Distinct time courses of word and context comprehension in the left temporal cortex

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Summary

The time course and cortical basis of reading comprehension were studied using magnetoencephalography. The cortical structures implicated most consistently with comprehension were located in the immediate vicinity of the left auditory cortex, where final words totally inappropriate to the overall sentence context evoked enduring activation starting ~250 ms and lasting up to 600 ms after word onset. Contextually appropriate but unexpected words produced weaker activation which terminated earlier. Highly anticipated words totally failed to activate this area, suggesting that the conceptual network became involved only if unexpected information was detected during the primary word identification process. We propose that the point in time (350 ms after word onset) where the response to appropriate but unexpected endings started to diverge from those to contextually inappropriate endings reflects the boundary between understanding a single word and the meaning of a whole sentence.

Keywords: reading; semantic processing; N400; functional brain imaging; magnetoencephalography

Abbreviations: ERP = event-related potential; fMRI = functional MRI; MEG = magnetoencephalography

Introduction

The rich interconnectivity of the cortex makes it an optimal structure for merging discrete pieces of information into a perceptual whole (Pandya and Seltzer, 1982; Goldman-Rakic, 1988; Mountcastle, 1997). For reading and understanding of written language, several hierarchical perceptual/cognitive processes must be mobilized (McClelland, 1987; Monsell, 1987; Patterson and Coltheart, 1987). The basic visual features must first be extracted and combined to form an image of a letter. Several letters must be processed as a whole to perceive a word. Successful lexical access based on, or accompanied by, phonological activation then opens the way for identifying the meaning of the word and, finally, for evaluating the word meaning in a particular context. On the basis of experimental psychology and specific deficits known to result from brain lesions, the analysis of written words is thought to consist of distinct subprocesses, such as orthographic/lexical, phonological, syntactic and semantic analysis.

Evidence for the neuroanatomical correlates of these still somewhat controversial modular subcomponents of linguistic processing is scarce and diverse (Frackowiak, 1994; Price et al., 1994; Poeppel, 1996). Traditionally, based on brain lesions that compromise linguistic capacities, the role of Wernicke’s area in the posterior third of the left superior temporal gyrus has been emphasized in understanding spoken and written language (Geschwind, 1970; Mesulam, 1990). Non-invasive functional imaging studies and intraoperative recordings have modified this view considerably during the last decade, indicating that several other areas besides Wernicke’s may be involved in the semantic processing of language (Petersen et al., 1988; Wise et al., 1991; Démonet, 1992; Nobre et al., 1994; Damasio, 1996; Martin et al., 1996; Binder et al., 1997). The non-overlapping results may derive partly from differences in methods—whereas functional imaging shows activations associated with the full range of processes involved in a certain behaviour, lesion studies reveal the structures essential for that behaviour (Steinmetz and Seitz, 1991).

Although cognitive models often postulate that the semantic system is multimodal (e.g. Ellis and Young, 1988) and thus common to the understanding of written and spoken words and pictures, functional imaging studies have suggested that the semantic processing of words versus pictures, for example, does not activate totally overlapping brain areas.
PET and functional MRI (fMRI) studies searching for brain areas involved in the semantic processing of written words have almost exclusively used isolated words as stimuli—the involvement of the left frontal areas (Petersen et al., 1988), the left superior temporal areas (Pugh et al., 1996) or (Vandenbergh et al., 1996) both has been indicated, depending on the particular task employed. A recent fMRI study on comprehension of written sentences (Just et al., 1996) showed activation of both left and right frontal and temporal areas. Due to the limited time resolution of haemodynamic measures, it is not possible to follow the progression of activation from one brain area to another. Thus, the analysis must rely heavily on the assumption that even the most complex cognitive operations are composed of well-defined, distinguishable modules that are extractable as invariable units through subtractions between specific tasks (see criticism of Sergent et al., 1992).

