has been applied in a variety of studies investigating temporal dynamics in the gamma frequency range (Basar, Schurmann, Demiralp, Basar-Eroglu, & Ademoglu A, 2001). The Morlet wavelet we used has the advantage of variable time and frequency specificity and can be adjusted to be sensitive for brief epochs of high-frequency oscillations (Bertrand, Bohorquez, & Pernier, 1994). We chose to model the data from 8-90Hz in bins of 2Hz. For each of the 197 locations, the RMS was computed over the resulting two orthogonal wavelet convolutions and the average baseline activity of the 300ms obtained before stimulus onset was subtracted for each frequency bin.

The whole procedure resulted in 197 wavelets reflecting the spectral activity in the corresponding locations in the brain.

Statistical Analysis:

Since the data we generated is a three-dimensional array of large extensions (356 time points x 42 frequency bins x 197 locations), it is obvious that we had to restrict our analyses. We used the grand average over all subjects and all words per condition and followed these steps:

1. Define areas of interest over the sphere.
2. Define frequency bands.
3. Define time range.

Our hypotheses specifically address the motor and pre-motor areas, therefore we constrained our analysis on locations within these areas. Per condition, the location with the maximal activity was chosen together with two of its strongest neighbours. The corresponding wavelet convolutions were plotted for all three conditions and all six areas (3 verb category x 2 hemisphere x region in motor cortex). The obvious activity peaks were defined by defining a frequency range and a time range.

The mean over time frame, frequency band and the three dipoles of a focus was computed resulting in one value per focus and six values per verb-subcategory. The 18 values were submitted to an ANOVA in the design VERB-CLASS (face, arm, leg) x HEMISPHERE (left, right) x REGION (leg-area, arm-area, face-area). The inference of distinct neural generators from significant region x condition interactions on ANOVA tests is not straightforward. Because changes in source strength (i.e. main effects) have a non-linear effect in event related field amplitudes across the scalp, significant region x condition interactions can result from changes in source strength as well as from genuinely different configurations of sources (McCarthy & Wood, 1985). This also holds true for linear Minimum Norm Estimates. Consequently, data was z-transformed for each individual subject and condition. This was done by subtracting the mean over dipoles of the motor cortex and dividing by the standard deviation. Before, non-z-transformed data was analysed to investigate main effects on the factor VERB-CLASS and thus to justify the data-analysis of the z-transformed data.

As recommended in the ERP guidelines by Picton et al. (Picton et al., 2000), we tested using univariate ANOVAs that assume equal covariance among all pairs of levels of the repreated measures (i.e. sphericity). As pointed out by Jennings (Jennings, 1987), this assumption is often violated in psychophysiological data. Degrees of freedom are usually Greenhouse-Geisser-corrected to compensate for such a violation. In the present study however, the sphericity was not violated (Mauchly's criterion) and a

Greenhouse-Geisser adjustment was therefore not necessary. Thus, all reported p-values are non-corrected values.

