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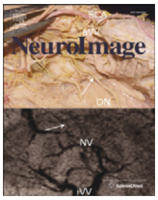

The time-course and spatial distribution of brain activity associated with sentence processing

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ABSTRACT

Sentence comprehension involves a host of highly interrelated processes, including syntactic parsing, semantic composition, and pragmatic inferencing. In neuroimaging, a primary paradigm for examining the brain bases of sentence processing has been to compare brain activity elicited by sentences versus unstructured lists of words. These studies commonly find an effect of increased activity for sentences in the anterior temporal lobes (aTL). Together with neuropsychological data, these findings have motivated the hypothesis that the aTL is engaged in sentence level combinatorics. Combinatoric processing during language comprehension, however, occurs within tens and hundreds of milliseconds, i.e., at a time-scale much faster than the temporal resolution of hemodynamic measures. Here, we examined the time-course of sentence-level processing using magnetoencephalography (MEG) to better understand the temporal profile of activation in this common paradigm and to test a key prediction of the combinatoric hypothesis: because sentences are interpreted incrementally, word-by-word, activity associated with basic linguistic combinatorics should be time-locked to word-presentation. Our results reveal increased anterior temporal activity for sentences compared to word lists beginning approximately 250 ms after word onset. We also observed increased activation in a network of other brain areas, extending across posterior temporal, inferior frontal, and ventral medial areas. These findings confirm a key prediction of the combinatoric hypothesis for the aTL and further elucidate the spatio-temporal characteristics of sentence-level computations in the brain.

Introduction

A broad neuroimaging literature has sought to identify neural activity associated with the cognitive operations engaged during the processing of sentences. A primary experimental design that has been used in this literature compares brain activity elicited when subjects read or listen to sentences to that observed for lists of words (Friederici et al., 2000; Humphries et al., 2005, 2006; Jobard et al., 2007; Mazoyer et al., 1993; Rogalsky and Hickok, 2009; Snijders et al., 2009; Stowe et al., 1998; Vandenberghe et al., 2002; Xu et al., 2005). This contrast has the desirable property that both conditions are likely to require an equivalent degree of word-level processing, but only the sentences are assumed to require processing associated with building and comprehending sentence structure. In this comparison, sentence-processing commonly leads to increased activity in the anterior temporal lobe (aTL; see e.g. Rogalsky and Hickok, 2009; Stowe et al., 2005 for discussion), a finding consistent across both the auditory (Friederici et al., 2000; Humphries et al., 2005, 2006; Jobard et al., 2007; Mazoyer et al., 1993; Rogalsky and Hickok, 2009) and visual (Jobard et al., 2007; Stowe et al., 1998; Vandenberghe et al., 2002) modalities. The majority of these studies report bilateral activation, with a stronger effect in the left hemisphere, while a subset have reported just a left-lateralized effect (Humphries et al., 2006; Vandenberghe et al., 2002).

Sentence processing is, of course, a complicated and multi-faceted task that is comprised of a host of separate computations, including the construction of sentence structure (syntactic parsing), the composition of complex meaning (semantic composition), the establishment of long distance dependencies, the determination of reference, and the drawing of pragmatic inferences. Thus, the cognitive operations involved in sentence processing differ substantially from those engaged by lists of words. While the functional role of the aTL is, accordingly, under-determined by the results from the sentence vs. word list comparison, the neuroimaging results together with deficit/lesion studies (Dronkers et al., 1994, 2004) have lead to hypotheses linking the aTL with aspects of linguistic composition (Pallier et al., 2011; Snijders et al., 2009), perhaps syntactic structure building (Grodzinsky and Friederici, 2006; Humphries et al., 2006), or incremental semantic composition (Stowe et al., 2005; Vandenberghe et al., 2002). A connection between this region and basic combinatory

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operations is also supported by recent work showing that the amount of sentence structure constructed word-by-word correlates with hemodynamic activity in the aTL (Brennan et al., in press). Additional evidence comes from comparisons of native language sentences to sentences in a foreign language (Mazoyer et al., 1993; Schlosser et al., 1998), non-linguistic sounds (Humphries et al., 2001), and rest (Bottini et al., 1994). Furthermore, evidence from eye-tracking and electrophysiology strongly suggests that sentence-level computations, such as syntactic and semantic composition, are engaged automatically and very rapidly word-by-word during language comprehension (Altmann and Kamide, 1999; Altmann and Steedman, 1988; Chambers et al., 2002; Friederici, 2002; Kamide et al., 2003; Kutas and Hillyard, 1980, 1984; Neville et al., 1991; Tanenhaus et al., 1995). Taken together, the basic composition hypothesis of the aTL and the immediacy of sentence structure-building predict that activation in this region should be time-locked to word presentation. To test this, we examined sentence-processing, in comparison to lists of words, using magnetoencephalography (MEG), which has a temporal resolution at the millisecond level, but which also provides spatial resolution on the order of centimeters (Hämäläinen et al., 1993), permitting comparison with the existing neuroimaging literature.

The use of MEG also offers an opportunity to investigate the spatio-temporal characteristics of sentence-level processes more broadly. In addition to addressing more general questions about the temporal profile of sentence comprehension, MEG may offer some insight into a somewhat puzzling aspect of the prior findings on sentences vs. lists; namely, although in some studies the aTL effect has been accompanied by effects in other regions, such as the posterior temporal lobe (Friederici et al., 2000; Jobard et al., 2007; Pallier et al., 2011; Snijders et al., 2009; Vandenberghe et al., 2002; Xu et al., 2005) and the inferior frontal gyrus (Pallier et al., 2011; Snijders et al., 2009; Xu et al., 2005), several studies have found a rather focal effect in the aTL (Humphries et al., 2006; Rogalsky and Hickok, 2009; Stowe et al., 1998). In light of the many computations affected by this manipulation, an effect limited to a single region is rather surprising. One possible reason for hemodynamic methods to potentially yield this type of focal finding has to do with the extreme speed of linguistic computation, which stands in contrast to the slow temporal resolution of the imaging methods. As noted above, there is a great deal of evidence that during comprehension, sentences are interpreted incrementally, word-by-word (e.g. Kutas and Hillyard, 1980; Marslen-Wilson, 1975; Tanenhaus et al., 1995). Thus perhaps hemodynamic methods, which integrate over brain activity across several seconds, may have reduced sensitivity to transient effects elicited word-by-word (see also Lau et al., 2008:926). If this is correct, then a faster technique such as MEG should yield a broad network of language-related regions for sentences over lists, including, but not limited to the aTL.