The temporal pattern of cortical activation with respect to a stimulus provides decisive clues to the functions of cortical areas. A powerful tool for characterizing the temporal aspects of language comprehension can be found in the EEG literature. When contextually constrained sentences end with a semantically inappropriate word, an event-related potential (ERP) is elicited 300–500 ms after the onset of the final word (Kutas and Hillyard, 1984). After their seminal finding, Kutas and Hillyard (1980) further demonstrated that semantic anomaly is not critical for eliciting this negative ‘N400’ response; it is also observed in response to semantically possible but unexpected sentence endings. In fact, all words were followed by an N400 response, but the response diminished towards the end of the sentence, with increasing contextual constraint (Kutas et al., 1988). For word pairs, the response is smaller to a word which is semantically related to the preceding word than to a totally unrelated word, and also to a repeated than to a novel word (Rugg, 1985). The N400 response does not seem to be specific to written words, because spoken words (McCallum et al., 1984; Holcomb et al., 1992; Connolly and Phillips, 1994) and pictures (Nigam et al., 1992; Ganis et al., 1996) can also elicit this response. However, the spatial distributions of the N400 response to words and pictures do not overlap perfectly (Ganis et al., 1996), in line with PET results from word and picture processing (Vandenbergh et al., 1996).

The precise cognitive processes associated with the N400 response remain unknown (Osterhout and Holcomb, 1995). It has been argued that the response reflects postlexical processes, either semantic analysis at the level of an isolated word or integration of the meaning of the whole sentence (Holcomb, 1993). The N400 response seems to increase with the amount of unexpected linguistic information the word (or picture) contains, whether lexical, semantic or syntactic, and with the difficulty of integrating the word into the context (Osterhout and Holcomb, 1995).

The N400 response is likely to arise from many generators that may be functionally (Nobre and McCarthy, 1994) and spatially (Halgren et al., 1994; McCarthy et al., 1995) segregated. The electric signal of the conventional scalp-recorded ERPs is blurred by conductivity changes at the skull and the scalp, complicating the interpretation and localization of the response. Further, the N400 deflection is normally reported as an average over several subjects.

Magnetencephalography (MEG) combines the excellent time resolution of the ERP with superior spatial resolution. MEG detects the magnetic field associated with synchronous electric currents in neurons. Since magnetic signals are not distorted by the structures surrounding the brain tissue, identification of the source areas, and interpretation of the signal, are more straightforward than with conventional ERPs. With MEG, we identified cortical correlates of semantic processing in individual subjects using the N400 paradigm.

Method

Subjects

We recorded MEG signals from 10 neurologically normal subjects: five females (age 20–37 years; mean 26 years) and five males (age 24–31; mean 28 years). All subjects were right-handed and their native language was Finnish. They had no history of reading disorders and their reading speed was found to be normal (see below). Informed consent was obtained from all subjects. The studies were approved by the Academy of Finland.

Materials and procedure

We employed four categories of sentence-ending words (Connolly et al., 1995). One sentence type was constructed to lead to a very strong expectation for a certain, probable final word (e.g. ‘The piano was out of... tune’). Sentences could also have semantically appropriate but unexpected, rare endings (e.g. ‘When the power went out the house became... quiet’; ‘dark’ would have been the most likely ending for this sentence), anomalous endings—totally inappropriate to the context (e.g. ‘The pizza was too hot to... sing’), or phonological endings which were semantically inappropriate but started with the same phonemes as the most probable word (e.g. ‘The gambler had a streak of bad... luggage’). Transparency of the Finnish language (practically one-to-one correspondence between phonemes and graphemes) means that the two to four letters and the phonemes forming the first syllable of the phonological final words were the same as those making up the beginning of the most probable final word. There were 100 sentences in each category. To ensure that the attention of the subjects was maximally engaged in reading the sentences, each sentence was used only once. The order of the 400 different sentences was randomized (no sentence type appeared more than three times in a row) and they were presented visually one word at a time (duration 330 ms, blank interval between words 750 ms). Subjects were instructed to concentrate on...
the meaning of the sentences. In total, the recording session lasted ~1 h.

The probability of a sentence ending with a particular word was tested on 30–63 university students instructed to fill in the best completion for each sentence. The cloze probability (Taylor, 1953) of the most often suggested ending was equal (0.73–1.00) for all four sentence categories. The number of words in the sentences ranged from four to 10 (mean 6.6, SD 1.1) and the length of the final words varied from five to 13 characters (mean 7.7, SD 1.8). Neither of these two measures differed among the four different sentence types. The distribution of different word classes was also the same for the four types of final word: 74–85% of the endings were nouns, 8–14% verbs and 7–18% adjectives or adverbs. The stimuli (yellow words on a black background) were projected onto a board, placed at a distance of ~1 m from the subject. The size of the word was on the average 5.3 cm (visual angle 6°).

