

## Sentence complexity and input modality effects in sentence comprehension: an fMRI study

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**Cortical regions engaged by sentence processing were mapped using functional MRI. The influence of input modality (spoken word vs. print input) and parsing difficulty (sentences containing subject-relative vs. object-relative clauses) was assessed. Auditory presentation was associated with pronounced activity at primary auditory cortex and across the superior temporal gyrus bilaterally. Printed sentences by contrast evoked major activity at several posterior sites in the left hemisphere, including the angular gyrus, supramarginal gyrus, and the fusiform gyrus in the occipitotemporal region. In addition, modality-independent regions were isolated, with greatest overlap seen in the inferior frontal gyrus (IFG). With respect to sentence complexity, object-relative sentences evoked heightened responses in comparison to subject-relative sentences at several left hemisphere sites, including IFG, the middle/superior temporal gyrus, and the angular gyrus. These sites showing modulation of activity as a function of sentence type, independent of input mode, arguably form the core of a cortical system essential to sentence parsing.**

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### Introduction

With continuing advances in functional neuroimaging tools such as fMRI, which can detect cortical regions implicated in a wide range of cognitive behaviors, the goal of mapping the language brain is within our grasp. Examination of patterns of co-varying regional brain activity across manipulations of sentence structure and input modality can help to narrow in on the brain circuitry that instantiates abilities essential to comprehension of spoken discourse and printed text. Identifying these critical

regions and their connections can also advance our understanding of the impact on language systems of developmental and pathologic conditions that affect brain function (Carpentier et al., 2001; Eden and Zeffiro, 1998; Pugh et al., 1996, 2001). An important potential application of mapping studies is to aid in planning for neurosurgical procedures in the treatment of focal epilepsy and other conditions (Binder et al., 1996; Bookheimer et al., 1997; Carpentier et al., 2001; Desmond et al., 1995; Simos et al., 1999; Springer et al., 1999). Before functional imaging paradigms can be used routinely in clinical practice, a fuller understanding of the functional anatomy of language must be obtained. Indeed, a clearer view is needed of how distributed neural systems function cooperatively in the performance of essential language abilities.

Until relatively recently, most knowledge of the neurological foundations of language had been gained from studies of patients with localized cortical damage. Specific deficits in language processing have been associated with damage to local cortical regions. Damage to Broca's area (BA 44, 45) in left inferior frontal gyrus (IFG) is associated with a range of deficits in spoken language production, including phonetic production of words and grammatical organization of sentences. Clinical and psycholinguistic studies also implicate this region in sentence comprehension, both in speech and reading. Recent neuroimaging studies have confirmed a strong role for pars triangularis (Brodmann area 45) and pars opercularis (BA 44) within IFG for core reading operations, including print-to-phonology decoding, working memory, and aspects of sentence parsing (Fiez and Peterson, 1998; Fiez et al., 1999; Hagoort et al., 1999; Herbster et al., 1997; Ni et al., 2000; Pugh et al., 1997).

Wernicke's area in the posterior portion of the left STG is the other classical language zone where lesions are known to produce major deficits in both spoken and written language comprehension. Imaging studies suggest that this region serves a multiplicity of functions, playing a role in ordered recall of words during verbal fluency tasks (Wise et al., 2001), phonological memory storage (Paulesu et al., 1993), phonological analysis, lexical semantic processing (Just et al., 1996; Keller et al., 2001; Michael et al.,

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2001; Pugh et al., 1996), and sentence interpretation (Helenius et al., 1998; Ni et al., 2000). Deficits in accessing visual word forms for reading have been associated with damage to the left angular gyrus while impairments in name retrieval and semantic processing of words have been associated with damage to the left basal temporal area (Hodges et al., 1992; Krauss et al., 1996; Roeltgen and Heilman, 1984).

At present, there is a good deal of evidence, stemming both from lesion studies and neuroimaging studies on neurologically intact persons, pointing to a role for multiple regions, beyond the classical Broca's and Wernicke's areas, in various aspects of language processing of spoken and printed materials (Caplan et al., 1996; Howard et al., 1992; Peterson et al., 1989; Pugh et al., 1996; Warburton et al., 1996). Thus, findings from both these sources converge on a complex, richly interconnected network of cortical and subcortical regions distributed in both hemispheres, but predominantly in the left, which are relevant to one or another aspect of language behavior.

