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fMRI Investigation of Sentence Comprehension by Eye and by Ear: Modality Fingerprints on Cognitive Processes

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Abstract: The neural substrate underlying reading vs. listening comprehension of sentences was compared using fMRI. One way in which this issue was addressed was by comparing the patterns of activation particularly in cortical association areas that classically are implicated in language processing. The precise locations of the activation differed between the two modalities. In the left inferior frontal gyrus (Broca's area), the activation associated with listening was more anterior and inferior than the activation associated with reading, suggesting more semantic processing during listening comprehension. In the left posterior superior and middle temporal region (roughly, Wernicke's area), the activation for listening was closer to primary auditory cortex (more anterior and somewhat more lateral) than the activation for reading. In several regions, the activation was much more left lateralized for reading than for listening. In addition to differences in the location of the activation, there were also differences in the total amount of activation in the two modalities in several regions. A second way in which the modality comparison was addressed was by examining how the neural systems responded to comprehension workload in the two modalities by systematically varying the structural complexity of the sentences to be processed. Here, the distribution of the workload increase associated with the processing of additional structural complexity was very similar across the two input modalities. The results suggest a number of subtle differences in the cognitive processing underlying listening vs. reading comprehension. *Hum. Brain Mapping 13:239–252, 2001.* © **2001 Wiley-Liss, Inc.**

Key words: sentence comprehension; comprehension; language; modality effects; fMRI

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INTRODUCTION

The study of visual vs. auditory sentence comprehension raises interesting questions about the nature of the psychological processes and the corresponding neural substrates that are involved in understanding language. By directly comparing cortical activation in the two modalities, we can begin to identify which components of the cortical language-processing network are shared across modalities and which components are modality specific. In addition to addressing language processing, this research question is of more general interest because much of cognitive science has been built on the assumption that higher cognitive processes manipulate only abstract information that is not particularly associated with or affected by the input modality. The present study investigated how far up the cognitive stream the sensory differences are manifest.

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In addition to examining the effect of modality, the current study also addressed the question of how the systems that support sentence comprehension respond to variations in workload. Cognitive workload, defined as the amount of processing and storage required for a given task, was manipulated by varying the structural complexity of the sentences to be comprehended, comparing the processing of a sentence with two conjoined active clauses to the processing of a more complex sentence containing a matrix clause with an embedded object-relative clause. Previous research has shown that a network of language areas respond to this type of increase in computational demand with increases in fMRI-measured activation [Just et al., 1996]. One goal of the current study was to determine whether there were differences in the response to increased workload as a function of input modality.

It is important to note that even when written and spoken language have the same content, the two modalities provide different information and make different demands on the comprehender. For example, spoken language provides the listener with prosodic cues that are not present in written language. Written language, on the other hand, offers parsing information in the form of punctuation. (In the current experiment, the visually presented sentences contained no punctuation other than a final period, and the auditorily presented sentences were spoken with little prosody and digitized). Another difference is that written language generally allows readers to control the rate of processing, and minimizes demands on working memory by allowing readers to re-read parts of the sentence that were problematic. We did not attempt to control for these differences. Indeed, these differences in the processing and storage demands of the two modalities may be precisely the interesting factors that could lead to different patterns of cortical activation for reading and listening comprehension.

There is no general agreement in the field about the precise relation between reading and listening comprehension. For example, many models of word processing [e.g., Patterson and Shewell, 1987] propose that reading and listening have separate input systems, but both input systems may then propagate information to a shared language processing system [also Coltheart et al., 1994; Lukatela and Turvey, 1994; Perfetti et al., 1992; Van Orden et al., 1988]. Similarly, according to Geschwind's [1979] description of word comprehension, both reading and listening involve a common pathway through Wernicke's area, but reading also involves a preceding pathway through additional temporo-parietal areas that transform the visual form of the word to its corresponding auditory form. Other theorists [e.g., Shallice, 1987] have argued for the existence of not only separate inputs, but also separate semantic systems. These accounts suggest that there might be some fundamental difference in the way the higher level comprehension processing is done in the two modalities.

On the other hand, there is also some degree of overlap between reading and listening comprehension processes. One argument in favor of a shared visual and auditory language processing system is that reading comprehension can be viewed as a second-order skill that is grafted onto existing listening-comprehension skills [e.g., Curtis, 1980; Horowitz and Samuels, 1985; Sticht and James, 1984]. A correlational study that compared reading and listening comprehension scores of students in grades 4, 6, and 8 found that the correlation between the two scores increased with age, presumably because students' reading skills caught up to their listening skills [Carlisle and Felbinger, 1991]. Moreover, the overall correlation of 0.52 in that study indicates some commonalities between reading and listening, but also leaves room for modality-specific processing. Additional evidence of partial sharing of neural systems between reading and listening arises from neuropsychological studies. A number of individuals, including the patient K.E., have demonstrated a homogeneous pattern of semantic errors across modalities, including spoken words, written words, pictures, objects, and tactile information, a pattern of results that has been interpreted as evidence for damage to a semantic system that is common to all lexical processes [Hillis et al., 1990]. However, stroke patient A.A. [Goodglass and Budin, 1988] suffered from a category-specific impairment in comprehending body parts, colors, numbers, and letters, but the deficit was present only for auditory comprehension. Given the mixed findings in both the behavioral and patient data, functional neuroimaging data may provide valuable information about the neural substrates of the comprehension processes in the two modalities.

Several neuroimaging studies have compared visual and auditory processing of single words, showing varying degrees of overlap and nonoverlap of the areas of activation. For example, in a PET study, reading visually presented words vs. repeating auditorily presented words produced areas of left temporal activation that were distinguishable but very close to each other [Howard et al., 1992]. (Word-reading produced activation that was superior and posterior to the activation for auditory word repetition). Similarly, in their classic PET study, Petersen et al. [1989] found some dissimilarity in the activation locus in the left inferior prefrontal region for generating an associated verb to a visually versus auditorily presented noun. In another study (fMRI), which required subjects to judge the concreteness of visually or auditorily presented words, both presentation modalities activated the left inferior frontal gyrus, but only the auditory task led to significant activation in the left posterior temporal region [Chee et al., 1999]. The results of the various single-word neuroimaging studies are difficult to compare because the tasks and subtraction control conditions differed. The results of all three studies, however, suggest that there are similar but distinguishable regions involved in the semantic processing of written and spoken words.