## X.4 Results

Figure 1 shows the wavelet convolution of the minimum norm estimate of the neuromagnetic brain response to each word category (face 1a, arm 1b, leg 1c) for the average of three dipoles over the motor areas leg, arm and face (from left to right) for both hemispheres (left hemisphere upper row).
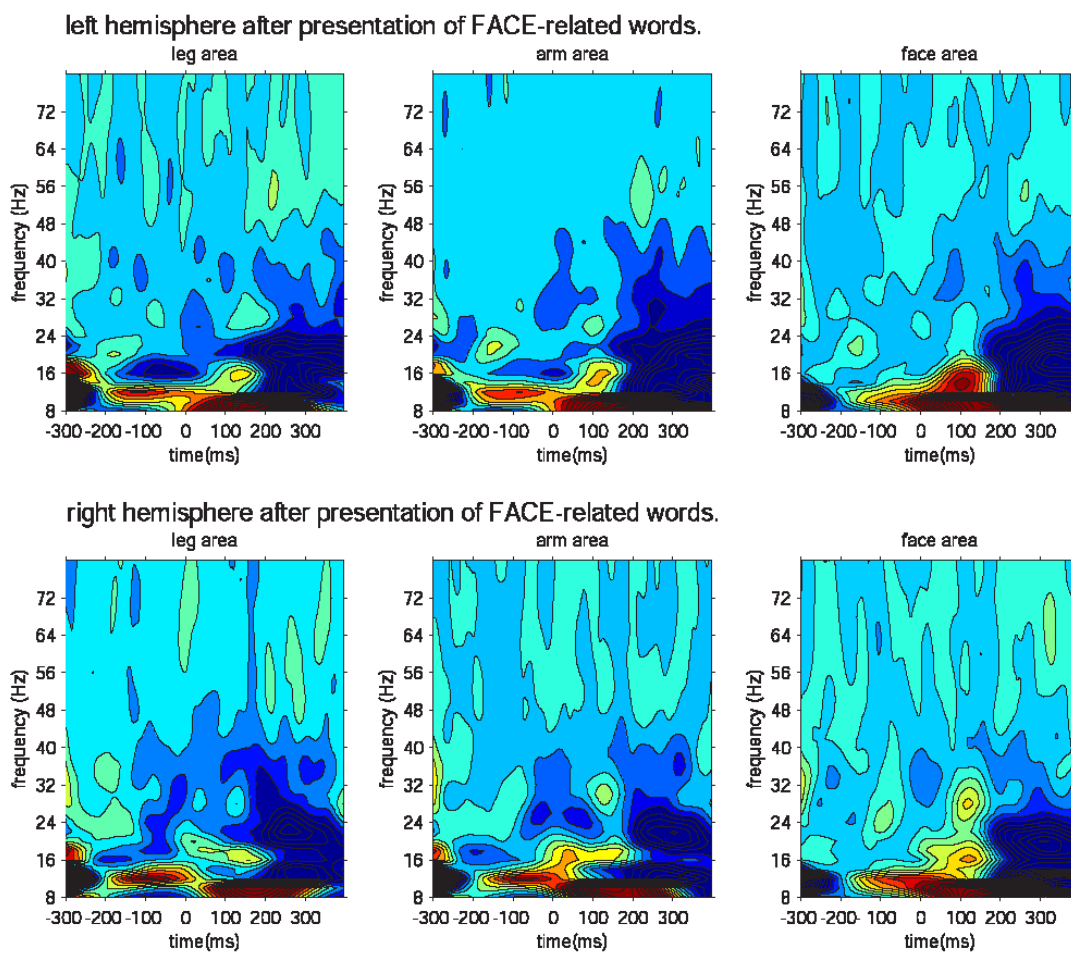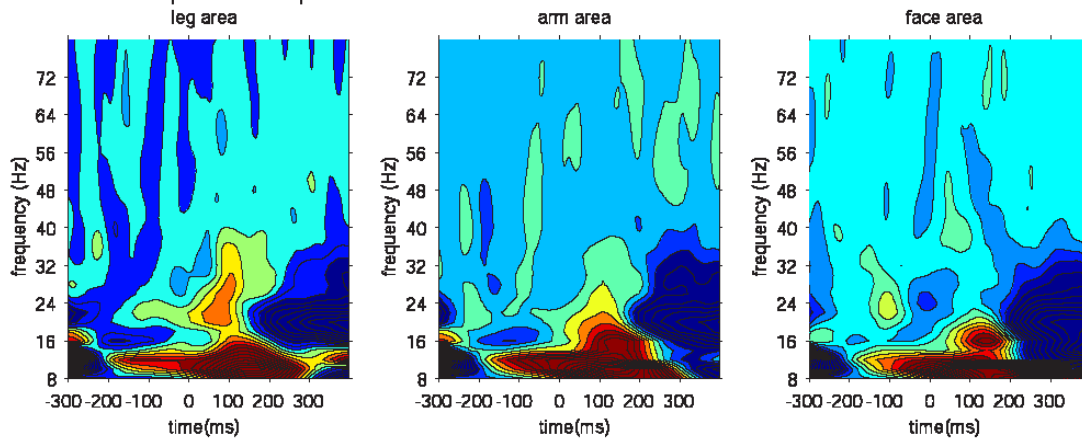
left hemisphere after presentation of ARM-related words.
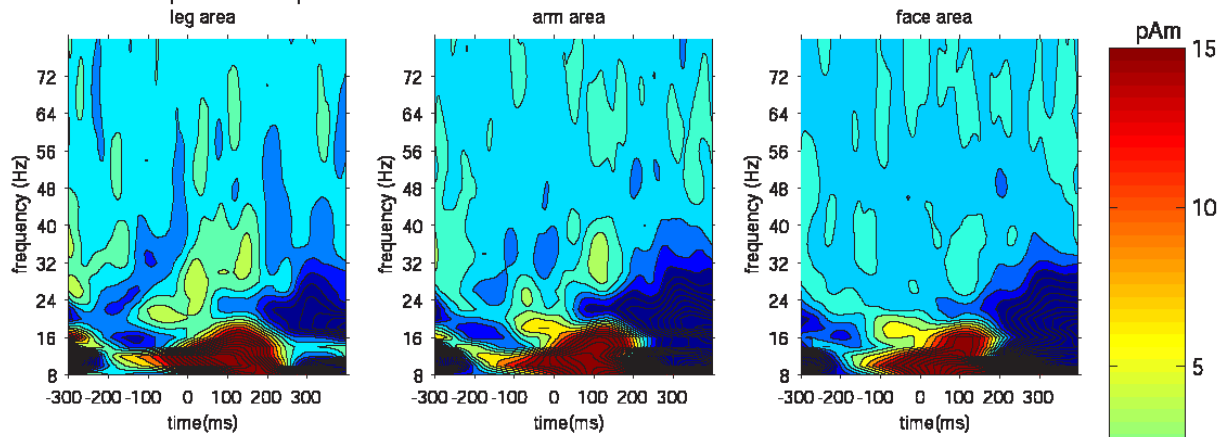
right hemisphere after presentation of ARM-related words.
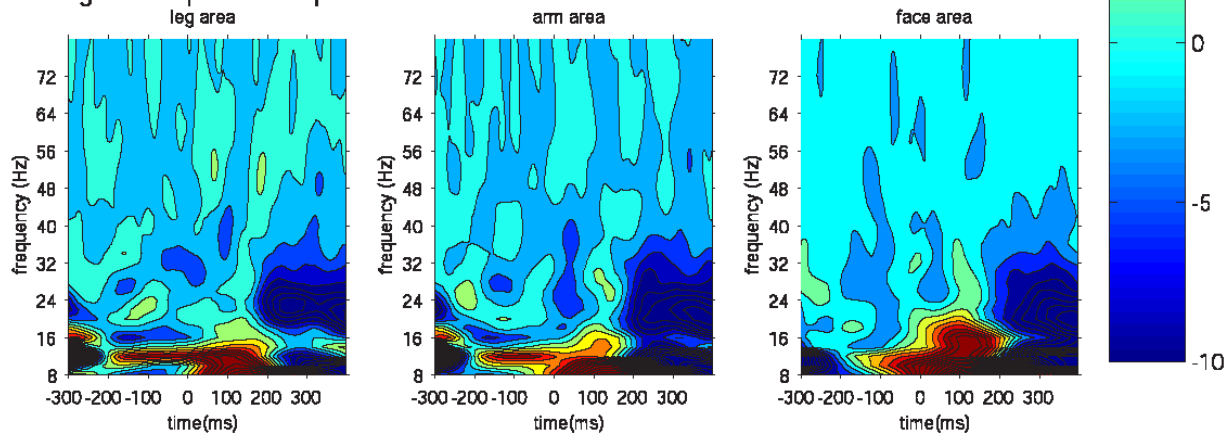
left hemisphere after presentation of LEG-related words.

