

Language outside the focus of attention: The mismatch negativity as a tool for studying higher cognitive processes

Friedemann Pulvermüller*, Yury Shtyrov

Medical Research Council, Cognition and Brain Sciences Unit, 15 Chaucer Road, Cambridge CB2 2EF, UK

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Abstract

Which aspects of language and cognitive processing take place irrespective of whether subjects focus their attention on incoming stimuli and are, in this sense, automatic? The Mismatch Negativity (MMN), a neurophysiological brain response recorded in the EEG and MEG, is elicited by attended and unattended stimuli alike. Recent studies investigating the cognitive processes underlying spoken language processing found that even under attentional withdrawal, MMN size and topography reflect the activation of memory traces for language elements in the human brain. Familiar sounds of one's native language elicit a larger MMN than unfamiliar sounds, and at the level of meaningful language units, words elicit a larger MMN than meaningless pseudowords. This suggests that the MMN reflects the activation of memory networks for language sounds and spoken words. Unattended word stimuli elicit an activation sequence starting in superior-temporal cortex and rapidly progressing to left-inferior-frontal lobe. The spatio-temporal patterns of cortical activation depend on lexical and semantic properties of word stems and affixes, thus indicating that the MMN can give clues about lexico-semantic information processing stored in long term memory. At the syntactic level, MMN size was found to reflect whether a word string conforms to abstract grammatical rules. This growing body of results suggests that lexical, semantic and syntactic information can be processed by the central nervous system outside the focus of attention in a largely automatic manner. Analysis of spatio-temporal patterns of generator activations underlying the MMN to speech may be an important tool for investigating the brain dynamics of spoken language processing and the activated distributed cortical circuits acting at long-term memory traces.

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* Corresponding author. Tel.: +44 1223 355294x770; fax: +44 1223 359062.

E-mail address: friedemann.pulvermuller@mrc-cbu.cam.ac.uk (F. Pulvermüller).

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1. The mismatch negativity: Change detection and memory trace indicator

Investigations of neuronal mass activity using electro- and magnetoencephalography (EEG, MEG) offer a unique opportunity to monitor non-invasively the spatio-temporal characteristics of brain processes. One of the most frequently investigated neuronal mass responses in Cognitive Neuroscience is the Mismatch Negativity or MMN. The MMN is an event-related response elicited by infrequent acoustic events, the so-called deviant stimuli, occasionally occurring among frequently repeated sounds, called the standard stimuli. Since the MMN was discovered (Näätänen et al., 1978), its properties were extensively studied using elementary acoustic events, such as brief tone pips, with the rare deviant stimuli differing from the repetitive standard stimuli in pitch, length, loudness, etc. In these experiments, the MMN was found to be an indicator of acoustic change detection, which, surprisingly, was present regardless of whether subjects focussed their attention on the stimuli or not. The MMN is therefore usually considered to be independent of focussed attention and it is, in this sense, an automatic brain response (Näätänen et al., 2001; Näätänen and Winkler, 1999). When claiming that the MMN indicates “automatic change detection”, it must, however, be taken into consideration that attentional load may influence the MMN (see Section 4.4) and that, in addition to its well-known role as an acoustic change detection indicator, the MMN reveals a range of higher cognitive processes.

Similar to most neurophysiological mass phenomena, the MMN can be recorded in the electric and in the magnetic brain response. In the latter case, it is also called the magnetic Mismatch Negativity or MMNm. Excitatory post-synaptic potentials arriving at the long apical dendrites of cortical pyramidal neurons give rise to an electric field that makes the cortex relatively negative at its surface and relatively positive at its basis (Mitzdorf, 1985). Concordant fields in thousands of neurons can be picked up in the EEG signal and in the averaged event-related potential or ERP. The current flow that leads to this polarity creates a magnetic field, which can be picked up by the superconducting quantum interference devices (SQUIDS) included in current magnetoencephalography (MEG) systems. As the main sources of the MMN are in superior-temporal cortex within the sylvian fissure, they are picked up by both EEG and MEG recordings and are revealed by both ERPs and event-related fields (ERFs). Apart from the superior-temporal sources, the MMN has been reported to have additional underlying cortical generators some of which change with the type of cognitive information that plays a role in eliciting the

MMN. These have been documented by fMRI, EEG and MEG studies (Opitz et al., 2002; Pulvermüller et al., 2003; Rinne et al., 2000). Differences may exist between the generator constellations inferred from EEG and MEG recordings, especially if some of the local generators are radial.

A main reason for the great importance of the MMN in cognitive neuroscience is the insight that it is linked to higher order perceptual processes underlying stimulus discrimination, rather than being triggered simply by physical differences between standard and deviant stimuli (Näätänen et al., 1993; Tervaniemi et al., 2001). Subjects exposed to a physical stimulus difference they are unable to discriminate may show only a minimal MMN, or even no MMN at all, to this acoustic contrast. However, as soon as the same subjects have learned to discriminate the critical stimuli, their MMN is reliably triggered by the acoustic stimulus contrast and MMN size is much increased (Kraus et al., 1995; Kujala et al., 2003; Näätänen et al., 1993; Schröger, 1996; Schröger et al., 1994). The MMN can even demonstrate a perception that does not have a direct physical basis in the acoustic input. Physiological manifestations of such perceptual illusions have been documented in a range of MMN studies (Colin et al., 2004; Micheyil et al., 2003; Ross et al., 1996; Stekelenburg et al., 2004; Tervaniemi et al., 1994). For example, a tone with a gap masked by broad-band noise elicits the so-called “continuity illusion”, the contra-factual perception of a continuous tone bridging the actual gap. The amplitude of the MMN has been shown to reflect this illusory-continuity perception. Furthermore, the MMN could be demonstrated to reflect abstract features of tone sequences. For example, in the context of stepwise upwards moving standard tones, an occasional downwards step presented as the rare deviant stimulus elicits an MMN irrespective of varying physical features of the sounds (Korzyukov et al., 2003; Paavilainen et al., 1995, 1998, 2001; Saarinen et al., 1992; Tervaniemi et al., 1994). This and similar evidence has led to the conclusion that, in addition to changes in the acoustic environment, higher level cognitive processes in the auditory system are reflected by the MMN (Näätänen et al., 2001).

Evidence for the usefulness of the MMN in the investigation of language was accumulated in recent years. When sounds of a linguistic nature were tested in oddball paradigms, it emerged that the MMN may indicate the presence of linguistic long-term memory traces. Stimuli representing typical examples of a phoneme category in a given language elicit a pronounced MMN in speakers of that language, whereas the MMN to the very same sounds was reduced in subjects whose language lacks a matching phoneme category (Dehaene-Lambertz, 1997;

Näätänen et al., 1997; Winkler et al., 1999b). It therefore appeared that, in addition to the change detection MMN elicited by the sounds per se, there is a phonological MMN response sensitive to native phonetic features. Experiments with young children indicated that this language specificity in MMN dynamics evolves with emerging language experience between 6 and 12 month of age (Cheour et al., 1998). A similar increase in phonetically elicited MMNs was shown in adults learning a foreign language (Winkler et al., 1999a). Unlike the acoustic change-detection MMNs, known to have bilateral or right-dominant distribution (Paavilainen et al., 1991), the phonological MMNs were lateralized to the left hemisphere as shown using MEG by Näätänen et al., 1997.

These results indicated that, on top of its known role as an automatic index of acoustic change detection, the electric and magnetic MMN may reflect the existence of learned neuronal representations or memory traces, conceptualized as large connected neuron ensembles, for the phonemes of languages one is familiar with. The strong internal connections within such neuron ensembles may provide the basis for cortico-cortical bottom-up and top-down activation following the presentation of learned acoustic elements, and the resulting neuronal mass response provides a tentative explanation for the enhancement of the MMN (Pulvermüller, 2001).

In subsequent research, it was shown that the MMN can indicate processes at other, “higher” levels of language processing as well. This evidence will be discussed in greater detail later in this paper. Here, we wish to highlight that MMN response characteristics were found to change with the lexical status of a stimulus, with grammaticality of a word string, and with the meaning of words used as deviant stimuli. We propose that the MMN is an objective and useful tool for investigating higher order language processes as they are elicited by spoken language stimuli, regardless of whether subjects attend to them or not. We use the results to draw careful conclusions on the time course of the cortical activation processes that manifest lexical access and selection, syntactic analysis, and semantic access. We also consider brain loci of these processes as suggested by neurophysiological source localization. First, however, we need to consider the motivations for using MMN to address language-related neural processes and a number of related theoretical issues.

2. Motivation for investigating brain processes of language using the MMN

Is the MMN elicited by speech an appropriate tool for studying brain basis of language? As there are already a number of neurophysiological dependent measures, components of the event-related potential and field, what are the specific advantages of using the MMN as a measure of brain activation to speech stimuli? Here are our main answers to these questions: The advantages of the MMN lie in its automaticity, earliness, and the perspective it opens on monitoring brain responses to individual linguistic items. We also discuss possible advantages of the oddball paradigm for controlling for physical features of the critical stimuli.

2.1. Automaticity

First, the MMN is automatic. This means, once again, that, for eliciting the MMN, it is not necessary that subjects perform an overt task or focus their attention on the stimuli, or on a specific processing aspect of these stimuli. Subjects can even be distracted – for example they can read a book or watch a silent film – while the acoustic stimuli are played. In spite of this distraction, the MMN is still elicited. Even highly demanding distraction is possible, for example by engaging the subjects in a demanding video game or by streaming their attention away from the stimuli to a competing task (see Section 4.4), and still there is an MMN, and sometimes even an unattenuated one (Alho et al., 1992; Surakka et al., 1998; Woods et al., 1992). This makes the MMN a measure that can monitor neural processes without being influenced by attentional biases and strategies so characteristic of cognitive tasks traditionally implemented in psychophysiological experiments.

To illustrate this, we would like to consider examples relevant to the investigation of brain mechanisms of language. In frequently used language tasks, the subjects have to indicate the meaningfulness of phoneme sequences or the grammaticality or intelligibility of word strings. In such tasks, it is likely that different stimulus types put different attentional demands on the cognitive system. Finding a lexical representation or syntactic tree structure for a stimulus may require less processing resources than searching in vain the lexicon or syntactic rule space. Even if no task is used and subjects are allowed to “just listen” to speech stimuli under investigation, it appears natural that different stimuli are approached with different strategies. For example, subjects may spend more effort on finding a match for an unknown pseudoword than on listening to a familiar word, or they may contemplate grammatical errors in an ungrammatical string and evaluate different strategies for repairing them, but prepare for the next trial immediately after a well-formed sentence. This implies differences in the amount of attention directed towards different stimulus types as well as differentially biased strategies for dealing with them. These differences in task-oriented and attentional strategies between stimulus types can have a manifestation in behavioral responses, such as response times or error rates, and can clearly also have a neurophysiological reflection picked up in the brain response—although they are irrelevant to the processes forming the basis of word or sentence comprehension. Here, an automatic brain response such as the MMN provides an obvious advantage: it can be recorded while subjects are discouraged from processing the stimuli actively and, therefore, the danger that different strategies are used to process different types of input is minimized. This probability is still not likely to be zero, but, as we would like to argue, the MMN paradigm with its characteristic distraction from the stimuli is the best possible approach to avoid attentional, task-related or strategic biases towards one stimulus type.

The first reason for choosing the MMN when studying speech processing is therefore that it can be elicited in the absence of attention actively directed towards the stimuli.

2.2. Earliness

The second reason for using the MMN in the investigation of language processes is its earliness. Psycholinguistic behavioral studies indicate that crucial information about incoming words and their context is processed already within the first ~200 ms after a critical word can be recognized (Marslen-Wilson, 1973, 1987; Mohr and Pulvermüller, 2002; Rastle et al., 2000). In contrast, the neurophysiological responses most frequently studied in current brain imaging research on language, however, have peak latencies of 400–600 ms. This discrepancy between early psycholinguistic processes and late brain responses raises doubts whether the latter can reflect the former directly and are appropriate for exploring brain processes crucial for language comprehension.