Neuroimaging studies of sentence comprehension have each examined only a single input modality, yielding only approximate comparisons across visual and auditory comprehension. Generally, comparisons across such studies have shown roughly similar areas of activation, nearly always including two cortical areas, the left inferior frontal gyrus (LIFG) and the left posterior superior and middle temporal gyri [e.g., Caplan et al., 1998, 1999; Just et al., 1996; Keller et al., 2001; Mazoyer et al., 1993; Schlosser et al., 1998; Stromswold et al., 1996].

A number of neuroimaging studies propose a role for the left inferior frontal gyrus (LIFG) in syntactic processing [e.g., Caplan et al., 1998, 1999; Just et al., 1996; Keller et al., 2001; Mazoyer et al., 1993; Schlosser et al., 1998; Stromswold et al., 1996] as well as a role in semantic processing and working memory [Fiez, 1997; Fiez and Petersen, 1998; Gabrieli et al., 1998; Petersen et al., 1989, 1990]. One possible role of LIFG in sentence comprehension is that it might be involved in generating a serial order-based representation that serves as input to other linguistic processes, a hypothesis intended to apply to the syntactic as well as other levels of representation [Keller et al., 2001]. Because of the transient nature of the stimulus, auditory sentence processing inherently imposes greater demands on working memory than does visual sentence processing. It is possible that listeners engage in more semantic processing than do readers in order to accommodate the greater memory demands of listening, by constructing a more complete semantic representation in which to store the information from earlier parts of the sentence. One might therefore expect to see more LIFG activation for the auditory conditions than for the visual conditions.

In addition, it is known from both reading comprehension [Just et al., 1996; Keller et al., 2001] and listening comprehension studies [Caplan et al., 1999] that greater sentence complexity produces more activation in the association cortical areas involved in language processing. These results are attributed to the greater computational workload imposed by the more complex sentences, leading to recruitment of more neural tissue and to higher intensities of activation [Just et al., 1996]. Therefore, the amount of activation in LIFG should increase with the complexity of the sentence for both visual and auditory comprehension.

The left superior and middle posterior temporal region is thought to be involved in many aspects of sentence processing, including lexical, semantic, phonological, and syntactic processing, based on results from both visual and auditory studies. Examples of task comparisons showing significant left posterior temporal activation include passive listening to sentences in a familiar as compared to an unfamiliar language [Schlosser et al., 1998], auditory semantic judgments compared to tone judgments [Binder et al., 1997], passive sentence reading compared to single-word reading [Bavelier et al., 1997], visual semantic categorization compared to visual letter recognition [Shaywitz et al., 1995], and visual rhyme judgment compared to visual letter recognition [Shaywitz et al., 1995]. This region also activates to nonlinguistic auditory input, possibly supporting the temporary storage of sound-based information [Petersen and Fiez, 1993]. Thus one might expect to observe left posterior temporal activation for both visual and auditory sentence comprehension because of the lexical, semantic, and syntactic requirements of the task, with more activation for listening than reading because of the hypothesized role of the left temporal region in processing auditory input. Because numerous processing and storage demands increase with sentence complexity, this region should show a sentence complexity effect in both modalities, as previously demonstrated for visual comprehension [Just et al., 1996].

Other areas involved in reading include the left ventral extrastriate and inferior temporal region. (This area will be referred to as the extrastriate region, but our use of this term also encompasses the inferior temporal gyrus.) The left inferior temporal gyrus and its surrounding regions have been implicated in the processing of visual form, such as in picture naming [Damasio et al., 1996], in processing visually presented words and pseudowords [Petersen et al., 1990], and in making semantic decisions to auditorily presented words, suggesting involvement of this region in semantic retrieval [Binder et al., 1997]. The retrieval and maintenance of semantic representations are processes that should operate during both visual and auditory comprehension. The extrastriate region is also believed to play a role in orthographic processing, which is a key component of visual comprehension [Keller et al., 2001]. We therefore expected extrastriate activation in both modalities but considerably more in the visual conditions than in the auditory conditions.

The left inferior parietal region is believed to be involved in the storage and processing of phonological representations [Awh et al., 1996; Paulesu et al., 1993], which are plausibly components of both reading and listening comprehension. The left inferior parietal region is also considered to be particularly involved in recoding visual input into an auditory form [Binder et al., 1997; Horwitz et al., 1998; Keller et al., 2001], which might lead to more inferior parietal activation for the visual conditions than the auditory conditions.

The study also directly compared the degree of left lateralization in reading and listening. Reading comprehension studies generally produce more activation in the left than the right hemisphere [Just et al., 1996]. In phonological tasks, Shaywitz et al. [1995] also reported strong left lateralization, but only for males; females showed a more bilateral pattern of activation. Few studies, however, have precisely documented the degree of left lateralization or provided a detailed analysis of the right hemisphere activation, making cross-modality comparisons of lateralization difficult. This comparison is permitted in the current study because of its within-participant design, using equivalent sentences and tasks in the two modalities.

In summary, to determine the degree to which the activation patterns in higher cortical areas are amodal or distinguishable between reading and listening comprehension, we looked for similarities and differences in the overall amount of activation in each region of interest (ROI), the location of activation within an ROI, and the degree of lateralization, as a function of input modality and sentence complexity.

METHOD

Participants

Nine college-age (mean 21.9 years, SD 4.2 years), native-English-speaking participants (five males) were included; data from another 10 participants were excluded because of excessive head motion.[1] All participants were right-handed as determined by the Edinburgh Handedness Inventory (mean score = 56.3, SD = 23.9). Volunteers provided informed consent based on a protocol approved by the Institutional Review Boards of the University of Pittsburgh and Carnegie Mellon University.

Experimental paradigm

The participant's task was to read or listen to a sentence and then answer a question by pressing one of two buttons to indicate whether the probe statement was true of the sentence. Seventy-five percent of the probes were true. The study involved four experimental conditions: two visual conditions in which the sentence and probe were written, and two auditory conditions in which they were presented auditorily over earphones. In both presentation modalities, the items were either simpler or more complex sentences. The simpler (Active) sentences consisted of two conjoined active clauses, such as, "The coach saw the actress and ran rapidly up the steep hill." The more complex (Object Relative) sentences contained an embedded object relative clause such as, "The monk that the astronaut watched entered the room quietly at noon." All probes were active statements such as, "The monk entered the room quietly. True or False." The two levels of sentence complexity were crossed with the two modalities; thus the four conditions were Visual Active, Visual Object Relative, Auditory Active, and Auditory Object Relative. Different sentences appeared in each of the four experimental conditions, but sentences were matched across condition for length and word frequency. Each sentence appeared only once in the course of the experiment.

