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Time Course of fMRI-Activation in Language and Spatial Networks during Sentence Comprehension

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Functional neuroimaging previously has been considered to provide inadequate temporal resolution to study changes of brain states as a function of cognitive computations; however, we have obtained evidence of differential amounts of brain activity related to high-level cognition (sentence processing) within 1.5 s of stimulus onset. The study used an event-related paradigm with high-speed echoplanar functional magnetic resonance imaging (fMRI) to trace the time course of the brain activation in the temporal and parietal regions as participants comprehended single sentences describing a spatial configuration. Within the first set of images, on average 1 s from when the participant begins to read a sentence, there was significant activation in a key cortical area involved in language comprehension (the left posterior temporal gyrus) and visuospatial processing (the left and right parietal regions). In all three areas, the amount of activation during sentence comprehension was higher for negative sentences than for their affirmative counterparts, which are linguistically less complex. The effect of negation indicates that the activation in these areas is modulated by the difficulty of the linguistic processing. These results suggest a relatively rapid coactivation in both linguistic and spatial cortical regions to support the integration of information from multiple processing streams.

INTRODUCTION

Ever since the time of Broca and Wernicke, behavioral data from aphasic patients have implicated the left inferior frontal and left posterior superior temporal regions in some aspects of language processing. With the onset of neuroimaging techniques, however, it has become possible to examine the involvement of various brain areas in language processing among normal subjects. The emerging view suggests a dynamic cortical involvement, determined by the quantitative difficulty as well as on the qualitative nature of the language processes. Specifically, in a functional magnetic resonance imaging (fMRI) study, we measured the amount of cortical activation while participants read and answered questions about structurally simpler sentences (conjoined active clauses) or more complex sentences (with embedded object-relative clauses) (Just *et al.*, 1996). The results showed that with increasing linguistic complexity, there were increasing amounts of fMRI-measured activation in the classic left cortical regions (roughly, Broca's and Wernicke's areas) as well as in their right homologues. Because the sentence types were balanced for word length and superficial lexical structure, the increases were attributed to the increased complexity of the underlying comprehension processes. Such data suggest that the mapping of language processing functions to the cortical systems that support them does not depend solely on the type of processing, but also on the quantitative difficulty of the processing.

The current study extends this approach by using an event-related method to examine the time course of activation that is associated with language processing in a complex cognitive task that involves intermodal integration. The task involves reading a sentence, such as, "It is (isn't) true that the star is above the plus," and then verifying it as true or false with respect to a subsequently presented picture, which might depict a star above a plus. The event-related method assesses the time course of activation during the sentence phase and then during the picture-processing phase, rather than relying on asymptotic activation that sums across different phases of the task. The averaged single-trial method has been used successfully to study simpler processes, such as the time course of activation while participants completed single word stems (Buckner *et al.*, 1996) or processed briefly flashed visual stimuli (Savoy *et al.*, 1995). The current study involves a more complex cognitive task.

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This study assesses whether fMRI-measured activation increases with the complexity of sentence processing, when complexity is operationalized by comparing the comprehension of negative sentences to their affirmative counterparts. Numerous behavioral studies indicate that negative sentences are more difficult to process than affirmatives, resulting in increased reading time and errors (Chase and Clark, 1972; Carpenter and Just, 1975). The modal processing model for negation suggests that negative sentences are encoded as an affirmative core with an additional linguistic marker signaling the negation. The participant initially processes the affirmative core and then must reverse the polarity of the representation to accommodate the negation. Both the construction and maintenance of the representation during comprehension is more complex for the negative sentences. It is this processing demand that leads to the prediction of higher levels of fMRI-measured activation during the comprehension of negative sentences than affirmative sentences in the left posterior temporal region, a region that is classically associated with language. Activation has been found in this region in several neuroimaging studies including sentence reading (Bavelier *et al.*, 1997; Just *et al.*, 1996) and sentence listening comprehension (Binder *et al.*, 1994; Mazoyer *et al.*, 1993). Although there is as yet no agreed upon characterization of its precise role in language comprehension, one hypothesis is that it participates in coordinating the linguistic representations used in interpreting speech and written text (Howard *et al.*, 1992; Mesulam, 1990).

