Research Focus

Tracking the time course of word recognition with MEG

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Twenty years ago it was discovered that recognition of semantically unexpected words is associated with a special ERP signature – the N400. Pinpointing the precise functional significance of the N400 has, however, been difficult. Recent MEG studies of word processing reveal that, in fact, the N400 decomposes into several functionally distinct subcomponents, allowing for more fine-grained investigation of its significance.

What happens in the brain when we recognize words? Within a few hundred milliseconds, we are able to perceive a string of sounds or letters and map the string to a single word representation among tens of thousands in our mental lexicon. Multiple rapidly changing processes must be involved and today's electrophysiological techniques allow us to monitor them on a millisecond basis. Perhaps surprisingly though, studies of the event-related potentials (ERPs) elicited by words have not revealed a rapidly changing profile of activity, but rather a single sustained negativity that onsets around 200 ms, peaks around 400 ms and offsets around 500 ms, that is, the so-called N400 (see [1] for a review).

Although twenty years have passed since the original discovery of the N400 [2], there is still no agreement even about basic aspects of the interpretation of the N400, such as whether it is associated with some stage of word recognition [3,4] or with the integration of new words into a preceding context [5]. Researchers have attempted to distinguish between these two hypotheses by making the preceding context invisible to consciousness [3,4,6–8], but the results obtained so far do not entirely converge.

Given that the N400 lasts for up to 300 ms, it seems unlikely that it indexes only a single linguistic processing stage. To understand the cognitive underpinnings of the N400, one would want to study its internal structure. Results from recent investigations using magnetoencephalography (MEG) suggest that MEG might be useful for decomposing the N400 [9,10]. MEG recordings of cortical activity related to visual-word processing show up to four prominent components with clearly distinguishable peaks between 150–500 ms post-stimulus onset. A recent study that simultaneously manipulated early and late stages of lexical processing showed that a peak at approximately 350 ms, the M350, is associated with the initial activation of word representations prior to the selection of one of them as the optimal match to the input [12]. This suggests that at 350 ms, N400 activity is still associated with lexical access, and not post-lexical integration processes.

MEG activity associated with word processing

MEG measures the magnetic fields generated by cortical currents. Although MEG and EEG both derive from largely the same neuronal currents, MEG differs from EEG in several ways. For example, unlike EEG, MEG is relatively insensitive to deep sources as well as to radially oriented gyral sources (although see [13]). Consequently, MEG field patterns plausibly reflect fewer overlapping fields and neural generators than EEG recordings. Importantly, data analysis in MEG is usually performed individually for each subject, allowing the detection of small latency differences invisible in ERP grand-averages, because of between-subjects variation in component latency.

The N400 ERP resembles a sustained field: the same scalp topography persists for several hundred milliseconds. In the same time window, a somewhat different waveform morphology is observed in MEG responses to visual words: between 200 and 500 ms after word-onset, a dipolar distribution with a posterior outgoing field and an anterior ingoing field appears and reappears over the left hemisphere sensors up to three times, as if roughly the same area activated repeatedly [12] (Fig. 1). This 'N400 complex' is preceded by a prominent peak at around 170 ms with a bilateral occipito-temporal distribution (M170) [11,12,14], reflecting pre-lexical visual processing.

The N400 time window has been investigated in MEG both via the classic N400 paradigm where predictions for sentence-final words are violated ('*He spread the warm bread with socks*') [9,10] and by manipulating properties of isolated words known to affect behavioral response times [11,12,15]. To localize the source of the N400 ERP in MEG, Helenius and colleagues manipulated the expectancy of visual sentence-final words and identified multiple areas sensitive to semantic congruity, with a distinct cluster in the superior temporal lobe, near auditory cortex [9]. A similar result was obtained when the sentences were presented aurally: the generators of the semantic congruity response localized within millimeters of the source of the auditory N100m response [16]. Intracranial recordings and distributed MEG source modeling have also identified additional N400 sources (see [10] for a summary).

The internal structure of the N400 has been further elucidated in a series of studies on lexical access.