A majority of neuroimaging studies of language processing to date have been carried out with simple materials, usually lists of isolated words. Examples of such studies include experiments aimed at identifying the brain systems active in the several component processes of word recognition, involving orthographic, phonological, and lexical semantic information, as well as those systems that support fluent word generation (Beaugregard et al., 1997; Pugh et al., 1996; Shaywitz et al., 1998). From the many studies of this type, there is an emerging consensus on the functional architecture of word recognition systems for print and speech (Hickok and Poeppel, 2000; Pugh et al., 2000, 2001; Tagamets et al., 2000). Neuroimaging studies have revealed a set of left hemisphere brain areas critical for word identification in reading. The left hemisphere reading circuit contains ventral (occipitotemporal), dorsal (temporoparietal), and anterior (inferior frontal gyrus) components.

A factor, which is sometimes neglected in analyses of language processing, is the influence of input modality. Both in the history of the human species and the development of the individual child, spoken language capacity is the secondary derived language abilities of reading and writing. Although parsimony would dictate that these secondary language functions would exploit much of the preexisting spoken language machinery rather than recreating it, nature does not always take the parsimonious route. Hence, the degree of overlap in regional brain activity underlying speech perception and reading is an empirical question. Studies that directly compare spoken with printed word identification are relatively few. These have generally found largely overlapping neural networks across left hemisphere cortex when activations associated with basic auditory and visual sensory processing are removed statistically (Chee et al., 1999; Howard et al., 1992; Michael et al., 2001; Shaywitz et al., 2001; Simos et al., 1999). While the center of activation induced by speech and printed material can vary somewhat within major left hemisphere regions (Howard et al., 1992), the overlap in activation is a more prominent feature of such comparisons than are the differences.

To illustrate, Shaywitz et al. (2001) examined auditory and visual word recognition across conditions that also modulated demands on selective and divided attention. This study revealed common activation for print and speech in left IFG, supramarginal gyrus, and occipitotemporal sites, with unique foci for spoken words in a localized region within the superior temporal gyrus (see

Chee et al., 1999; Howard et al., 1992 for similar findings). Thus, it appears that lexical access and lexical semantic processing of single printed and spoken words share many neural networks within left perisylvian language areas. There is evidence for a language modality that transcends sensory modality.

Although much valuable information has been obtained from controlled studies of processing isolated words, such studies necessarily present an incomplete and possibly a distorted view of brain operations occurring during the processing of language in sentence contexts. Those circuits that are responsible for linking words in text or discourse and that underlie multiword syntactic and semantic operations are relatively less well charted (Hagoort and Brown, 2000). Accordingly, this study focused on sentence processing. Given the high degree of overlap of structures engaged by speech and print at the word level, it is reasonable to expect that the processing of connected text or discourse will conform to this picture of largely overlapping foci for the two input modalities. Nevertheless, lesion studies have occasionally shown selective loss of comprehension for spoken discourse or text, so there is reason to believe that the neural systems supporting abstract components of language processing in the two modalities are partially non-overlapping (Shallice, 1987).

Previous investigations of sentence processing with PET or fMRI have consistently shown broad regions of activity across left perisylvian areas irrespective of mode of presentation, though few studies have directly contrasted speech and print input within the same study under controlled conditions (Bookheimer et al., 1997; Carpentier et al., 2001; Michael et al., 2001). In two recent studies by our group, subjects heard or read sentences that were either well-formed or syntactically or semantically anomalous (Carpentier et al., 2001; Ni et al., 2000). In Carpentier et al., there was an explicit speech–print comparison, which showed that many left hemisphere regions were activated in common across both modalities. Greater levels of activity for spoken sentences were found primarily in bilateral auditory cortex and at several sites in the superior temporal gyrus, while printed sentences showed heightened responses at ventral occipitotemporal sites and some temporoparietal sites. Within IFG, common activation was seen anteriorly in BA 45, but posteriorly in BA 44, greater activation for printed than spoken sentences was observed. This led us to speculate that BA 44 is associated with orthographic-to-phonological recoding for print, in keeping with some previous studies of processing isolated individual words (Fiez and Peterson, 1998; Herbster et al., 1997; Pugh et al., 1997). It would also suggest that BA 45, an area that was insensitive to modality of presentation, might be a good candidate for higher order processing related to sentence parsing operations and/or language-related working memory (a speculation which is also consistent with the findings of Ni et al., 2000).