Psycholinguistic research has demonstrated that subjects can already make reliable button-press motor responses to spoken words according to their evaluation of aspects of phonological and semantic stimulus properties within 400–450 ms after their onset (Marslen-Wilson and Tyler, 1975). Therefore, the earliest word-related psycholinguistic processes must take place substantially before 400–450 ms. At these early latencies, linguistic processing is already influenced by syntactic and semantic information (Marslen-Wilson and Tyler, 1975). Consistent with this, studies using the shadowing technique demonstrated that subjects can repeat an incoming sentence almost immediately, at a latency of as little as 300 ms or less, suggesting extremely rapid processing of speech (Marslen-Wilson, 1985): “If we assume that some component of the shadowing delay is taken up with the process of response integration and execution, then these subjects are able to initiate their output when they have heard no more than 150–200 ms of the input of each word they are repeating” (p. 59). Again, response latencies were influenced by syntactic and semantic context, demonstrating early near-simultaneous processing of different types of linguistic information (Marslen-Wilson, 1985). The early psycholinguistic effects were also documented in cross modal priming (Moss et al., 1997; Tyler et al., 2002; Zwitserlood, 1989), where specific semantic knowledge about an upcoming spoken word could be demonstrated to be present well before its end, within 200 ms after the acoustic signal allows for unique word identification or even earlier. The view that it takes only 100–200 ms to gain access and select an item from the “mental lexicon” is further substantiated by eye-tracking experiments demonstrating that a range of psycholinguistic properties of words influence short-latency eye movement responses (Serenó and Rayner, 2003).

As there is strong evidence for early psycholinguistic information access and processing, any direct neurophysiological reflections of psycholinguistic information access must be present at similar, if not shorter, latencies, likely within 200 ms. Therefore, the short latency of the MMN, which peaks between 100 and 250 ms after the deviant stimulus differs from the standard stimulus (physical divergence point), suggests that it may be a potential tool for studying the physiological basis of the early speech comprehension processes demonstrated by behavioral studies. The linkage found earlier between the

MMN and cognitive processes, and, more specifically, with memory traces for native phonemes, is supportive of this suggestion. As a range of results document early neurophysiological reflections of lexical and semantic features of written words (e.g., Assadollahi and Pulvermüller, 2003; Hauk et al., 2006a; Pulvermüller et al., 1995; Sereno et al., 1998), it is important to achieve a methodological standard for investigating early brain responses to spoken words and sentences, too.

2.3. Suitability for studying individual linguistic items

The third reason for using the MMN in language research is that it can reveal the brain basis of the processing of individual language stimuli. Why should this be an advantage? In most brain imaging studies of language, large groups of stimuli are investigated and compared with each other. In such experiments, the brain responses are averaged across entire groups of stimuli to draw generalized conclusions on all language materials falling into a certain category. However, this inference scheme is deficient for the following reason: If ERP or ERF averages over large stimulus groups yield a result, this does not demonstrate that all members of the stimulus groups contribute equally to the observed physiological difference. It could instead be that effects are due to a fraction of the group members, to a few outliers in the extreme. Even more devastating problems are entailed by the fact that words differ in their physical features (Fig. 1). For example, the earliest brain responses to long written words may be almost twice as large as that to short ones (see, e.g., Assadollahi and Pulvermüller, 2001), and the vast variability of physical features of spoken words likely leads to even more substantial variation. It was shown, for example, that early negative ERPs change with word length (Hauk and Pulvermüller, 2004a; Osterhout et al., 1997) and that physical stimulus parameters are of crucial importance for obtaining ERP effects of syntactic processes (Gunter et al., 1999). Differences even in basic physical features may lead to differential brain activation (Korth and Nguyen, 1997; Näätänen and Picton, 1987) that could overlap with, or be misinterpreted as, language-related effects. Controlling for such stimulus variation effects becomes utterly impossible if large groups of 50 or more spoken words are under study. The problem that arises in such cases is that the variation in physical stimulus features inevitably leads to variability in the early brain responses. If the latter are to reflect the neural basis of the early cognitive processes of language comprehension, this variability acts as noise, which can mask or even cancel the brain’s evoked potentials and/or fields of cognitive origin. We call this the physical variance problem (for discussion, see Pulvermüller, 1999).

An additional specific problem of stimulus group studies of spoken language is that speech unfolds in time and the psycholinguistic processes of interest follow word onset at variable latencies (Fig. 1). However, the neurophysiological brain responses are usually calculated from the onset of the critical word or phrase. This raises problems, since, if lexical, syntactic or semantic processes are under investigation, the relevant point in time is not the onset of a critical word, but

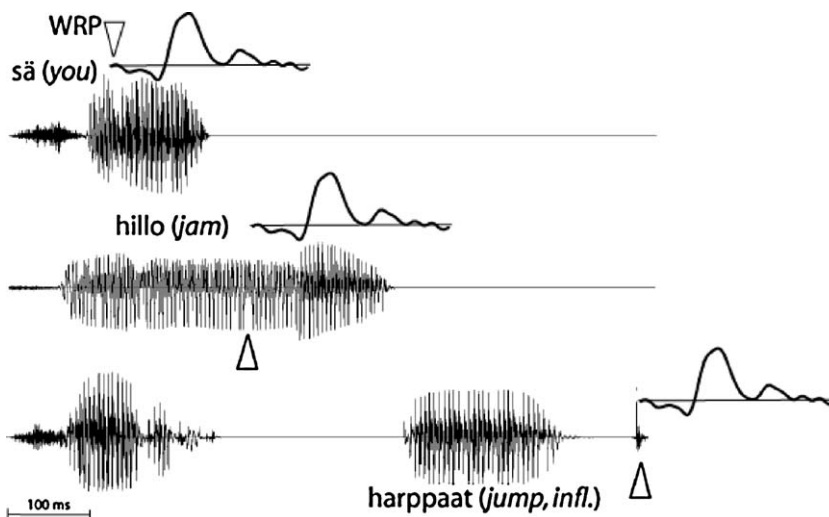


Fig. 1. Physical and psycholinguistic variance between different spoken words: acoustic waveforms of three example words of Finnish language (English translations in parentheses). Approximate positions of individual word recognition points (WRP) are marked with white arrowheads. A hypothetical short-lived brain response that might reflect the comprehension of each word shortly after the point in time when it can be uniquely recognized from the acoustic signal is schematically indicated. Please note that physical features and WRP latencies differ substantially between words. Averaging of neurophysiological activity over such variable stimulus sets will therefore blur and thus minimize or remove any early short-lived brain response locked to the recognition point.

rather the point in time when the word becomes distinct from its lexical competitor environment and can therefore be recognized with certainty, the so-called word recognition point or WRP (Marslen-Wilson, 1987).¹ Now one may argue that, to reveal physiological-linguistic correspondence, one can always relate the average word recognition point for a stimulus group to the onset or peak latency of the averaged physiological response, as we and others have done in the past (e.g., Pulvermüller et al., 1999). However, this strategy is still imperfect for the following reason: If word recognition points differ between stimuli, word comprehension and the other “higher” syntactic and semantic processes will occur at different points in time for different stimuli. If the brain responses reflecting the higher processes are early and therefore short-lived and focal, this temporal variance may not only reduce but also remove any effect from the average. We call this the psycholinguistic variance problem and it is clear that, apart from word recognition latencies, the variability of numerous other psycholinguistic variables could play a role in reducing early averaged brain response (for discussion, see Pulvermüller, 1999).

Considering the physical and psycholinguistic variance problems, it is not surprising that many studies following the “mix and average” strategy could reveal late long-lasting and

widespread language-related responses, such as the N400 or the P600 (see Section 3.2), but not early, brief and focal lexical, syntactic and semantic effects. In order to obtain the early effects it may be best to reduce stimulus variance. It has therefore been proposed to keep factors known to influence early brain response, such as word length, lexical frequency and recognition latency, to a minimum in word group studies that aim at documenting early linguistic brain activity (Pulvermüller, 1999). The maximal reduction of such variance can be achieved in studies of single items where all relevant physical and psychophysiological factors have been carefully controlled. This means adopting in-depth investigation of single stimuli, a strategy with a long tradition in psychoacoustics (Carlyon, 2004), for investigating the neurophysiological basis of psycholinguistic processes (Pulvermüller et al., 2001c; Shtyrov et al., 2003). Demonstrating a physiological basis of a psycholinguistic process for an individual speech stimulus provides an existence proof for such a correspondence. It does not in itself allow for generalized conclusions for all stimuli of the same kind, but replicating results for different individual stimuli can provide a basis for generalized conclusions and complementary studies using a greater set of stimuli with minimal acoustic-psycholinguistic variance may further strengthen generalized conclusions.

The single item approach to the neurophysiology of spoken language would, as we would like to submit, avoid some of the shortcomings of the conventional stimulus group approach, especially the physical and psycholinguistic variance problems. We therefore believe that stronger conclusions on early cognitive brain responses can be based on single item studies than on the stimulus group approach. At the least, single item studies are necessary to complement neurophysiological studies of speech stimulus groups. On the other hand, because, naturally, also the single item strategy has its limitations, for example, those grounded in the fact that stimuli must be repeated within the experiment, it would be ideal to confirm

¹ The word recognition point is the point in time during listening to a spoken word when subjects are relatively certain about which word they are hearing. Hearing “cro”, there is a range of possible candidates, a “cohort” of words that could continue the stimulus. The cohort is narrowed down when the input string becomes larger: (“croc”, “croco”, “crocod”) and at one point subjects report to be reasonably sure about the word. The point in time within a spoken word where subjects judge that they are 80% sure is called the Word Recognition Point, WRP, and the point in time when there is objectively only one possible continuation left is sometimes called the isolation point of a spoken word. The gating task, where subjects have to judge fragments of different length obtained from spoken words is used to obtain information about word recognition dynamics (Marslen-Wilson, 1990).

results from single item studies by investigations of low variance stimulus groups. When applying a single item approach, recording MMN is an optimal option, since the very paradigm of MMN studies implies recording and analyzing responses to one or few well-controlled deviant stimuli.

2.4. Control of the effect of physical stimulus features: Identity MMN and theory

As an additional advantage, the oddball paradigm opens the possibility to control for physical stimulus properties in a much more stringent manner than it was possible in previous work. Not only is it possible to minimize physical and psycholinguistic variance and exactly match individual speech stimuli for length, F0 frequency, word recognition points and a range of physical and psycholinguistic factors. It is also possible to record and “subtract-out”, or minimize, the neurophysiological manifestations of physical stimulus features, including those immanent to the early event-related components P1 and N1. If the stimulus used as the deviant in the MMN oddball design is, in a separate control experiment, being used as a frequently repeated item, it will elicit its obligatory, or exogenous, evoked potential components but not an MMN. In this case, an “identity MMN” can be calculated by subtracting the ERP to the deviant stimulus by the ERP to the identical frequently repeated “control standard” stimulus so that, ideally, the P1 and N1 contribution is removed (“subtracted out”). It is necessary to note that this technique does not guarantee removal of all contributions of the P1 and N1 components, because a phenomenon called N1 enhancement (see for example, Teder et al., 1993) may be less pronounced in the “control standard” ERP than in the deviant ERP. However, the identity MMN technique allows one to minimize the possible influence of the physical stimulus properties on the MMN response as far as this seems possible. In conventional ERPs, obtained without any subtractions, the neurophysiological activity is always under the strong influence of physical stimulus features.