In the visual conditions, each written sentence was presented for 5 sec with a 1-sec pause before the written probe was presented; the participant's response terminated the presentation of the probe. There was no time limit for participants' response to the probe. The written sentence and probe were rear projected onto a screen 20 cm from the participant. In the auditory conditions, each sentence presentation took approximately 5 sec with a 1-sec pause before the probe, which took approximately 2 sec. There was a 0.5-sec pause after the probe in which the participant could respond. The auditory sentences and probes were digitized by a male speaker at a normal speaking rate.

A series of five successively presented sentences of the same type (e.g., Auditory Object Relative) constituted an epoch. There were four separate epochs for each of the four experimental conditions, resulting in a total of 16 experimental epochs. The 16 epochs were

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[1] The number of excluded participants was high, partly because of discomfort of the headphones pressing against an ear. Five of the excluded participants had head motion greater than 0.3 voxels. Several others had excessive head motion primarily in the auditory conditions.

divided into a sequence of four blocks, with each block containing one epoch of each condition in a different permutation. The baseline was a total of five 24-sec fixation epochs in which the participant fixated on an asterisk. The experiment began with a fixation epoch, and an additional fixation epoch was presented at the end of each block. Finally, 6-sec rest intervals occurred between experimental epochs. Data from the 6-sec rest intervals as well as the first 6 sec of each experimental epoch were not included in the analysis to accommodate the hemodynamic response.

fMRI acquisition parameters

The fMRI data were collected using a GE Medical Systems 3.0T scanner at the Magnetic Resonance Research Center of the University of Pittsburgh Medical Center. The scanner used a commercial birdcage, quadrature-drive radio-frequency whole-head coil. The study was performed with a gradient echo, resonant echo planar pulse sequence with TR = 3,000 ms, TE = 25 ms, and a 90° flip angle. Fourteen oblique-axial slices were imaged, and each slice was 5-mm thick with a gap of 1-mm between slices. The acquisition matrix was 128 × 64 with 3.125-mm × 3.125 × 5-mm voxels. Structural images for anatomic localization were taken in the axial plane and then resliced to correspond to the functional images. They were a 124-slice SPGR volume scan with TR = 25 ms, TE = 4 ms. The acquisition matrix was 256 × 256, with 1.5-mm slice thickness.

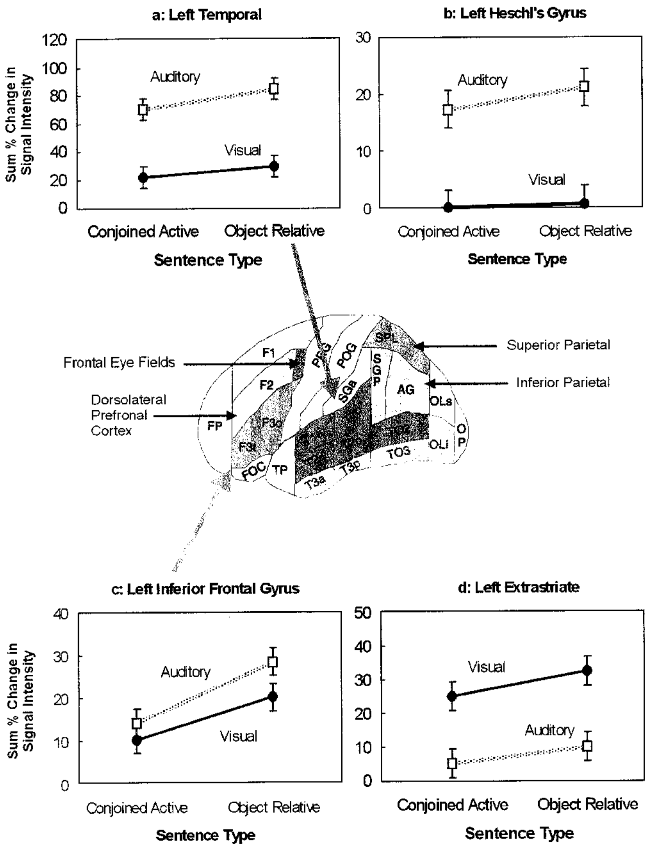

Figure 1.
The schematic drawing in the center of the figure shows several of the left hemisphere ROIs, adapted from the parcellation scheme described and depicted in Caviness et al. [1996]: Inferior Frontal Gyrus, Temporal, Extrastriate (which also includes inferior temporal), Inferior Parietal, Superior Parietal, Dorsolateral Prefrontal Cortex, and the Frontal Eye Fields. Each area shaded in gray represents an ROI, as indicated by the arrows and associated labels. The associated graphs depict the amount of activation in a given ROI as a function of modality and sentence complexity. Amount of activation is defined as the percent change in signal intensity (as compared to fixation) summed across all voxels in an ROI that are active ($t > 5.0$) in any condition. Note that the graphs are not all on the same scale. Error bars represent 95% confidence intervals calculated as the square root of MS_e /n, where MS_e is the pooled error term for both of the independent variables [Loftus and Masson, 1994]. Confidence intervals that descended below zero were truncated at the abscissa.

Anatomical regions of interest

To compare the amount of activation in a given area across experimental conditions, anatomically defined ROIs were drawn for each participant using the parcellation scheme described by Rademacher et al. [1992] and further refined by Caviness et al. [1996]. In order to examine not just the location of the activation but also how input modality and sentence complexity affected the volume and amplitude of the activation in each of these regions, it was important to use an a priori, independent method of defining the ROIs. The schematic drawing in the center of Figure 1 displays the set of ROIs that were defined, with the exception of Heschl's gyrus, the calcarine sulcus, and the supplementary motor area, which are not shown. This method uses limiting sulci and anatomically landmarked coronal planes to segment cortical regions. The ROIs were defined by a staff research assistant after extensive training on the Rademacher/Caviness parcellation scheme. The anatomical information in the structural images was displayed in the three orthogonal planes simultaneously and the ROIs were manually drawn on each functional slice. The interrater reliability of this ROI-defining procedure between two trained staff members was evaluated for four of the 18 ROIs in two participants in another study. The interrater reliability measure speaks to the general reliability of the ROI-defining procedure. The reliability measure was obtained by dividing the size of the set of voxels that overlapped between the two raters by the mean of their two set sizes. The resulting eight reliability measures were in the 78–91% range, with a mean of 84%, as high as the reliability reported by the developers of the parcellation scheme.