Contrary to much of the prior literature (but cf. Xu et al., 2005), we also aimed to characterize sentence processing in a relatively natural setting. Many previous sentence vs. list studies have used explicit meta-linguistic tasks, having subjects judge meaningfulness (Humphries et al., 2006), identity (Mazoyer et al., 1993), or syntactic and semantic errors (Friederici et al., 2000), while others have used a passive listening task with isolated sentences devoid of any context (Humphries et al., 2005; Rogalsky and Hickok, 2009). Such stimuli and tasks, however, may lead to brain activity that is not necessarily related to core language comprehension computations. To address these concerns, our stimuli were embedded within a narrative. While this design may lead to processing associated with both sentence-level and discourse/narrative-level computations, it is not clear whether operations associated with constructing higher-level narrative representations are time-locked to individual words, which is the only type of effect we analyzed here. Psychologically plausible parsing models clearly predict that syntactic and semantic operations are engaged incrementally, word-by-word (e.g. Hale, 2011; Stabler, 1991; Steedman, 2000; Vosse and Kempen, 2000) and thus should be reflected in brain activity that is time-locked to word presentation. However, to our knowledge, there are no models of discourse-level processes in which these processes are computed word-by-word. To improve the sensitivity of our analysis, we also sought to maximize the similarity of the low-level visual properties of our stimuli by restricting our analysis to just open-class words that were three to eight characters long (cf. Pulvermüller, 2001).

What brain regions are candidates for sentence level processing? If the aTL is indeed associated with basic combinatory operations, as discussed above, then clearly sentences should elicit more aTL activity than lists, as reported in the previous imaging studies. A second candidate is the ventromedial prefrontal cortex (vmPFC), which has been implicated for semantic composition by a growing body of MEG studies (Brennan and Pylkkänen, 2008, 2010; Pylkkänen and McElree, 2007; Pylkkänen et al., 2008, 2009). The vmPFC has also been observed to become more active as comprehension of a story increases (Maguire et al., 1999) and when subjects are asked to complete sentences with a word which fits with a given sentential context as opposed to one that does not (Nathaniel-James and Frith, 2002). Further, it forms part of a network of strongly connected regions observed during reading (Kujala et al., 2007).

Finally, and most famously, the left inferior frontal gyrus (LIFG; Broca's area) has long been considered a sentence processing related region, based on deficit/lesion research (Caramazza and Zurif, 1976; Zurif, 1995) and a variety of neuroimaging studies, including research on the processing of long-distance linguistic dependencies (Ben-Shachar et al., 2003, 2004; Caplan et al., 2008; Grodzinsky, 2001; Just et al., 1996; Santi and Grodzinsky, 2007a, 2007b, 2010; Stromswold et al., 1996), non-standard word order (Bornkessel et al., 2005; Bornkessel-Schlesewsky et al., 2009; Grewe et al., 2005, 2006), and selective attention to syntactic aspects of a stimulus (Dapretto and Bookheimer, 1999; Embick et al., 2000; Hashimoto and Sakai, 2002). Specific functional hypotheses have linked this region with syntactic movement (Grodzinsky, 2001; Grodzinsky and Friederici, 2006), working memory demands (Fiebach et al., 2005), and linearization computations (Bornkessel et al., 2005). The LIFG has also been associated with a range of lexical-level processes, including semantic retrieval (Bookheimer, 2002), cognitive control mechanisms engaged by ambiguous words or structures (Bedny et al., 2007; Thompson-Schill et al., 1997), and the evaluation of word meaning in the context of world knowledge (Hagoort et al., 2004; Lau et al., 2008). Although LIFG effects are observed in a myriad of manipulations, the sentence vs. word list contrast employed here has *not* systematically shown LIFG effects in fMRI or PET (but cf. Pallier et al., 2011; Snijders et al., 2009; Xu et al., 2005; see also Lerner et al., 2011), leading to a controversy about the centrality of the LIFG in processing sentence structure (Rogalsky and Hickok, 2010; Stowe et al., 2005). However, given the grossness of the sentence vs. word list contrast, a LIFG effect for this manipulation would be compatible with many of the above hypotheses, as long as they relate to combinatory processing in some way, even if indirectly (e.g., modulation of lexical access via sentential context).

To summarize, this experiment compared the processing of open-class words which were either presented in randomized word lists or embedded in a narrative using MEG. Analysis was done time-locked to word onsets to identify spatio-temporal patterns of brain activity associated with rapid, word-by-word sentence-level computations.

Methods

Participants

9 subjects from the New York University community participated in the experiment. Participants ranged in age from 18 to 30 (median 21) and 6 of the participants were women. All subjects were right-

handed (assessed using the Edinburgh Handedness Inventory; Oldfield, 1971) and were native speakers of English with normal vision.

Stimuli

Participants were presented with the story "Sleeping Beauty" (Marshall, 1917; text available at http://www.gutenberg.org/etext/20748). The text contains 82 sentences composed of 1404 words. Word lists were created by pseudo-randomly re-ordering the words in the story. The randomization was constrained as to avoid pairings of words that constituted partial phrases. Specifically, the following orders were disallowed: *Article–Noun*, *Adjective–Noun*, *Preposition–Noun*, *Noun–Verb*, *Verb–Noun*. The stimuli were presented to participants in two blocks, first the word lists and then the sentences. This was done to prevent the possibility that increases for the narrative condition might reflect de-activation due to lexical-level priming in the list condition instead of sentence processing the narrative condition, as well as to prevent words from the list condition from being recognized from their use in the sentence condition, which may evoke sentential and/or pragmatic processing related to the previously seen sentences. There remained the possibility of repetition priming effects in the sentence condition, potentially reducing language related activation for the sentences, however, this property of our design biased the experiment against our hypotheses.

The sentence block and the list block were further divided into nine segments containing approximately eight sentences (130 words) each. After each segment a fixation cross was presented on the screen indicating the end of the segment, followed by a yes/no question pertaining to the segment just seen. For the sentence condition, subjects were asked a comprehension question concerning the immediately preceding segment of the story (e.g. "Did the cook hit the kitchen boy?"); the questions were designed to require subjects to parse and understand the sentences. After the list condition, subjects were asked a recall question concerning the immediately preceding list (e.g. "Did you see the word 'horse'"?). Subjects used a button box placed underneath their left hand to register a response.