The reading speed of the subjects was tested separately from the MEG measurement in a computerized lexical decision task. Sitting in front of a computer screen, subjects indicated with a response key whether they saw a word or an orthographically legal non-word, as quickly as possible. The target word or non-word was preceded by a prime word of short duration (200 ms), which was, or was not, semantically related to the following word. The word recognition speed was estimated as the time to correctly recognize a Finnish word preceded either by an associated or non-associated prime word (number of averages 45–48).

**Magnetic measurements**

The magnetic activity was measured using a Neuromag-122™ device (Neuromag, Helsinki, Finland), which employs planar gradiometers arranged in a helmet-shaped array to cover the whole head (Ahonen et al., 1993). Neuromagnetic fields which are detectable outside the head are typically generated by the simultaneous activation of ~1 000 000 synapses in the parallel apical dendrites of pyramidal cells. As MEG is most sensitive to the cortical currents tangential to the surface of the head, the recorded signals mainly reflect activity in the fissural cortex (Hämäläinen et al., 1993). Approximately two-thirds of the entire cortex lies in the fissures (Zilles, 1990; Armstrong et al., 1995), and even activation arising from the gyral cortex usually has at least a small tangential component, rendering essentially all cortical activations detectable with MEG. The MEG signals were averaged for each subject with respect to the onset of the final word (four categories) of each sentence. Epochs contaminated by eye blinks were discarded.

**Source analysis**

The whole-head field patterns were scanned for stable dipolar field distributions, signalling local coherent brain activation, up to 900 ms after word presentation. The source areas were modelled as equivalent current dipoles, and the average strength of the source current and its three-dimensional location and orientation, representing the centre of gravity of the activated area and the mean current flow therein, were determined from the measured field (Hämäläinen et al., 1993). To estimate the source strengths as a function of time, the isolated equivalent current dipoles (seven to nine in each individual subject), localized from subsets of 12–20 sensors, were introduced simultaneously into a multidipole model, keeping their locations and orientations fixed while their strengths were allowed to vary to achieve the optimal explanation of the data measured with all sensors. The source area sensitive to the meaning of the words within sentences was determined either in the anomalous or phonological condition, showing a clear dipolar field distribution with minimal interference from simultaneous activation of other brain regions. The same equivalent current dipoles adequately explained the activation elicited by all sentence endings.

**Functional landmarks**

To identify the auditory and hand somatosensory cortices of the individual brains, we also recorded responses to 50-ms, 1-kHz tones, delivered alternately to the left and right ears every 1.2 s (Mäkelä et al., 1994), and to self-paced left and right index finger lifts, performed approximately every 3 s (Salmelin et al., 1995).

**Statistical analysis**

A repeated measures analysis of variance (ANOVA; the within-subjects factor was sentence type) was performed to reveal statistically significant differences in the strength of the N400 response. The temporal pattern of the response was characterized by measuring, in individual subjects, the latencies at which the source strength had reached 0% (onset/offset), 25%, 50%, 75% and 100% of the maximum on the ascending and descending slopes. The temporal patterns were tested with a repeated-measures ANOVA (the within-subjects factors were sentence type and latency). A detailed description of the statistical findings are given in the legend of Fig. 3.

**Results**

Figure 1A illustrates the whole-head responses of one subject (S1) to the four different sentence endings. A striking difference between categories was observed in the left temporal sensors, where the anomalous and phonological sentence endings (incongruent with the established context of the sentence) elicited a strong sustained activity. The activation was smaller for the rare endings and totally missing for the probable sentence endings. A smaller and later effect of word congruity arose in the right hemisphere too. Figure 1B depicts, for each of the other nine subjects, the channel displaying the strongest congruity effect in the left hemisphere.
**Fig. 1** (A) Variation in the cortical magnetic signal as a function of time in one subject (S1), recorded with the 122-channel neuromagnetometer. Responses are shown from 100 ms before to 800 ms after presentation of the final word. The sensor array is viewed from above with the nose pointing upwards. Variation in the magnetic field was measured at 61 sites over the head both latitudinally and longitudinally (see pair of traces), as illustrated on the schematic heads. The Neuromag-122™ detects the strongest signal just above an active brain area. The sensor displaying the strongest effect of sentence context (over the left temporal area in this subject) is shown enlarged in the upper left corner. Responses to the four types of final words are displayed in different colours, as demonstrated at the bottom. The large magnetic deflection in the upper, but not in the lower, sensor of each channel pair indicates that the underlying current was flowing longitudinally, directed laterally from the vertex; note that the magnetic field changes most in the direction orthogonal to the electric current. (B) The output of the sensor displaying a distinct effect of sentence context in the other nine subjects. The maximum was recorded over the left temporal area in subjects S1–S8, and more frontally in subjects S9 and S10.