Greater activation in this region for negative than affirmative sentences would support the more general hypothesis that the cortical activation in a region is related to the amount of demand for the processes executed in that cortical region (Just *et al.*, 1996). The effects of task demand on cortical activation have been found not only in language processing, as in the Just *et al.* (1996) study, but also in neuroimaging studies that have examined mental rotation (Carpenter *et al.*, 1999), short-term memory word span (Grasby *et al.*, 1994), and *n*-back short-term letter recognition (Braver *et al.*, 1997). Although such conventional blocked-design studies of task difficulty demonstrate more activation for more demanding task items, the more demanding items typically take a longer time to process. So, the comparison of activation levels is somewhat compromised by the inequality of the processing times (although the processing times can be statistically equated). An advantage of an event-related paradigm is that it reveals not just the amount, but the time course of the brain activation. Consequently, the activation in the easier and harder conditions can be compared at various time intervals after the stimulus onset, regardless of whether there is any difference in their total processing times.

A second contribution of the study is that it examines activation not just in the posterior temporal region but also in the parietal regions, which are associated with various visuospatial processes, such as mental rotation, and covert and overt changes in spatial attention and eye movements (Alivisatos and Petrides, 1997; Carpenter *et al.*, 1999; Cohen *et al.*, 1996; Corbetta *et al.*, 1998; Luna *et al.*, 1998; Lynch *et al.*, 1977; Tagaris *et al.*, 1997). The reason for examining activation in the parietal regions is that during sentence reading in this task, the participant is preparing to compare the linguistic representation to a picture. On one hypothesis, the initial sentence reading consists of linguistic processing that is encapsulated from any representation or processing of the spatial configuration to which the sentence refers. According to this linguistic encapsulation hypothesis, the reading of the sentence entails the representation of its lexical and syntactic content, without immediately constructing a spatial representation of the sentence referent. In that case, one would expect little or no activation in the parietal regions related to the initial sentence comprehension. (Parietal activation related to the processing of the picture would not be expected until after the picture had been presented.) Alternatively, according to a more interactive hypothesis, the neural processing of sentences that refer to a spatial configuration is not encapsulated but also involves some activation in the parietal system that may participate in constructing a representation of the sentence's spatial referent. The study examined the degree and onset time of the activation in parietal regions during the processing of the sentence only, before the picture was presented, to adjudicate between the encapsulation hypothesis and the interactive hypothesis. The experiment's ability to make this adjudication was increased by the manipulation of the linguistic variable of negation-affirmation. If this variable, namely the presence or absence of negation, were to affect the activation in the parietal areas prior to picture onset, it would constitute strong evidence for the interactive hypothesis. Also, an effect of negation on parietal activation greatly decreases the plausibility that the parietal activation is due to processes unrelated to language processing, such as the eye movements in reading.

Finally, we also examined the activation in these cortical regions during the picture-processing phase. Because the picture presentation almost immediately followed the sentence presentation, the fMRI-measured activation during this phase is likely to reflect some combination of the activation due to the preceding sentence processing and to the picture processing.

In sum, the study examined the time course of fMRI-measured activation in posterior temporal and parietal regions while the participant read a sentence that described a spatial configuration and verified it against a subsequently presented picture. In order to sample the activation frequently during sentence reading, we restricted the study to a short TR (1.5 s) and seven coronal slices, which excluded the frontal and occipital regions from the field of view. In addition, to further control the temporal relation between the task and MR imaging, the MR data acquisition was coordinated with the sentence presentation and with the subsequent picture presentation, as shown in Fig. 1.

MATERIALS AND METHODS

Subjects

The participants were eight healthy, right-handed college student volunteers (four males, four females) who gave signed, informed consent that had been approved by the University of Pittsburgh and the Carnegie Mellon Institutional Review boards. The participants were familiarized with the sentence-verification task before the imaging study through instructions and participation in a short pilot study. They were also familiarized with the scanner and the scanning procedure before the actual study began.

Task and Stimulus Materials

Each trial began with either an affirmative or negative sentence, such as, “It is (not) true that the star is above the plus.” The sentence was rear-projected on a screen 45 cm away from the participant on a single line that subtended approximately 15° of visual angle. When the participant finished reading the sentence, he/she pressed a button to terminate the sentence and start the pictorial display. The latter displayed a picture (such as a plus above a star or a star above a plus), to which participants responded by pressing a button to indicate “true” or “false.” The baseline activation was the mean of the activation observations for the last 14 s of the 20-s fixation intervals that intervened between each trial.