The computations of interest that our stimuli were designed to elicit, including lexical access and basic sentence composition and interpretation, are understood to be largely automatic (see e.g. Dehaene et al., 1998; Martens et al., 2002; Rastle et al., 2000; Shapiro et al., 1997 for lexical semantic processing, and Gunter and Friederici, 1999; Hahne and Friederici, 1999 for syntactic analysis). Accordingly, the tasks were selected to monitor basic attention in our subjects, and were necessarily slightly different between the two experimental blocks since sentence processing, by definition, engages different computations than lexical access. These differences, however, plausibly biased the experiment against finding increased activation for sentences, which is the only type of activation we sought to interpret. Specifically, since the lists in the word recall task were quite long, the sentence comprehension task was likely to be somewhat easier (and this is what our results also revealed), but under the assumption that harder processing leads to more brain activity, this difference would work against our goal of identifying increases in brain activity for the sentences. Further, it was also possible that subjects might attempt to create phrases out of the lists of words in the list condition (although it has not been our experience with these stimuli that such parsing takes place, at least not consciously). Note that this possibility, shared by all studies that have used this paradigm, would also work against our hypotheses by reducing the difference in cognitive operations engaged by the two conditions.

Procedure

Prior to recording, the head shape of each participant was digitized to allow source localization and co-registration with structural MRIs (Fastscan; Polhemus, VT). We also digitized three fiducial points (the nasion and the left and right pre-auricular points) and the position of five coils, placed around the participants face. Once the participant was situated in the magnetically shielded room for the experiment, the position of these coils was localized with respect to the MEG sensors, allowing us to assess the position of the participant's head for source reconstruction. Data were recorded continuously at the KIT/NYU facility with a 157-channel axial gradiometer (Kanazawa Institute of Technology, Kanazawa, Japan) in a dimly lit magnetically shielded room while the stimuli were projected onto a screen approximately 50 cm away. The stimuli were presented word-by-word for 500 ms each with a 300 ms ISI in gray courier font, size 18, on a black background using Psyscope software (Cohen et al., 1993). Words subtended a visual angle of approximately 1° vertically, and an average of 2.5° horizontally (with a range of 1.5° to 5° for trials included in the analysis). Data were recorded continuously at 1000 Hz with a 200 Hz low pass filter.

Data processing

Environmental noise was removed from the data by regressing signals recorded from three orthogonally oriented magnetometers approximately 20 cm away from the recording array against the recorded data using the continuously adjusted least squares method (CALM; Adachi et al., 2001). The data were then low-pass filtered to 40 Hz, resampled to 250 Hz to facilitate analysis, and high-pass filtered at .1 Hz. Individual channels with zero signal or showing excessive noise relative to neighboring channels were excluded from further analysis. At most eleven such channels were observed per subject (Median = 1).

To compare activity between the sentences and list conditions, we focused on data from epochs following the presentation of open-class words with length of three to eight characters to maximize the similarity of the low-level visual properties of our stimuli. This limited the data set to 597 epochs per condition. We did not analyze epochs from segments where participants registered incorrect responses, and we also set aside all epochs where the peak-to-peak magnetic flux at any channel exceeded 2000 fT between −100 and 600 ms of the stimulus onset. This relatively conservative artifact threshold led to the exclusion of 33% of the data across all subjects. Data for the remaining epochs spanning from −100 to 600 ms post stimulus onset were considered for further analysis ($M = 209$ for the list condition and $M = 277$ for the story condition.) While this resulted in a somewhat unbalanced dataset, as performance was poorer in the list condition than the sentence condition, our statistical inferences were based on mixed-effects regression which is robust against unbalanced data (Baayen et al., 2008; Gelman and Hill, 2006).

Source-space analysis

MNE software (Martinos center MGH, Boston) was used to estimate neuroelectric current strength based on the recorded magnetic field strengths using minimum *l2* norm estimation (Dale and Sereno, 1993; Hämäläinen and Ilmoniemi, 1984), following the recommendations of (Hauk et al., 2006) for analyzing data with a low SNR (e.g. single-trial data) and when the number and distribution of underlying sources is unknown. We note that the minimum *l2* norm is biased towards distributed patterns of activation. Current sources were modeled as three orthogonal dipoles spaced approximately 5 mm apart across the cortical surface (Dale et al., 2000), yielding approximately 2500 potential electrical sources per hemisphere. For four of nine subjects, structural MRIs were available and their cortical surface was reconstructed based on their structural MRI using Freesurfer (Martinos center MGH, Boston). For the five remaining subjects, a cortical surface based on an averaged brain provided by Freesurfer was used. The neuromagnetic data was co-registered with the structural MRI (four subjects) or the averaged cortex (five subjects) using MNE by first aligning the fiducial points, and then using an Iterative Closest Point algorithm to minimize the difference between the points defining the head shape of each participant, and the scalp.

The forward solution was calculated for each source using a single-layer boundary element model (BEM) based on the inner-skull boundary (Hämäläinen and Sarvas, 1989). As the variance of noise may vary across the cortex, the estimated activation was normalized by dividing the estimated activation by the predicted standard error of the estimate due to additive noise, yielding noise-normalized dynamic (time-varying) statistical parametric (dSPM) maps of cortical activation (Dale et al., 2000). The root mean square value of each triplet of sources was taken and baseline corrected by subtracting the mean amplitude per source for a 100 ms interval preceding the presentation of each word.

To reduce the dimensionality of the data, individual subject cortices were automatically parcellated into anatomically-based regions spanning the cortex (Fischl et al., 2002), based on the Desikan–Killiany gyral atlas (Desikan et al., 2006), using Freesurfer. We further manually subdivided four regions in each hemisphere as follows. We divided the inferior, middle, and superior temporal gyri into anterior and posterior portions, using the anterior edge of the transverse temporal gyrus to define the division along the anterior–posterior axis. We also divided the superior frontal gyrus into anterior and posterior regions, using the anterior–posterior midpoint per subject to define the division. This yielded a total of 39 regions per hemisphere spanning the lateral and medial surfaces of the cortex, shown in Fig. 1. This parcellation excluded a central portion of the medial wall, inferior to the corpus collosum, and the deep portion of the sylvian fissure. Estimated source activations were averaged together within these regions.

Our first analysis focused on a set of eight left hemisphere regions of interest (ROIs) that have been previously associated with language processing. These included anterior portions of the superior and middle temporal gyri (aSTG, aMTG), the Pars Triangularis and Pars Opercularis of the left IFG (Broca's area; PTr, POp), and the ventromedial prefrontal cortex (vmPFC). We also included three posterior temporal ROIs: the posterior superior temporal gyrus (pSTG), superior temporal sulcus (STS) and middle temporal gyrus (pMTG).