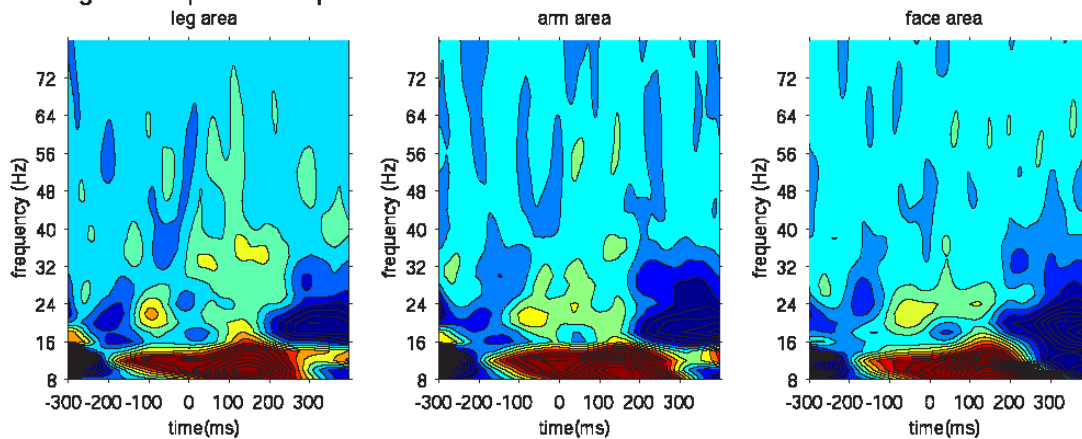right hemisphere after presentation of LEG-related words.