The piano was out of tune (probable)
The power went out, the house became quiet (rare)
The pizza was too hot to sing (anomalous)
The gambler had a streak of bad luggage (phonological)

Figure 2 shows the source areas contributing to the congruity effect in all subjects. Eight of 10 subjects showed distinct activation in the left superior temporal cortex, which could be unequivocally localized in seven subjects (S1–S7, black dots). The origin of this activation within the upper bank of the superior (four subjects) or middle temporal gyrus (three subjects) was confirmed by the orientation of the current flow, perpendicular to the sulci. In two subjects (S9 and S10), no congruity effect was observed in the left middle temporal region, but it was in the left frontal lobe (grey triangles). In addition, sources in the temporoparietal area surrounding the posterior end of the sylvian fissure (grey squares) were identified in these two subjects and in three of the seven subjects showing the more anterior temporal lobe congruity effect. The left middle temporal and the more posterior temporoparietal sources did not differ from each
activation, lasting until ~600 ms after word onset, whereas the rare endings resulted in a significantly weaker \((P < 0.0001)\) response, in agreement with previous ERP results (Connolly et al., 1995). The response to rare endings also terminated earlier \((P < 0.002)\). Interestingly, no activation exceeding the background noise was observed after the probable sentence endings in six of these seven subjects.

The activity elicited by the three unexpected endings always began 250 ms after word onset, with no statistically significant differences according to the type of incongruency. The responses to the rare final words culminated, on average, at 350 ms. The activations elicited by the anomalous and phonological final words continued to increase after this time point, but the waveforms started to diverge, the phonological activation lagging behind the anomalous waveform by ~35 ms \((P < 0.02)\).

Figure 4 depicts the relationship between the behaviourally measured word recognition speed and the latency of activation in the left superior temporal cortex, represented by the time at which the source strength had reached 50% of the maximum. A statistically significant correlation between word recognition speed and latency of the neuromagnetic response was observed with anomalous \((\text{Pearson } r = 0.84, P < 0.02)\) and phonological \((r = 0.89, P < 0.007)\) final words; in the rare condition the correlation \((r < 0.63)\) failed to reach significance in this small sample.

**Discussion**

We employed MEG to track the time course of comprehension of written sentences using final words which varied in their semantic appropriateness to the overall sentence context. We were able to identify, in individual subjects, multiple, widely distributed cortical areas that were sensitive to the meaning of the final word in a sentence context. Areas surrounding the left auditory cortex, in the upper banks of the left superior and middle temporal gyri, were found to be most consistently involved in understanding written sentences.

Evidence from behavioural studies indicates that both primary visual analysis and perception of the global form of the word have been achieved by 200 ms after word onset (e.g. Balota and Chumbley, 1985). The fairly late onset (250 ms) of the left temporal activation thus strongly suggests that this response is related to the analysis of the meaning of the word and its role in the context created by the sentence. The virtually identical onset of activation for the different final words further suggests that, up to this point, the basic visual/linguistic processing is largely independent of semantics, as suggested also by reaction time studies (Taft, 1991). Thereafter, a distinct stage of cognitive processing begins, with the intensity and duration of the cortical response heavily dependent on comprehension of the word and sentence. The interpretation that the left temporal response reflects purely postlexical processes is also in perfect concordance with previous ERP studies, indicating that the N400 effect is not reduced by stimulus degradation thought
The time course of source activation in the left superior temporal cortex in subjects S1–S7. Since the average activity following the probable sentence endings (5.4 ± 1.5 nAm; mean ± SEM) did not differ from the prestimulus noise level (2.9 ± 0.6 nAm), the probable condition was not included in further analysis. The average peak amplitudes differed significantly for the three types of unexpected endings \( F(2,12) = 23.4, \; P < 0.0001 \). Planned contrasts between the peak amplitudes of anomalous (20.5 ± 2.4 nAm) and phonological (20.7 ± 2.4 nAm) endings revealed no difference. Rare sentence endings produced a significantly smaller response (14.2 ± 2.0 nAm) than either anomalous (\( P < 0.0001 \)) or phonological (\( P < 0.0001 \)) endings. Colour coding as in Fig. 1. (B) Time behaviour of normalized waveforms (mean ± SEM) of the three unexpected sentence endings in the left superior temporal cortex. The source amplitudes were scaled individually, setting the maximum activation in the phonological condition equal to 1. The latencies and relative amplitudes were measured at points where the source amplitude reached 0% (onset/offset), 25%, 50%, 75% and 100% of the maximum source strength in each condition, and averaged over subjects (S1–S7). The dashed line shows the average prestimulus noise level. The temporal patterns of the responses to three types of unexpected final words differed significantly, both when compared with respect to their overall shape \( F(2,12) = 20.6, \; P < 0.0001 \) and when the ascending \( F(2,12) = 6.0, \; P < 0.02 \) and descending \( F(2,12) = 22.9, \; P < 0.0001 \) slopes were considered separately. On the ascending slope, planned contrasts revealed statistically significant differences between categories only when 75% of the peak activity had been reached; both anomalous (\( P < 0.03 \)) and rare endings (\( P < 0.0009 \)) reached 75% of their maximum strength earlier than phonological endings. The rare sentence endings peaked earlier than the anomalous (\( P < 0.02 \)) and phonological (\( P < 0.0001 \)) endings. In an analysis combining the ascending and descending slopes, the time behaviour of the anomalous and phonological endings was also different (\( P < 0.008 \)), the phonological ending tending to peak later (\( P < 0.08 \)).
(James, 1975), a stage probably reflected in the rising slope of the left superior temporal activation, this correlation is not surprising. This kind of correlation should be of particular interest when disorders of language, e.g. dyslexia, are studied.