The inferior frontal ROI included areas F3t and F3o referring to the Caviness et al. [1996] nomenclature, or approximately BA 44 and 45. The dorsolateral prefrontal cortex (DLPFC) consisted of the middle frontal gyrus (F2; BA 6, 8, 9, and 46), with the exception of the two posterior-most voxels. The excluded area constituted the frontal eye fields ROI. The temporal ROI included the superior (T1a and T1p, BA 22) and middle temporal gyri (T2a, T2p, and TO2; BA 21, and 37). The superior and middle temporal gyri were combined into one ROI because previous studies of language processing have often found activation centered in the superior temporal sulcus between them [Keller et al., 2001]. Heschl's gyrus consisted of parcellation unit H. The parietal lobe was divided into two separate ROIs— superior parietal and inferior parietal. The superior parietal ROI consisted of area SPL (BA 5 and 7). The inferior parietal ROI included both the supramarginal gyrus (SGp, BA 40) and the angular gyrus (AG, BA 39). The extrastriate ROI included the inferior temporal gyrus (TO3 and TFp, BA 37 and 20), the fusiform gyrus (TOF and TF; BA 36, 37, and 20), and parts of the lateral inferior occipital cortex (OF, T3a, T3p, and Oli). The calcarine sulcus consisted of parcellation units SCAL and CALC. The supplementary motor area consisted of parcellation unit JPL. For all areas except the calcarine sulcus and supplementary motor area, the ROIs were drawn separately for the left and right hemispheres.

fMRI data analysis

Image preprocessing used FIASCO to correct for signal drift and head motion [Eddy et al., 1996]. The mean of the maximum head motion per participant was less than 0.1 voxels, and never exceeded 0.3 voxels. The fMRI procedure relies on BOLD contrast (blood oxygenation level dependent) [Ogawa et al., 1990] to measure the oxygen level in the microvasculature supporting neuronal activity. In order to eliminate potential effects of macrovasculature, we discarded data with greater than 6% change in signal. This procedure resulted in the exclusion of less than 1% of voxels in all ROIs except the calcarine sulcus, in which 1.58% of the voxels were excluded.

Activation within each condition was assessed by calculating voxel-wise t statistics for the comparison of images collected within each of the four experimental conditions with those acquired during the fixation condition. The total number of voxels in all 18 ROIs ranged from 5,052 to 6,830 across subjects, with a mean of 5,904. A t-threshold of $t > 5.0$ was selected to give a Bonferroni-corrected alpha level of $P < .05$ after taking into account the average number of voxels and approximately 50 degrees of freedom for each of the voxel-wise t tests within a participant.

The primary dependent measure was the percent change in signal intensity (as compared to fixation) summed across all voxels in an ROI that are active ($t > 5.0$) in any condition. This measure was chosen because it provides an integral of the total volume of activation and the strength of activation [Xiong et al., 1998]. For each ROI, the data were subjected to an analysis of variance with modality (visual vs. auditory) and sentence complexity (conjoined active vs. embedded object relative) as within-subjects factors.

RESULTS

Region of interest (ROI) analyses

Summary

The left perisylvian language areas (inferior frontal and superior/middle posterior temporal) showed a significant increase in activation with increasing sentence complexity and more activation for the auditory than visual conditions, as shown in Figure 1; these results are consistent with a hypothesis that these regions are part of a highly connected language network. In addition, the analyses of the location of activation for both regions indicated systematic, interpretable differences between the two modalities. Several other ROIs also showed modality differences in the amount of activation, but no other region showed a significant increase in activation with increasing sentence complexity. There was no significant interaction between modality and sentence complexity for any region except the calcarine sulcus. Table I shows the amount of activation for each condition in each of the 18 ROIs. Also shown in Table I are the average centroids of activation for each ROI. Because the centroids did not differ much as a function of sentence complexity, data are presented for only the Visual Object Relative and Auditory Object Relative conditions. The coordinates of the centroids of activation within each ROI were calculated by separately averaging the x, y, and z coordinates of each active voxel for each condition. These centroid coordinates were then transformed to a standardized space [Talairach and Tour-

TABLE I. Amount and location of activation as a function of condition for 18 regions of interest

	Sum % change in signal intensity					Talairach coordinates[a]					
						Visual object relative			Auditory object relative		
ROI	Visual active	Visual object relative	Auditory active	Auditory object relative	SE[b]	x	y	z	x	y	z
Left temporal	21.1	28.8	69.6	83.9	7.62	−52	−36	5	−52	−29	5
Right temporal	1.7	1.3	56.6	49.8	6.24	38	−27	7	53	−24	6
Left Heschl's gyrus	0.0	0.7	17.3	21.2	3.21	−55	−13	16	−46	−20	11
Right Heschl's gyrus	0.0	0.2	13.7	13.1	1.95	38	−20	11	49	−16	13
Left inferior frontal gyrus	10.5	20.2	14.3	28.4	3.24	−42	11	26	−43	15	24
Right inferior frontal gyrus	1.7	2.2	3.4	8.3	1.30	45	15	28	41	16	20
Left extrastriate	25.1	32.4	5.1	9.9	4.31	−29	−70	−7	−44	−49	−12
Right extrastriate	22.3	24.1	3.2	1.8	3.80	27	−70	−8	43	−44	−9
Calcarine sulcus	79.3	105.3	6.8	8.7	13.84	1	−70	5	3	−66	12
Left inferior parietal	11.0	15.2	5.3	8.4	2.55	−33	−62	40	−34	−61	37
Right inferior parietal	3.0	3.7	5.1	6.7	2.09	31	−61	37	43	−46	30
Left superior parietal	7.0	8.5	2.5	3.1	2.06	−23	−60	44	−12	−61	49
Right superior parietal	4.3	5.6	1.5	1.8	1.68	22	−64	48	26	−64	49
Left DLPFC	7.8	8.2	7.2	10.1	1.83	−37	22	36	−34	30	31
Right DLPFC	4.2	4.0	3.3	9.3	2.58	34	35	32	37	28	32
Left frontal eye fields	4.1	6.3	4.1	3.8	1.21	−38	0	45	−41	−3	47
Right frontal eye fields	0.5	1.1	0.0	1.2	0.57	35	−3	49	45	−2	50
Supplementary motor area	8.2	10.8	9.1	10.2	1.65	−4	−9	60	−4	−12	64

[a] Positive numbers indicate right (x), anterior (y), and superior (z) directions.

[b] SE = standard error, a 95% confidence interval calculated as the square root of MS_e/n, where MS_e is the pooled error term for the two independent variables [Loftus and Masson, 1994].

noux, 1988] using *MCW-AFNI* software [Cox, 1996]. The following sections describe the results for individual ROIs.

