Differential components of sentence comprehension: Beyond single word reading and memory

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A number of studies have used functional neuroimaging to examine the neural mechanisms of sentence comprehension; however, few fMRI studies have examined activation patterns associated with sentence comprehension after accounting for activation attributable to single-word-level tasks important for sentence comprehension. To investigate the patterns of activation associated with sentence comprehension *after* controlling for single word reading and maintaining single words in memory, 20 unimpaired adult readers completed a block design paradigm which included sentence comprehension, single word reading, and short-term memory (for words) tasks. Results indicated that, regardless of the aspect of sentence comprehension being controlled for, activation was observed in bilateral temporal lobes (left > right) as well as bilateral occipital lobes and middle frontal gyri. Additional findings showed that bilateral superior parietal lobe activation was greatest for short-term memory for words, while left anterior inferior frontal gyri activation (centered around Brodmann's area 47) was greatest for single word reading. Results suggest that temporal cortex (left > right) is a core region important for sentence comprehension beyond the short-term memory and semantic requirements inherent in processing sentences.

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Advances in functional neuroimaging have allowed for the neural mechanisms of reading to be extensively studied, which has offered insight into the neural circuitry associated with this cognitive process. While the neural circuitry of both single word reading and sentence comprehension has been studied, to date there has been a greater focus on understanding the neural mechanisms of processing words in isolation, vs. in connected text (cf. Constable et al., 2004; Gernsbacher and Kaschak, 2003; Capek et al., 2004). The neurobiology of processing single words and/or nonwords has been studied in different populations and age groups, including skilled and impaired child, adolescent, and adult readers (e.g., Eden et al., 2004; Turkeltaub et al., 2003; Pugh et al., 2000; Shaywitz et al., 2002; Shaywitz et al., 2003; Simos et al., 2000; Simos et al., 2002). Converging results from these studies indicate that skilled readers tend to rely on a left hemisphere network for reading single words that includes the inferior frontal gyrus and posterior regions (occipitotemporal and temporo-parietal). In contrast, impaired readers tend to underactivate the left hemisphere posterior regions, and instead utilize the homol-ogous right hemisphere posterior regions (e.g., Eden et al., 2004; Pugh et al., 2000; Shaywitz et al., 2002; Shaywtiz et al., 2004; Simos et al., 2000). By studying single word reading in impaired and skilled readers, a more comprehensive understanding of the phenotype of impaired reading (at least at the single word level) has emerged, which has yielded a greater understanding of the identification and treatment of reading disability.

While the ability to read single words is undoubtedly important for reading, the higher-level skill of sentence comprehension is also critical. Most functional neuroimaging sentence comprehension studies, with the exception of two studies by Booth et al. in children (Booth et al., 1999; Booth et al., 2000), have been conducted with adult skilled readers (e.g., Ben-Shachar et al., 2004; Caplan et al., 2001; Capek et al., 2004; Ferstl and von Cramon, 2001; Friederici et al., 2003; Grossman et al., 2002;

Hashimoto and Sakai, 2002; Keller et al., 2001; Keller et al., 2003; Meyer et al., 2000; Ni et al., 2000). These studies have begun to identify regions critical for sentence comprehension in skilled readers; overall, findings indicate that sentence comprehension tasks show a network of activation that appears to be overlapping, but more widespread, than that reported for neuroimaging of single words. Generally, sentence comprehension tasks activate the inferior frontal gyrus and the posterior superior and middle temporal gyri (L > R; e.g., Caplan et al., 2001; Ferstl and von Cramon, 2001; Friederici et al., 2003; Grossman et al., 2002; Keller et al., 2001; Meyer et al., 2000). Several studies have also reported dorsolateral prefrontal cortex (DLPFC) activation (e.g., Bavelier et al., 1997; Capek et al., 2004; Kang et al., 1999; Hashimoto and Sakai, 2002) and parietal lobe activation (e.g., Booth et al., 2000; Carpenter et al., 2000; Keller et al., 2003). Although sentence comprehension tasks presented in auditory and visual formats tend to activate similar areas (e.g., Constable et al., 2004; Homae et al., 2002; Michael et al., 2001), additional activation in the extrastriate areas, as well as more left lateralization, has been reported when sentences are visually presented (e.g., Caplan et al., 2001; Constable et al., 2004; Grossman et al., 2002; Keller et al., 2001; Keller et al., 2003).