**Figure 1. Time/frequency plots over motor areas for the three verb-classes (1a: face-verbs, 1b: arm-verbs, 1c: leg-verbs). From left to right activity over leg-, arm- and face areas is depicted. Upper rows are areas over the left hemisphere, lower rows are areas over the right. Face-related verbs lead to a strong activation around 28 Hz over the right face-area (lower row, right most plot), arm-words (1b) lead to strong gamma-band responses from 30 to 40 Hz over the left leg- and arm-area (upper row, left and middle plots), leg-words (1c) lead to even stronger gamma-band response over leg-areas in the left hemisphere (20-40Hz, upper row, left most plot),**

There is a clear peak in the activation over leg areas after the presentation of leg words starting already at 80ms (figure 1c upper row, left most plot). This activity extends to about 120ms, the frequency of this activation from 20-40Hz. In this time frame, also the other two word classes elicited maximal activity at their corresponding area of the motor cortex: arm-related words lead to the strongest gamma-band activity in the left hemisphere over arm-areas (28-40Hz, 1b, upper row, middle plot) while face-related words activated face areas in the right hemisphere in the frequency range from 24 to 34Hz (1a, lower row, right most plot). Generally, we had the impression that frequencies were lower in the right hemisphere than in the left (e.g. figure 1c, lower vs upper row).

Since there were no other strong activations in the frequencies of interest (> 20Hz) in the first 400ms after stimulus-onset, we chose to analyse the time frame from 80-120ms (a minor peak in the upper gamma-band from 50-74 Hz around 300ms was observed for all three verb-classes and analysed statistically but did not reveal any significant effects).

Analysis of non-z-transformed data:

We chose to analyse frequency bins of 8Hz from 40-32Hz, 32-24Hz, 24-16Hz and 16-8Hz to ensure that effects on higher frequency-bands were not merely due to harmonics of lower-bands.

Indeed, the analysis of lower bands up to 24Hz did not yield any significant effects. The p-values decreased from lower to upper frequencies. We observed a marginally significant ($p = 0.06$) interaction of the factors VERB-CLASS and REGION in the band from 24-32Hz.

The band from 32-40Hz finally, yielded multiple significant interactions. There was a main effect on VERB-CLASS ($F(2,20) = 5.8$, $p = 0.01$) indicating that leg-words induced the strongest activity followed by arm-related words. Weakest brain responses

were induced by the face-related words. However, post-hoc tests only confirmed a difference between leg- and face-related words ($F(1,10) = 15.3$, $p = 0.002$). The difference between face- and arm-related words was marginally significant ($p = 0.06$).

This main effect for the non-z-transformed data justified the analysis of z-transformed data as we were not interested in the absolute strengths of the brain responses between classes but in their distribution over the cortex. The significant interactions of VERB-CLASSxREGION ($p = 0.01$) and HEMISPHERExREGION ($p = 0.02$) were thus not analysed any further. Before going into detailed statistical analyses of the z-transformed data, we will describe the topographies of the brain-responses in the gamma band from 32-40Hz.

Topography of the gamma-band response:

The topography of the minimum norm estimate of the brain response in this time/frequency-range (80-120ms, 32-40Hz) is given in figure 2.
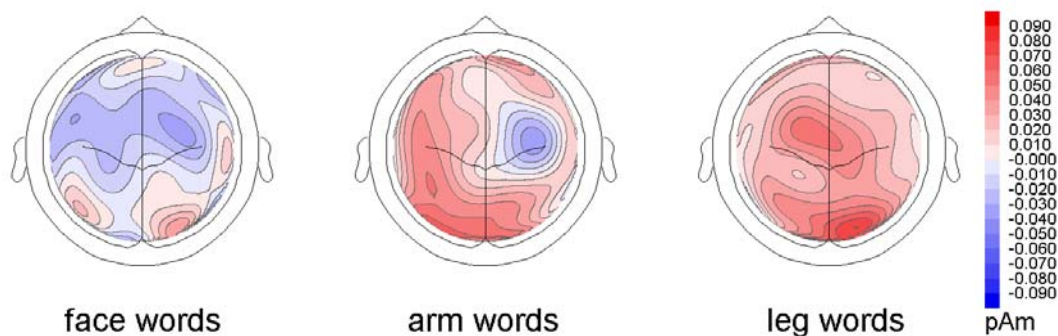


**figure 2:**
**The topography of z-transformed minimum norm estimates of the brain response to the three verb-classes (left: face-words, middle: arm-words, right: leg-words) in the gamma-band range from 32 to 40Hz in the time frame from 80 to 120ms. Activity is strong (strong activation: red, activation under baseline-level: blue) over the visual cortex but there are also activations over motor cortices. In the top-view (up-most row) there is a clear difference between responses to arm-verbs and leg-verbs, where the focus of the latter is more central. Activity to face-verbs is strong over right hemispheric face-areas and virtually absent over other areas.**

All maps (left: face-verbs, middle: arm-verbs, right: leg-verbs) have strong activations (red, lower row) over visual cortices in common. This strong activation is most probably a part of the activation related to the visual N1 component. We analysed this prominent activation separately.