The use of the brain responses to the same stimulus in one case presented as the rare deviant stimulus and, in the other case, frequently and repeatedly presented as the standard stimulus of the control experiment, has an obvious theoretical and neurophysiological reason: Neurophysiological research has shown that stimuli are represented in the brain by neuronal populations that serve as a substrate of stimulus recognition and of short-term active memory (Fuster, 1997, 2003, 2004). Intracortical neurophysiological recordings revealed that neurons activated when specific stimuli were perceived and kept in active memory usually show an initial strong activation followed by exponential decline of their activity with time. Over 20 s, these “memory cells” lose activity continuously. Therefore, re-appearance of a stimulus at a delay of 20 s leads to a strong re-activation of the network, whereas, if the stimulus is presented at a short latency, the memory network will still be strongly active so that only little additional activity enhancement is possible. This provides a reason why the oddball paradigm, where deviant stimuli are repeated with a long average stimulus onset asynchrony of around 10 seconds or

even longer, can reveal the activation of memory networks in the brain. By subtracting the deviant stimulus ERP by the ERP to the identical stimulus presented as the “control standard”, it may even be possible, as we would suggest here, to obtain the relatively pure contribution of the memory network by minimizing bottom-up perceptual process contributions.²

We note that the oddball paradigm is not strictly necessary for implementing a long SOA between stimuli, which, according to this view, should be crucial. However, by presenting stimuli with long gaps of up to >10 seconds of silence in-between, it might be impossible to control the subjects’ attention and direct it away from these rare stimuli during the long pauses. In this case, the possibility exists that they continue to process the previous stimulus, or fail to disengage from processing it, thus making it impossible to achieve network deactivation, which, in turn, may make it difficult to see memory trace related cortical activity. The oddball paradigm, where the standard stimulus intervenes among consecutive presentations of the deviant stimulus, may facilitate the necessary disengagement (cf., Posner and Raichle, 1994) from the deviant stimulus and therefore help to deactivate its memory trace. We therefore suggest that the MMN recorded in the oddball paradigm is a brain response that is unique in allowing the researcher relatively direct access to the memory networks that underlie cognitive processing. Consistent with this, the set of cortical sources revealed by the MMN in the processing of higher language functions by far exceeded those of classic sensory components such as the N1 to elementary acoustic stimuli (Pulvermüller et al., 2004, 2005b).

In sum, we propose to use the MMN in neuropsycholinguistic studies of spoken language, because it does not require focussed attention (automaticity), has short latency (earliness), and can be used to study individual speech stimuli exactly matched for physical and psycholinguistic features. Furthermore, it allows one to “subtract out” major manifestations of the physical stimulus features at the neurophysiological level and obtain a relatively pure measure of memory trace activity, especially if the identity MMN is calculated. There are other early neurophysiological brain responses that share some of these advantages, but these responses are primarily driven by physical stimulus features. In contrast, the MMN’s unique role as an index of early higher cognitive processes (Näätänen et al., 1978, 2001) suggests to explore its usefulness in pursuing investigations of “higher” aspects of human language.

3. Theoretical issues: Functional seriality or parallelism in spoken language processing?

3.1. Serial models of language processing

If we conceptualize the speech perception system in a traditional way, as suggested by many cognitive models, we may envisage the level of phonological analysis to follow the level of acoustic information extraction. “Above” these

² The relationship between the N1 and the MMN is a topic of an ongoing debate (e.g., Jääskeläinen et al., 2004; Näätänen et al., 2005).

“basement” and “ground floor” systems, “higher” levels can be envisaged, one for word – or lexical – processing, which is sometimes conceptualized as the “lookup” of a lexical item in a “mental lexicon” comprising only word forms but not their meaning or other word related information. At this level or slightly later, syntactic information bound to a lexical item may also be processed. A separate (second) higher level may exist for semantic information defining the meaning of words and longer utterances by listing their essential semantic features, but not arbitrary memories attached to language elements. Finally, a further (third) level of higher language processes can be envisaged for syntax and the grammatical information immanent in word combinations and sentences. This “town-house model” of language comprehension is an echo of early psycholinguistic models (Dell, 1986; Fromkin, 1973; Garrett, 1980; MacKay, 1987; Morton, 1969) also resonating in current approaches to speech comprehension and production (Levelt et al., 1999; Norris et al., 2000). There is some discussion on whether the individual components should be added, omitted, or merged with others (e.g., Caramazza and Miozzo, 1998), or arranged differently (Gaskell and Marslen-Wilson, 2002), but it is generally agreed that these types of information need to be processed when words and sentences are to be comprehended.

The question of where in the brain these different information types are processed is still under discussion, in spite of much imaging work done in recent years. As an example, the cortical locus of semantic information integration has been discussed controversially, and, although several researchers now attribute semantic information processing to areas in inferior-temporal lobe (Price, 2000; Rogers et al., 2004), there is evidence for a contribution of frontal lobes to semantics as well (Bak et al., 2001; Hauk et al., 2004; Posner and Raichle, 1998; Pulvermüller, 2005). Other linguistic processes, for example syntax, have tentatively been localized in different parts of the perisylvian cortex in the dominant left hemisphere (Friederici, 2002; Kaan and Swaab, 2002).

Psycholinguistic models postulating processing stages that receive their information in a linear serial order can be used to make predictions on the time course of the processing of different types of linguistic information (phonological, lexical, semantic, syntactic). Because the time delays that may occur between different types of information access can be in the range of hundreds or tens of milliseconds, fast neurophysiological imaging techniques are necessary for the testing of these theories at the level of the brain. Slow haemodynamic imaging methods, including PET and fMRI, are not sufficient, as they do not have the necessary time resolution in the millisecond range. In contrast, fast neurophysiological imaging studies, for example using EEG and MEG whose millisecond-by-millisecond time resolution is unrivaled, can provide the necessary grain to distinguish potentially minimally different activation time courses.

3.2. Neurophysiological evidence for serial information access in language comprehension

A great debate about whether processing of psycholinguistic information types is stepwise, that is, serial or cascaded, so that

access onsets differ substantially in time between information types, or whether they take place near-simultaneously instead, can potentially be decided on the basis of neurophysiological data. Physical (20–200 ms latencies, Krumbholz et al., 2003; Lutkenhoner et al., 2003) and phonological (100–200 ms latencies, Obleser et al., 2004; Poeppel et al., 1996; van den Brink et al., 2001) processes are reflected in the brain response already before 200 ms after the relevant stimulus information is available. According to the stepwise models, the “higher” (lexical, semantic, syntactic) processes follow later. The N400 component, which peaks around 400 ms after the onset of a critical visual word (Kutas and Hillyard, 1980) is traditionally considered the main neurophysiological index of semantic processes. Kutas and Hillyard found that it is elicited by “senseless sentences”, more precisely words presented in a sentence context where they are grammatically possible, but semantically unexpected. The N400 is elicited by written and spoken words presented in and outside sentence context and its size appears to reflect the degree to which a word is expected semantically. Semantic differences between words may lead to N400 responses with different topographies (Kiefer, 2001). The N400 component, or perhaps its slightly earlier peaking sub-component called N350 (M350 in MEG recordings), is also considered to be an index of lexical processing (Holcomb and Neville, 1990; Pyllkanen and Marantz, 2003; Stockall et al., 2004); but see also Bentin et al., 1999. For syntax, an even later component, the P600, has been reported that differentiates between well-formed and grammatically incorrect word strings (Hagoort et al., 1993; Osterhout and Holcomb, 1992), although an early component, the early left anterior negativity (ELAN) peaking at 100–250 ms, has also been found to be associated with grammaticality (Friederici et al., 1993; Neville et al., 1991). Therefore, the classical neurophysiological studies allow us to tentatively label the different linguistic information types with the putative times (in milliseconds after the respective information is present in the input) of the neurophysiological processes that manifest their access in the brain (Table 1).

These data appear to support stepwise, serial or cascaded, access to linguistic information types. Phonological and, for written language, orthographic processing seems to precede

Table 1

Time course of the processing of different linguistic information types according to classical studies of event-related potentials (ERPs)

Classical ERP components and language processes			
Information type	Topography	Delay (ms)	Component
Syntactic	Centro-parietal	500–700	P600
	Left anterior	100–250	ELAN
Semantic	Centro-parietal	300–500	N400
Lexical	Centro-parietal	250–500	N350
Phonological		100–400	N100, N200
Acoustic		20–200	P20-N100

The scalp topographies, typical latencies and labels are indicated for a selection of components that reflect processing of acoustic, phonological, lexical, semantic and syntactic information. Topographies are omitted if several components are listed. Latencies are relative to onset of the critical stimuli. The letters N and P in component labels, respectively, indicate negative- or positive-going ERP components.

lexical and semantic access, with a potential serial alignment of the latter two processes as well (Bentin et al., 1999). The N350 index of lexical processes seems to peak slightly earlier than the semantic N400 (Pykkänen and Marantz, 2003). Syntactic processing has at least two temporal loci within this sequence, possibly reflecting initial access to syntactic information and later grammatical reanalysis, respectively (Friederici, 2002).

3.3. Neurophysiological evidence for early psycholinguistic information access

The processing sequence indicated in Table 1 is still sometimes being considered the mainstream view on the neurophysiology of information access in language recognition (see also Fig. 2, left side). However, a different picture of the linguistic information processing sequence arises from neurophysiological studies looking in detail at the early brain responses peaking between 50 and 250 ms after the critical information is available in the input (right side of Fig. 2). In these studies, lexico-semantic and word frequency effects were seen already at 100–250 ms after visual word onset (Assadollahi and Pulvermüller, 2003; Hauk and Pulvermüller, 2004a; Martin-Loeches et al., 1999; Sereno and Rayner, 2003; Sereno et al., 1998), shortly after, if not near-simultaneous with, the effects of physical stimulus features. Neurophysiological differences between lexico-syntactic categories, such as content and function words or nouns and verbs, were also seen early (150–250 ms, Dehaene, 1995; Hinojosa et al., 2001a; Preissl et al., 1995; Pulvermüller et al., 1995), as were brain reflections of semantic properties of single words (80–250 ms, Ortigue et al., 2004; Pulvermüller et al., 1999, 2001a, 2001b; Skrandies, 1998; Skrandies and Chiu, 2003). A brain response peaking around 250 ms called the recognition potential (Rudell, 1992) could also be shown to be sensitive to lexical status (Martin-Loeches et al., 1999), word frequency (Rudell, 1999), lexical category (Hinojosa et al., 2001a) and meaning of words (Hinojosa et al., 2004; Martin-Loeches et al., 2001). As mentioned in the previous paragraph, there is also evidence for

early syntactic processing (100–250 ms, Friederici et al., 1993; Neville et al., 1991). These results speak in favor of parallel models postulating near-synchronous access to all types of linguistic information in word and sentence comprehension (Marslen-Wilson and Tyler, 1975, 1980; Pulvermüller, 2001). This near-simultaneous information access would, accordingly, occur at 100–250 ms, the exact point in time probably depending on stimulus and task properties.

However, most of the results reviewed above in this section are based on studies of written language. The lion's share of neurophysiological studies of spoken language is still consistent with step-wise information access. However, whereas visual presentation of a word implies simultaneous presence of different kinds of psycholinguistic information, spoken language unfolds over a considerable length of time with acoustic and phonological information usually preceding the availability of lexical, semantic and syntactic stimulus features (see Section 2.3 and Fig. 1). This implies that investigations of spoken language are confounded by the simultaneous versus serial availability of different kinds of linguistic information. The serial availability of psycholinguistic information types in spoken language comprehension can be controlled for by exact evaluation of psycholinguistic properties of individual stimulus items, and by relating the psycholinguistic data to neurophysiological dynamics. In this endeavor, the MMN can serve an important function.

For the reasons described, we consider it important to use the MMN to properly explore the neurophysiological basis of the time course of access to different types of psycholinguistic information in spoken language comprehension. In the following sections, we will discuss the evidence emerging from studies undertaken with this aim.