To test this speculation about division of labor within IFG and other regions, it is critical to experimentally cross the factors of speech/print modality with sentence complexity to isolate modality-independent areas that modulate activity in response to differences in sentence complexity. This approach was adopted in the present investigation. The underlying premise can be stated simply: Sentence-level processing of linguistic information should be largely independent of input modality because it is carried out on linguistic representations that are neither specifically auditory nor visual. Accordingly, we could expect that the neural substrate of parsing operations comprises those regions that are activated by both spoken and written sentences and that

also respond differentially to sentences that are easier or harder to parse.

Sentence complexity effects involving subject- and object-relative clause structures have been demonstrated both in behavioral and imaging studies. The restrictive relative clause is one structure that has received much study. Relative clauses can be distinguished by the syntactic role of the noun phrase within the matrix sentence that bears the relative clause (subject or object) and the role of the missing noun phrase within the relative clause (again, subject or object). With respect to the latter distinction, object relatives have uniformly been found more difficult and slower to process than subject relatives (Hamburger and Crain, 1984; Just et al., 1996; Ni et al., 1996). There are a variety of theories to explain the greater difficulty of processing object relatives (Gibson and Pearlmuter, 2000). For the most part, these focus on the problems of assigning thematic role to the head noun of the relative clause. Apparently, object relatives present greater processing difficulties than subject relatives because the assignment of thematic role is more difficult in these cases.

Recently, in a design similar to the one employed in the current report, Michael et al. (2001) varied sentence complexity for spoken and written sentences. Subjects either heard or read two kinds of sentences: Compound simple sentences containing two clauses joined by the word and (“The coach saw the actress and ran rapidly up the steep hill”) and complex sentences with an embedded clause (“The monk that the astronaut watched entered the room quietly at noon”). Each condition was examined relative to a rest/fixation baseline condition. Using anatomically defined regions of interest (ROI), Michael et al. found sentence complexity effects that were modality independent in the IFG ROI and in the temporal lobe ROI. Increased activation for spoken sentences was seen at anterior temporal lobe sites and in anterior aspects of IFG (probably BA 45), while print showed reliable increases in a broadly defined extrastriate ROI. Moreover, as in the study by Carpentier et al. (2001), spoken sentences were associated with greater right hemispheric activity (especially in STG and IFG) than printed sentences. The use by Michael et al. of anatomically defined ROIs does, however, limit the grain-size of spatial resolution. Moreover, the use of rest/fixation as a baseline task does not permit subtraction of primary visual and auditory processes. The present study employs modality-specific control tasks and voxel-based analyses.

Several other studies have examined whole sentence processing in one or the other modality to map activity associated with particular demands placed on the brain in comprehending sentences (Caplan, 2001; Caplan et al., 2000, 2002; Carpentier et al., 2001; Michael et al., 2001; Muller et al., 1997; Ni et al., 2000; Kang et al., 1999; Schmolck et al., 2000). The most frequent finding in studies that examine sentence complexity is that sites in IFG, particularly BA 45, consistently discriminate easy-to-parse from difficult-to-parse structures. Less consistently reported effects have been reported in posterior STG, MTG, and in one recent study, effects of complexity were observed in the angular gyrus (Caplan, 2001). The current study examines all of these regions (i.e., whole brain analyses are employed), with both auditory and visually presented sentences to distinguish possible modality-specific from modality-independent sentence complexity effects. While STG and IFG activations are anticipated, the angular gyrus finding by Caplan et al. stands as unexpected. Given that stimuli in this event-related experiment were presented visually, it remains to be seen if such effects in this putatively reading-related region are

modality specific or, alternatively, whether they cut across both speech and print modes.

The present study examined the influence of sentence structure (center-embedded, object-relative clause vs. subject-relative clause) and input modality (print vs. speech) in a sentence comprehension fMRI paradigm with full brain coverage. As noted, a reason to examine sentence processing of comparable materials presented in both spoken and written form is to clearly distinguish regions that are active in one modality or the other from those that show overlapping excitation. The latter amodal areas likely constitute the critical sites for the more abstract dimensions of linguistic processing. A candidate neural system for sentence parsing is one that is both modality independent and discriminates subject-relative from object-relative sentences. This approach allows us, in principle, to examine sentential and modality effects and their interactions.

### Methodology

Subjects were healthy right-handed individuals aged 18–40, mean 24, 10 males and 10 females. A total of 21 subjects were studied, with 1 subject discarded who was judged to be right hemisphere dominant for language (based on a laterality score from the main subtractions in both the visual and auditory presentation modes). Final analysis was performed on 20 left hemisphere dominant subjects. All participants gave informed consent, had normal or corrected-to-normal vision, and were paid \$40 for their participation. Approval for this study was obtained from the Yale Medical Human Investigation Committee.