Beyond the occipital activation, the gamma-band response to face-verbs is strong over the right supra-temporal face-area, parts of Wernicke and the auditory cortex. In the corresponding area of the left hemisphere, face-verbs also seem to lead to some

activation compared to the other verb-classes, whose activation is zero (white, arm-verbs) or below baseline (blue, leg-verbs).

Arm-verbs lead to a strong activation extending well into frontal areas and more lateral compared to leg-verbs. The activation seems to be confined to the left hemisphere whereas the corresponding arm-area over the right hemisphere elicits an activity below baseline-level (which is also true for the non-z-transformed data).

Clearly, the activation due to leg-verbs is restricted to pre-central areas of the central fissure at the vertex. Compared to the other verb-classes this activity is thus most central. Although the main activity is in the left hemisphere, it extends to the right hemisphere. Activity over face-areas in the right hemisphere seems to be in between the activation level of faces (strongly red) and legs (light blue).

The separate statistical analysis of the occipital part of the gamma band response revealed a significant interaction of the factors HEMISPHERE and VERB-CLASS ($F_{(2,20)} = 3.7$, $p = 0.04$). Post-hoc tests revealed that arm related verbs induce stronger activity than leg verbs in the left occipital lobe ($F_{(1,10)} = 8.3$, $p = 0.016$) whereas the reverse was true in the right hemisphere ($F_{(1,10)} = 8.3$, $p = 0.016$). No other post-hoc tests were significant.

The statistical analysis of this z-transformed data revealed a significant interaction of the factors HEMISPHERE and REGION ($F_{(2,20)} = 3.7$, $p = 0.04$) suggesting that gamma-band responses were stronger in the left hemisphere over leg and arm regions and that face regions in the right hemisphere elicited stronger activation than in the left. However, post-hoc-tests only confirmed the difference in hemispheric activation over leg-areas ($F_{(1,10)} = 6.8$, $p = 0.02$).

Further, the factors VERB-CLASS and REGION interacted ($F_{(4,40)} = 2.85$, $p = 0.03$, figure 3). Post-hoc tests were performed per VERB-CLASS to test hypothesis 2 and per REGION to test hypothesis 3.
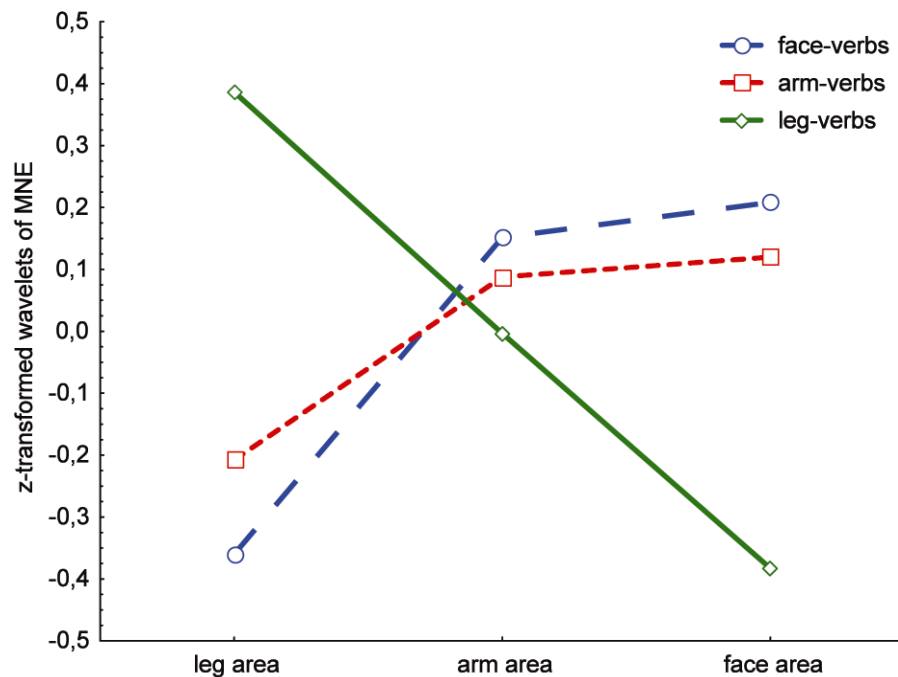
**Figure 3. Interaction of the factors VERB-CLASS and RE-GION (F(4,40) = 2.85, p =0.03). The plot is suggesting that leg-verbs lead to stronger gamma-band activity over leg-areas than face-verbs and that this relation is reversed over face-areas.**

Tests per VERB-CLASS:

- For **face-verbs** the difference for arm vs the leg-regions was marginally significant (p = 0.10).