The ROI analysis was followed up with an analysis of activity across all 39 regions per hemisphere, providing almost complete coverage of the cortex.

Statistical analysis

The effect of condition (sentences vs. lists) was evaluated using mixed-effects regression over the single-trial data (Baayen et al., 2008; Gelman and Hill, 2006) with the *lme4* package (Bates and Maechler, 2009) in R (R Development Core Team, 2006). Analyzing the single-trial data rather than data averaged by condition allowed us to incorporate several potentially confounding factors into our analysis, including word frequency, trial order, and sentence position, and also provided statistical inferences that were robust against unbalanced data of the sort introduced after our dataset was trimmed due to behavioral performance and artifacts. Separate models were fit per time-point, per ROI, for all time points between 200 and 500 milliseconds post-stimulus onset. These times were chosen to span a window within which effects associated with sentence processing have been reported in the electrophysiogy literature (e.g. Friederici, 2002).

The regression models included our factor of interest which was coded as a binary predictor set to 0 for the list condition and 1 for the sentence condition, along with several potentially confounding variables, treated as fixed effects: word frequency (log-transformed and mean centered, derived from the HAL written-language corpus of 160 words), word length in orthographic characters (mean centered), epoch order (residualized against condition label), sentence position, measured from the first word in a sentence (these values were also ascribed to the same items when appearing in the random word lists to reduce co-linearity between this predictor and condition label). We also included interaction terms between condition and epoch order and condition and sentence position, and a random intercept for subjects.

Statistical significance was evaluated using a non-parametric permutation test. We first identified time points t for each region k where the magnitude of the normalized estimated coefficient for the effect of condition β_{cond} was greater than or equal to a pre-defined height threshold s:

$$\left\{ t_k : \left| \frac{\beta_{cond}(t_k)}{SE_{\hat{\beta}_{cond}(t_k)}} \right| \geq s \right\}. \qquad (1)$$

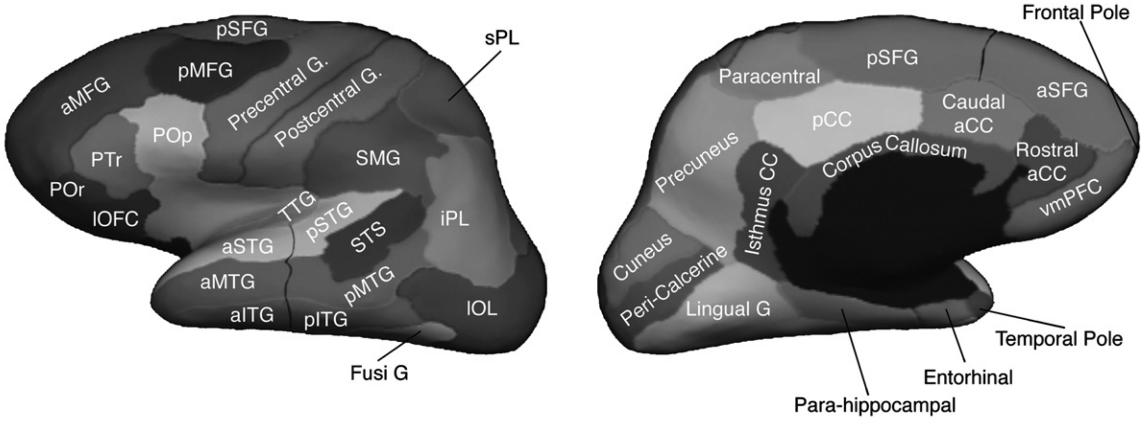

Fig. 1. Cortical regions used in our analysis were determined using an automated anatomical parcellation following Desikan et al. (2006) in combination with manual division of the STG, MTG, ITG and SFG into anterior and posterior portions. This parcellation covered most of the lateral and medial cortex, but excluded a central portion of the medial wall, inferior to the corpus collosum, and the deep portion of the sylvian fissure. aSTG, anterior superior temporal gyrus; pSTG, posterior superor temporal gyrus; aMTG, anterior middle temporal gyrus; pMTG, posterior middle temporal gyrus; aITG, anterior inferior frontal gyrus; pITG, posterior inferior temporal gyrus; STS, superior temporal sulcus; TTG, transverse temporal gyrus; SMG, supramarginal gyrus; sPL, superior parietal lobe; iPL, inferior parietal lobe; iOL, inferior occipital lobe; Fusi G, fusiform gyrus; aMFG, anterior middle frontal gyrus; pMFG, posterior middle frontal gyrus; aSFG, anterior superior frontal gyrus; pSFG, posterior superior frontal gyrus; POr, pars orbitalis; PTr, pars triangularis; POp, pars opercularis; lOFC, lateral orbitofrontal cortex; vmPFC, ventromedial prefrontal cortex; aCC, anterior cingulated cortex; pCC, posterior cingulated cortex.

Time points for each region were grouped into a set of clusters G based on temporal adjacency, and we discarded all clusters shorter than 20 ms. We report results for comparisons with two planned height thresholds, s, one which allowed increased sensitivity to shorter, punctuated effects, and one which allowed increased sensitivity to longer-lasting effects ($s = 1.64$ or .67, respectively, which correspond to α of .1 and .5 when evaluated against the standard normal distribution). Note that this threshold does not affect the false alarm rate of the non-parametric statistical test (Maris and Oostenveld, 2007). We then formed a summary statistic C describing each cluster g in G by dividing the coefficient for condition at each time-point by its standard error and summing the resulting normalized coefficient within each cluster:

$$C_g = \sum_{t\in g} \frac{\hat{\beta}_t}{SE_{\hat{\beta}_t}}. \tag{2}$$

To evaluate the statistical reliability of each cluster, we estimated the distribution of these cluster-level statistics under the null hypothesis using the following permutation test (Maris and Oostenveld, 2007):

1. The condition label (lists or sentences) was shuffled across epochs within subjects.
2. Regression models were re-fit per time-point, per region.
3. Clusters were identified as described above and cluster-level statistics were re-computed for each permutation.
4. The largest cluster-level statistic per region was selected.