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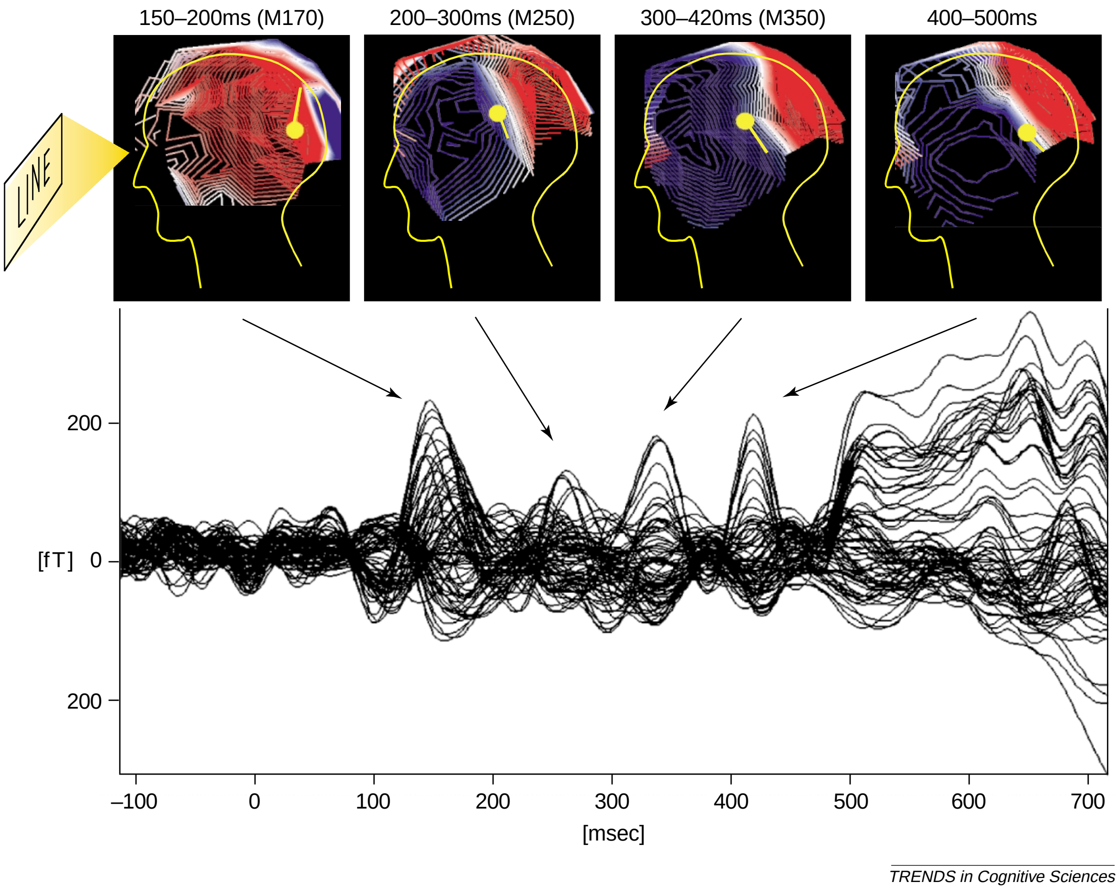

Fig. 1. A waveform illustrating the averaged MEG response of one subject to 69 presentations of visual words recorded with a 93-channel axial gradiometer whole-head system (Kanazawa Institute of Technology, Japan). Activity from all sensors is shown in the bottom panel; the magnetic field patterns of the major response components and their estimated current sources are in the top panel (single dipole modeling). The strong activity after 500 ms reflects the motor activity of the button press of the experimental task (lexical decision). Recent MEG results suggest that activity at 150–200 ms in the left hemisphere (M170) is associated with letter-string processing [14] and activity at 300–400 ms with lexical activation [11,12]. The functional significance of the activity in the 200–300 ms and 400–500 ms time windows is less clear. However, results obtained so far suggest that phonological stimulus factors, such as the frequency of the sounds in the word, affect the M250, and that activity at 400–500 ms is sensitive to the magnitude of interlexical competition [12]. The electrical N400, which is sensitive to both lexical and post-lexical stimulus factors [1], might be a summation of the M250, M350 and the post-M350 activity.

Embick *et al*. [11] and Pylkkänen *et al*. [15] used the lexical decision task and manipulated lexical frequency and repetition, i.e. factors that affect the timing of lexical access. Both studies identified three consistent MEG components elicited by visual words. The first, the M170, peaks between 150–200 ms over occipito-temporal sensors bilaterally. The second, the M250, peaks at approximately 250 ms and is associated with a left-lateralized distribution with a posterior outgoing and an anterior ingoing magnetic field. The third component, the M350, peaks about a hundred milliseconds later and exhibits a field pattern similar to the M250, although source localization has revealed the current source of the M350 to be more anterior than the generator of the M250 [12]. Of these three components, only the latencies of the M350 were found to be predictive of the behavioral effects of lexical frequency and repetition. High frequency and repetition decreased both M350 latencies and behavioral reaction times.