### Materials

The stimulus materials consisted of 120 center-embedded sentences containing relative clauses. Half of these were subject relatives (as in example 1 below) and half were object relatives (as in example 2 below). Within each pair, the sentences contained the same words; only the structure of the relative clause varied.<sup>1</sup>

- (1) The biologist—who showed the video—studied the snake.
- (2) The biologist—who the video showed—studied the snake.

All sentences were syntactically correct but some sentences in each block (1–2) could be considered pragmatically

<sup>1</sup> There could be concern that the sentence judgment task is rendered ambiguous by the failure to observe the who/whom distinction for the subject and the object case, respectively. In preparing these materials, we followed the principle of keeping the actual words the same for both subject-relative and object-relative sentences, making word order the only distinguishing feature. This is the control we have incorporated in most of our earlier studies of relative clause constructions. The issue of who/whom was explicitly studied by two of us, Ni and Shankweiler (unpublished data), using eye-tracking to compare the online reading of subject-relative and object-relative sentences, with materials in which the who/whom distinction, was observed. Inserting whom or the pronoun in the objective case (in the object-relative clauses) made essentially no difference for subjects who, like the subjects of the present study, were young adults. That is, object-relative sentences, despite the additional cue, were more difficult to process than subject-relative sentences by about the same margin. For these reasons, we are therefore comfortable not observing the who/whom distinction in these stimuli.

Table 1  
Location of activations in sentence comprehension task

| ROI                        | Brodmann area | Visual input modality sentence—lines |     |    |         | Auditory input modality sentence—tones |     |    |         |
|----------------------------|---------------|--------------------------------------|-----|----|---------|--|-----|----|---------|
|                            |               | x                                    | y   | z  | Z score | x                                      | y   | z  | Z score |
| <i>Left hemisphere</i>     |               |                                      |     |    |         |  |     |    |         |
| Posterior parietal         | BA 40         | -58                                  | -47 | 4  | 3.1     | -61                                    | -42 | 5  | 3.7     |
| Temporal                   | BA 22         | -56                                  | -32 | 3  | 2.9     | -57                                    | -22 | 8  | 3.1     |
| Inferior frontal           | BA 44/45      | -43                                  | 30  | 9  | 2.4     | -46                                    | 27  | 12 | 3.7     |
| Superior temporal/parietal | BA 39         | -54                                  | -52 | 15 | 3.1     | -36                                    | -81 | 26 | 2.0     |
| Anterior cingulate         | BA 6/24       |                                      |     |    |         | -1                                     | -2  | 57 | 2.6     |
| Posterior cingulate        | BA 30         | -7                                   | -54 | 29 | 2.3     |  |     |    |         |
| <i>Right hemisphere</i>    |               |                                      |     |    |         |  |     |    |         |
| Posterior parietal         | BA 40         | 59                                   | -49 | 0  | 1.8     |  |     |    |         |
| Right temporal             | BA 22         | 55                                   | -25 | 5  | 2.2     | 55                                     | -19 | 4  | 3.9     |
| Inferior frontal           | BA 44/45      | 36                                   | 25  | 6  | 1.7     | 32                                     | 19  | 13 | 1.9     |
| Superior temporal/parietal | BA 39         | 53                                   | -63 | 14 | 1.7     |  |     |    |         |
| Anterior cingulate         | BA 6          | 2                                    | 14  | 49 | 2.4     | 1                                      | -2  | 57 | 2.6     |

anomalous. Examples of such pragmatically anomalous sentences include

- (3) The thief who chased the policeman was slow.
- (4) The man who the dolphin loves eats seafood.

Across all 10 runs, the number of anomalies among the object-relative and subject-relative sentences was balanced and the location of these anomalous sentences within a block was random. Each sentence occurred in two forms, a printed form and a spoken form. Nonlinguistic control stimuli consisted of tone pairs (low