This procedure was repeated 1000 times, creating a distribution of cluster maxima per region that would be expected under the null hypothesis that that there was no difference between the sentences and list condition. For the ROI analysis, we report as significant those clusters for which the cluster-level statistic was seen in fewer than .625% of the simulated runs (corresponding to family-wise error rate of .05 with a Bonferroni adjustment for multiple comparisons across ROIs). For the whole brain analysis, cluster p-values were corrected for multiple comparisons across regions using the False Discovery Rate (Benjamini and Yekutieli, 2001; Genovese et al., 2002).

Results

Sensor waveforms of the sentence and list conditions for a representative subject are shown in Fig. 2. There is a visually salient increase of activity in a component spanning from approximately 250 to 450 ms. Fig. 3 shows snapshots of estimated source activity in the left hemisphere across time, grand-averaged across subjects. Visual inspection shows increased inferior frontal and anterior temporal activation between 300 and 500 ms.

Region of interest analysis

Waveforms from the eight regions of interest are shown in Fig. 4. Using clusters defined based on a pointwise height threshold sensitive to longer-lasting effects, significant effects were observed for the entire duration of the time-window of interest (200–500; black bars) in the in the aSTG, aMTG, and pSTG and marginal effects ($p<.05$ corrected for multiple comparisons across time-points, but not across regions) were additionally observed in the vmPFC, pMTG, STS, and POp. With a pointwise height threshold more sensitive to shorter effects, effects between approximately 230 to 390 ms were seen in the pSTG. Marginal effects were observed between 230 and 290 ms in the pMTG and STS, and between 290 and 340 ms in the aMTG, aSTG, vmPFC. Detailed results for all ROI effects are given in Tables 1 and 2.

Our results are consistent with the basic combinatoric hypothesis of the aTL in that we see increased activity in the anterior temporal lobe beginning between 200 and 300 ms after word presentation. We also see increased activation in a set of other language-related regions, consistent with the hypothesis that sentence processing should engage a number of regions associated with the many processes required for comprehension.

Whole brain analysis

Across all cortical regions, clusters derived using a lower pointwise height threshold, which identified clusters that spanned the entire time-window of interest, were significant (q(FDR)$<.05$) in six of

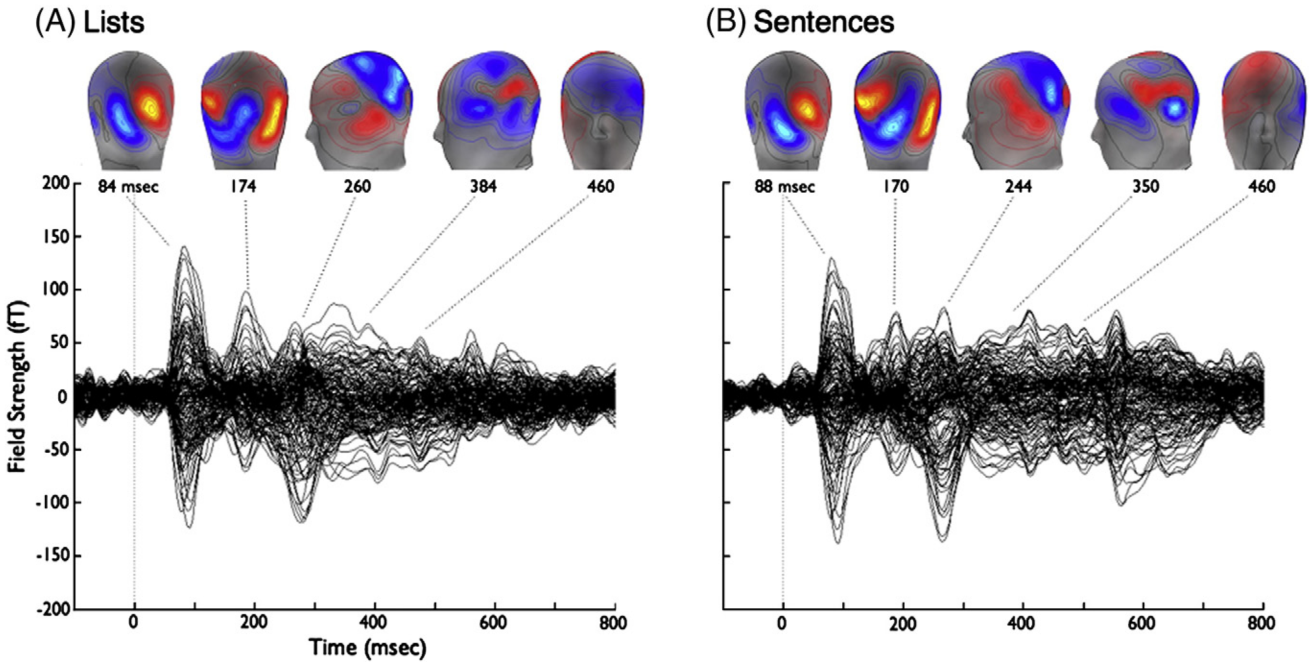

Fig. 2. Overlay of averaged waves for all 157 sensors from a single subject along with magnetic flux topographies in the list (A) and sentence (B) conditions. Waves are time-locked to word presentation. Early components at approximately 100, 170 and 250 are clearly visible as well as an extended complex component peaking between 300 and 400 ms which shows a larger effect in the sentence condition, compared to lists.