The stimuli consisted of 14 affirmative and 14 negative randomly ordered sentences that included variation in the preposition (*above* or *below*), figures (star/plus/dollar), and truth value (true/false). To defeat the strategy of simply preparing for a fixed picture, half of the pictures included a symbol (a 135° arc terminating with an arrow), indicating that the picture should be mentally rotated by 135° counterclockwise prior to comparison to the sentence. To further discourage participants from mentally converting negative sentences into an affirmative converse, a third symbol was sometimes used. For example, the sentence might be, “It is not true that the star is above the plus,” and the picture might show a star above a dollar sign. Such stimuli were used frequently in the practice pilot session to decrease the likelihood that the participant would adopt a conversion strategy, but they were used only twice in the actual study.

Scanning Procedures

Both the sentence and picture presentations were synchronized electronically with the scanner. The acquisition interval to acquire all seven slices was 1500 ms. For the five slices (of the seven total) that defined the posterior temporal regions, the center of *k*-space was

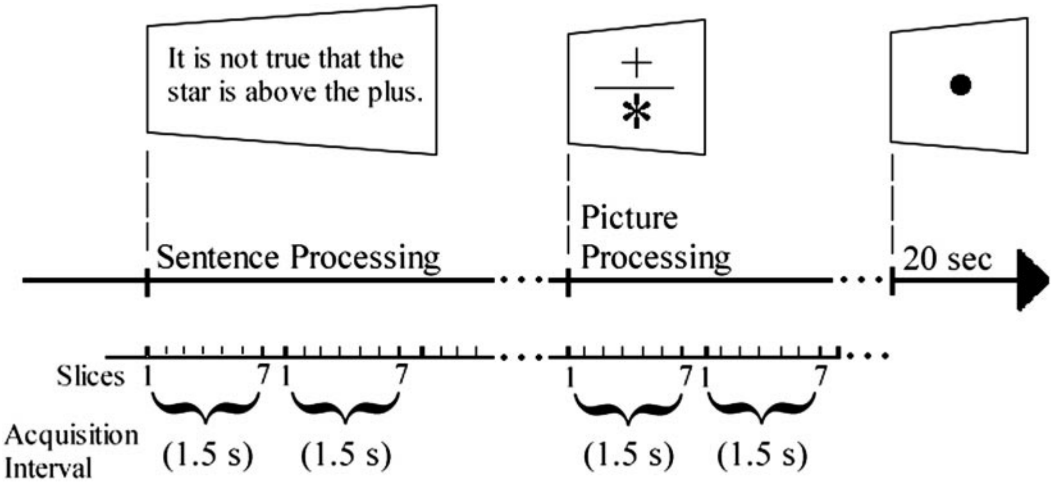

FIG. 1. The time line for a trial. A trial began with either an affirmative or negative sentence, such as, “It is (not) true that the star is above the plus.” The participant read the sentence and then pressed a button to terminate the sentence display and start the pictorial display, such as a star above a plus. The participant responded by pressing a button to indicate true or false and terminate the picture. Then the participant viewed a fixation point during a 20-s intertrial interval, the last 14 s of which were used to measure the baseline activation level. The beginning of the sentence presentation and picture presentation were synchronized electronically with the MR scanner, indicated schematically by the seven slices being acquired in successive 1500-ms acquisition intervals.

acquired approximately 0.4, 0.6, 1, 1.2, and 1.4 s from the sentence onset, with a mean elapsed time of 940 ms for the first acquisition interval, 2440 ms for the second, and 3940 ms for the third interval. For the five slices that defined the parietal regions, the corresponding times were approximately 0.2, 0.4, 0.6, 1.2, and 1.4 s, with a mean elapsed time of 850 and 2350 ms for the first and second acquisition intervals.

Cerebral activation was measured using blood oxygenation level-dependent (BOLD) contrast. Imaging was on a 1.5T scanner at the MR Research Center at the University of Pittsburgh Medical Center (Thulborn *et al.*, 1996a,1996b). The acquisition parameters for the gradient-echo EPI with 7 coronal slices were TR = 1.5 s, TE = 50 ms, flip angle = 90°, 128 × 64 acquisition matrix, 5-mm thickness, 1-mm gap, RF whole-head coil. The structural images were high-resolution T1-weighted spin echo images, with TR = 400 ms, TE = 11 ms, 256 × 256 acquisition matrix, 5-mm slice thickness, and 1-mm gap.