The similar onset latencies of the left temporal responses to the two semantically anomalous endings suggest that fluent readers perceived a word as a whole, or at least in units larger than a few letters—the ‘correct’ letters at the beginning of the phonological final words did not clearly delay the onset of analysis of word meaning. However, at the later stage, probably reflecting integration of the word to the entire sentence, the phonological response showed a systematic 35-ms time lag in comparison with the anomalous condition. Processes based on the analysis of sublexical units as opposed to whole words (Patterson and Coltheart, 1987) may thus mainly delay the beginning of the context-sensitive stages of word analysis. In the auditory domain, where the input is necessarily serial, a delayed N400 response to final words beginning with the same phonemes as the most probable word has been reported in an ERP study (Connolly and Phillips, 1994).

Although all words in a sentence (Kutas et al., 1988), and even isolated words (Salmelin et al. 1996), are known to result in a clear activation peaking 300–500 ms after word onset, the probable endings totally failed to activate the left temporal cortex or any other area sensitive to sentence meaning, or the activation was so minor as not to be detected with MEG. This observation suggests that the word had already been recognized as the one expected at the level of lexical access, at the latest, thus rendering further processing unnecessary. In this study the sentences were constructed to lead, with little ambiguity, to the expectation of one particular terminal word. The relatively slow presentation rate of the words ensured that the subjects had adequate time to become aware of the sentence context. The lack of activation with probable final words is thus likely to be the result of top-down build-up of anticipation (Neely, 1977, 1991). It would seem that the only truly efficient and economic way for the brain to work would be to ignore the fulfilment of the anticipated scenarios and instead concentrate on new, aberrant information.

The neural generators of the widespread scalp-recorded N400 response, with the maximum around the vertex or in the parietal sensors, have remained unestablished (Nobre and McCarthy, 1994). Intracortical depth recordings have provided more information about the neural generators of language-related processing (Smith et al., 1986; Halgren et al., 1994; Guillem et al., 1995; McCarthy et al., 1995; Nobre and McCarthy, 1995). When written words have been used as stimuli the role of the medial temporal structures near the hippocampus and amygdala have been emphasized in the generation of the N400 response (Smith et al., 1986; Halgren et al., 1994; McCarthy et al., 1995; Nobre and McCarthy, 1995). However, Halgren et al. (1994) reported N400-like responses also from more superficial cortical structures, including the region of the superior temporal sulcus.

The emphasis on lateral rather than medial temporal activations in the present MEG data may be associated with the rapid decay of the magnetic field as a function of distance from the sensors (Hari, 1993). Also, field patterns arising from currents, e.g. in the inferior surface of the temporal pole (McCarthy et al., 1995; Nobre and McCarthy, 1995) would not be covered adequately by the MEG helmet used, thus making them even less likely to be identified, especially in the presence of the dominant lateral neocortical activation. It also seems that the intracortical recordings, done on patients, oversample the medial temporal structures compared with the quite infrequently (if at all) targeted lateral neocortex (Smith et al., 1986; Halgren et al., 1994; Guillem et al., 1995; McCarthy et al., 1995; Nobre and McCarthy, 1995).