Some sentence comprehension studies have attempted to isolate regions associated with specific components of sentence comprehension, such as syntax, semantics, inferences, and verbal short-term/working memory[1] (e.g., Caplan et al., 2001; Dapretto and Bookheimer, 1999; Ferstl and von Cramon, 2001; Grossman et al., 2002; Ni et al., 2000). In general, findings from these studies suggest that separate regions subserve different components of sentence comprehension, in addition to core regions of activation within the left temporal lobe, which are present regardless of which aspect of sentence comprehension is being targeted (e.g., Cooke et al., 2001; Grossman et al., 2002). A commonly discussed distinction, historically rooted in lesion studies, is that syntax is subserved by Broca's area and that semantics is subserved by Wernicke's area; however, these broad distinctions so far have not been fully supported by functional neuroimaging studies, suggesting a more complex picture (see Ben-Shachar et al., 2004; Constable et al., 2004; Friederici et al., 2003). For instance, with regard to Broca's area/left inferior frontal gyrus, studies have hypothesized distinctions between Brodmann's areas 44, 45, and 47, but the processes thought to be associated with each have varied. For example, Carpentier et al. (2001) proposed that area 44 is related to orthographic-to-phonologic recoding of print and 45 is related to higher order processing related to sentence parsing; in contrast, Dapretto and Bookheimer (1999) proposed that area 44 was related to syntax and 47 was related to semantics. Nevertheless, in general, findings across studies appear to support the idea that Broca's area/left posterior inferior frontal gyrus is associated with syntax, while left anterior inferior frontal gyrus (Brodmann's area 47) is associated with semantics (see Bookheimer, 2002). There is also interest in distinguishing between regions associated with verbal short-term/working memory and syntax. Because the two are heavily intertwined, there are debates about whether activation, particularly in Broca's area, reflects syntax per se or the verbal short-term/working memory demands associated with syntax. Studies

that have manipulated syntactic complexity have found that increasing syntactic complexity results in increased Broca's area activation, particularly posteriorly (Ben-Shachar et al., 2003; Constable et al., 2004; Michael et al., 2001), and thus far, findings suggest that the Broca's area activation is related more to syntactic difficulty than short-term/working memory for words (e.g., Cooke et al., 2000, 2001; Grossman et al., 2002; Hashimoto and Sakai, 2002). Nevertheless, some studies have indicated that examining coordinated communication between different brain regions over different levels of demand on cortical resources, rather than linking discrete processes to specific anatomical areas, is needed (e.g., Keller et al., 2001).

One aspect of sentence comprehension that has received less attention is that of probing for those neural mechanisms that are distinct from single word reading. Knowing which regions are responsible for single word reading vs. sentence comprehension in skilled readers is important for advancing our knowledge of language functions in general, but is especially important for laying the foundation for studying and understanding the neural mechanisms of impaired reading beyond the single word level. While comparison of results from single word reading studies and sentence comprehension studies suggests that sentence comprehension tasks activate a neural network that is similar to that observed for processing of single words, few studies have actually examined these two processes conjointly. In studies that have included comparisons of sentences vs. single words, findings have indicated that sentence comprehension, in general, elicits more activation than single words, particularly in the left middle and superior temporal gyri and in the right hemisphere (Bottini et al., 1994; Stowe et al., 1994, 1998, 1999). Greater activation for sentences vs. words has also been reported in the temporal poles bilaterally (Brodmann's area 38), left frontal lobe, and left parietal lobe (Bottini et al., 1994; Stowe et al., 1999). Additionally, although verbal short-term/working memory for words has also long been known to be an essential component of reading in behavioral studies (see Perfetti et al., 1996), at this time, few sentence comprehension studies involving functional neuroimaging have examined the specific contribution of short-term memory for single words to reading sentences (Hashimoto and Sakai, 2002).

In an effort to explore the contributions of different component processes to the complex task of sentence comprehension, we designed an fMRI experiment to compare the neural correlates of a task requiring sentence comprehension with the neural correlates of two single-word-level reading tasks that tap processes inherent to comprehending a written sentence: (1) reading single words and (2) maintaining single words in short-term memory. In particular, we intended to use the principle of cognitive subtraction to examine regions of activation present during sentence comprehension after controlling for the activation attributable to the single-word-level tasks. We hypothesized that core regions of activation in the left temporal lobe would correlate with sentence comprehension and would persist on contrast images that controlled for the effect of either of the two single-word-level tasks on sentence comprehension. We also hypothesized that subtracting the effect of single word reading from sentence comprehension activation would produce a contrast image with relatively decreased activation in the left hemisphere network associated with single word reading, but increased activation in homologous right hemisphere regions. When subtracting the activation associated with short-term memory for words from sentence comprehension activation, we hypothesized that we

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[1] We include both terms because operational definitions of short-term memory and working memory are often not clearly distinguished in the literature.

would observe decreased activation in DLPFC and/or parietal cortex, i.e., areas associated with verbal short-term memory (Braver et al., 1997; Honey et al., 2002; Smith et al., 1998; Wagner and Smith, 2003) in addition to the previously described activation changes due to subtracting single word reading, which is a component of holding written single words in memory.

Materials and methods

Participants

Participants in this study were 20 right-handed adult volunteers (10 males, 10 females) between the ages of 19–35 (mean = 27.4, SD = 5.1). All subjects were screened prior to entry in the study for past history of reading disability, psychiatric disorders (including ADHD), and for any contraindications to the MR environment. Written consent was obtained from each participant at the start of the study in accordance with the Johns Hopkins Medical Institutional Review Board.