Data Analysis

The functional activation was assessed in two major regions of interest (ROI's) that were defined in each hemisphere using a parcellation method that relies on limiting sulci and anatomically landmarked coronal planes to segment cortical regions (Caviness *et al.*, 1996; Rademacher *et al.*, 1992). The ROI's in the functional images were defined for each participant with respect to coregistered structural images that had been acquired during the same scanning session. The temporal ROI's included the posterior superior (T1p or BA 22) and the middle temporal gyrus regions (T2p, and TO2 or BA 22 and 37). The parietal ROI's included the superior parietal lobule (SPL, BA 5, and 7), the posterior supramarginal gyrus (SGp, BA 40) and the angular gyrus (AG, BA 39), as shown in Fig. 2.

The voxels of interest were identified by first computing separate voxel-wise t statistics (using a threshold of $t \geq 4.5$) that compared the activation for the affirmative condition and negative condition to the baseline activation during the sentence presentation and separately, during the picture presentation (including 6 s beyond picture offset to take advantage of the lag in the hemodynamic response). The voxels of interest were those that reached significance in either the affirmative or negative conditions for either presentation phase, and it was the time course of their averaged activation that was of primary interest. The mean activation level for a time period for a voxel was based on the raw time-series data for any subset of the 14 sentences of that type that were still processed during that 1.5-s acquisition interval. The average time-series data for each voxel were fit with a mixed linear model, with voxels nested within subjects and crossed with acquisition interval and sentence type (affirmative or negative).

The image preprocessing corrected for in-plane head motion and signal drift using procedures and software developed by Eddy *et al.* (1996). The in-plane head motion of the data sets averaged less than 0.2 voxels, and data sets with greater in-plane or out-of-plane motion were discarded without further analysis.

RESULTS

As expected, negative sentences took longer to process than affirmatives. The mean reading time was 3511 ms for affirmative and 4100 ms for negative sentences ($t(7) = 3.09$, $P < 0.01$), and the picture processing times were 2924 and 4266 ms for the affirmative and negative conditions ($t(7) = 3.91$, $P < 0.01$), respectively. The times for the combined picture processing and verification phase were substantially greater for the negative condition than for the affirmative condition for seven of the eight participants. This suggests that the sentences were maintained in a verbal code rather than converted into images during the sentence presentation phase because the conversion to an image would have (a) eliminated or lessened the difference between the conditions during the picture-presentation phase and (b) consumed substantially more time during the sentence-presentation phase for the negative sentence. The maintenance of a verbal code would also be consistent with earlier behavioral studies of the processing of negative sentences that used this paradigm (Chase and Clark, 1972; Clark and Chase, 1972). Those studies found that image generation was less likely to occur if the picture immediately followed the sentence. Finally, the differences in processing time between affirmative and negative sentences cannot account for the differences in activation, which were observed at fixed intervals after stimulus onset for both types of sentences. Of primary interest was the growth of fMRI-measured activation during the sentence-processing phase.

The total number of activated voxels across the eight participants was 118 in the left temporal ROI. In the left temporal region (Fig. 3a), the average percentage change in signal intensity over the baseline was significantly greater overall for the negative than the affirmative sentences, $F(1, 110) = 10.30$, $P < 0.01$. The greater activation for the negative sentences indicates that the amount of neural activity is influenced by sentence complexity. In the first acquisition interval, acquired an average of 940 ms after sentence onset, the activation for negative sentences was significantly above the resting baseline, $t(117) = 3.30$, $P < 0.01$. In the second interval, acquired on average 2440 ms after the sentence presentation, the activation was significantly above baseline for both negative and affirmative sen-