Temporal region

The left temporal ROI showed substantially more activation (three times as much, by the sum % change measure) in the auditory than in the visual conditions, $F(1, 8) = 18.77$, $P < .01$. The right temporal region (see Fig. 2a), like the left, showed considerably more activation in the auditory than in the visual conditions, $F(1, 8) = 24.02$, $P < .01$; in fact, there was almost no activation in the right temporal ROI in the visual condition.

As predicted, and shown in Figure 1a, the left temporal ROI showed significantly more activation for object relative than for active sentences, $F(1, 8) = 5.78$, $P < .05$. Moreover, the size of the sentence complexity effect was similar for reading and listening. (The right temporal region enigmatically showed slightly more activation for active sentences than for object relative sentences in the listening condition).

The centroids of activation in the left temporal region differed for the two modalities, as indexed by the x, y, and z coordinates for the auditory object relative vs. visual object relative conditions for each participant.[2] For this analysis, the averages of the coordinates were not transformed into Talairach space, but the average Talairach coordinates (see Table I) are consistent with this more precise analysis. The voxels activated in the Auditory Object Relative condition were significantly more anterior and somewhat more lateral than the voxels activated in the Visual Object Relative condition ($t(7) = 5.20$, $P < .01$ for y coordinates; $t(7) = 1.88$, $P = .05$ for x coordinates). The average z coordinates for the two conditions were very similar. This location difference is visible in individual data sets, such as that shown in Figure 3, which shows the significantly activated voxels for a single slice through the superior/middle temporal region for one participant.

Heschl's gyrus

As would be expected for the primary auditory region, both left and right Heschl's gyri (see Fig. 1b

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[2] One participant who had no active voxels in the Visual Object Relative condition was excluded from this analysis.

and 2b) showed significantly more activation in the auditory conditions than in the visual conditions, F(1, 8) = 12.24, $P < .01$ (left), F(1, 8) = 20.80, $P < .01$ (right) but no reliable effect of sentence complexity.

Inferior frontal gyrus

In LIFG, increasing sentence complexity led to similar amounts of increase in activation for visual and auditory sentence processing (see Fig. 1c). Across both modalities, there was significantly more activation for object relative sentences than for active sentences, F(1, 7) = 7.67, $P < .05$.

The total amount of activation in LIFG was significantly greater in the auditory conditions than in the visual conditions, F(1, 7) = 11.20, $P < .05$.[3] The same direction of effect, but with an even greater magnitude, was mentioned above for the temporal regions.

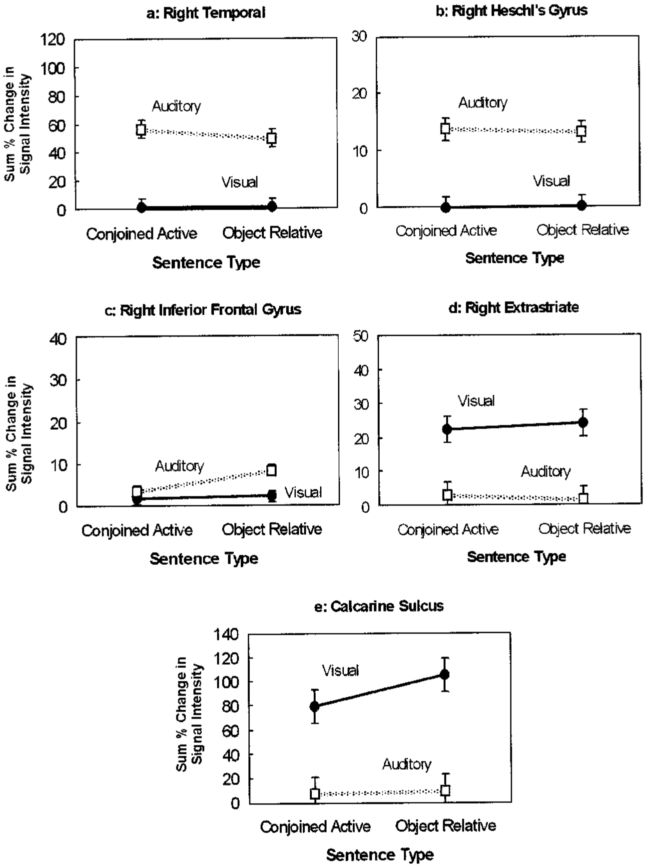

Figure 2.
Each graph depicts the amount of activation, defined as in Figure 1, in a given ROI as a function of modality and sentence complexity for the right homologues. Most show patterns similar to those for the corresponding left hemisphere region, with the exception of the right temporal region. In each graph the scale is the same as that of its left homologue in Figure 1.

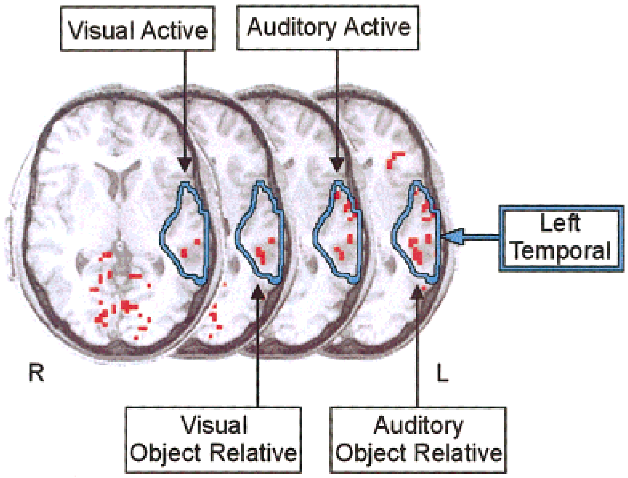

Figure 3.
An activation image of one slice for one participant, with the left temporal ROI outlined, for each of the four experimental conditions (Visual Active, Visual Object Relative, Auditory Active, and Auditory Object Relative). The volume of activation was greater in the auditory conditions than in the visual conditions, and the amount of activation increased with increasing sentence complexity.