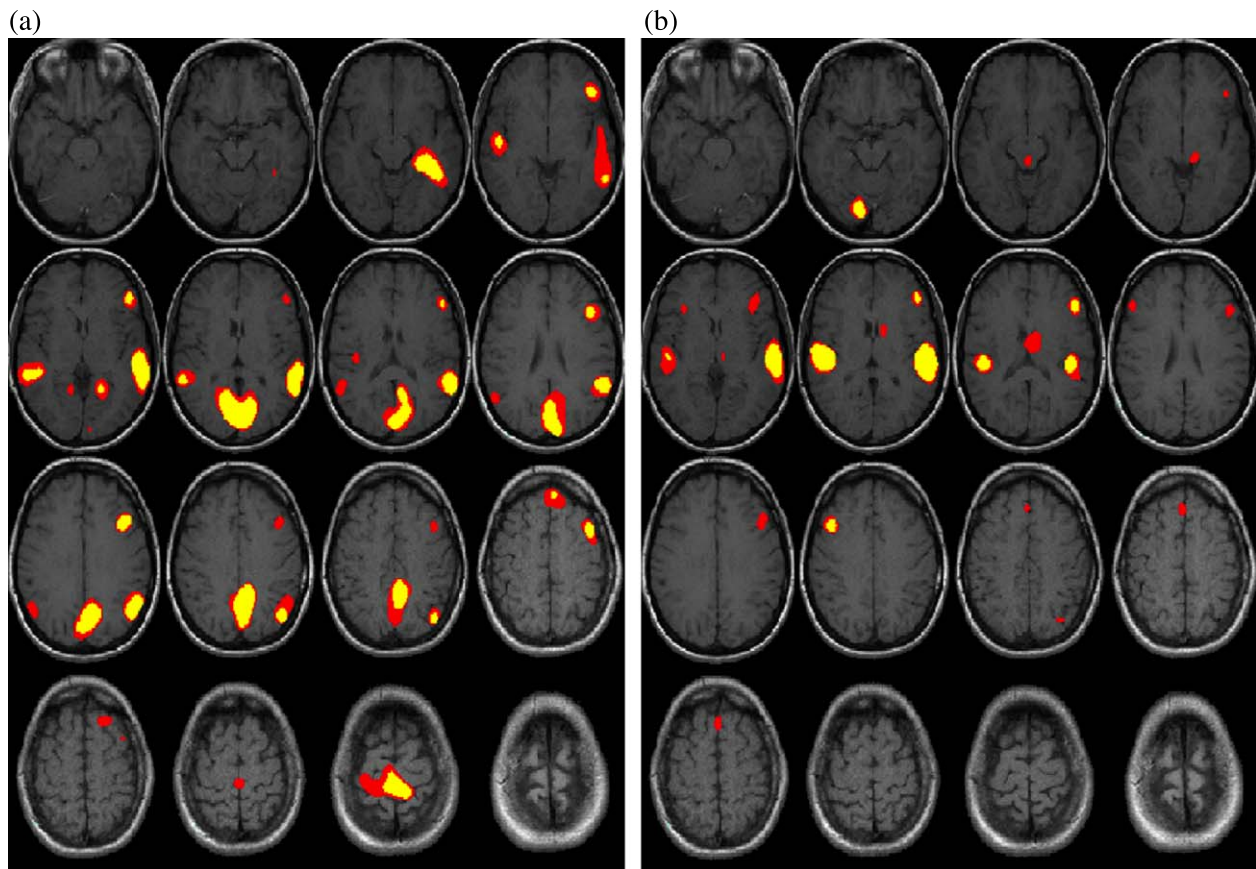


Fig. 1. Main subtractions averaged across 20 subjects: (a) visual input (sentence—line), (b) auditory input (sentence—tone). All results are shown at  $P < 0.01$ . Following established radiological convention, the left hemisphere was shown on the right. Note the strong left basal temporal-fusiform gyrus activity evoked by visual input, and left posterior parietal activation associated with this modality. Posterior portion of left Wernicke's region is activated more strongly by visual input than auditory input; auditory input activates STG bilaterally. Left anterior prefrontal cortex (BA 8 and 9) is activated by both auditory and visual input modalities, only on the left with the visual input.

tone, 220 Hz; high tone, 329.6 Hz, where pairs were formed randomly low–low, high–high, low–high, or high–low) and the subject made a same/different pitch judgment, which served as the baseline for spoken sentences, and pairs of line sequences (with same or different orientation) which served as the baseline for print. The line sequences consisted of two rows of five oblique lines ( $\backslash \backslash \backslash \backslash$  and  $\backslash \backslash / / \backslash$ ), one immediately above the other, for which the participant had to decide whether the lines in the upper and lower row matched in orientation.