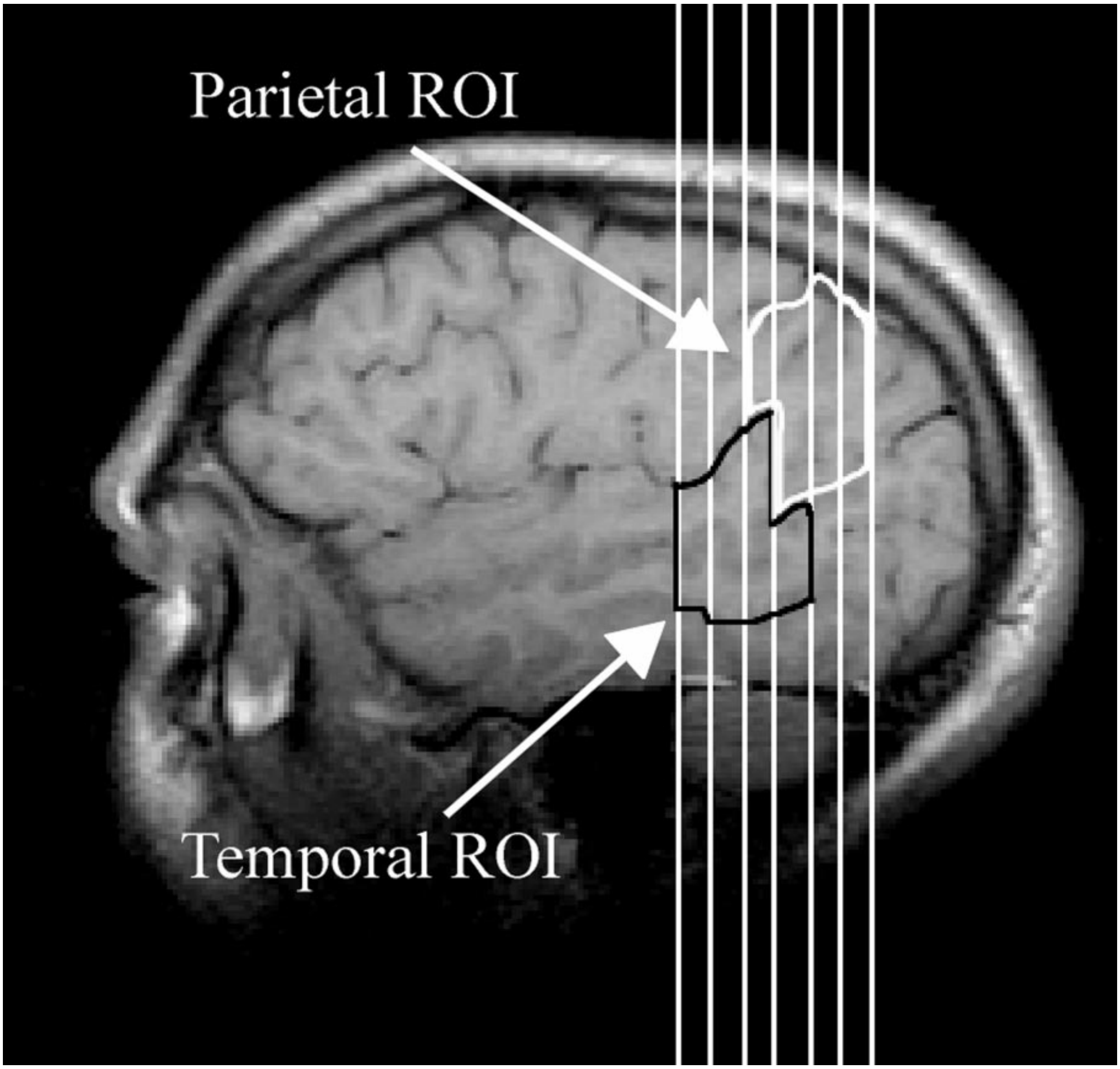

FIG. 2. The slice prescriptions and the temporal and parietal ROI's for a typical participant.

tences, $t(117) = 7.34$ and 3.16, respectively. The activation in the negative condition was not significantly greater than in the affirmative during the picture-processing phase. As mentioned earlier, the activation during the picture-processing phase reflects some combination of processes associated with sentence comprehension and picture processing.

A total of 95 voxels was significantly activated in the right posterior temporal region across the eight participants, but the activation was not significantly higher for the negative condition than for the affirmative during either sentence processing or picture processing phases. This comparatively high proportion of activated voxels in the right homologue is more than we have observed in other fMRI studies involving sentence comprehension, and it may be partially related to the pictorial referents of the sentences in the current task.

A total of 434 voxels were activated in the left parietal region (Fig. 3b). The activation level of these voxels was significantly above baseline for the negative sentences during the first acquisition interval of sentence processing ($t(433) = 2.22$, $P < 0.05$) and overall, negative sentences induced higher activation levels than affirmatives, $F(1, 426) = 4.68$, $P < 0.05$. (The negative condition also had significantly greater activation than the affirmative during the picture processing phase, $F(1, 421) = 15.47$, $P < 0.01$.) These results strongly support the interactive hypothesis over the encapsulation hypothesis; the processing of sentences with spatial referents is accompanied by activation in the parietal areas related to spatial processing.