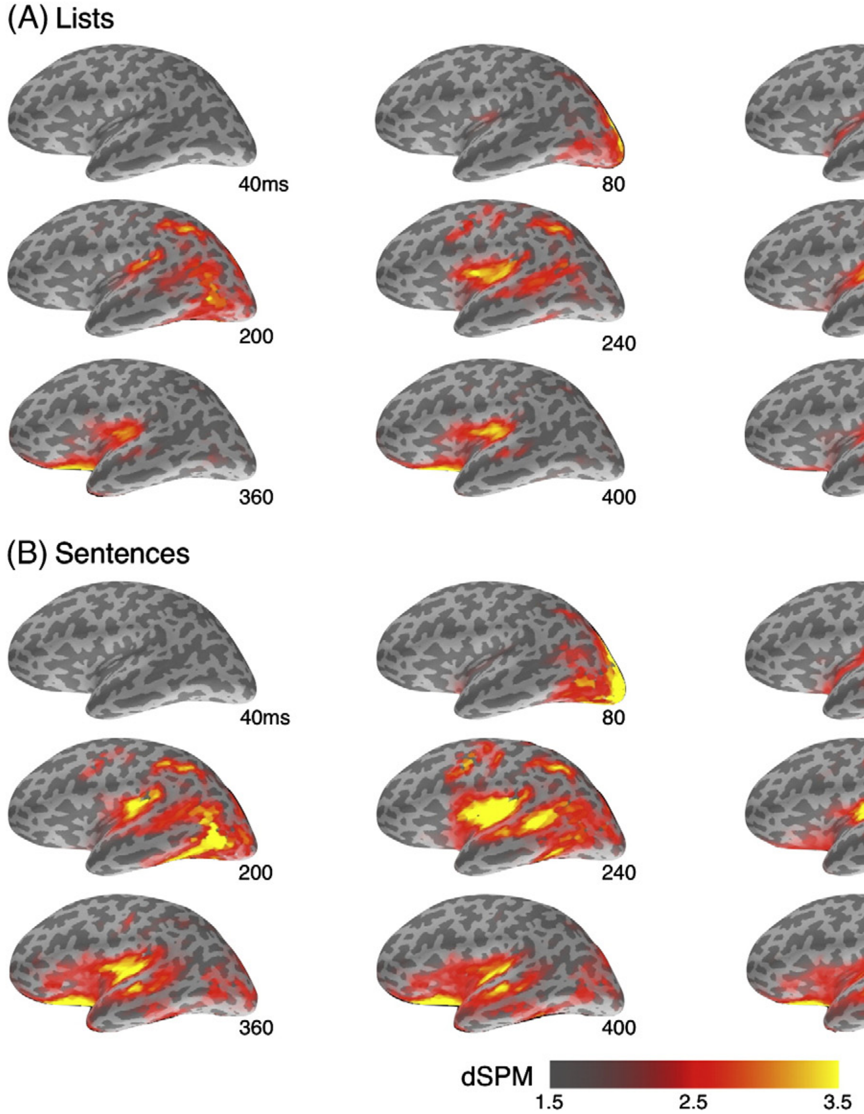

Fig. 3. Grand-averaged left hemisphere source-space activation in the list (A) and sentence (B) conditions shown at 40 ms intervals. Centered at approximately 360 ms, increased activation in the temporal lobe and inferior frontal gyrus is apparent. There also appears to be increased activation in the occipital and parietal lobes starting around 120 ms. Thresholds for displayed activation reflect the range of activity observed across the epoch. dSPM, noise normalized source estimates (Dale et al., 2000).

the eight regions of interest (aMTG, aSTG, pMTG, pSTG, STS, POp) and marginal ($q(\mathrm{FDR}) = .06$) in the vmPFC. Significant effects were also observed in left pars orbitalis, postcentral gyrus, inferior parietal gyrus, and transverse temporal gyrus, as well as right hemisphere anterior temporal lobe, portions of the inferior frontal gyrus, anterior cingulate, and regions surrounding the central sulcus bilaterally. Table 3 describes the significant clusters in detail. No clusters derived using the higher pointwise threshold survived multiple comparisons across the whole brain.

Sensory responses

Inspection of Fig. 4 shows a visually salient increase in early activity in posterior temporal regions for sentences over lists, peaking approximately 130 ms after stimulus onset. Fig. 3 also shows a trend towards increased early occipital activity for sentences compared to lists in the same time window. While sentence-level processes have been observed to influence early sensory responses due to top-down effects (Dikker and Pylkkanen, 2011; Dikker et al., 2009, 2010; Herrmann et al., 2009), it is possible that a difference in early responses might be due to attention-related effects owing to the different tasks used for sentences and word lists.

To evaluate this possibility, we conducted a post-hoc analysis of activity in a window from 0 to 200 ms in our eight regions of interest following the same statistical procedures described in the Methods section. No significant clusters were observed in this analysis. We conducted a second post-hoc comparison in the early 0–200 ms window using eight bilateral occipital ROIs: iOL, cuneus, lingual gyrus, and peri-calcarine cortex (see Fig. 1). Though defining these ROIs based on observed trends in the data introduces a degree of statistical circularity to our analysis (Kriegeskorte et al., 2009), we do so here to allow maximal power to detect early effects that may be indicative of attention-related confounds. However, even using targeted occipital ROIs, we found no significant differences between sentences and lists in the earlier time-window. Finally, we repeated our whole-brain analysis over the earlier 0–200 ms time-window. Again, no significant effects were observed. The absence of detectable early sensory effects suggests that increased activation for sentences over lists observed in temporal and frontal regions was not due to lower-level, attention-related, differences between our conditions.