Paradigms

To examine different aspects of sentence comprehension, participants completed a paradigm that alternated a sentence comprehension task with two separate control tasks: a single word reading task and a short-term memory task for words. Participants then also completed a separate paradigm (with different stimuli) in which the single word reading and short-term memory tasks were alternated; this was done in order to understand more about the differences between the two control tasks for the sentence comprehension conditions. Participants viewed the paradigms via an LCD projector on a rear projection screen at the head of the scanner via a 45° angled mirror affixed to the MRI head coil. The paradigms were computer-controlled with E-Prime (Psychology Software Tools, Pittsburgh, PA, USA), which was used to present the task and record the timing of both stimulus presentations and participant responses. Participants responded by pressing a button with either their right index finger or their right middle finger via a button box that was held in their right hand.

Sentence comprehension task

The sentence comprehension (SC) task consisted of having participants read a sequence of six words that formed a sentence. The task was designed for participants to decide whether the sentences were meaningful or nonmeaningful. Nonmeaningful sentences contained both semantic and syntactic errors. All sentences were composed of words with an overall mean frequency of 62 and higher (Carroll et al., 1971), mean length of 30 letters, and mean number of 9 syllables. Stimuli were presented word-by-word and participants pushed a button with their right index finger for every word in the sentence. At the end of the sentence, participants indicated by button press if the sentence was meaningful or not by pressing with their right index finger for meaningful sentences and right middle finger for nonmeaningful sentences. Fifty percent were meaningful. Each block was 15 s in length: a 2000 ms instruction screen (indicating task switch), a 2000 ms rest, 6 stimuli appearing on the screen for 1000 ms with an interstimulus interval of 500 ms (thus comprising one sentence), and a 2000 ms decision screen. The

instruction and rest screens were not included in the modeled analyses.

Single-word reading task

A single word reading (SWR) task was used to control for the single word reading requirements of the sentence comprehension task. In this task, participants viewed a sequence of six words in which some of the six words were names of living objects and some were names of nonliving objects. Each six-word sequence was matched to the sentence comprehension task on overall word frequency, length, and number of syllables. Fifty percent of the stimuli were names of living object; all other words were nouns. The participants pushed a button with their right index finger when they saw a word that denoted a living object, and pressed a button with their right middle finger when they saw a word that denoted a nonliving object. Each block was 13 s in length: a 2000 ms instruction screen (indicating task switch), a 2000 ms rest, and 6 stimuli appearing on the screen for 1000 ms with an interstimulus interval of 500 ms. The instruction and rest screens were not included in the modeled analyses.

Short-term memory task

The short-term memory (STM) task consisted of having participants view a string of six words. They pressed a button with their right index finger every time they saw a word for the first time within a block. During the string of six words, if they had seen a word previously, they pressed a button with their right middle finger. Approximately 58% of the blocks consisted of a word repeated once, 20% of the blocks consisted of a word repeated twice, and 22% of the blocks consisted of no repeated words. Thus, this task was expected to control for the single word reading and short-term memory (for words) requirements of the sentence comprehension task. The stimuli were also matched to the sentence comprehension task on overall word frequency, length, and number of syllables. All words were nouns. Each block was 13 s in length: a 2000 ms instruction screen (indicating task switch), a 2000 ms rest, and 6 stimuli appearing on the screen for 1000 ms with an interstimulus interval of 500 ms. The instruction and rest screens were not included in the modeled analyses.

Task alternation

The scanning session consisted of six runs. In each run, there were 9 blocks of each task type, yielding 18 blocks total (i.e., sentence comprehension vs. STM or sentence comprehension vs. SWR, or SWR vs. STM). There were two runs for each combination: Runs 1 and 2: sentence comprehension block alternated with STM block (×9); Runs 3 and 4: sentence comprehension block alternated with SWR block (×9); Runs 5 and 6: STM block alternated with SWR block (×9).

Scan procedure

Scanning was carried out in a 1.5 T ACS-NT Powertrack 6000 MRI scanner (Philips Medical Systems, Inc.) using body coil transmission and quadrature end-capped head coil reception. Single shot echo planar images were coronally acquired with a 40 ms echo time (TE), a 2.6 s repetition (TR), 64 × 64 acquisition matrix, 230 mm field of view (FOV) with 41 volumes consisting of 4.0 mm slices, and a 0.5 mm gap, yielding a nominal acquisition voxel size of 3.579 × 3.579 × 4.5 (to provide whole brain coverage).

Image processing and data analysis

Post acquisition image processing was carried out using SPM99 (http://ww.fil.ion.ucl.ac.uk/spm/) on Matlab (Mathworks, Inc., Natick, MA). Images from the scanner were converted to Analyze format and then time corrected to adjust for within volume time of acquisition differences (Calhoun et al., 2000), realigned, and smoothed using a Gaussian kernel that was half the resolution of the acquisition matrix ($7 \times 7 \times 9$ mm³; Friston et al., 1995). Prior to estimation, the data were spatially normalized to Montreal Neurological Institute (MNI)-labeled space (Evans et al., 1993), resampled into (2 mm)³ voxels, and temporally smoothed with a high-pass filter cutoff of 37–41 s and the low-pass filter achieved by convolving with the SPM hemodynamic response function.