The 336 voxels that were significantly activated in the right parietal region showed a pattern similar to those in the left parietal region, including significantly

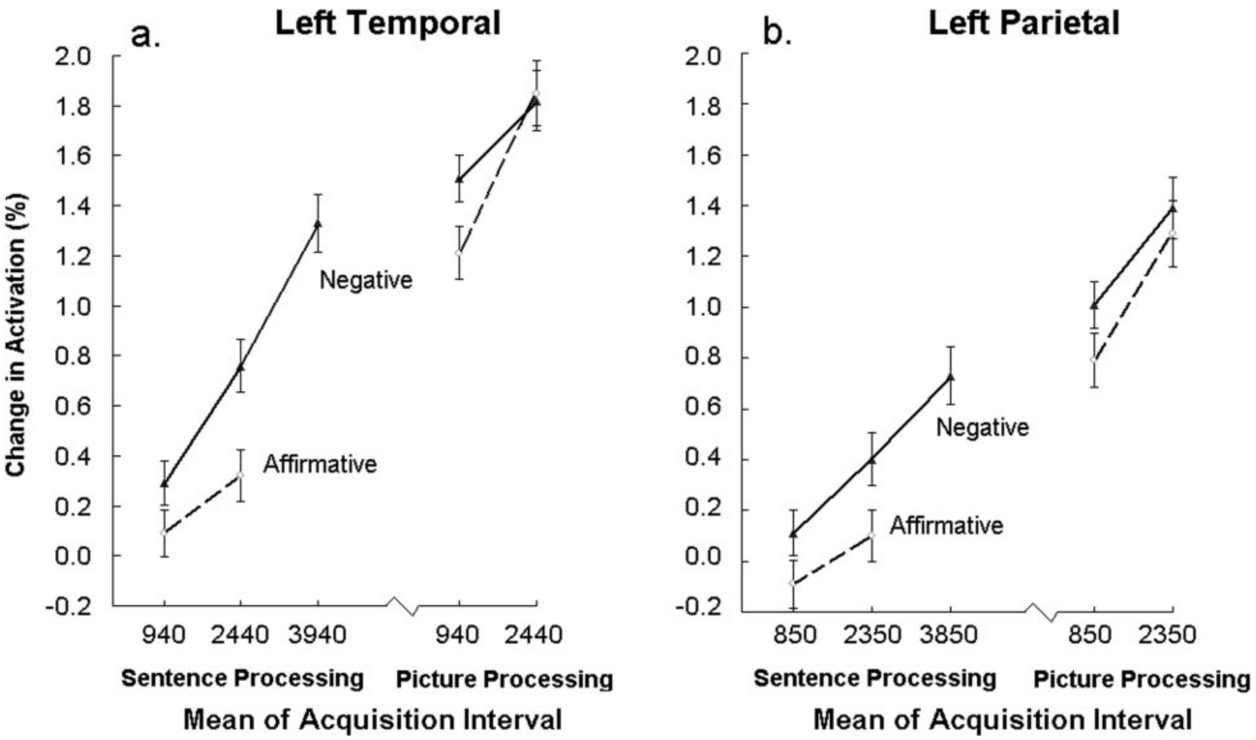

FIG. 3. The percentage of change in MR signal over the resting baseline for successive acquisition intervals for relevant voxels in the left temporal ROI (a) and left parietal ROI (b) for the sentence and picture processing phases. There is a significant effect of negation during sentence processing in both regions. For the temporal region, the activation was significantly over the baseline for the negative sentences during the first acquisition interval and significant for both sentence types during the second acquisition interval. The error bars represent the standard errors of the means. Only two acquisition intervals are plotted for the affirmative condition because the subject-controlled sentence processing time was shorter for the affirmative than the negative sentences, resulting in fewer (over 30%) observations in this condition during the third data acquisition interval.

more activation for negative than affirmative conditions during the sentence and picture processing phases, $F(1, 328) = 7.7$, $P < 0.01$ and $F(1, 321) = 14.30$, $P < 0.01$, respectively. The lower activation in the parietal region than in the temporal region is suggestive of a cascade of activation during sentence processing in which the processing in the temporal region has a slight temporal precedence over the processing in the parietal region. However, this conclusion must be tempered by the possibility that the parietal and temporal regions may be differentially activated during the intertrial interval; this could differentially affect the baseline activation measures in the two regions and, hence, make it difficult to compare the intercepts across regions.