Separating access from decision

Although the sensitivity of the M350 to frequency and repetition suggests its involvement in word processing, the results outlined above do not prove that the M350 directly reflects any aspect of lexical access. As facilitation at one processing stage is bound to have effects at later stages, the effects of lexical frequency and repetition on the M350 could be downstream consequences of an earlier facilitation. To narrow the interpretation of the M350, Pylkkänen, Stringfellow and Marantz used stimuli designed to facilitate early lexical processing while simultaneously inhibiting the decision stages of the lexical decision task [12]. The M350 was predicted to show a facilitory effect if it was an automatic early component and an inhibitory effect if it indexed the decision stage.

To achieve early facilitation and later inhibition, the phonotactic probabilities (frequencies of the sounds and sequence of sounds in words) and the densities of the similarity neighborhoods (number of words that sound similar to the target stimuli) of words and pseudowords were manipulated. These two factors are highly correlated, but they have opposite effects on processing. High phonotactic probability (i.e. high sub-lexical frequency) facilitates sub-lexical processing, whereas high neighborhood density inhibits recognition, owing to intense competition between many similar sounding representations [17,18]. Pylkkänen, Stringfellow and Marantz asked how stimuli with high phonotactic probabilities *and* dense similarity neighborhoods would move the M350. Decreased M350 latencies would indicate that the M350 reflects a processing stage before competition, which benefits from the facilitory effect of high phonotactic probability. By contrast, if latencies increased, the M350 would be associated with some processing stage already affected by competition, potentially the post-lexical decision stage. Results confirmed the first prediction: the M350 latencies of high probability and high density stimuli were shorter than those of low probability and low density stimuli. A facilitory effect of high probability was also seen in M250 amplitudes: they were reduced for high probability words, suggesting that the M350 latencies were a downstream effect of the M250 amplitude reduction. Even though the M250 or M350 showed no inhibitory effect of competition, this effect was clearly seen in lexical decision times: high probability/high density stimuli elicited significantly longer reaction times than low probability/low density stimuli.

In most models of word recognition, competition precedes recognition, that is, the identification of the optimal match to the input [19–21]. Pylkkänen, Stringfellow and Marantz did not identify any MEG component predictive of the inhibitory effect of high neighborhood density on reaction times. However, when reaction times were delayed owing to competition, the M350 field distribution was generally associated with two prominent peaks as opposed to one for low probability/low density stimuli. The interpretation of this result remains inconclusive, but it does suggest the possibility of a recognition-related component in the latter part of the N400 time window.

Concluding remarks

Much behavioral research on cognition, including language, has focused on finding paradigms and experimental tasks where automatic mental operations, such as lexical access, could be measured without interference from strategic, task-related processes. The MEG results described here suggest that automatic lexical processing can be measured directly with the M350, making it a powerful new tool for testing hypotheses about language processing.

Collectively, the MEG studies summarized here suggest that the brain activity in the N400 time window decomposes as follows. At 250 ms, pre-lexical processing, which is sensitive to sub-lexical frequency [12] but not to lexical frequency [11], occurs in the posterior parts of the left superior temporal cortex. At 350 ms, the mental lexicon is activated. At this point, processing is sensitive to factors such as lexical frequency [11] but not to competition among the representations activated by the stimulus [12]. After the mental lexicon has been activated, recognition of the optimal match to the stimulus must occur.

Imagine then, that the N400 ERP is really a conglomeration of the M250, M350 as well as the mysterious second peak of the M350 field distribution. This type of negativity would as a whole be sensitive to all sorts of factors, lexical and post-lexical. This is precisely what the N400 literature indicates and is the reason why it has been difficult to point to a single processing stage that could be hypothesized to underlie the component [22]. Clearly then, the combination of different methodologies is imperative for obtaining a full picture of the temporal and spatial dynamics of linguistic processing in the brain. In the case of MEG, the fact that it allows us to distinguish subsets of activity identified by EEG should be able to add an important dimension to electrophysiological investigations of language, and cognition in general.

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