- Post-hoc tests for **arm-verbs** did not yield any significant effects.

- For the **leg-verb-class** there was a highly significant difference between leg- and face-regions (F(1,10) = 11.9, p = 0.006). In contrast to face-verbs, leg-verbs led thus a focus of activity over centro-central sites.

Tests per REGION:

- Over the **face-region**, only face- and leg-verbs differed reliably (F(1,10) = 4.8, p = 0.05), indicating that face-verbs lead to a stronger activation than leg-verbs.

- There were no significant effects over the **arm-region**.

- Face- and leg-verbs elicited a significant difference over the **leg-region** (F(1,10) = 9.2, p = 0.01). Also, there was a significant difference between leg- and arm-verbs (F(1,10) = 4.6, p = 0.05). This indicates that leg-verbs lead to a stronger gamma-band response than other words over leg-areas of the cortex.

There was also a significant three-way interaction of the factors VERB-CLASS, HEMISPHERE and REGION (F(4,40) = 3.15, p = 0.02, figure 4). This interaction allowed us to comfortably test hypothesis 4 in addition to the other hypotheses.
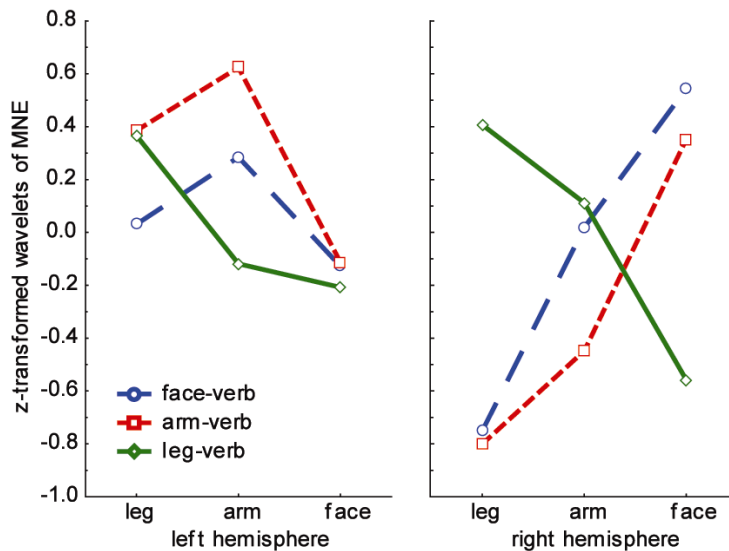


**figure 4:**
Interaction of the factors VERB-CLASS, HEMISPHERE and REGION (F(4,40) = 3.15, p = 0.02). This plot refines the impression from figure 3, in that responses differ over the hemispheres. For leg-verbs responses are still strongest over leg-areas in both hemispheres, but face-verbs only lead to stronger activation over face-areas in the right hemisphere. Arm-verbs lead to a significantly stronger activation over the left arm-area. Arm-verbs are the only verb-class whose brain response lateralises to the left.

Post-hoc tests per VERB-CLASS:

- There were no significant differences for **face-verbs** in the left hemisphere. In the right hemisphere, there was a significant difference between the leg- and face-areas (F(1,10) = 9.5, p =0.01) while differences for leg- and arm-areas were marginally significant (p = 0.07).

- For **arm-verbs**, the left hemisphere elicited a significant difference between arm- and face-areas (F(1,10) = 7.7, p = 0.01). Thus, the seemingly similar distribution of activity over regions for face- and arm-verbs was statistically different: Arm-verbs lead to stronger brain-responses over arm-areas compared to face-areas whereas face-verbs did not. However, in the right hemisphere arm-verbs lead to unexpected differences between leg- and face-areas (F(1,10) = 8.7, p = 0.01) mimicking the results from the face-verbs.

- The difference in activity over face- and leg-regions after **leg-verbs** was marginally significant (p = 0.1) in the left hemisphere while it gained significance in the right hemisphere (F(1,10) = 5.6, p = 0.03), thus undermining the findings from the two-way interaction.