Most of the parietal activation was in and around the intraparietal sulcus (as illustrated in Fig. 4), a region also activated by spatial processes such as mental rotation (Carpenter *et al.*, 1999) and variation in spatial attention, including those accompanying eye fixations (Luna *et al.*, 1998). A smaller proportion of the activation was in the superior parietal gyrus and the angular gyrus, a region (on the left) that is more associated with the visual aspects of reading.

DISCUSSION

The results support the two major hypotheses that motivated this study. The first was that the comprehension of linguistically more complex negative sentences would result in more fMRI-measured cortical activation than the comprehension of affirmative sentences in the left temporal region. This result supports the general view that fMRI-measured activation in the task-relevant cortical regions increases with cognitive demand (Just *et al.*, 1996). The second main result, the effect of negation on activation in the parietal region, indicates that the impact of linguistic difficulty extends to regions other than the traditional language processing areas, supporting an interactive rather than an encapsulated view of sentence comprehension. The activation in the parietal regions, which are associated with visuospatial processes, suggests that comprehending a locative sentence may involve accessing some features of the spatial representation of the sentence's referent. In this section, we consider some alternative interpretations of these results as well as their further implications.

Some of the parietal activation may be attributable

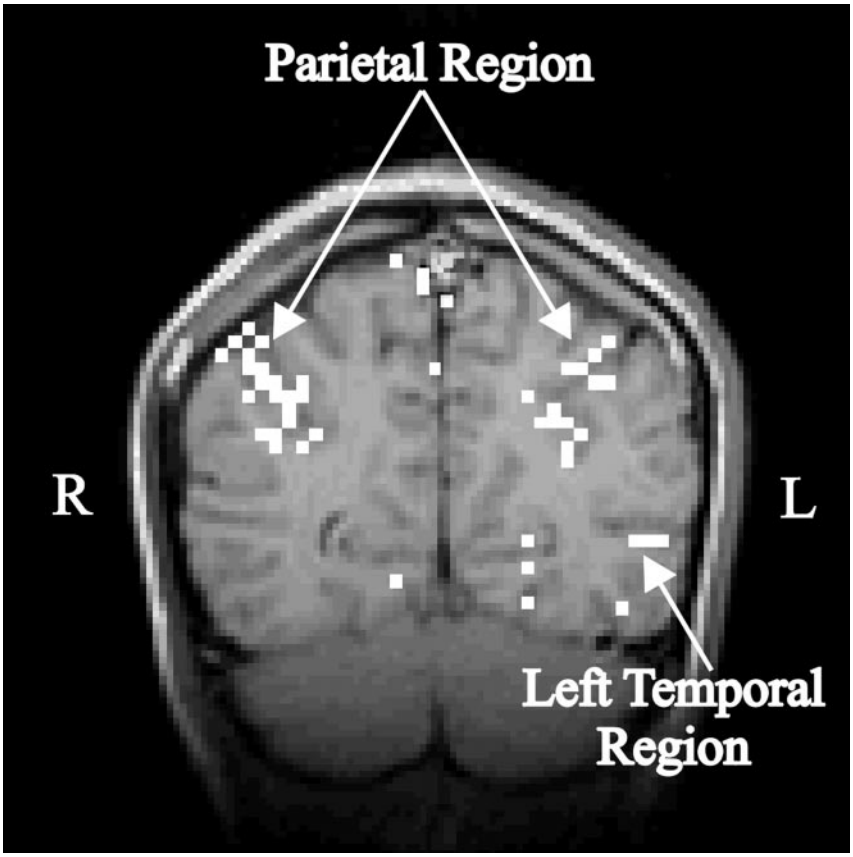

FIG. 4. An activation map showing one slice from one participant (the same one as in Fig. 2). The white voxels are those that were significantly above threshold, and their activation levels, along with those of other voxels in the ROI's, entered into the analyses. (The activated voxels toward the center bottom of the cortex above the cerebellum represent visual regions that were not included in the analysis. Those toward the center top region also were not analyzed and represent voxels associated with the superior sagittal sinus.)