The location of the activation within the left inferior frontal gyrus also differed for the two modalities. Overall, the voxels activated in the two modalities were in overlapping locations and interspersed throughout the region. However, a comparison of the auditory versus visual activation for the two object relative conditions within each participant revealed that the centroids in the Auditory Object Relative condition were significantly more inferior and anterior than in the Visual Object Relative condition ($t(8) = 3.43$, $P < .01$ for the comparison of z coordinates; $t(8) = 2.42$, $P < .05$ for y coordinates). In a number of the participants, this effect appeared to result from a small number of voxels in the Auditory Object Relative condition that were considerably anterior and inferior to any of the activated voxels in the Visual Object Relative condition. In at least four of these participants, this extra auditory activation was in the

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[3] One participant's data were excluded from the LIFG analyses because of an unusually high amount of activation in the region, 10 standard deviations above the mean for the visual conditions and five standard deviations for the auditory conditions. The data from this participant did not look unusual in any of the other regions and were included in all other analyses. The statistical results with and without this participant were the same other than in LIFG.

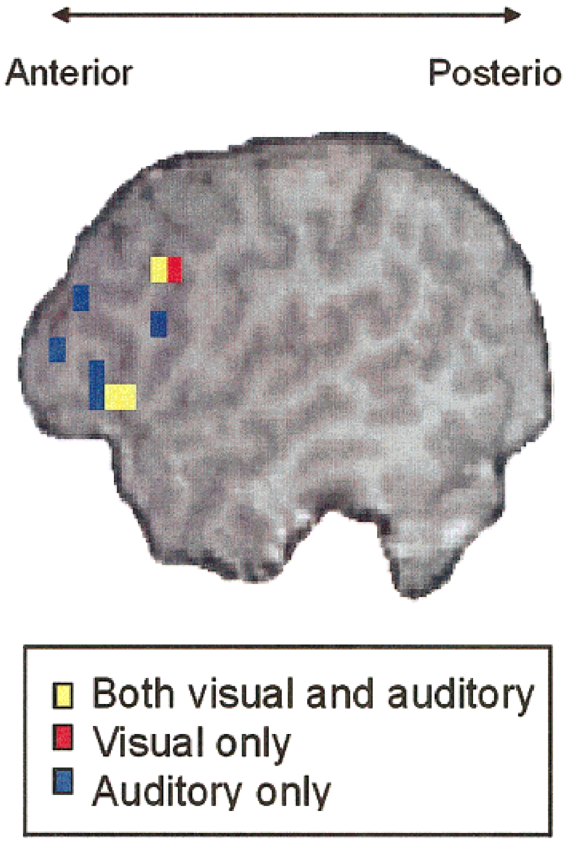


Figure 4.
The effect of presentation modality in left inferior frontal gyrus for Object Relative sentences is shown for one representative sagittal slice of one participant. Yellow voxels were active in both the visual and auditory conditions, the single red voxel was active in only the visual condition, and blue voxels were active in only the auditory condition.

pars triangularis. The activation locations of one participant who displayed this pattern of results are shown in Figure 4. As in the left temporal analysis, the average Talairach coordinates are consistent with this more detailed analysis by individual participant.

In the right inferior frontal area (see Fig. 2c), the pattern of results was similar to that in the left hemisphere, with significantly more activation in the auditory conditions than in the visual conditions, F(1, 8) = 9.49, $P < .05$. As in the left area, there was more activation for more complex sentences, although not significantly more. Overall, in both hemispheres the inferior frontal regions showed more activation for more complex sentences and more activation for auditory comprehension than visual comprehension; there was also considerably more activation in the left ROI than in the right homologue.

Extrastriate

Figures 1d and 2d show much more activation in the visual conditions than in the auditory conditions in both hemispheres, F(1, 8) = 13.87, $P < .01$ (left), F(1, 8) = 13.13, $P < .01$ (right). In the left extrastriate region, there was a trend toward more activation for object relative sentences than for active sentences, F(1,8) = 3.39, $P = .10$, a finding that has been obtained for reading comprehension [Keller et al., 2001]; the difference was not significant for the right extrastriate region. The activation for the visual condition was more posterior than for the auditory condition.

Calcarine sulcus region

As expected for this region (Fig. 2e), there was significantly more activation in the visual than auditory conditions, F(1, 8) = 14.12, $P < .01$. The small amount of activation in the auditory conditions may result from the visual true/false cue that was displayed along with each auditory comprehension probe. The calcarine sulcus also showed a significant interaction with complexity, such that the visual conditions showed more activation as sentence complexity increased, but not surprisingly, the auditory condition did not show an effect of sentence complexity, F(1, 8) = 5.94, $P < .05$.

Other regions

Table I provides the results for several additional ROIs in which activation was observed but modulation by either of the independent variables within the ROI did not attain statistical significance. These ROIs included the parietal regions (both inferior and superior), dorsolateral prefrontal cortices (DLPFC), the frontal eye fields, and the supplementary motor area. In all of these regions, except the right frontal eye fields, seven or more of the nine participants showed some activation. The left inferior parietal region showed a marginally significant trend toward more activation in the visual conditions than in the auditory conditions, F(1, 8) = 4.01, $P < .10$. A small amount of frontal eye field activation was observed not only in the visual conditions but also in the auditory conditions, which may be a result of, in part, the visually presented true/false cue (even in the auditory conditions). This region has been shown to be sensitive to cognitive variables in reading comprehension [Keller et al., 2001], so it may play some role in comprehension itself.

TABLE II. Laterality ratios for selected ROIs[a]

	Visual	Auditory
Inferior frontal gyrus	0.80	0.59
Temporal	0.63	0.07
Inferior parietal	0.57	0.22

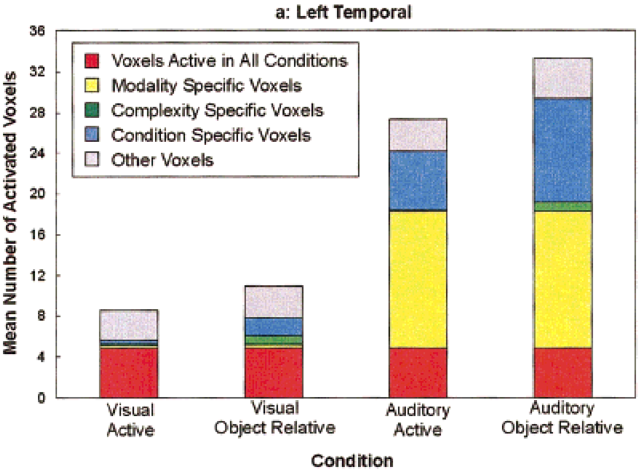
[a] Each laterality ratio was calculated by dividing the difference between the two hemispheres' voxel counts by the sum of the two hemispheres' voxel counts. A ratio near zero indicates bilateral activation, and a ratio near 1 indicates left lateralization.