Post-hoc tests per REGION:

- Activity in the left **face-region** could not differentiate between verb-classes while in the right hemisphere there was a significant difference between face- and leg-verbs ($F(1,10) = 8.3$, $p = 0.01$). The difference between arm-and leg-verbs was not significant, again stating a different result for the face-verbs compared to the arm-verbs.

- Over the **arm-region**, arm- and leg-related words tended to differ ($p = 0.09$) in the left hemisphere indicating the strongest activation for arm-words, in the right hemisphere there were no statistically significant differences.

- Over the **leg-regions** of the motor cortex in the left hemisphere, leg-related words lead to stronger gamma-activity than arm-related words ($F(1,10) = 6.0$, $p = 0.03$) and face-related ones ($F(1,10) = 4.9$, $p = 0.05$). Over the left leg-area, leg-verbs thus lead to the strongest activity.

Post-hoc tests for HEMISPHERE:

- There were only differences for the **arm-verbs** over arm-regions (left>right, $F(1,10) = 6.1$, $p = 0.03$) and leg-regions (left>right, $F(1,10) = 7.7$, $p = 0.01$).

- Notably, no other post-hoc tests yielded a significant level.

## X.5 Discussion

We investigated brain responses to visually presented face-, arm- and leg-related verbs in the MEG. Our main findings are:

- In a very early time frame, 80-120ms, we found the topographies of brain responses to action related verbs to be differed between the brain areas that are responsible for carrying out the actions the verbs refer to.

- This differential topography was found in the frequency range from 32-40Hz (gamma-band) but not in lower frequencies.

- Gamma-band responses to verbs related to hand- and arm-movements were stronger in the left hemisphere than in the right. In contrast, brain responses to leg- and face-verbs did not differ in their laterality.

Early gamma band responses:

Pantev et al. (1991) also found gamma-band responses occurring very early on (100-150ms), although in the evoked gamma. Pulvermüller et al (Pulvermüller et al., 1996) point out that the MEG might be better suited for detecting high frequency responses as there is no attenuation of the magnetic brain response as compared to the electric brain response. As amplitudes generally decrease with their frequency the attenuation observed in the EEG is stronger for higher frequencies. Moreover, we can rule out that the differential activation in the gamma-band is caused by harmonics in lower frequency bands as all statistics on lower frequency band did not attain significance.

In an earlier study (Pulvermüller, Assadollahi, & Elbert, 2001), we found differences due to word classes in neuromagnetic brain responses very early on (90-120ms). Studies concerning length and frequency of words also reported early word dependent brain responses (Assadollahi & Pulvermüller, 2001: 90-120ms, Assadollahi & Pulvermüller submitted: 60-90ms, 90-120ms)

Thus the present study again confirms that early differences related to linguistic word properties are detectable.


Specific hypothesis concerning different topographies due to verb-classes:

Hypothesis 1.)

A neurobiological approach to language suggests **different word classes** and their subclasses **activate different brain areas**. This postulate leads to the prediction that different topographies of brain responses to words from different word classes will be found when presented to the brain. Consistent with this general claim, the statistical significance of the VERBxREGION interaction indicated that topographies of brain responses vary between verb-classes. Further, the significant VERBxHEMISPHERExREGION interaction indicated that they do so differentially for the hemispheres.

Hypothesis 2.)

Hypothesis 1 only postulates *that* the topography of the verb dependend brain responses varies, but not *in what way*. However, based on the neurobiological theory of

language the more specific prediction can be made, that there are differences in the topography over the areas around the central sulcus (Brodman areas 1-4) which are responsible for executing actions (pre-central motor areas) and receiving the feed-back of these actions (post-central sensory areas). The significant interaction of RE-GION and VERB-CLASS we found clearly undermines this postulation. However, additional differences were observable over visual cortices. Although we closely matched stimulus groups for word length, word form- and lemma-frequency, there might be other word-properties that influence early visual processing. Earlier studies (Pulvermüller, Hummel, & Härle, 2001; Hauk & Pulvermüller 2002) reported a difference for arm-words compared to both other stimulus classes in the right frontal area. The gamma-band response to arm-verbs in figure 2 (middle column) suggests that such an activity might be found in the present study as well.