The lateral temporal origin of the N400 response is further supported by a recent seven-channel MEG study; in five of the seven subjects N400-like activation to sentence endings was localized close to the left superior temporal sulcus (Simos et al., 1997). An obvious approach for the future is to combine whole-head MEG and ERP recordings. The readily identified MEG sources would serve as the initial estimate for the distribution of activity, and additional sources (possibly also subcortical) could then be determined based on the remaining unexplained electrical activity.

Comparison of haemodynamic (PET, fMRI) and electrophysiological (MEG, ERP) measures is not straightforward. While MEG records the synchronous postsynaptic currents in neural populations with millisecond time resolution, PET and fMRI measure the overall level of blood flow (oxygen consumption) with respect to a certain task over several seconds or even minutes. Thus the results cannot be expected to overlap perfectly, even if the stimulus parameters are essentially the same. It is also worth noting that even minor changes in stimulus parameters (e.g. prolonging the duration of a stimulus) can change the haemodynamic activation patterns radically (Price et al., 1994). Sentences may well tap semantic processing.
significantly more efficiently than isolated words, and thus the results of the present study should be compared primarily with PET/fMRI studies in which the stimuli have been as similar as possible to those in the present study.

Just et al. (1996) used three types of sentences designed to differ in structural complexity. The fMRI signals were monitored around Wernicke's and Broca's areas and their right-hemisphere homologues. All these areas showed increased activation with increasing linguistic complexity. The present results and those reported by Just et al. (1996) thus differ mainly with respect to the frontal activation. However, as pointed out in the comment by Kapp and McCloskey (1997), the syntactic complexity of the sentences used in the study of Just et al. (1996) covaried with their semantic complexity, which could account for the inferior frontal activation. In another recent fMRI study, Bavelier et al. (1997) contrasted sentence reading with the viewing of consonant strings. The subtracted activations thus reflected all aspects of sentence processing from lexical access to semantic and syntactic processing. Multiple perisylvian structures were found to be involved in sentence reading, most consistently in Broca's area and along the left superior temporal sulcus, in accordance with the temporal activation detected in our study. The frontal activation may again reflect the more general activation associated with reading in the study of Bavelier et al. (1997) compared with the targeted semantic processing of the present experiment. Bavelier et al. (1997) analysed activations elicited by sentence-reading individually in each subject and found that the activation pattern was composed of several small patches, variable across subjects, rather than of large well-circumscribed centres of activity. The large variation among individuals may explain some of the inconsistencies found between methods based on averaging across subjects (e.g. PET) and on individual analysis [e.g. lesion studies and MEG; see also Steinmetz and Seitz (1991)].

Although both hemispheres may be involved in the processing of written language (Price et al., 1994; Just et al., 1996), an unequivocal left-hemisphere dominance, based on the number of identified sources, was detected in nine of our 10 right-handed subjects. This is concordant with the findings of, for example, Just et al. (1996), who found that the overall level of activation during sentence reading was significantly higher in the left than in the right hemisphere. More specifically, we also noted that the responses in the left hemisphere were systematically ~25 ms earlier than in the right hemisphere, although the small number of right-hemisphere observations prevents us from drawing firm statistical conclusions about the latency difference.

The magnetic signal probably reflects synchronous activation of focal nodes within a distributed conceptual network, which could involve all aspects of language reception and production (Mesulam, 1990). The balance of the network undoubtedly depends on the task (Ganis et al., 1996; Vandenbergh et al., 1996) and shows some individual variation; in the present study the congruity effect was detected in the left frontal, rather than the superior, temporal cortex in two subjects. While many brain areas are certainly involved in semantic processing (Just et al., 1996; Vandenbergh et al., 1996; Bavelier et al., 1997), the strong dominance of the temporal activation may well be related to the closeness of the auditory cortex, the primary route for language acquisition.

We propose that it is possible to separate out a specific context-sensitive stage of word processing from activation related to lexical semantic analysis. The reliability with which this activation can be detected, and both spatially and temporally characterized in individual subjects, holds promise for further studies of more specific features of the neural networks subserving the perceptual and cognitive processes of language.

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