Task associated brain activation was assessed using a block design. SPM99 was used to construct and test the fit of the image data to a general linear model (Friston et al., 1995). Statistical parametric maps were created corresponding with the time-courses for the following contrasts: sentence comprehension greater than single word reading (SC-SWR), sentence comprehension greater than short-term memory (SC-STM), short-term memory greater than single word reading (STM-SWR), and single word reading greater than short-term memory (SWR-STM). Two additional contrasts, i.e., single word reading greater than sentence comprehension (SWR-SC) and short-term memory greater than sentence comprehension (STM-SC), were also generated solely for use in the final conjunction analysis step of the data analysis. Voxel-wise *t*-maps were constructed for each of the subjects as a first level analysis and the amplitude maps were then carried to a second level analysis to test for significant group effects. The two-level strategy described is equivalent to a random effects analysis in that the analysis is dominated by intersubject variance (as opposed to interscan variance) in order to provide a better idea of the average activation of a given population (Holmes and Friston, 1998). The location of voxels significantly associated with the tasks was summarized by their local maxima, separated by at least 4 mm. The maxima coordinates were then converted from MNI to Talaraich coordinate space using the formulas provided by Matthew Brett (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html). These coordinates were finally assigned neuroanatomic and cytoarchitectonic labels using the Talaraich Daemon (http://ric.uthscsa.edu/ projects/talairachdaemon.html). Peak voxels of activation for each cluster, as provided by the Talaraich Daemon, are reported in Tables 2–6.

Whole brain random effects analyses for each contrast (SC-SWR, SC-STM, STM-SWR and SWR-STM) were conducted using SPM99 by performing one-sample *t* tests on the individual contrast images. Each of the contrasts are reported at uncorrected $P < 0.0001$ with an extent threshold of 300 voxels, which is equivalent to a false positive rate of <0.001 over the whole brain based on Monte Carlo simulations run using AlphaSim (NIMH, Bethesda, Maryland http://afni.nimh.nih.gov/afni/about/afni_summary/ view?searchterm=alphasim).

Region-of-interest (ROI) analyses were conducted using the Wake Forest University PickAtlas (Wake Forest University School of Medicine, 2003, http://www.fmri.wfubmc.edu/downloads/ WFU_PickAtlas_User_Manual.pdf) in order to confirm findings from random effects analyses. The voxel counts for each individual were recorded from their own contrast images (SC-SWR, SC-STM, STM-SWR and SWR-STM) for the superior parietal lobe (Brodmann's areas 5/7/31) and the inferior frontal gyrus. The

individual voxel counts were then analyzed using paired *t* tests to determine if there were significant differences between contrasts.

Regression analyses were executed on each contrast over the group using simple regression analyses with each individual's reaction time and accuracy (separately) for each task as regressors. Additional analyses included using a two-sample *t* test with gender as the variable of interest to look at differences between males and females.

A conjunction analysis was performed on the SC-SWR and SC-STM contrasts to determine areas of activation common to both of the contrasts involving sentence comprehension. The resulting image is referred to as the SC conjunction. Similarly, conjunction analyses were performed on the SWR-SC and SWR-STM contrasts to reveal areas of common activation for both contrasts involving single word reading (i.e., SWR conjunction), and on the STM-SC and STM-SWR contrasts to generate the STM conjunction. To perform these three conjunction analyses, three multiple regressions without constant terms were conducted for each of the two contrasts and then a conjunction analysis was done using the approach outlined by Nichols et al. (2005). The statistical parametric maps are reported at uncorrected $P < 0.00023$ which is equivalent to the *T*-height threshold used for the random effects contrast maps.

Results

Task performance

For each task, the participant's performance was recorded via E-Prime. Table 1 shows the overall percentage accuracy and reaction time (RT) for each task (SC decision, SWR and STM). Accuracy on SWR was significantly lower than accuracy for both STM and SC; however, there was no significant difference in accuracy between STM and SC. All RT measures were statistically different from each other, with participants showing the fastest RTs on STM, and the slowest RTs on SWR. No statistical differences were found between males and females for either accuracy or RT measures.

Whole brain and region of interest analyses

The SC-SWR contrast included areas of significant activation in bilateral temporal and bilateral superior parietal regions (see Table 2 and Fig. 1).

The SC-STM contrast yielded significant activation in bilateral parietal and occipital regions, but unlike the SC-SWR

Table 1
Behavioral results

	Percentage accuracy		Reaction time (in milliseconds)	
	Mean	SD	Mean	SD
Sentence comprehension (decision)	96.11%	5.13	635.65[a]	191.11
Single word reading	92.78%[b]	4.00	706.19[c]	51.04
Short-term memory	95.79%	6.93	514.75	47.82

[a] Sentence comprehension > short-term memory.
[b] Single word reading < short-term memory and sentence comprehension.
[c] Single word reading > sentence comprehension and short-term memory.