4. MMN evidence

Here, we will focus on the time course of higher language processes, i.e. on lexical, semantic and syntactic processing, as

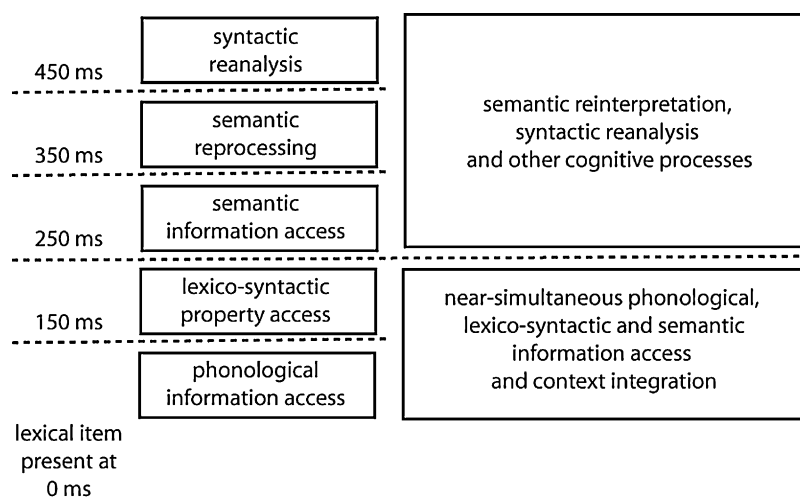


Fig. 2. Time course of psycholinguistic information access in word recognition. After the information in the input is sufficient for identifying a word in the input, serial and cascaded models (left side of the diagram) postulate a sequence of processing steps that start at different times. In contrast, parallel psycholinguistic models (right side) postulate near-simultaneous access to different types of psycholinguistic information, which may be followed by second order computations and reprocessing of already accessed information.

they are revealed by the Mismatch Negativity, or MMN, brain response. Separate sections will be devoted to words as units stored in memory or in a “mental” lexicon (lexical processing), to word meaning (semantic processing), and to sentence structure (syntactic processing). A final section will focus on the possible role of attention in the neurophysiological study of language.

As mentioned in Section 1, the MMN was found to reflect phonological properties of speech sounds. Following studies by Näätänen’s and Dehaene-Lambertz’s groups (Dehaene-Lambertz, 1997; Näätänen et al., 1997), there was a series of contributions agreeing on greater MMNs to known language sounds as compared with unknown sound that were not part of the subjects’ phonological repertoire (e.g., Koyama et al., 2000; Shestakova et al., 2002). In addition, acoustic contrasts that cross a phonemic boundary led to larger MMN responses than comparable acoustic contrasts that did not (Aaltonen et al., 1997; Dehaene-Lambertz, 1997; Phillips et al., 2000). Furthermore, there were reports that the MMN can reflect a range of additional processes related to phonology, including those of language-specific phonotactic and statistical constraints (Bonte et al., 2005; Eulitz and Lahiri, 2004) and the integration of visual with auditory information in phoneme perception (Colin et al., 2002; Mottonen et al., 2002). As mentioned, the neurophysiological signs of learning of phonological memory traces occur in the second half of the first year of life (Cheour et al., 1998), but phoneme learning can be neurophysiologically traced also later in life (Winkler et al., 1999a). Phonological processes reflected by the MMN have been localized in space to the superior-temporal cortex, with laterality to the left dominant hemisphere. In time, the phonological effects are early, usually occurring between 100 and 200 ms after onset of vowels or CV syllables (Näätänen, 2001). This confirms a left-hemispheric early locus of phonological processing.

4.1. Lexical access and selection

When does a spoken word presented in the input activate its lexical entry? The “lexical entry” can be conceptualized as a network of neurons that has been formed during learning, which is likely housed in the perisylvian (especially inferior frontal and superior-temporal) cortex and lateralized to the language dominant hemisphere. For convenience, we can call the connected neuronal network of the lexical entry a cell assembly (Hebb, 1949) or word web (Pulvermüller, 2003). The activation of a strongly connected neuronal set leads to spreading of activity within the feedforward and feedback connections within this set. Due to this feedback and feedforward activation, the amount of overall neuronal activity should therefore be larger when a cell assembly is being activated than in a condition where no such network becomes active.

To properly investigate the distinction between activation of a lexical representation and the failure of such activation, it is necessary to compare physically identical stimuli that nevertheless differ in their lexical status (in being either a word or not). Otherwise, the physical stimulus differences, which are, as

we argued above, near impossible to control, will confound what may appear to be a lexicality difference. In this situation, the MMN, which is elicited by contrasts between standard and deviant stimuli rather than by stimulus features per se, may be particularly useful.

In MMN studies of lexical access the physical variance problem can be solved by placing the same syllables in contexts where they either complete words or fail to do so and thus, terminate meaningless pseudowords in the testing language. Given that the acoustic contrast between standard and deviant stimuli is kept constant between words and pseudowords, a fully crossed design can be applied to control for the influence of context and critical syllables. In a number of studies, Finnish was used as the testing language as this language is one of the few in which long pauses within words can have the linguistic status of a phonological distinctive feature. Geminate stop consonants of Finnish include a pause of 200–250 ms followed by the plosion of the stop consonant. In neurophysiological studies, this pause makes it possible to record a pre-stimulus baseline before the first acoustic signal of the critical syllable is presented.

In such an experiment, which compared the magnetic responses elicited by the syllable [ko] completing the Finnish word “pakko” (Engl.: compulsion) with that elicited by the identical syllable stimulus completing the pseudoword “takko”, a larger MMN in the word context as compared with the pseudoword context was found (Fig. 3). A larger MMN in word context than in pseudoword context was also seen for the syllable [ku], which, in sharp contrast to [ko], forms a word with the syllable [ta] (“takku”, Engl.: tangle) but not with [pa]. All words under study had their recognition points at 30–40 ms after onset of the critical acoustic signal, that is, after the end of the pause of the geminate stop consonant. This elevation of the MMN is apparently due to a process separate from acoustic change detection and may reflect the activation of long-term memory traces for meaningful language elements in the brain. Such memory traces, instantiated as neuronal ensembles distributed over the perisylvian language areas, should incorporate multiple connections between the participating neurons and local neuron groups, as discussed above. We hypothesize that it is activation within these strongly connected networks that accounts for the increase of magnitude of the event-related response in meaningful word contexts, as compared with pseudoword contexts. Note that the orthogonal design applied not only controls for physical differences between the critical syllables eliciting the MMN and their preceding context syllables, but also for possible effects of the sequential probabilities with which phonemes follow each other. Therefore, the results rule out an explanation in terms of bi- or trigram frequencies of the critical phonemes.

In an EEG study on lexicality effects, Korpilahti et al. (2001), who used a contrast between the same long and short Finnish vowels incorporated in either words or pseudowords, also found a significantly enhanced MMN response for the native words. Using MEG, Kujala et al. (2002), found an increased MMN for words using three-syllabic words and pseudowords differing only in one (middle) syllable. In an

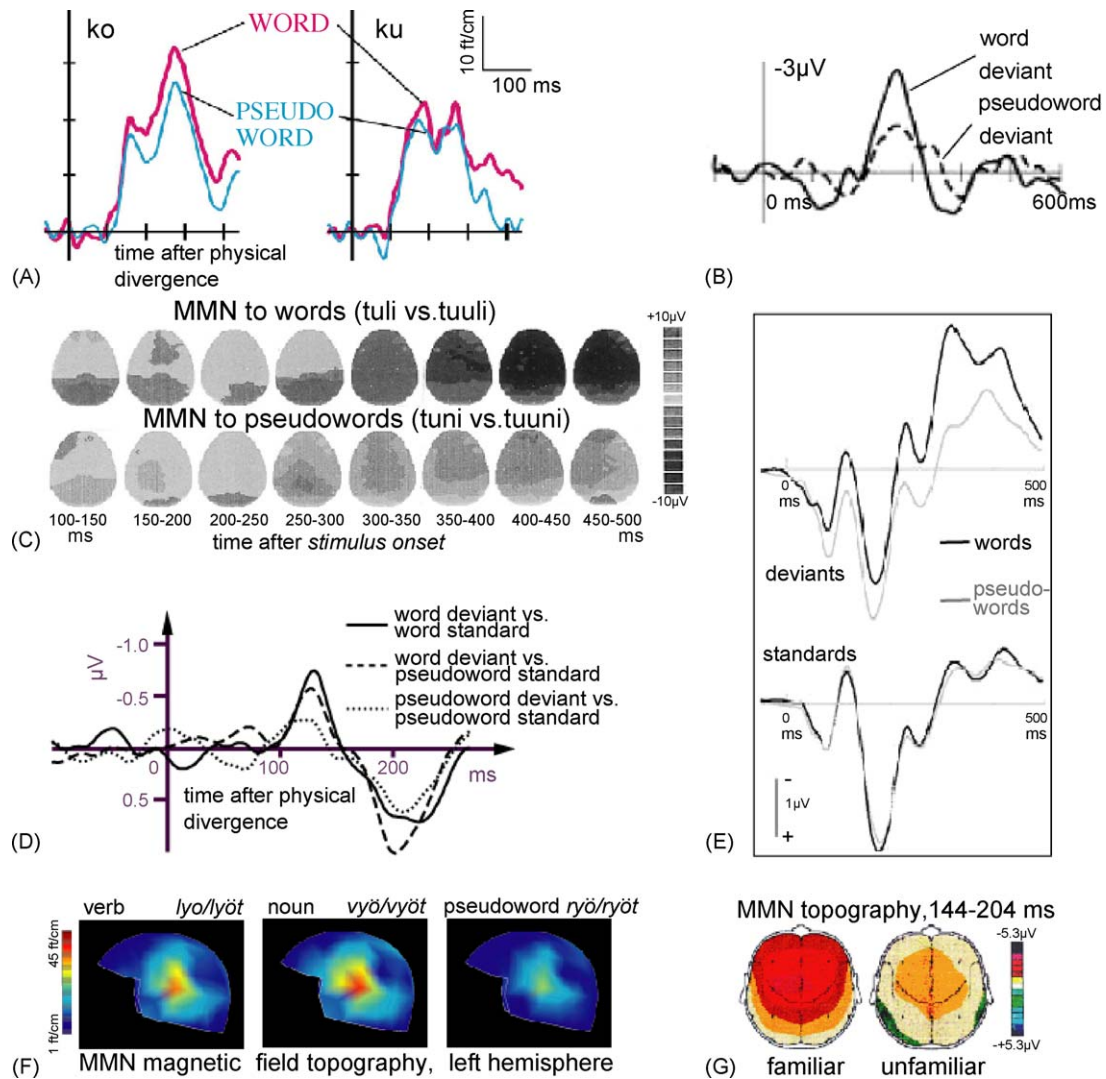


Fig. 3. Enhancement of the Mismatch Negativity in word context relative to pseudoword context: overview of recent results: (A) magnetic MMN elicited by identical CV-syllables completing either Finnish words or pseudoword (after Pulvermüller et al., 2001c); (B) EEG data using English stimuli (after Pettigrew et al., 2004a); (C) spatio-temporal patterns of MMN activation elicited in Finnish-speaking children by words and pseudowords incorporating the same vowel contrasts (after Korpilahti et al., 2001); (D) EEG study using identical acoustic contrasts but varying lexical contrasts between the standard and deviant stimuli (after Shtyrov and Pulvermüller, 2002): the results indicated that the enhanced MMN is elicited whenever the deviant stimulus is a word, but irrespective of presence/absence of lexical contrasts; (E) MMN enhancement to German function words vs. pseudowords: The difference is clearly generated by neurophysiological responses to deviant items, not by those to the standard stimuli (after Endrass et al., 2004); (F) magnetic MMN responses elicited by identical contrasts (presence/absence of stimulus final plosion [t]) in verb, noun, and pseudoword contexts (after Shtyrov et al., 2005): A clear increase in response amplitude is seen in both word contexts as opposed to the pseudoword context; and (G) MMN responses elicited by tonal contrasts incorporated in familiar words and unfamiliar syllables of Thai (after Sittiprapaporn et al., 2003, 2004): In Thai speakers, the MMN to native meaningful words was enhanced.

attempt to delineate the nature of the MMN enhancement to words, we looked at the MMN elicited by word and pseudoword deviants in the context of different kinds of standard stimuli, keeping constant the acoustic difference between standard and deviant stimuli between conditions (Shtyrov and Pulvermüller, 2002). An MMN was elicited either by rare English words occasionally presented (i) among repetitive words (deviant stimulus “tight” versus standard stimulus “type”) or (ii) among pseudowords used as standard stimuli (“bite” versus “bipe”), or (iii) by pseudowords presented among words (“pite” versus “pipe”). If the lexical contrasts were critical for the MMN enhancement, only conditions (ii) and (iii) should lead to the enhancement; if the

lexical status of the deviant stimulus was relevant but that of the standard stimulus irrelevant, the lexical enhancement would be predicted specifically in conditions (i) and (ii). The latter hypothesis matched the outcome of the experiment: MMNs elicited by word deviants were found to be larger than the MMN elicited by the deviant pseudoword, but the lexical status of the standard stimulus was not reflected by the size of the MMN. This pattern of results indicates that the MMN enhancement is indeed due to the activation of long-term memory traces for the deviant items rather than to an overall lexical contrast between the standard and deviant stimuli. This conclusion was also supported by another study using monosyllabic English stimuli (Pettigrew et al., 2004a).