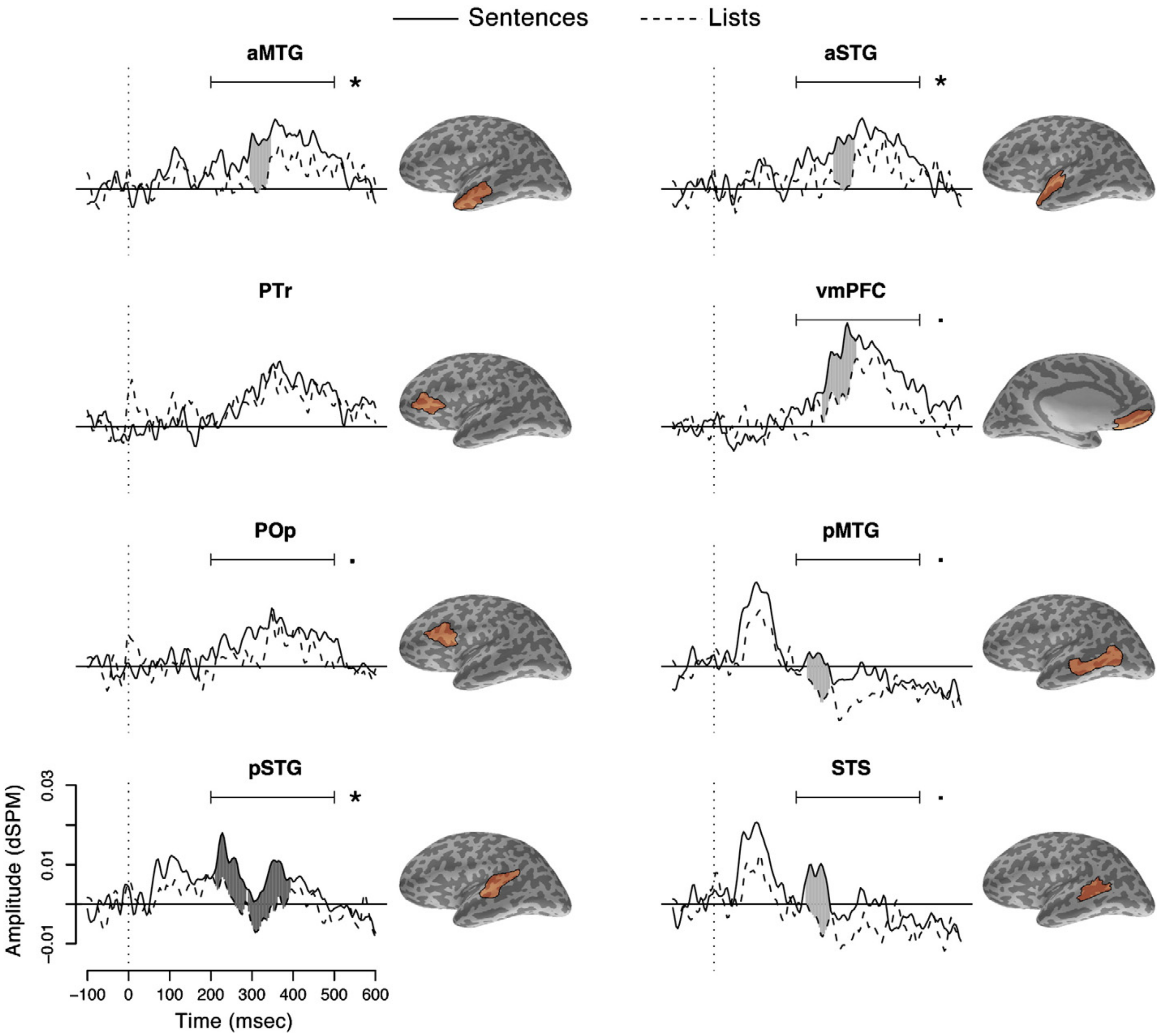

Fig. 4. Mean source waveforms for eight regions of interest (ROIs) in the sentence (solid) and list (dashed) conditions, between −100 and 600 ms from word onset. ROIs are marked on the inflated cortex of a representative subject (see also Fig. 1). Horizontal bars indicate significant ('*' p<.006) and marginal ('.' p<.05) differences in the 200–500 ms time-window of interest (see Table 1). Gray shading indicates significant (dark gray; $p<.006$) and marginal (light gray; $p<.05$) contiguous clusters of activation within the time-window of interest (see Table 2).

Table 1
Region of Interest results, pointwise height = .67 (see Methods), time window from 200 to 500 ms. Cluster p-value is corrected for multiple comparisons across time using a permutation test, and evaluated against a Bonferroni-adjusted alpha level of .006 to correct for multiple comparisons across regions. '*' $p<.006$; '.' $p<.05$.

Region	Cluster statistic	Cluster *p*-value	
Left hemisphere			
aMTG	97.88	.006	*
aSTG	109.86	.005	*
pMTG	80.76	.008	.
pSTG	122.54	.000	*
STS	90.68	.007	.
PTr	50.39	.061	
POp	80.26	.010	.
vmPFC	106.87	.023	.

Behavioral results

Accuracy in the list condition ($M=57\%$, $SEM=5.3\%$) was significantly reduced compared to the sentence condition ($M=74\%$, $SEM=2.6\%$), $t(8)=2.94$ $p<.05$. Performance in the sentence condition was evaluated in comparison to nine control subjects, who completed the sentence questionnaire without having participated in the reading experiment. Control subjects performed significantly worse ($M=47\%$, $SEM=3.6\%$), $t(16)=6.01$, $p<.001$, indicating that the experimental subjects attended to the sentences. The low accuracy observed in the list condition was unexpected. In order to have the questions appear at roughly equivalent intervals across the two conditions, the lists were a bit too long for memorization to be entirely successful. However, for the purposes of this study, what was needed was for subjects to read the words, not to memorize them. As comprehension is automatic upon encountering a word (Dehaene et al., 1998; Gunter and Friederici, 1999; Hahne and Friederici, 1999;

Table 2
Region of Interest results, pointwise height = 1.64 (see Methods). Cluster p-value is corrected for multiple comparisons across time using a permutation test, and evaluated against a Bonferroni-adjusted alpha level of .006 to correct for multiple comparisons across regions. ‘*’ $p<.006$; ‘.’ $p<.05$.

Region	Time (ms)	Cluster statistic	Cluster p-value	
Left hemisphere				
aMTG	296–344	29.38	0.028	.
aSTG	292–340	29.83	0.040	.
vmPFC	264–344	41.85	0.034	.
pMTG	228–280	26.35	0.022	.
pSTG	212–284	42.74	0.003	*
pSTG	292–392	53.55	0.001	*
STS	224–280	36.37	0.009	.

Martens et al., 2002; Rastle et al., 2000; Shapiro et al., 1997) and performance on the task indicated that participants were attending, we believe it is unlikely that the difference in performance seriously affects the interpretation of our results, which relied only on epochs for which participants registered a correct response.

Discussion

In this work we investigated the neural correlates of sentence-level processing using MEG to address two goals. First, we evaluated whether anterior temporal activity, observed in previous neuroimaging studies, is time-locked to word presentation, as expected under the hypothesis that activity in this region is associated with basic combinatoric processing (Brennan et al., in press; Dronkers et al., 2004; Grodzinsky and Friederici, 2006; Hickok and Poeppel, 2007; Humphries et al., 2006; Rogalsky and Hickok, 2009; Stowe et al., 2005; Vandenberghe et al., 2002) in combination with evidence that sentence-level processes are engaged word-by-word (Altmann and Steedman, 1988; Chambers et al., 2002; Marslen-Wilson, 1975; Tanenhaus et al., 1995). Consistent with this view, we observed a time-locked effect in the left aSTG and aMTG, occurring between 290 and 340 ms after word onset. We also examined the time-course and spatial distribution of sentence processing more broadly. Our results showed activation a broad network of regions beginning around 250–300 ms after word onset. Specifically, increased activity was observed in anterior temporal regions bilaterally, posterior temporal regions, the left ventromedial pre-frontal cortex, as well as the left pars opercularis.

Table 3
Whole brain analysis results, pointwise height = .67 (see Methods), time window from 200 to 500 ms. Only effects with q(FDR) < .05 are shown. Cluster p-value is corrected across time but not regions; q(FDR) indicates the false discovery rate across all regions.