Table 2
Sentence comprehension greater than single word reading

Cluster size	Region(s) included	BA	Side	Coordinates			Z value
				x	y	z	
5140	Medial frontal gyrus	6	R	2	−24	55	4.64
	Precentral gyrus		R	14	−24	64	4.68
	Paracentral lobule		L	−6	−34	53	4.56
			R	2	−28	62	4.66
	Cingulate gyrus	31	R	6	−47	39	5.71
	Posterior cingulate		R	10	−52	14	4.58
	Precuneus	31	R	2	−69	26	3.84
	Cuneus	19	L	−4	−78	32	4.90
		18/19	R	26	−86	36	5.49
	Parahippocampal gyrus	19/30/36/37	R	−12	−76	0	5.36
	Lingual gyrus	18/19	R	10	−64	3	4.14
	Superior occipital gyrus	19	R	38	−82	32	5.91
	Middle occipital gyrus		R	51	−72	7	4.34
3726	Fusiform gyrus	20	L	−51	−3	−25	4.95
	Inferior temporal gyrus	20	L	−50	−3	−28	4.98
	Middle temporal gyrus	19/21	L	−51	5	−29	5.36
	Superior temporal gyrus	22/39	L	−48	−52	10	5.13
	Inferior parietal lobule	39/40	L	−51	−62	40	4.41
	Supramarginal gyrus		L	−55	−51	28	5.26
1492	Middle temporal gyrus	21	R	65	−45	2	4.99
	Superior temporal gyrus		R	48	−23	1	4.54
	Transverse temporal gyrus		R	44	−27	11	4.38
397	Posterior cingulate		L	−16	−61	14	4.81
	Precuneus	31	L	−14	−71	22	3.75
	Lingual gyrus		L	28	−45	−6	4.57

BA = Brodmann's area.

contrast, the temporal lobe activation was only on the left (see Table 3 and Fig. 2). There was also activation in the left inferior frontal gyrus (Brodmann's areas 44 and 47) and bilateral middle frontal gyri.

The SWR-STM contrast revealed significant activation in left inferior temporal gyrus (Brodmann's area 20) and several left frontal regions, including inferior frontal gyrus (Brodmann's area 47) and middle and superior frontal gyri. Further significant activation was seen in the left occipital lobe (see Table 4).

The STM-SWR contrast included significant activation in right frontal gyri and bilateral parietal lobe (Brodmann's area 7 and precuneus bilaterally, as well as left paracentral lobule; see Table 5).

Region of interest analyses confirmed that significantly greater activation was observed in superior parietal lobe bilaterally for the SC-SWR and STM-SWR contrasts compared to the SC-STM and SWR-STM contrasts (all *P* < 0.0001).
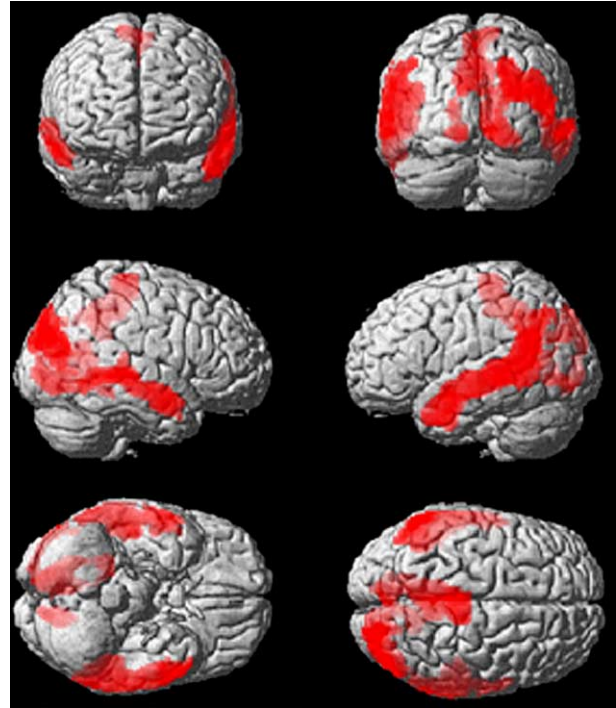

Fig. 1. SC-SWR contrast.

Region of interest analyses also confirmed significantly greater left inferior frontal gyrus activation for the SC-STM and SWR-STM contrasts compared to the SC-SWR and STM-SWR contrasts (all *P* < 0.0001).

Table 3
Sentence comprehension greater than short-term memory for words

| Cluster size	Region(s) included	BA	Side	Coordinates			Z value
				x	y	z	
12479	Fusiform gyrus	37	R	32	−47	−9	4.37
	Inferior temporal gyrus		L	−53	−61	−10	4.49
	Middle temporal gyrus	21/38/39	L	−59	−58	3	6.04
	Superior temporal gyrus	38/39	L	−46	18	−21	5.38
	Inferior frontal gyrus		L	−53	29	6	6.03
	Middle frontal gyrus		L	−48	10	47	4.74
	Precentral gyrus	44	L	−51	16	7	5.26
	Angular gyrus		L	−46	−76	30	5.31
	Posterior cingulate	23	L	−6	−56	14	5.51
	Parahippocampal gyrus	30	L	−12	−48	4	5.62
		30	R	12	−46	4	6.79
	Cuneus	19	L	−18	−90	23	4.16
		19	R	24	−92	25	5.05
	Lingual gyrus	18	L	−14	−52	4	5.63
			R	12	−62	5	6.96
	Superior occipital gyrus		L	−32	−76	28	6.77
		19	R	40	−82	24	4.37
	Middle occipital gyrus	18/19/37	L	−40	−87	12	4.33
		19	R	46	−77	11	5.14
1229	Inferior frontal gyrus	47	R	55	33	−3	5.13
	Middle frontal gyrus	9	R	57	19	34	4.24
912	Cerebellum		R	20	−75	−23	8.45