Research on the lexicality contrast and the neurophysiological differences between words and pseudowords has recently been extended to tonal languages where words (and pseudowords) can be differentiated by pitch (Sittiprapaporn et al., 2003). This research showed a reliable MMN enhancement for words as compared with pseudowords in native speakers of Thai. A study investigating the MMN elicited by German words and pseudowords presented to either the left or right ear or simultaneously to both ears of experimental subjects found a greater MMN to words than pseudowords in the binaural condition (Endrass et al., 2004). Importantly, this study used function words that do not have specific referential meaning but are used to convey grammatical information, whereas most earlier work focussed on meaningful content words; it thus appears that important neuronal substrates are similar between the neuronal processes for these different vocabulary types.

Thus, the lexical enhancement of the MMN has to date been confirmed by a number of studies (Endrass et al., 2004; Korpilahti et al., 2001; Kujala et al., 2002; Pettigrew et al., 2004a, 2004b; Pulvermüller et al., 2001c, 2004; Shtyrov et al., 2004; Shtyrov and Pulvermüller, 2002; Sittiprapaporn et al., 2003) using different languages, imaging techniques, and a range of word stimuli (see Fig. 3). In contrast to these results, Wunderlich and Cone-Wesson did not find larger MMNs to CVC words (e.g., [bæd]) than to CV pseudowords ([bæ]). In this study, however, physical stimulus properties were obviously not matched, as this study focused on psychoacoustic issues (Wunderlich and Cone-Wesson, 2001) rather than on the word-pseudoword distinction. Pettigrew et al. (2004b) have reported lack of robust MMNs elicited by speech stimuli with fine acoustic contrasts, especially in voiced English stop consonants, and such MMNs might be particularly vulnerable to a change in syllable context. Therefore, the reduced MMN to CVC syllables relative to CV syllables might be due to physical stimulus features.

Similarly, Jacobsen et al. (2004) did not replicate the lexical MMN enhancement, although they claimed having matched all relevant factors. On closer examination, however, it turns out that what they used as their German pseudoword was, in fact, a word with low lexical frequency ([ʃa:p], an imperative form of the verb “schaben”, engl.: scrape). As a further possibly relevant feature, we should mention that the few studies that failed to replicate the lexical enhancement of the MMN reported so far have used synthesized word and pseudoword stimuli, whereas most studies confirming the word enhancement used naturally spoken words and pseudowords that were selected and processed to control for physical stimulus features. It is possible that, apart from other features, a critical question in MMN research on language is whether speech stimuli are naturally spoken and sounding or are synthesized.

As previously discussed, studies from our lab indicated that the lexical status of the deviant stimulus was relevant for eliciting the MMN, but the lexical status of the standard stimulus did not significantly affect the MMN amplitude (Shtyrov and Pulvermüller, 2002). However, others have reported that the event-related brain response evoked by the speech standard stimulus may also be affected by its lexical status (Diesch et al., 1998; Jacobsen et al., 2004), a claim which is not in direct conflict with the MMN evidence and opens perspective for future research.

In most studies, the lexical enhancement of the MMN was found around 130–150 ms after stimulus information allowed for unique word identification. There was some variation between studies and, in some cases, a longer lasting effect persisted up to 250 ms (Pulvermüller et al., 2004). The main cortical sources of the word-evoked MMN revealed by Equivalent Current Dipole analysis were in superior-temporal cortex, anterior to Heschl’s gyrus. Distributed source analysis indicated a spread-out superior-temporal source and an additional inferior frontal one peaking shortly after the former (time difference ~ 20 ms, see Fig. 4 and Pulvermüller et al., 2003).

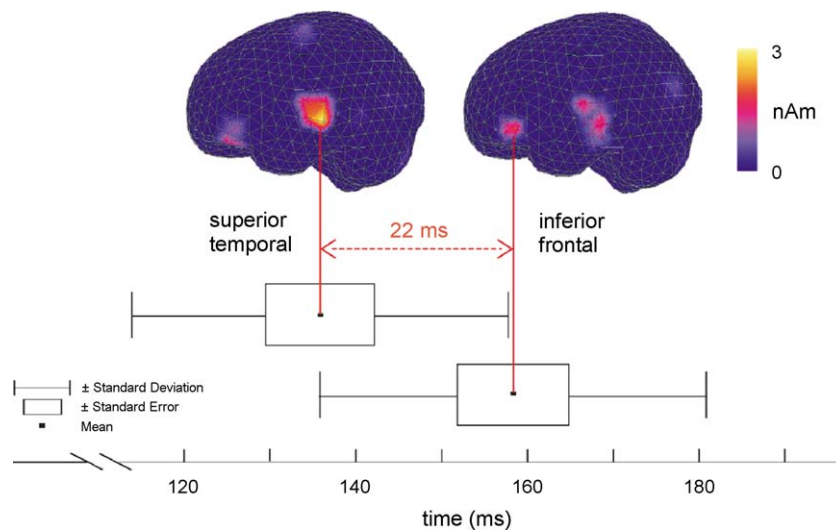


Fig. 4. Cortical sources of the magnetic Mismatch Negativity elicited by a spoken word and the time course of maximal activation of these sources: Time is given relative to the recognition point of the word presented as the deviant stimulus in a passive oddball paradigm. Note that a superior-temporal source peaked at 130–140 ms, closely followed by an inferior frontal source at 150–160 ms. This spatio-temporal pattern of cortical activation may be related to the activation of a word-related neuronal assembly (adopted from Pulvermüller et al., 2003).

On the basis of these data, we hypothesized that the MMN might include information about the point in time when cortical memory networks for lexical items become active. This leads to the prediction that the point of word recognition in the ongoing acoustic signal has a correlate in the MMN. This issue could be approached by using physically different word stimuli with different word recognition latencies. Indeed, in a study, where ERPs to two similar English words (kick versus pick) were studied (Shtyrov et al., 2004), a remarkably similar difference between the MMN latencies (30 ms) and word-recognition points (38 ms) was found between the two individual word stimuli. However, in this design, physical differences between stimuli are an unavoidable confound. We therefore chose to look at stimuli for which speakers showed massive differences in the use of subphonemic co-articulatory cues, so that different subjects identified the same words at different latencies. With this design, it was possible to compare the different time courses of psycholinguistic processes in different speakers while keeping physical stimulus properties constant. In a gating task, word recognition points were determined for each stimulus word and subject separately, and an acoustic discrimination task was used to examine psychoacoustic processes elicited by the stimuli. In addition, magnetic MMNs were recorded to the same stimuli in each subject. The correlation between word recognition points and peak latencies of the MMN sources in the left superior-temporal lobe was significant, therefore suggesting that MMN latency indexes word recognition processes (Pulvermüller et al., 2006b).

We therefore conclude that MMN amplitude and latency can reveal information about cortical processes of lexical access and selection. The latency at which the lexical selection process becomes manifest neurophysiologically varies slightly between studies but was in most cases present around 130–150 ms after the acoustic input allowed for identification of the critical word. External validation for early brain indicators of lexical access and selection comes from conventional EEG studies of written word processing (Assadollahi and Pulvermüller, 2001, 2003; Compton et al., 1991; Hauk and Pulvermüller, 2004a; Sereno and Rayner, 2003; Sereno et al., 1998) and from studies using intracortical recordings (Halgren et al., 1994).

Other representational MMN responses have meanwhile been documented for familiar meaningful non-language sounds, too. These include familiar melody patterns (Jacobsen et al., 2005), whistling patterns (Frangos et al., 2005), and even clicks produced by human finger and tongue (Hauk et al., 2006b). Similar to words, these meaningful stimuli elicited larger MMN responses compared with matched meaningless and unfamiliar sounds. In one case, it could even be demonstrated that the cortical sources of the sound-elicited MMN reflected the body parts used for generating the sounds: finger snaps elicited cortical sources in the sensorimotor cortex dorsal to those of tongue clicks. These results show that the memory traces demonstrated for meaningful familiar units of speech have similar memory trace mechanisms as meaningful non-language sounds. Future research may fruitfully investigate whether there are systematic differences in the cortical source constellations underlying the MMN to meaningful linguistic and non-linguistic sounds.

4.2. Semantic processes

When in the course of spoken language understanding is the specific semantic information tied to a lexical item accessed in the brain, and could the MMN help to reveal this process? Some brain models of language postulate that semantic concepts linked to words are housed in different brain regions, reflecting the kind of meaningful information stored (Martin and Chao, 2001; Pulvermüller and Preissl, 1991; Warrington and Shallice, 1984). If correct, this provides a basis for neurophysiological experiments of meaning access, because one could then make specific predictions from aspects of a word's meaning on the brain areas it activates and investigate the time course of this excitation (Pulvermüller, 1996, 2005).

We tried this strategy with a pair of words clearly differing in meaning, a concrete visually well-imageable word (the Finnish word “lakki”, Engl.: cap) and a more abstract and less imageable word (“lakko”, Engl.: strike, walkout), hypothesizing that only the concrete imageable word would elicit strong activity in both cerebral hemispheres, whereas the word lacking clear referential meaning might be predominantly stored by circuits in and close to the left-hemispheric perisylvian language areas (Pulvermüller, 1996). We controlled for the physical differences between the stimuli by comparing the electric MMN to the word final syllable to that elicited by a pseudoword ending in the same syllable. Again, physically identical control stimuli were used and the preceding context syllables were also identical between the two pseudowords. The words “lakki” and “lakko” were compared with the pseudowords “vakki” and “vakko”. All stimuli included a pause of 250 ms as part of the “double k”.

Source estimates of the lexical MMN enhancement elicited by the two words showed primarily left-lateralized sources for the abstract word and a bilateral slightly right-lateralized source constellation for the concrete imageable word, thus supporting the prediction (Pulvermüller et al., 2004). Unfortunately, the word pair was not matched for standardized lexical frequency; however, assuming that a word frequency difference cannot account for a rightward shift of word-evoked sources (cf., Assadollahi and Pulvermüller, 2003; Hauk and Pulvermüller, 2004a; Sereno et al., 1998), the semantic explanation of the observed difference in cortical generators appears plausible. The between-word differences were present already 100–150 ms after stimulus information allowed for unique word identification, suggesting surprisingly early access to aspects of word semantics. This study also makes it clear that the previous findings of predominant left-hemispheric (Pulvermüller et al., 2001c) versus right-hemispheric sources (Kujala et al., 2002) of the lexical MMN are compatible with each other and may be grounded in word specific differences, possibly in their semantic meaning.