to the attentional switches and the accompanying eye fixations that are associated with reading sentences, but these processes are unlikely to account for all of it. It is known that activation in the parietal region is associated with overt switches in visual attention accompanied by saccadic eye movements (Corbetta *et al.*, 1998; Luna *et al.*, 1998). However, the event-related paradigm permits the analysis of the amount of activation associated with processing the affirmative and negative sentences at the same points in time. Because most eye fixations in reading consume approximately 230–300 ms (Just and Carpenter, 1987), it is unlikely that many more fixations occurred for the negative sentence than the affirmative within the same fixed acquisition interval. Moreover, the hypothesis that eye movements are unlikely to be the main source of the parietal activation is also supported by a listening comprehension study in our laboratory. In that study, significantly more parietal activation was associated with sentences that had visuospatial referents (e.g., "On a map of Europe, Spain is to the left of France") than with sentences of the same length that had abstract referents. Thus, parietal activation can be significantly associated with processing visuo-spatial sentences, even when no reading eye fixations are involved. Such evidence is consistent with the current hypothesis that the parietal activation is not simply due to eye movements and that the additional parietal activation for negative sentences is due primarily to comprehension-related processes.

Several features of the experimental method discouraged generation of the entire image before the picture was displayed. The success of these precautions was indicated by the fact that participants required more time to complete the picture phase with the negative sentences than with the affirmative sentences. However, even when a complete image is not explicitly generated, comprehending locative sentences may involve activating a representation of some aspects of their referents, resulting in the co-activation of the temporal and parietal regions. This conclusion is supported by a recent fMRI experiment in which participants performed the sentence-picture verification task using two strategies: a verbal strategy (i.e., what subjects in the current study did) and a visual-imagery strategy (i.e., subjects generated mental images of the sentences before the picture was presented) (Reichle *et al.*, in press). Although the strategies tended to differentially activate the language and parietal regions, the two strategies also produced a substantial level of coactivation. Thus, language comprehension (at least in the case of locatives) may be partially dependent upon those cortical systems that mediate visuospatial processing.

The greater activation in the temporal region for the negative sentence condition is likely to reflect the added computational demand associated with understanding such sentences. Negative sentences by definition have an additional morpheme (the negation), but the additional encoding of this small marker by itself consumes very little time (Clark and Chase, 1972) and is unlikely to account for much of the added activation in the temporal region. Moreover, the current results are consistent with those from the study by Just *et al.* (1996) cited earlier, in which the comprehension of structurally more complex sentences evoked more temporal activation than did the comprehension of structurally simpler sentences, even though those sentences were matched for length and lexical content. More generally, these results are consistent with a resource view of comprehension (Just and Carpenter, 1992). The comprehension of more complex structures requires more work and hence, may consume more biological resources, a facet of which is reflected by the hemodynamic response that is assessed by fMRI-measured activation.

The time-locked and rapid effect of negation on fMRI-measured activation is likely to reflect the added computational burden imposed by the processing of the negation and cannot be due to longer processing time associated with negative sentences per se. The rapid coactivation of the parietal region during sentence reading suggests that the interpretation of the locative sentence entails the representation of the spatial referent. This suggests that the difficulty of the language-initiated computational processing is a determinant of the amount of activation in more than one node in a network of cortical areas. Neuroimaging studies (with multiple trials per epoch) have shown that the difficulty of a cognitive operation affects the amount of cortical activation in one or more centrally involved cortical regions for the domains of language comprehension (Just *et al.*, 1996), mental rotation (Carpenter *et al.*, 1999), and short-term word or letter recognition (Braver *et al.*, 1997; Grasby *et al.*, 1994). The converging results in these various domains suggest that the relation between computational load and neural activation may be a general principle that applies across various types of cognitive computations.

The temporal resolution of echoplanar fMRI can distinguish between differential levels of cortical activation within 1.5 s of stimulus onset and can trace the growth of activation over the course of 3 s of sentence processing and a similar amount of time for the subsequent picture processing. The time-series data are noteworthy in view of previous findings indicating that the rise time of localized blood oxygenation concentrations in the primary visual cortex in response to visual stimuli is also between 1 and 2 s (De Yoe *et al.*, 1994). The fact that robust activation is detectable within the first acquisition interval indicates that fMRI should be useful in tracking the coordination of cortical activation in multiple regions in complex cognitive tasks that require the integration of multiple information streams.

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