Region	Cluster statistic	Cluster p-value	Cluster q(FDR)
Left hemisphere			
aMTG	97.88	0.006	0.040
aSTG	109.86	0.005	0.039
STS	90.68	0.007	0.041
Caudal aCC	80.83	0.015	0.046
iPL	116.48	0.005	0.039
POp	80.26	0.010	0.042
POr	100.45	0.011	0.042
pMTG	80.76	0.008	0.041
pSTG	122.54	0.000	0.000
Postcentral G	75.71	0.009	0.042
TTG	87.51	0.007	0.041
Right hemisphere			
aITG	104.05	0.014	0.043
aMTG	95.49	0.012	0.042
aSTG	118.10	0.008	0.041
STS	76.44	0.015	0.046
Caudal aCC	76.02	0.012	0.042
pMFG	84.85	0.015	0.046
Entorhinal	105.44	0.015	0.046
Paracentral G	87.27	0.006	0.040
PTr	110.07	0.015	0.046
pSFG	90.30	0.013	0.043
pSTG	111.47	0.005	0.039
Precentral G	88.50	0.014	0.043
sPL	83.14	0.015	0.046
TTG	119.98	0.005	0.039

This study did not aim to shed light on the specific sub-functions of the areas showing an effect; the sentence vs. list comparison was a simple gross contrast which aimed to identify a sentence processing network. Crucially for our purposes, increased activation for sentences was observed in a wide range of regions that have been previously implicated in various aspects of sentence processing (Ferstl et al., 2008; Friederici, 2002; Hickok and Poeppel, 2007; Kaan and Swaab, 2002; Vigneau et al., 2006).

In addition to the anterior temporal, inferior frontal, and ventral medial regions discussed in our introduction, we observed a robust effect for sentences vs. lists in the left posterior temporal lobe. This result is consistent with a selection of previous sentence vs. list studies (Friederici et al., 2000; Jobard et al., 2007; Pallier et al., 2011; Snijders et al., 2009; Vandenberghe et al., 2002; Xu et al., 2005), and with recent meta-analyses of sentence-level processing (Ferstl et al., 2008; Vigneau et al., 2006). While not standardly associated with sentence-level computations (Hickok and Poeppel, 2007), posterior temporal cortex has been associated with lexical-level processes that have been observed to be sensitive to contextual effects (see e.g. Lau et al., 2008 for a review). Given the robust contextual support provided by sentences, it is quite plausible that some aspects of context-sensitive lexical processing were manipulated in our study.

Differences between current results and previous sentence vs. list studies

The finding that a network of language-related regions was selectively activated during sentence processing is consistent with the hypothesis that the focal results reported by some previous studies may be due to reduced sensitivity of hemodynamic techniques to some word-by-word sentence-level processing. However, there are also several alternative possibilities. One alternative is that activation in a larger number of regions in our results is a simple consequence of different statistical criteria. However, we do not believe that our results can be attributed to a difference in statistic threshold, as several of the fMRI studies under consideration employed very liberal thresholds (e.g. $p<.01$, uncorrected across the MRI volume; Rogalsky and Hickok, 2009). Another possibility is that the larger number of regions we report is an artifact of the reduced spatial resolution of the MEG source solution such that activation from a single focal source is spreading into adjacent regions. Evidence against this interpretation comes from the fact that we observe increased activation in regions that are not adjacent (e.g. pSTG and vmPFC) while intermediate regions, do not show increased activation (e.g. the lateral orbitofrontal cortex).

We suggest that rapid sentence-level computations lead to changes in cortical activity that may be difficult to detect with hemodynamic methods which integrate across several seconds. Reduced signal to noise for some sentence-level computations may contribute to inconsistent findings across studies and lab groups. One possible mechanism for this reduced sensitivity follows from observations that the evoked hemodynamic response exhibits a non-linear reduction in amplitude to stimuli presented visually with inter-stimulus-intervals of less than 4 s (e.g. de Zwart et al., 2009; Liu et al., 2010; Zhang et al., 2008). That is, the amplitude of the hemodynamic response is reduced to rapidly presented stimuli in comparison to stimuli that are spaced more than four seconds apart, with the effect most pronounced for presentation rates of less than 1 s. Accordingly, there is a concern that rapid word-by-word presentation in previous sentence vs. word list experiments could lead to a reduction in the hemodynamic response associated with the sentence-level computations that are engaged many times a second during incremental language comprehension.

While previous studies have been careful to ensure that there is an adequate inter-stimulus interval between sentences and word lists, the individual words within each sentence or list have been presented serially and rapidly, with several words appearing each second.

The time-course of activation

The fine temporal resolution of MEG allows the examination of the temporal characteristics of the activation patterns observed for sentences, compared to lists. All of the observed activations peak between 250 and 450 ms after stimulus onset, consistent with a large number of studies from electrophysiology on the time-course of sentence processing, where effects of semantic congruity and syntactic analysis are commonly observed starting at about 300 ms (e.g. Friederici, 2002; Kutas et al., 2006). Interestingly, the time-course of separation in each of the regions is roughly similar. Wave separation begins between 250 and 300 ms after stimulus onset and continues to 500 ms post stimulus onset, although the time points at which the differences are statistically reliable show variability.

The parallel time-course across regions observed during the narrative could be construed as evidence for parallel processing of multiple different computations (MacDonald et al., 1994; Marslen-Wilson, 1975; Marslen-Wilson and Tyler, 1980; McRae et al., 1998). However, our results cannot be used to reject the hypothesis of seriality in syntactic and semantic processing (e.g. Ferreira and Clifton, 1986; Frazier and Fodor, 1978; Friederici, 2002). For instance, a serial model could accommodate these findings if it included the possibility that top-down predictive processes and bottom-up stimulus-driven processing may be engaged simultaneously. Finally, our analysis collapses over words at different points in the sentence, and it is plausible that both syntactic and semantic operations are processed more rapidly as a sentence progresses and a rich prior context constrains possible analyses.

Conclusion

Brain activity associated with processing sentences was examined using MEG to test whether anterior temporal activation for sentence processing is time-locked to word presentation and to better understand the puzzling neuroimaging finding that sentences may lead to a focal increase of activation in the anterior temporal lobes, compared to word lists. Comparing the processing of sentences embedded in a story with the same words in random lists, more activation was found for sentences between 250 and 500 ms post stimulus onset in the anterior temporal lobes, consistent with the hypotheses linking this region with basic combinatorics; further activation was seen in medial prefrontal cortex, the left inferior frontal gyrus, and posterior temporal lobes, consistent with much literature connecting these regions with various aspects of sentence level processing.

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