In further studies, we used action words referring to different body parts, e.g., “pick” and “kick”. Referential meaning is an integral part of a word's semantics (Frege, 1980). These words' regular usage for referring to arm/hand actions or leg/foot actions, respectively, is therefore an essential characteristic of their meaning, although their semantics can certainly not be

exhaustively described by these features. In this logic, lexical representations become manifest cortically as perisylvian cell assemblies and the motor actions referred to by these words are laid down in motor areas of the brain, in particular premotor and primary motor areas. Therefore, the semantic links between neuronal sets in these cortical regions should realize the semantic relationship between the word forms and their actions (somatotopy of action word model, Pulvermüller, 2001). Crucially, this leads to the specific prediction that action words with different reference domains in the body also activate the corresponding areas of motor cortex, a claim which receives strong support from conventional neuroimaging studies (Hauk et al., 2004; Hauk and Pulvermüller, 2004b; Tettamanti et al., 2005). We used the MMN to determine whether meaning access in word recognition requires focussed attention and, if so, when semantic access in spoken action word recognition takes place.

Two MMN experiments were performed, one using 64 channel EEG and English stimuli, using the words “pick” and “kick” (Shtyrov et al., 2004) and one using 306 channel MEG and words of Finnish, the word forms “hotki” and “potki” meaning ‘eat’ and ‘kick’ (Pulvermüller et al., 2005b). In both experiments, the classical superior-temporal MMN sources became maximally active at the usual time, at 130–150 ms. Activation elicited by the words referring to face and/or arm movements activated inferior fronto-central areas in the vicinity of the cortical representation of the upper body. Critically, the leg words elicited a stronger superior central source, compatible with leg area activation. This leg word specific superior fronto-central activation was seen later than the inferior fronto-central activation predominating for face- and arm-related words. In one of the studies, inferior fronto-central activation was seen 140–150 ms after the word recognition point, whereas the superior activation focus evoked by leg words was maximal at 170–180 ms ($\Delta t = 30$ ms; see Fig. 5). These spatio-temporal characteristics suggest that MMN sources in perisylvian areas along with near-simultaneous activation in other cortical areas can reflect access to word meaning in the cortex. The minimal delays between area activations may be mediated by cortical conduction delays caused by the travelling of action potentials in relatively fast-conducting cortico-cortical axons (~ 5 m/s). The fast myelinated axons of 0.5–1 μm diameter, which are known to be the most frequent cortico-cortical axon type and therefore carry the main burden of long-range communication within cortex, would cause a delay of ~ 20 ms for a travelling distance of ~ 10 cm and can therefore explain the delays measured (see also Fig. 4, Pulvermüller, 2000).

Based on these data, we suggest that processing of semantic features of action words is reflected in the MMN as early as 140–180 ms after acoustic signals allow for unique word recognition. Similarly early influences of word semantics were suggested by a recent study using the MMN to assess how semantic violations are processed by the brain; in this case, the authors used full length sentences and stimulus features were well-controlled for by using the same contrasts in a semantically neutral condition (Menning et al., 2005). They found semantically-driven MMN modulation at 150–200 ms

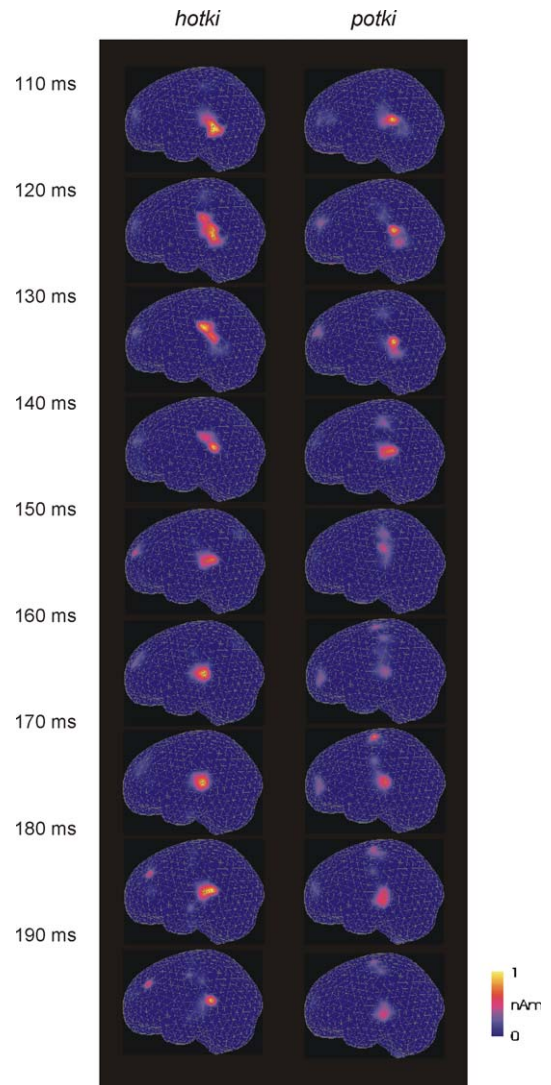


Fig. 5. Spatio-temporal patterns of the activation of cortical sources constellations elicited by the Finnish face- and arm-related action word “hotki” (English, EAT) and the leg-related word “potki” (KICK): Word stimuli were presented as deviant stimuli in an MMN experiment against meaningless standard stimuli composed of the same first syllable as the respective word stimulus ([hot] or [pot]) but ending in the syllable [pi]. Note the difference in topographies of cortical sources, especially the superior fronto-central activation elicited by the leg word. Times give latencies relative to the point in time when words could be uniquely recognized (adopted from Pulvermüller et al., 2005b).

thereby confirming earlier findings on the time course of semantic information access in the brain, now adding the insight that even semantic context integration can be cortically reflected by the MMN within a fifth of a second. It therefore seems that, similar to lexical access and selection, meaning access and integration may be an early neural process occurring within the first 200 ms after critical syllable onset, and even slightly earlier if the point of unique word recognition is used as the reference point. The lexical and semantic access can thus be conceptualized as near-simultaneous. Slightly increased delays seen for the presumably semantically related activations to some word categories (relative to lexical ones) can, in part, be explained by larger cortical distances that need to be bridged

when the distributed neuronal networks binding word form and meaning are being accessed.

External validation for early semantic access in word recognition comes from EEG and MEG studies converging on the result that semantic features of a word are reflected within 200 ms after written word onset (Hauk and Pulvermüller, 2004b; Hinojosa et al., 2004; Martin-Loeches et al., 2001; Ortigue et al., 2004; Sereno et al., 2003; Skrandies, 1998; Skrandies and Chiu, 2003). This evidence for early neurophysiological indicators of semantic processes reflecting aspects of word meaning does not devalue earlier findings about the N400 response as an index of semantics. The N400 is typically elicited by words that do not fit into a given semantic context. It may be that the early neurophysiological responses, including the MMN, reflect initial access to semantic information related to a word and its immediate integration into context, whereas the N400 response could index additional late semantic processes. These putative additional late semantic processes include, for example, second attempts at integrating a word's meaning into a meaningful context, a process of search for a more appropriate word in a given context, or the thought processes arising from confrontation with unlikely cognitive links.

4.3. Syntactic processes

A conventional way of studying syntactic processing in the brain is to compare the neurophysiological responses to well-formed grammatical sentences (for example “we sing”) with those to ungrammatical strings (“we sings”). In recent research, this strategy in MMN was used to look at syntactic processing under conditions where subjects were discouraged from attending to language stimuli and focus their attention on other tasks. Would the previously known neurophysiological indicators of syntactic processing, such as the early left-anterior negativity and the late positivity at 600 ms (cf. Section 3.2), persist under such attentional withdrawal?

Neurophysiological indicators of syntactic agreement were studied, because this grammatical phenomenon has earlier been reported to elicit both early and late neurophysiological grammar indicators (e.g., Deutsch and Bentin, 2001; Gunter et al., 2000; Hagoort et al., 1993; Münte et al., 1997; Osterhout et al., 1996; Barber and Carreiras, 2005; Osterhout et al., 1996). To control exactly for physical stimulus properties, identical naturally spoken linguistic stimuli were presented in different contexts, in minimal phrases consisting of two words. The critical second word occurred after a context word with which it matched in syntactic features or mismatched syntactically. For example, in one study (Shtyrov et al., 2003), the context word was a pronoun and the critical word an inflected verb of the Finnish language so that subject-verb agreement was the syntactic feature of interest. The minimal phrases of the Finnish language differed only in one single phoneme, the inflectional affix at the end of the verb, which rendered the entire phrase either grammatical or ungrammatical. Acoustic and lexical differences were controlled for by using an orthogonal design in which the phoneme's effect on grammaticality was inverted. The same physical contrast (in this case between verb final [n]

and [t] sounds indicating first versus second person singular) made a phrase grammatical or ungrammatical dependent on context determined by the preceding pronoun, so that, once again, an orthogonal design could be benefited from.

MMNm responses to the syntactically incorrect phrases were always larger than those to the correct phrases ending in the same word regardless of the direction of the acoustic contrast or of the preceding pronoun. The modulation of MMN by grammaticality under non-attend conditions clearly suggested that early syntax processing in the human brain may take place outside the focus of attention. Source analysis (single-dipole models and minimum-norm current estimates) indicated grammaticality-dependent differential activation of the left superior-temporal cortex suggesting that this brain structure may play an important role in such automatic grammar processing (Shtyrov et al., 2003).

In principle, the syntactic enhancement of the MMN could be related to processes that detect the feature that a word string is ungrammatical and includes a syntactic violation. In contrast to violation detection, there is a second possibility: that the critical word, which violates the grammatical structure, is unexpected in a given context, whereas the word placed in a correct sentence is primed through the grammar network. The MMN could thus indicate syntactic priming or lack thereof. To decide between these possibilities, words can be presented (a) in syntactic context; (b) in ungrammatical context; and (c) out of any linguistic context. The prediction of the grammatical violation theory is that a syntactic MMN is seen only in ungrammatical context (b), whereas the syntactic priming theory predicts enhanced MMN responses in both ungrammatical and out-of-context conditions but not in syntactic context.

Additional experiments were conducted now investigating the electric MMN response elicited by English syntactic and a syntactic phrases (“we comes”, “we come”) and comparing them with the MMNs elicited by the same critical words outside of linguistic context, after a noise burst with similar acoustic characteristics as the pronouns used as the context words (Pulvermüller and Shtyrov, 2003). As in the MEG study, syntactically incorrect stimuli elicited stronger MMN response than the grammatical ones. Crucially, when comparing the MMNs to the critical word in linguistic context with those obtained outside of linguistic context (after noise), it emerged that the MMNs were similar between syntactic violation and noise conditions. In contrast, the MMN elicited by grammatical phrases was markedly reduced compared with the MMN to the same critical words presented out of context.

This pattern of results indicates that the syntactic MMN is not triggered by a brain mechanism related to the detection of syntactic anomalies, a syntactic violation detection system. Rather, it appears that it is related to priming of a critical word by its canonical syntactic context. The syntactic priming effects may be mediated by neuronal assemblies specialized for processing regular serial order relationships between lexical items (Knoblauch and Pulvermüller, 2005; Pulvermüller, 2002). Source localization performed on the syntactic MMN effect obtained in the EEG indicated a strong contribution of left inferior frontal cortex already 100–150 ms. These results

complement the findings obtained with MEG and together are consistent with the suggestion that both inferior frontal and superior-temporal areas in the left perisylvian language region specifically contribute to syntactic processes (Friederici and Kotz, 2003; Kaan and Swaab, 2002).

A more recent confirmation of the syntactic role of the MMN came from an MMN experiment of syntactic violations (determiner-noun agreement in grammatical case) in naturally spoken sentences of German (“Die Frau düngt den *Rosen im Mai”, Engl. approximately: “The woman fertilizes this *roses in May”); the suffix of the word indexed with an asterisk syntactically mismatches with its context, as it does not agree in case and number with the determiner). The authors found an increased MMN amplitude elicited by the critical word (“Rosen”) placed in ungrammatical context (Menning et al., 2005). This effect emerged already at 150–200 ms with activity sources (equivalent current dipoles) located in the left-temporal lobe, close to Heschl’s gyrus, and was near-simultaneous with the effect of semantic anomaly seen in a different condition.