BA = Brodmann's area.
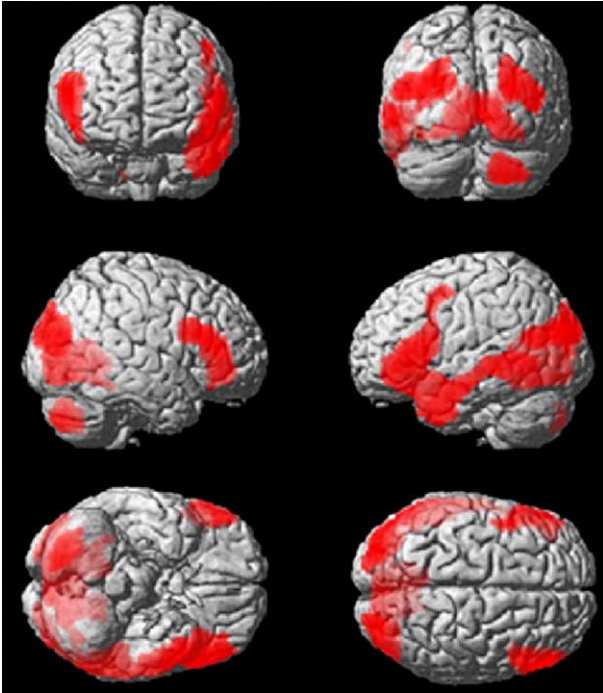
Fig. 2. SC-STM contrast.

Regression analyses

Accuracy and reaction time regression analyses were performed, with percentage accuracy or reaction time as independent variables. Results revealed no statistically significant effects across all tasks. No statistically significant differences were found between males and females on any of the contrast images (SC-SWR, SC-STM, SWR-STM, nor STM-SWR). The fact that we did not find significant correlations between behavioral task performance and activation patterns is not altogether surprising, given the limited variability across subjects in accuracy as well as reaction time on most tasks. The exception to this was the sentence comprehension task, for which there was a wide range of reaction times across participants; however, given the overall high performance on this task (96% accuracy), reaction time may not have been a sensitive enough measure to show a relationship with cortical activation.

Table 4
Single word reading greater than short-term memory for words

Cluster size	Region(s) included	BA	Side	Coordinates			Z value
				x	y	z	
1697	Inferior frontal gyrus	46/47	L	−46	36	−14	5.71
	Middle frontal gyrus	11	L	−22	25	15	4.47
648	Superior frontal gyrus		L	−10	56	27	6.05
	Medial frontal gyrus	10	L	−4	63	14	3.87
530	Cuneus		L	−16	−97	−2	5.75
	Middle occipital gyrus	18	L	−32	−91	0	4.74
	Inferior occipital gyrus	19	L	−38	−76	−5	3.98
302	Fusiform gyrus	37	L	−48	−53	−11	4.29
	Inferior temporal gyrus	20	L	−50	−49	−11	4.19

BA = Brodmann's area.

Table 5
Short-term memory for words greater than single word reading

Cluster size	Region(s) included	BA	Side	Coordinates			Z value
				x	y	z	
4828	Paracentral lobule	5	L	−8	−38	48	5.47
	Postcentral gyrus	7	R	8	−53	63	4.42
	Inferior parietal lobule	39/40	R	42	−66	42	4.70
	Superior parietal lobule	7	R	22	−67	53	5.50
	Supramarginal gyrus		R	50	−39	37	4.61
	Cingulate gyrus	31	R	4	−39	42	6.22
	Precuneus	7	L	−2	−44	46	3.75
		7/19	R	12	−58	45	5.69
616	Superior frontal gyrus	8	R	24	35	44	3.98
515	Middle frontal gyrus		R	38	51	20	5.33

BA = Brodmann's area.

Conjunction analyses

The SC conjunction showed significant clusters of activation in left inferior temporal gyrus (Brodmann's area 20), bilateral middle and superior temporal gyri (Brodmann's areas 21 and 22), bilateral middle frontal gyrus, left posterior cingulate, and bilateral occipital regions (Brodmann's areas 18 and 19).

The SWR conjunction showed significant activation in several areas, including left inferior frontal gyrus (Brodmann's areas 46/47), right inferior frontal gyrus (Brodmann's area 47), and right middle frontal gyrus.

The STM conjunction showed significant clusters of activation in right middle frontal gyrus, right superior parietal lobe (Brodmann's area 7), and right cingulate gyrus. See Table 6 and Fig. 3 for results of the three conjunction analyses.