Laterality

To assess the degree to which language processing is lateralized for the three main language-processing regions, we computed the number of significantly activated voxels for each region, averaging over the two levels of complexity, and calculated a ratio of the difference between the two hemispheres' voxel counts and the sum of the two hemispheres' voxel counts. A ratio near zero indicates bilateral activation, and a ratio near 1 indicates strong left lateralization. As shown in Table II, in both the inferior frontal and the posterior temporal ROIs, the activation was significantly more left lateralized for reading than for listening, $t(8) = 3.34$, $P < .01$ (inferior frontal), and $t(8) = 3.15$, $P < .01$ (temporal). The directionality of this effect held for eight of the nine participants. The inferior parietal ROI showed a similar trend, although the pattern held for only six of the nine participants and was not statistically different, $t(8) = 1.56$, $P < .10$.

Individual voxel characteristics

To determine whether some of the activating voxels were differentially sensitive to one or the other independent variable, we examined how the activated voxels in each of the four conditions behaved in the other three conditions. For example, we examined each activated voxel in the Visual Active condition, and we assessed whether that voxel was activated in Visual Object Relative, Auditory Active, and Auditory Object Relative conditions. Each voxel's behavior was classified into one of $2^3 = 8$ sets, representing the binary possibilities of significantly activated vs. not, in each of the remaining three conditions. (Of course, not being significantly activated does not imply that the voxel's activation was at baseline in the other conditions.) Consider the graph in Figure 5a, which shows such a classification for the left temporal ROI. There was one set of about five voxels per participant (shown in red) that was activated in all four conditions, and presumably reflects processes that are common across conditions. Two other sets of voxels were modality specific. One of these two sets, shown in blue, consisted of voxels whose significant activation was specific to only that one condition. For example, in the Auditory Object Relative condition (the rightmost bar), there were about 10 voxels, depicted in blue, that significantly activated only in that condition. The other set of modality specific voxels was significantly active only in the given condition and in the other condition with the same input modality (yellow). Another voxel set was specific to a given level of



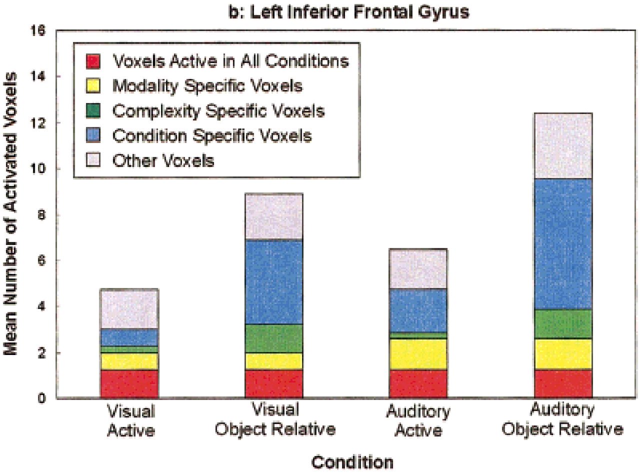


Figure 5.

For each condition, the voxels that activated above threshold in that condition were divided into sets according to the other conditions in which they were also active. The height of each bar segment represents the number of voxels in that set. Note that the upper panel (left temporal) and lower panel (left inferior frontal gyrus) use different scales.

sentence complexity (green), significantly activating only for the given condition plus the condition with the same syntactic structure in the other modality. The remaining four sets were combined (depicted in gray) and consist of voxels that were activated in each possible combination of three conditions (e.g., a voxel could be activated in all conditions except for Auditory Active). These sets correspond to patterns that are less interpretable and cross modalities.

The main new information that this analysis provides about the left temporal ROI is that for the two auditory conditions, a large majority of voxels (70%) were modality specific (blue and yellow), whereas for the two visual conditions, very few voxels were modality specific. Even though the left temporal activation was much greater in the auditory conditions than in the visual conditions, the activated voxels in the visual conditions could have been different voxels than those that were activated in the auditory conditions. Instead, the visual voxels seem to be primarily a subset of the voxels activated in the auditory condition. The presence of many auditory specific voxels in this region is consistent with the finding of a more anterior centroid for the auditory conditions, a direction that points toward primary auditory cortex. By contrast, the pattern in the left inferior frontal ROI was quite different (shown in Fig. 5b). Here, there were many fewer modality specific voxels and many condition-specific voxels. At the least, this analysis reveals different patterns of modality specificity in the left temporal and left inferior frontal regions.

Behavioral results

As predicted, response times were significantly longer for object relative sentences than for active sentences, F(1, 8) = 5.51, $P < .05$, both in the visual modality (487 ms difference) and the auditory modality (179 ms difference). Response times were measured from different initial times in the two modalities, and thus cannot be directly compared. Participants also made significantly more errors (13%) on the object relative sentences than on the active sentences, F(1, 8) = 18.64, $P < .01$. The overall error rates were slightly higher (a difference of 6%) in the auditory than in the visual conditions, F(1, 8) = 7.39, $P < .05$. However, the mean error rate in both modalities (overall, 15%) was well below chance. For both response time and error rate there was no interaction between modality and sentence complexity.

DISCUSSION

A major premise underlying many theories of cognition is that higher-level cognition is a process of abstract symbol manipulation. This assumption of amodality leads to the prediction that higher-level comprehension processes, such as lexical access, syntactic analysis, semantic interpretation, and integration, should produce similar cortical activation for reading and listening. However, many aspects of the current results indicate that the input modality leaves its imprint on subsequent processing. For example, many of the voxels in the temporal ROI were modality and condition specific, and the centroid of activation was more anterior for the auditory conditions than for the visual conditions. By contrast, in the inferior frontal region, the percentage of activated voxels that are activated only in a given modality or condition is lower, hovering around 50%, a classic "half full, half empty" situation in terms of modality specificity. Finally, the degree of lateralization was greater for the visual modality. All of these results indicate modality effects at higher levels of processing.

The finding of more left and right temporal activation in the auditory than the visual conditions is consistent with the view that the temporal region is involved in the processing of auditory input [e.g., Petersen and Fiez, 1993]. Although Heschl's gyrus was excluded from the temporal ROI, evidently the secondary and tertiary association areas in the temporal lobe are activated to a greater extent for auditory than visual processing of sentences, and this pattern appears to be true for both the left and right hemispheres.