All MMN studies of syntactic processing conducted so far failed to find evidence for any P600-like dynamics in the brain response. The late positivity emerging if subjects attend to ungrammatical sentences (Hagoort et al., 1993; Osterhout and Holcomb, 1992) thus seems to be absent when attention is withdrawn from speech input in the MMN paradigm.

It should again be noted that the cortical locus where the main sources of the syntactic MMN were localized varied: MEG studies indicated a superior-temporal main source and some weak effects in inferior frontal cortex whereas EEG results suggested the opposite, a most pronounced grammaticality effect in inferior frontal cortex. This slight divergence matches well the neuroimaging literature on the cortical basis of syntax, where this module is sometimes localized in frontal areas (e.g., Musso et al., 2003) and sometimes in temporal lobes (e.g., Meyer et al., 2000). The best way to make sense out of this state of affairs seems to us to assume that different areas in perisylvian cortex contribute to grammatical and syntactic processing. In addition, the differential sensitivity of MEG and EEG and possibly different orientations of generators contributing to syntactic processing in frontal and temporal perisylvian cortex may further help to account for the observed difference.

The early syntactic MMN resembles the ELAN component (Friederici et al., 1993; Neville et al., 1991), which has been interpreted as an index of syntactic structure building (Friederici, 2002). Correspondence exists with regard to latency, topography including laterality, and most of the functional characteristics. However, the syntactic MMN can be elicited even if subjects do not attend to the word strings that elicit it, whereas the ELAN is usually recorded when subjects attend to language or even perform an attention demanding linguistic task to evaluate the word strings. However, our results converge on the interpretation that ELAN and syntactic MMN reveal related syntactic brain mechanisms. The MMN work complements the literature on the ELAN by showing that the early syntactic brain response does not require that attention be directed towards language stimuli. In this sense, early syntactic processing seems to be automatic (see also Section 4.4).

Because the MMN paradigm failed to reveal late grammatically related differences resembling the late positivity characteristic of syntactic violations in experiments where subjects are encouraged to attend to speech stimuli (see Section 3.2), these results confirm that the late positivity is under strong influence of attention (Hahne and Friederici, 1999). Therefore, the late positivity may reflect secondary controlled attempts at reparsing a string after the initial analysis has failed (cf. Friederici, 2002; Osterhout and Holcomb, 1992).

4.4. Varying attentional withdrawal in the study of language

The MMN has been proposed as an indicator of automatic, attention-independent processing. However, although some studies reported that the MMN does not change as a function of attentional distraction from the stimuli eliciting it, there is evidence indicating that the size of the MMN is larger if subjects attend to the stimuli, as compared with conditions where they are instructed to ignore them (see Section 2.1, Alho et al., 1992; Surakka et al., 1998; Woods et al., 1992). As it can be modulated by the level of attention, the MMN is not attention-independent in the sense that it does not reflect attentional processes at all. However, it can still be called attention-independent in the sense that it persists even under heaviest distraction. We may, for the purposes of an unambiguous discussion, call it “semi-automatic” in this review from now on.

In the study of language, it appears of greatest theoretical importance to find out to what degree MMN responses are subject to attention modulation. Are the lexical, semantic and syntactic modulations of the MMN response immune to attentional factors, and, if they are being modified by attention, when does this influence start? Is there, for example, evidence for an initial period of full automaticity where no influence of the load of distraction tasks can be documented, and for later stages where semi-automaticity can be postulated, that is, persistence of MMN responses modulated by attentional factors? Future research into the neurophysiology of language and attentional processing might greatly profit from a systematic experimental approach to these questions.

A first attempt in this direction was made in the syntactic domain. One may argue that demonstrating language-related effects in a paradigm where subjects are instructed to attend to a video film or book while language stimuli are presented does not control strictly for attention withdrawal. To draw conclusions on the automaticity of the processes investigated from such studies, subjects must strictly follow the instruction to try to ignore the speech stimuli, which they sometimes may fail to do (Carlyon, 2004). It would thus be desirable to control for the attention withdrawal in each subject throughout the experiment. Therefore, an experiment was performed to further investigate the role of attention in language processing by comparing the classic MMN paradigm with its moderate attention withdrawal by a silent video film with a distraction task where subjects had to continuously perform an acoustic signal detection task. In such a streaming condition, subjects

had to press a button to a deviant acoustic non-speech stimulus in the left ear while, at the same time, the language stimuli were played to the right ear; the conventional video presentation took place simultaneously with acoustic streaming task thus providing both across- and intra-modality distraction. In another condition, subjects were allowed to watch a video as usual, without further motor-task distraction, while the same stimuli, sounds and language stimuli, were played. Results showed a replication of the grammaticality effect, i.e. stronger MMNs to ungrammatical word strings than to grammatical ones up to a latency of ~ 150 ms., with no difference between task conditions varying attentional withdrawal. Only later, we found significant interactions of the task and attention factors indicating that at these later stages the grammar processes revealed by the MMN were influenced by attention and task demand. We interpret this as strong evidence for the attention independence of the early part of the MMN and for the automaticity of early syntactic analysis, and for a switch from strict automaticity to semi-automaticity at 150 ms, shortly after the peak of the MMN response (Pulvermüller et al., 2006a).

5. Conclusions

5.1. *The time course of information access in spoken language comprehension*

MMN studies of language processes suggest that all types of linguistic information are processed near-simultaneously shortly after the incoming acoustic signal allows for identification of the critical language sounds and words. The lexical MMN is generated in superior-temporal and possibly inferior frontal cortex at 130–150 ms. Correlates of semantic meaning access in action word recognition were seen at 140–180 ms in the same areas but also in cortical areas further away from the Sylvian fissure. The syntactic MMN was seen in several time windows starting as early as 100 ms and extending up to above 200 ms. Phonological MMN indicators of vowel processing were also seen in a wider time interval, at 100–200 ms after stimulus onset (Dehaene-Lambertz, 1997; Eulitz and Lahiri, 2004; Näätänen, 2001; Näätänen et al., 1997). These latencies are extracted from studies with methodological differences, for example with different stimulus intensities, artificially generated or naturally spoken speech. These and other methodological features can influence the latency of the MMN (see, for example, Tiitinen et al., 1994) and it is therefore not feasible to make comparisons in the millisecond range between studies. However, it clearly emerges from MMN research on language that specific neural processes reflecting lexical, syntactic and semantic processing can be documented within the first 200 ms after auditory information allows for recognition of critical lexical items, and that the early processing indicators of different kinds of linguistic information occur near-simultaneously.

As comparisons of time courses obtained between experiments on different types of psycholinguistic information processing are difficult, due to variance between stimuli and experimental subjects, studies investigating the same set of

subjects using the same acoustic contrasts that nevertheless provide information at different linguistic levels are of particular relevance. One recent study of this kind looked at the stimulus contrast resulting from the addition of a brief noise burst to the end of standard stimuli. If the standard stimulus was itself a non-linguistic sound, the MMN elicited by the noise burst peaked 138 ms after burst onset. After a speech stimulus, a meaningless pseudoword, the same noise burst was perceived as the plosion of a stop consonant, the phoneme [t], and its corresponding MMN was maximal at 155 ms. The sound was also perceived as a [t] in the context of meaningful words, where the MMN it elicited peaked at 138–148 ms (Shtyrov et al., 2005). As latency differences were not supported statistically, this study using identical stimuli carrying, in different conditions, acoustic, phonological or lexical information, does not support a serial order of the access processes to these different information types, but rather further argues in favor of their near-simultaneity. Furthermore, as already mentioned in Section 4, the study by Menning and colleagues suggested near-simultaneous access to semantic and syntactic information (Menning et al., 2005). In other studies (Pulvermüller et al., 2005b; Shtyrov et al., 2004), it emerged that the time delay between the peak activation of generators known to distinguish between lexical items and pseudowords (in superior-temporal cortex) and those reflecting aspects of referential semantics (in different areas of fronto-central cortex) is small and best accounted for by conduction delays related to cortico-cortical information transmission.

As mentioned in Sections 3.2 and 4.1–4.3, the MMN studies are complemented by work in the visual modality that further established early neurophysiological indicators of lexical, semantic and syntactic processes within 200 ms after stimulus information allows for word identification (Hinojosa et al., 2004; Sereno and Rayner, 2003). These studies of early responses with peak latencies between 100 and 250 ms after written word onset agree with findings summarized here, as they all suggest an early locus of lexical and semantic information access. The recognition potential, for example, indicates that lexical and semantic word categories, and also effects of semantic context, become manifest at or before 250 ms (Hinojosa et al., 2001a, 2001b, 2001c, 2004; Martin-Loeches et al., 1999, 2004). Conventional studies of lexical and semantic processes using a range of paradigms, including passive reading, visual lexical decision and memory tasks, even support lexical and semantic effects at 120–200 ms after written word onset (see Section 3 and Hauk and Pulvermüller, 2004a; Pulvermüller et al., 1995, 2001a; Sereno et al., 1998, 2003). The main conclusions implied by current MMN research, that language processing is rapid and different information types are accessed near-simultaneously, is therefore also corroborated by conventional ERP studies of visual language processing. Together, the two research domains provide cross-validation of these main conclusions.

There is an apparent incompatibility between the serial interpretation of linguistic information processing as put forward on the basis of classical, mainly N400- and P600-based evidence (see Section 3 and Table 1) and the parallel processing perspective opened by recent MMN studies

(Table 2). We would like to offer the following view to reconcile these (Fig. 2, right side): the early information access and selection reflected by early neurophysiological components may be followed by later language-related processes (Friederici, 2002), but also by more general thought processes triggered by the unexpected access to linguistic memory representations. In contrast to the more automatic early processes, these later processes of linguistic re-processing or successional cognitive activity heavily depend on attention and task-related strategies. The late optional processes (latencies >250 ms) may thus underlie the classical language potentials, for example the N400 and P600. This secondary processing account seems compatible with current proposals about the function of these neurophysiological indexes as indicators of grammatical reanalysis or second-path semantic context integration (Friederici, 2002; Hagoort, 2005; Osterhout and Holcomb, 1992).

5.2. Change detection MMN and representational negativity

We propose that the MMN as an early neurophysiological indicator of lexical, semantic and syntactic information processing reflect the early access to stored linguistic representations or symbols. An MMN would thus indicate the match or mismatch between a stimulus and its corresponding symbolic memory trace in the brain. These memory traces can be thought to be realized as discrete strongly connected networks of cortical neurons, sometimes called cell assemblies (Hebb, 1949), neuronal ensembles (Braitenberg and Schüz, 1998; Palm, 1982), distributed functional networks (Roland and Gulyas, 1994), neurocognitive networks (Mesulam, 1998) functional circuits (Feldman and Narayanan, 2004) or cognits (Fuster, 2003). It might therefore be sensible to think of the MMN as consisting of two parts: a part which reflects the automatic – or semi-automatic – detection of a change in the acoustic environment (Näätänen, 1990) and a part that reflects the activation of cortical cell assemblies forming the long-term memory traces for learned cognitive representations (Näätänen, 2001). If one wishes to distinguish the two, it might be

appropriate to call them classic or change-detection MMN and Representational Negativity, RN, respectively. Speech-elicited activity patterns coming in through sensory modalities may activate their matching memory traces at different levels, a process so robust that it even takes place if subjects try to ignore stimuli and focus their attention elsewhere, although it might be possibly modulated by attentional load (semi-automaticity).