Discussion

Overall, we found that sentence comprehension was associated with greater activation in temporal cortex (left > right) when compared to either a single word reading task or a short-term memory task. Specifically, the sentence comprehension conjunction analysis revealed left inferior, middle, and superior temporal lobe activation, plus right middle temporal lobe activation. This is consistent with previous literature contrasting sentence comprehension with single word reading (Bottini et al., 1994; Stowe et al., 1994, 1998, 1999) or controlling for other components of sentence comprehension, e.g., syntax, short-term/working memory (Cooke et al., 2001; Grossman et al., 2002). Bilateral occipital lobe and middle frontal gyri activation was also found on the conjunction analysis for the sentence comprehension contrast images, although these areas appeared to be less exclusive to sentence comprehension, as they were also activated significantly in the single word reading and/or short-term memory contrast images (see Table 6). Previous sentence comprehension studies have demonstrated that regardless of the component of the sentence comprehension being isolated or controlled for (e.g., syntax, working memory, single word reading, etc.), there appear to be core regions of activation present, located predominately in the left temporal lobe (e.g., Cooke et al., 2001; Grossman et al., 2002). The fact that core

Table 6
Results of conjunction analyses

Cluster size	Region(s) included	BA	Side	x	y	z	Z value
Sentence comprehension conjunction							
1942	Inferior temporal gyrus	20	L	−48	−5	−32	4.59
	Middle temporal gyrus	21	L	−53	7	−22	5.79
	Superior temporal gyrus		L	−48	−55	19	5.22
1816	Posterior cingulate		L	−14	−60	14	5.13
	Parahippocampal gyrus	30	R	12	−48	4	5.59
	Lingual gyrus	18	L	−10	−74	0	5.47
		18	R	18	−78	−3	6.09
865	Precuneus	19	R	34	−82	35	5.24
	Cuneus	19	R	28	−80	28	5.78
	Superior occipital gyrus	19	R	40	−82	24	5.07
	Middle occipital gyrus		R	46	−79	17	4.83
261	Cuneus		L	−26	−84	28	5.38
	Superior occipital gyrus	19	L	−34	−84	32	5.32
155	Middle temporal gyrus	21	R	61	−39	0	4.54
65	Middle frontal gyrus		L	−46	10	47	5.13
24	Superior temporal gyrus	22	R	59	−25	0	4.61
21	Middle frontal gyrus		R	51	43	−4	4.77
Single word reading conjunction							
161	Inferior frontal gyrus	46/47	L	−44	34	11	5.06
68	Cerebellum		L	−34	−53	−18	4.98
59	Cerebellum		R	30	−48	−25	4.87
20	Cuneus	18	L	−16	−99	−2	4.58
11	Inferior frontal gyrus	47	R	36	31	−12	4.65
11	Fusiform gyrus		L	−50	−57	−11	4.32
4	Inferior occipital gyrus		L	−38	−89	−1	4.14
3	Middle frontal gyrus		R	42	32	15	4.15
1	Brainstem/midbrain		L	−8	−22	−17	4.17
Short-term memory conjunction results							
366	Middle frontal gyrus	6	R	24	11	58	5.33
75	Precuneus	7	L	12	−58	45	4.87
30	Cingulate gyrus		R	4	−23	40	4.75

BA = Brodmann's area.

regions appear to be active no matter what aspect of sentence comprehension is being probed suggests that certain areas are essential for sentence comprehension above and beyond any unique components of different types of sentences/contrasts (cf. Grossman et al., 2002).

Aside from the core regions of commonality, our study revealed that each sentence comprehension contrast (SC-SWR and SC-STM) was associated with distinct patterns of activation. The SC-SWR contrast included superior parietal lobe activation, consistent with the activation in the parietal cortex on the STM conjunction image, while the SC-STM contrast included left inferior frontal gyrus activation (peak activation in Brodmann's area 47), consistent with the left inferior frontal gyrus activation on the SWR conjunction. This suggests that the activations associated with short-term memory and single word reading had distinguishable components. This finding is in contrast to our assumption that

short-term memory activation (for single words) would be explained as a linear combination of adding a memory component to the activation associated with single word reading.

Our finding of left anterior inferior frontal gyrus (Brodmann's area 47) activation associated with both contrasts modeling SWR (SWR-STM and SWR conjunction) as well as on the SC-STM contrast suggests that our single word reading task preferentially activated the anterior portion of the left inferior frontal gyrus, i.e., Brodmann's area 47. This is consistent with previous literature that has found linkages between Brodmann's area 47 and semantic processing (Bookheimer, 2002; Leube et al., 2001).