The total amount of activation was also significantly greater in the auditory conditions than in the visual conditions in LIFG, particularly in the anterior, inferior portions of this area. The difference in relative amounts of activation may stem from the fact that auditory input is by nature transient and information from earlier parts of a sentence must be internally maintained. The additional activation in LIFG for auditory comprehension could reflect two mutually compatible ways of coping with the additional storage burden. First, there could simply be additional storage-related activity (a working memory function). Second, there could be additional semantic and thematic analyses during listening comprehension, in order to generate a more complete representation in which to store the thematic relations among the sentence elements (e.g., who is the agent, what is the action, who is the recipient of the action). In addition, the priority of acquisition of listening comprehension or its evolutionary and practical prominence in human life might give it a greater cortical representation, even in the frontal region where there is no direct sensory input.

Other regions show the opposite pattern, namely more activation in reading than in auditory comprehension. The finding of more visual than auditory activation in the left and right extrastriate regions supports the consensual view that these areas contribute to the processing of the visual form of words. The trend toward more visual than auditory activation in the left inferior parietal region is consistent with the idea that this region is involved in recoding visual input into an auditory form [Binder et al., 1997; Horwitz et al., 1998; Keller et al., 2001]. In the calcarine sulcus, there was not only a finding of greater activation in the visual than auditory conditions but also a significant interaction between modality and sentence complexity. This pattern of results may arise from computations that are specific to this region, such as more visual processing initiated by the slower reading for the object relative sentence; alternatively or in addition, the effect may be a result of feedback from processes that are further upstream and are directly affected by the added complexity of the object relative sentences.

In addition to the finding that many ROIs showed more activation for one modality than the other, the partial overlap of the voxel sets that activate in reading and listening is also reflected by the different centroids of activation for the reading and listening conditions. For the left temporal region, the finding of more anterior and lateral centroids for the Auditory compared to the Visual Object Relative conditions is partially consistent with the findings of Howard et al. [1992], who found that for single words, left temporal activation in response to auditory input was more anterior (and more superior) than activation in response to visual input. This pattern of activation may be partially explained by the proximity of the anterior portion of the ROI to the primary auditory processing in Heschl's gyrus.

In the left inferior frontal gyrus, the more inferior and anterior activation for the auditory compared to visual Object Relative conditions is paralleled by the results of the two Caplan et al. studies [1998, 1999]. In the visual study [Caplan et al., 1998], the increase in activation was located in the pars opercularis, whereas in the auditory study [Caplan et al., 1999] the increase in activation was located in the more inferior and anterior pars triangularis. Although the current study showed that the two modalities produced overlapping areas of left IFG activation, visual inspection of each participant's activated voxels superimposed on their structural images revealed four participants with activation of the pars triangularis only for auditory processing; none of the nine participants showed activation in pars triangularis for visual processing. Taken together, these findings indicate that visual and auditory sentence processing activate distinguishable but overlapping locations within left IFG, with pars triangularis activation being primarily associated with auditory comprehension. This extra activation in inferior/anterior left IFG associated with listening comprehension may reflect the greater demand that listening comprehension (compared to reading comprehension) places on working memory storage and perhaps on thematic/semantic processing, consistent with previous interpretations of the processing associated with this area [Fiez, 1997; Fiez and Petersen, 1998; Gabrieli et al., 1998; Petersen et al., 1989, 1990].

The existence of varying degrees of cortical overlap as a function of both the modality and the cortical region may help illuminate our understanding of the diverging patterns of stroke-induced language impairment among individuals. Some individuals show modality specific deficits, whereas others show impairments that cross modalities. The existence of both separable and overlapping activating neural areas revealed by the fMRI results leaves room for both types of impairment. Future fMRI studies of patients with brain damage may eventually reveal why a given patient has a particular type of comprehension deficit [cf. Thulborn et al., 1999].

Another striking modality difference was the significantly greater bilaterality of the auditory than visual processing in the temporal ROI and also the inferior frontal regions. There are several mutually compatible possible explanations for this phenomenon. One possibility is that auditory sentence processing is more bilateral than visual sentence processing because the sensory processing of auditory sentences entails a fairly bilateral activation of Heschl's gyrus, which could induce more bilaterality in nearby language areas, even though Heschl's gyrus itself was not included in this analysis of lateralization. Of course, it is interesting that this asymmetry was also observed in the inferior frontal region, a region that has no primary sensory input but which may work in tandem with the more posterior temporal region [Just et al., 1996]. Another possibility stems from auditory comprehension being acquired long before reading: once the relative dominance of the left hemisphere is established for auditory language, this pattern may be exaggerated or enhanced when reading comprehension is grafted onto listening comprehension. Finally, the two modalities in this study may have differed in the difficulty of the processing, which may impact on the degree of lateralization. At the very least, this study reveals two new crucial facts about lateralization, namely, that it is modulated by the modality and varies among language-related cortical regions. Furthermore, the degree of lateralization may also vary as a function of the task difficulty. These observations raise a caution about generalizations about lateralized processing of language, particularly if they are based on studies using only the visual modality or only simple language tasks.

Despite differences in the location of activation, the visual and auditory modalities showed similar increases in the activation in the left inferior frontal region and the left posterior temporal region with sentence complexity. In visual sentence comprehension, this result for the inferior frontal region is consistent with findings in several studies [Caplan et al., 1998; Just et al., 1996; Stromswold et al., 1996] that vary in the tasks, baselines, and sentence types, but which all reported an increase in the activation in this region with increasing complexity. The results are also consistent with an auditory study that found increases in the inferior frontal region for more complex sentences [Caplan et al., 1999]. The results of the current study add the valuable information that the increase occurs not just in the left inferior frontal region but the left temporal region as well, i.e., in a network of areas. An additional important contribution of the current study is the finding that there is a functional similarity in the increase in activation with complexity for both reading and listening, suggesting that the functional impact of the sentence structure is independent of the input modality.

The increase in activation with increases in complexity suggests that the neural systems subserving listening and reading both have the capability to dynamically recruit additional tissue as the task demand increases. Thus, this type of response to task demand appears to be a general characteristic of some of the main cortical regions involved in language comprehension. An obvious interpretation of increased activation with sentence complexity is that the area in question is directly supporting more computations necessitated by the greater complexity.

CONCLUSION

This study allowed us to compare directly the effect of visual and auditory input on sentence comprehension in numerous cortical areas, and we found differences in activation amounts, brain locations, lateralizations, and voxel characteristics. At the same time, the increase in activation with increasing sentence complexity was similar regardless of the modality of the input, indicating a commonality in dealing with additional structural analysis. Like many new findings, the results answer some old questions and frame the beginnings of new questions concerning the origin and functional significance of the differences in brain activation between reading and listening comprehension. The richness and variety of language behavior makes it a leading venue for using fMRI to understand the relation between sensory processing and cognitive processing.

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