The cell assembly theory is not specific about the activation of other assemblies whose sub-assemblies might lie in vicinity or even overlap with active cell assemblies. To some degree a co-activation could occur, it might also be possible that other assemblies might stay silent completely. Therefore, a stronger and even more specific prediction would be that **areas not involved** in the performance of the particular action **should not be activated** by the presentation of this word. This strong claim would imply that for leg-related words the areas responsible for arm movement are as inactive as areas for face movement. However, there are arguments why this strong claim may not be tested adequately. Often, the representation of a word emphasises the movement of a certain extremity but does not explicitly exclude the movement of others, like in the word 'to dance'. Dancing involves the movement of legs but is often accompanied by the movement of the arms or the whole body. These words are often referred to as "gestural postures". In fact, we found leg-related words to activate arm areas as well, although not as strongly as leg areas. This effect was found for both hemispheres. Other words refer explicitly to a certain part of the body but implicitly involve the coordination of other body parts. 'to bite' involves the movement of the jaw and the mouth, but very often implies that one is grabbing the item that is bitten by using her hands. Therefore some association with the hands

is imaginable that in turn is represented neuronally in the motor cortex. Again, this is reflected in our data: face-related words co-activate arm areas to some degree.

The degree to which additional areas might be involved is hard to determine. This leads to a somewhat weaker claim that **areas** that are **not involved** in the prominent part of a verb's representation are **activated to a lower degree** than areas that directly refer to the core meaning ('to bite' = to move one's jaw in a way that the teeth get into something). From this perspective, when comparing sub-classes of action words such as leg-related words and arm-related words one might expect a preponderance of activity over the area that reflects the core of the word's meaning. This might also partially account for the fact that Pulvermüller et al (Pulvermüller, Hummel, & Härle, 2001) and Hauk and Pulvermüller (2002) were not able to find specific differences for arm-related words as arm-areas might be co-activated by face-verbs and leg-verbs. In a recent review, Rizzolatti and Luppino (Rizzolatti & Luppino, 2001) came to the conclusion, that arm and face areas are not easy to distinguish as they overlap considerably, which is especially true for the pre-motor areas. This might in part account for the absence of strong differences between arm and face related words in the two studies mentioned above as well as for the gros similarity of the activations by face and arm words in the present study (cf. figure 3). In agreement with the hypothesis, post-hoc tests confirmed that arm-verbs induced a significantly stronger activation over the arm-area compared to the face-area of the left hemisphere. However, a contradicting finding is that arm-verbs led to stronger activations in the face area of the right hemisphere than in the arm area. Figure 2 suggests that the gamma-suppression (blue, gamma-activation below baseline level) might be responsible for this effect. In sum, only this single post-hoc test contradicts the hypothesis.

Hypothesis 3)

Related to the last postulation is a third postulation, namely that the activation evoked by a **certain verb-class** in its related brain area is **stronger** than the activation in this area evoked by **verbs of other classes**. In the present study leg-verbs lead to stronger brain responses over centro-central areas (coordinating leg movements) than face-related words in the left hemisphere and they were stronger than responses

to both other categories in the right. Arm-verbs tended to lead to stronger responses over arm-areas than leg words and face-verbs lead to stronger activations in face-areas in the right hemisphere than leg-words. In sum, we think to have found many indices that such this hypothesis can be accepted, especially as there were no results in the post-hoc test that directly contradict it.

Hypothesis 4):

Some verb-classes involve the movement of both limbs ('to walk', 'to grin'), some only involve one ('to write'). If we investigate the three grand classes, leg-, arm-, face-related words, then it is evident that the majority of leg- and face-related words tend to involve both sides of the body (and thus: hemispheres) in contrast to arm-related words that have a greater degree of freedom. One could therefore postulate that arm-related words have a stronger degree of lateralisation (to the left hemisphere in right-handers) than the other two classes. Our data, for the first time, confirms this claim. Only arm-verbs lead to significantly stronger brain responses in the left hemisphere than in the right.

Of course this finding must be replicated in order to find its way into theorising, but if it turns out that this left-lateralisation for arm-verbs is stable one postulation of the neurobiological theory of language must be modified: closed class words with grammatical function ('the', 'from') are postulated to be lateralised to the left as they do not have associations to movements or objects. In contrast, content words ('sun', 'to drink') are postulated to not to be lateralised as they refer to things and movements that are represented in both hemispheres (Pulvermüller & Mohr, 1996). The present data however, suggests that some content words (like arm-related verbs) can be strongly lateralised as the neuronal substrate for processing the underlying meaning is naturally (by the handedness of the subject) lateralised.


## X.6 Conclusions

We found differential topographies to verb-class in the brain response. These differences occurred relatively early after visual presentation (80-120ms). Moreover, they could only be observed in the gamma band range from 32 to 40 Hz. The topographies

reflected the verbs' meanings in that they activated areas in the motor cortex that are related to the verb's meanings: Activations to leg words were strongest over cortical leg areas, for example. Actions that are conducted with one preferred hand (arm-verbs) lead to brain responses that were stronger over the corresponding hemisphere.

## X.7 References

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