On the contrast images that reveal activation associated with the short-term memory task (i.e., the STM-SWR contrasts and the STM conjunction analysis), activation was observed in superior parietal lobe; parietal lobe activation was also observed on SC-SWR contrast. The finding of superior parietal lobe activation being associated with short-term memory is supported by previous literature (e.g., Braver et al., 1997; Honey et al., 2000, 2002; Nystrom et al., 2000; Wagner and Smith, 2003). However, there are a number of other brain regions that have also been linked with short-term/working memory, including DLPFC and inferior frontal gyrus (e.g., Bookheimer, 2002; Crottaz-Herbette et al., 2004; Gerton et al., 2004; Linden et al., 2003, Rama et al., 2001). Many studies have linked phonological short-term memory to activation

■ Sentence comprehension

■ Short-term memory for words
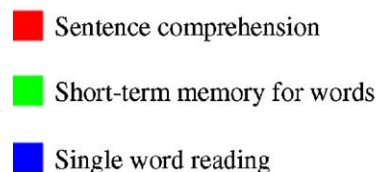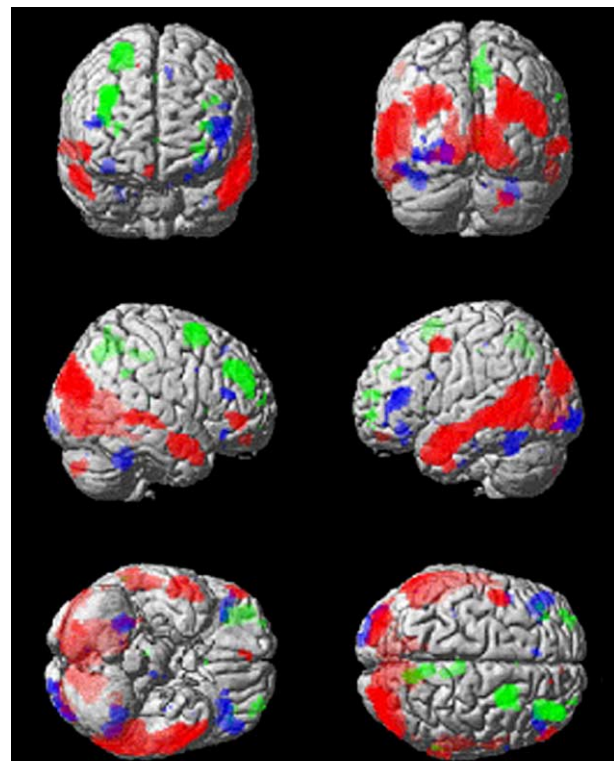
■ Single word reading

Fig. 3. Results of conjunction analyses.

in Brodmann's area 44/45 (Bookheimer, 2002). Our short-term memory task was intended to tap subjects' ability to remember words that they have read (i.e., encoded phonologically) but our short-term memory findings did not appear to correspond to Brodmann's area 44/45. This could be interpreted as supporting previous findings that left inferior frontal gyrus (Brodmann's area 44/45) activation during sentence tasks is more associated with syntax than short-term/working memory (Cooke et al., 2000, 2001; Grossman et al., 2002; Hashimoto and Sakai, 2002). Alternatively, it may be that because our short-term memory task was relatively easy that it did not tap phonological memory. For example, if participants were doing the task largely via orthographic means, rather than phonological, they may not have been using the articulatory loop to keep the words active (i.e., phonological memory). Nevertheless, it is important to note that without inclusion of a baseline rest, we are somewhat limited in being able to make firm conclusions regarding the activations associated with the single word reading and short-term memory tasks.

In summary, our study offers an initial examination of two components of sentence comprehension, single word semantic processing and maintaining single words in memory. However, it is important to point out that, in the current study, without a rest baseline, we cannot rule out the possibility, for example, that the parietal activation observed on the SC-SWR and STM-SWR contrasts could have been due to reduced parietal activation during the SWR task, rather than increased parietal activation during sentence comprehension and STM. Additionally, further studies are needed to sort out the functional and neuroimaging relationships between these and other cognitive components of sentence comprehension (e.g., comprehending different syntactical structures and making inferences). In particular, including the use of two or more levels of syntactic complexity and varying the type and difficulty of the memory demands would be interesting extensions of this study that could help localize the various functions of the left inferior frontal gyrus. Also, including a nonword reading control and/or assessing single word reading in other ways could help distinguish phonological activation from semantic. Furthermore, future studies should investigate how differences in task design, such as the effects of switching between tasks and the types of decisions required, may influence findings. Although we carefully matched stimulus materials for length, frequency, and number of syllables, the activation associated with each task (beyond the motor requirements that we controlled for) could potentially be associated with different decision requirements. Use of event-related designs would also be valuable, allowing for examination of activation associated with correct vs. incorrect responses. Future studies will need to consider these aspects in their designs in order to fully understand the complex interactions between and differential contributions of word level (phonological and semantic), syntactical, short-term/working memory, as well as other processes to sentence comprehension and the brain regions (and/or coordinated networks) that subserve them.

Conclusion

The purpose of this study was to examine the fMRI correlates of sentence comprehension activation that remain after eliminating the contribution from word-level processes inherent to the task. Our results indicate that, after eliminating activation associated with two single-word-level subcomponents of the task (i.e., single word reading and short-term memory for single words), sentence comprehension is consistently associated with core regions of bilateral (left > right) temporal cortex activation. Bilateral occipital lobe and middle frontal gyri activation was also observed. Additionally, we found tentative support for single word reading (including semantic processing) being associated with the left anterior inferior frontal cortex (Brodmann's area 47) and short-term memory for words being associated with the superior parietal cortex activation.

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