It is important to note that the memory trace-MMN or RN is conceptualized as a neurophysiological index of the activation of a strongly connected cortical network possibly distributed over a range of cortical areas. As mentioned in Section 2.4, the properties of the oddball design might be ideal for revealing the activation of such networks. First, these memory networks are known to retain activity for seconds (Fuster, 2003; Fuster and Alexander, 1971; Fuster et al., 2000; Fuster and Jervey, 1981) so that repeated consecutive presentation of the same stimulus is insufficient for substantially activating the network, as it remains at its ceiling activation level. Second, the frequent standard stimuli intervening between subsequent deviant stimuli may be important for disengaging the attentional system (Compton et al., 1991; Posner and Raichle, 1994) from processing the deviant stimulus at a high activity level, thus facilitating the decline of activation of memory networks necessary for their later re-activation. Third, as also outlined in Section 2, using the MMN paradigm has a number of advantages for studying the brain basis of language, including its semi-automaticity, earliness, and the possibility it opens for precise stimulus matching. These advantages make the MMN paradigm a unique tool for investigating cognitive representations, especially of spoken language elements.

Although these advantages make the MMN paradigm an unrivaled procedure for recording the physiological correlates of memory networks activated by acoustic input, we should stress that there are also other methods that allow to reveal memory traces. This is evident from the fact that memory networks have first been demonstrated in monkey experiments where delayed matching to sample tasks were applied (Fuster, 2003). Also, in our own research, we could document language-related early processes indicating lexical and semantic

Table 2

Latencies and main cortical sources of neurophysiological indicators of acoustic, phonological, lexical, semantic and syntactic information processing as revealed by the Mismatch Negativity (MMN)

Time course of linguistic information access according to MMN studies

Information type	Cortical sources	Latency (ms)	Example reference
Syntactic	Left inferior frontal and superior-temporal	*100–250 130–280	Pulvermüller and Shtyrov (2003), Menning et al. (2005)
Semantic	Left inferior to superior fronto-central	*120–180 170–210	Shtyrov et al. (2004), Pulvermüller et al. (2005b)
Lexical	Left inferior frontal and superior-temporal	*130–150 160–190	Pulvermüller et al. (2001c), Pettigrew et al. (2004a)
Phonological	Left superior-temporal	100–200	Näätänen et al. (1997)
Acoustic	Superior-temporal and right frontal	90–170	Rinne et al. (2000), Opitz et al. (2002)

Latencies are given relative to critical stimulus onset; for higher linguistic processes above the phonological level, numbers marked by asterisks indicate latencies relative to the point in time when stimulus information allows for unique identification of the critical words. The second set of numbers given without asterisks indicates latency relative to critical syllable onset or to the relevant perceivable acoustic change.

networks by using a range of techniques (Pulvermüller, 2005). It should therefore be clear, that, although the MMN technique appears as an optimal tool for revealing the effects of memory network activation to acoustic input, it is not the only paradigm that allows one to investigate the neural basis of higher cortical functions.

Whereas the acoustic change detection MMN may have its cortical generators in superior-temporal lobe, the memory networks may be distributed over various cortical areas. They may involve frontal, parietal and occipital cortices, and some of their parts may be distributed over temporal sites. Recent claims that the seat of all sources of MMN-like activation are localized in superior-temporal cortex (e.g., Jääskeläinen et al., 2004) fall short of an account why the cortical distribution of the MMN can change dramatically, for example between linguistic stimuli with similar, even identical physical features but different semantic implications (Pulvermüller et al., 2005b; Shtyrov et al., 2004). The distributed source constellations underlying the MMN are best explained on the basis of memory networks with different cortical distributions whose activation is reflected by a sub-component of the MMN. This sub-component, which we referred to as a representational negativity, RN here, would be conceptualized as a memory trace indicator.

5.3. *The contribution of fronto-central cortex to attention switching and language comprehension*

Source localization performed on the acoustic MMN revealed a range of underlying cortical generator constellations, including sources in superior-temporal lobes and inferior frontal cortex (see also Fig. 4, Näätänen et al., 2001; Rinne et al., 2000). For speech stimuli, these generators are in most cases stronger in the left language-dominant hemisphere compared with the right hemisphere (Näätänen, 2001; Shtyrov et al., 2000). However, the range of generators underlying the MMN seems to vary as a function of linguistic element under processing. Considering the idea that part of the MMN may be a representational negativity whose generators reflect the extent and specific distribution of long-term memory networks instantiating cognitive representations at the cortical level, it becomes relevant to discuss their possible specific contributions to higher brain functions. What, therefore, is the specific role of frontal circuits in the early automatic access to linguistic information? What do the frontal activity “blobs” obtained from the source estimates actually tell the cognitive scientist?

One possibility is that the inferior frontal generators of the MMN reflect attention. This is not to say that they reflect selective attention, as it emerges when subjects prepare for processing a stimulus or making a response, but rather automatic re-orientation of attention triggered by a stimulus (Näätänen, 1990). Activation of frontal MMN sources (Molholm et al., 2005), in the right hemisphere in particular (Doeller et al., 2003), has been suggested to reflect attention-switching, the automatic re-direction of attention towards an unexpected or new stimulus (Näätänen, 1995). The frontal sources sparked by elementary acoustic stimuli (tones, pips) predominate in the right hemisphere whereas the language-evoked sources are stronger in the

left than in the right frontal cortex. Therefore, it seems reasonable to suggest that for linguistic processes, left inferior frontal areas may predominantly play the role of attentional re-orientation. This view would predict similar frontal activation patterns for different types of linguistic information, possibly engaging the same frontal attention system (Posner and Raichle, 1995) to different degrees for different linguistic information types. However, the frontal sources seem to vary between different studies of psycholinguistic processes and, more strikingly, different types of linguistic information even elicited differential source constellations in fronto-central cortex that could be linked to different types of linguistic information access (Pulvermüller et al., 2005b; Shtyrov et al., 2004). These differential frontal sources to linguistic stimuli are left unexplained by the attention-switching theory.

An additional and complementary interpretation is offered by brain theories inspired by recent findings about the cortical processing of actions and their corresponding perceptual patterns. Mirror neurons found in inferior frontal lobe (Gallese et al., 1996; Rizzolatti et al., 1996), but possibly more widely scattered throughout different parts of premotor and other areas (Buccino et al., 2001; Hauk et al., 2004), appear to be a cortical basis of knowledge about actions linked to sensory perceptions. The stimuli whose perception can spark action-specific mirror neurons include sounds associated with body actions, such as sounds resulting from dropping a stick or cracking a nut (Kohler et al., 2002). It is feasible to assume that action-perception circuits are being set up for spoken phonemes and syllables, as the articulatory patterns necessary to produce these speech items have a distinctive mapping onto specific perceptual patterns. The resulting distributed neuronal assemblies may bind perceptual and action-related information characteristic of speech items such as phonemes and word forms and may play a role in both perception and action. This is reminiscent of language theories in the tradition of the motor and direct realist theories of speech perception claiming that action related mechanisms play a crucial role in phoneme perception (Fowler et al., 2003; Liberman and Whalen, 2000). Likewise, strong linkage, within the phonological loop, between articulatory and acoustic phonological components, likely housed in perisylvian cortex, was postulated to be the basis of short-term verbal memory (Baddeley, 2003). Neurophysiological evidence obtained from monkeys provided direct support for fronto-temporal neuronal assemblies that bind action-related and perceptual information and form the biological basis of memories kept active in the short term (Fuster, 2003; Fuster and Alexander, 1971; Fuster and Jervey, 1982). More recently, a direct link between the perception of specific speech sounds and equally specific motor activity patterns in precentral cortex could be demonstrated (Pulvermüller et al., 2006c).

Distributed perisylvian neuronal assemblies linking together perceptual information stored in superior-temporal cortex and articulatory action-related information in inferior frontal cortex have been postulated at different levels of linguistic information processing, including the level of language sounds and that of meaningful words (Pulvermüller, 2001). The topography and time course of generator activations seen for word-related

MMNs confirm predictions of this model of distributed neuronal assemblies. It may therefore be that the inferior frontal activation, which followed superior-temporal activation elicited by speech, may index the activation of stored action programs related to speech sound and word articulation which is bound to the respective acoustic stimulus representations by distributed neuronal assemblies. Differential activation along the motor and premotor cortex in fronto-central cortex elicited by action words related to different parts of the body may reflect the specific semantic coupling of word forms and the representations of non-linguistic actions critical for action words. Inferior frontal activation related to syntactic anomalies may, in this logic, reflect the motor component of circuits for serial alignment and hierarchical or heterarchical structuring of words and morphemes in sentences. In this view, the different frontal areas activated when specific linguistic information types are being processed are related to different types of action programs intimately linked to and therefore contributing to language comprehension (Fig. 6).

According to this view inspired by the existence of action-perception networks, any phonologically regular stimulus would therefore activate a left-lateralized inferior-frontal source indicating the activation of the articulatory motor program associated with the sound or sound sequence. A spoken word form would activate the complex articulatory pattern related to the pronunciation of the word, which may spark an even stronger inferior frontal source, because, in the case of words, the individual speech sound representations are bound into a larger scale word-related cell assembly. If the perceived word's meaning relates to an action that usually involves the mouth, face, hand or arm, additional inferior and lateral frontal areas sources are sparked which indicate the semi-automatic mental processing of motor movements semantically associated with the word form. If a leg-related

word is under processing, the additional sources sparked are in dorsal fronto-central cortex, close to the vertex, and indicate the processing of leg movements the word form denotes. In this view, the full activation of the cortical cell assemblies linking action and perception representations to each other would be the basis of a strong activation process, once termed “ignition” (Braitenberg, 1978), which can be thought of as a possible basis of the automatic switching of attention elicited by an incoming stimulus. Although more evidence is needed to further bolster this view on the neurobiological basis of action programs linked to spoken language, it is already supported by a range of imaging results on language and memory processes in the human brain (Pulvermüller, 2005; Rizzolatti et al., 2001) and offers perspectives for a better understanding of the neurobiological basis of language and other higher cognitive processes.

6. Summary

We reviewed Mismatch Negativity (MMN) studies of lexical, semantic and syntactic processing. These studies suggest that these different “higher” linguistic information types are accessed and processed near-simultaneously within 200 ms after stimulus information allows for unique identification of the critical meaningful language unit. This time range overlaps with and may be identical to that of the MMN reflecting phonological and acoustic stimulus features. This evidence, together with other neurophysiological studies of early language-related brain responses, call into question serial models of language comprehension and weigh in favor of parallel models.

The MMN indicated early linguistic information access that does not require that subjects focus their attention on language or intentionally perform lexical, semantic or grammar tasks. In this sense, the MMN or its representational subcomponent, RN, reflects early automatic processes of lexical access and selection, semantic information processing and syntactic analysis. The frontal sources of the MMN, whose locus varied with linguistic information type under processing, may indicate the automatic access to action-related information relevant in the language comprehension process at different levels of processing.

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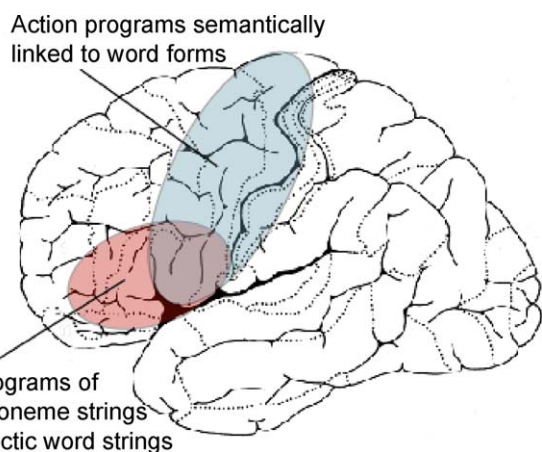


Fig. 6. Functional significance of frontal sources according to the language-action model: Speech stimuli automatically activate areas in frontal lobes. Areas in left inferior frontal cortex (Broca's area and anterior to it) house circuits binding speech signals to articulatory motor programs and syntactic circuits. Words semantically related to actions involving specific parts of the body activate semantic circuits binding word form knowledge to action knowledge. These occupy premotor and motor cortex (Pulvermüller, 2005). Word form/syntactic and semantic circuits can both involve posterior inferior frontal areas (overlap of ellipses).

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