## Procedure

The task involved reading or listening to the sentences and making a sentence goodness judgment following each sentence, or a line orientation or a pitch judgment for the control stimuli. Subjects were instructed to press the yes key if the sentence seemed to be grammatical and to make sense, otherwise they were to press the no key (criteria employed for making this judgment were not controlled and presumably varied across subjects; our primary consideration was to ensure that subjects were trying to comprehend the tokens). Each subject received all sentences twice, once in spoken form and once in print. Reading and listening trials were separately grouped, the order counter-balanced across subjects. Different orderings of sentences were used in auditory and visual presentations. A single run consisted of alternating blocks of sentences and control stimuli; four blocks of sentences alternated with five blocks of control stimuli (each run starting and ending with the control condition). Within each block, there were six sentences of a given type, example 1 or 2 above. The block order of sentence types was randomized across each run. The structure of a run and its timing are schematized in Table 1.

Sentence task structure and timing<sup>a</sup>

| Visual<br>or auditory<br>presentation | LP or TP  | Sentence<br>type 1 | LP or TP  | Sentence<br>type 2 | LP or TP  | Sentence<br>type 1 | LP or TP  | Sentence<br>type 2 | LP or TP  |
|---------------------------------------|-----------|--------------------|-----------|--------------------|-----------|--------------------|-----------|--------------------|-----------|
| Timing                                | 0.00:0.20 | 0.21:1.00          | 1.01:1.20 | 1.21:2.00          | 2.01:2.20 | 2.21:3.00          | 3.01:3.20 | 3.21:4.00          | 4.01:4.20 |

<sup>a</sup> LP = line pairs, TP = tone pairs, 1 = subject-relative sentence structure, 2 = object-relative sentence structure.

MR compatible headphones (RTC Technologies) were used to provide the auditory stimuli during the task. An LCD panel (Sharp Instruments, Mahwah, NJ) was used to project output from a PowerPC (Macintosh, CA) laptop running Psyscope onto the back-projection screen. Studies began with a sagittal localizer scan (T1-weighted spin echo, TE/TR = 11/500 ms,  $256 \times 192 \times 2$  nex, FOV = 24 cm, 6 mm skip 0.5 mm) from which the anterior commissure (ac) and posterior commissures (pc) were identified. T1-weighted, spin echo, axial-oblique slices, parallel to and through the ac–pc line (5th slice centered on the ac–pc line), were then acquired (T1-weighted spin echo, TE/TR = 11/500 ms,  $256 \times 192 \times 2$  nex, FOV = 20 cm, 6 mm skip 0). These images served as the anatomic images for activation overlay. The BOLD gradient echo imaging during the activation paradigms was then run (gradient echo EPI,  $\alpha$ /TE/TR = 80/50/1800 ms) with the same FOV, slice thickness, as in series 2, and a  $64 \times 64$  matrix, and 62.5 kHz bandwidth. Four warm-up pulses were used to ensure steady-state magnetization and then 140 images per slice per run were obtained. Each of the auditory and visual

The spoken sentences were recorded at a comfortable speaking rate with each presentation lasting less than 4.8 s and with the ISI adjusted such that net time per sentence plus ISI was 6.5 s. Each tone in a tone pair was presented for 500 ms, with 500 ms between tones within a pair, followed by a 1.5 s ISI, which was sufficient to allow time for the button press response. For the reading condition, the printed versions of the sentences were divided into three segments (as illustrated in 1 and 2). The three-part presentation was used to minimize eye movements and prevent re-reading. Each sentence segment was presented for 1.6 s with an ISI of 1.7 s. Line pairs were presented for 2 s each with an ISI of 1.5 s. Thus, the timing of both versions of the sentence task and their corresponding control tasks were comparable. The subject was asked to decide, and respond with a yes/no button press, if the sentences made sense and were correct grammatically. There was no cue for the subjects to respond. They simply responded at the end of each sentence. No feedback was given.

## Image acquisition

Imaging was performed using a 1.5 T GE, Signa LX system (General Electric, Waukesha, WI). Subjects were placed supine in the MR scanner, and their heads were placed within the standard quadrature head coil. Care was taken to ensure that the subjects were looking straight up; foam was placed on either side of the head to minimize motions. Also to minimize motion, a piece of tape was placed across the forehead of each subject and attached to the head holder within the head coil. Once inside the magnet, subjects could view a back-projection screen placed at their feet, through a mirror assembly in the head coil. A fiber optic button box was used to record the subject's response, and

input paradigms was repeated five times (with different sentences each time) to maximize the statistical power.

## Data analysis

Data were motion corrected using SPM-99 (Friston et al., 1995) and aligned to a reference anatomic scan taken at the beginning of the study (Studholme et al., 2001). A Student's *t* test was applied to the task/control conditions within a run using in-house developed software. Specifically, within each run, the two subject-relative blocks were compared with the baseline blocks on either side of each activation block, in a single *t* test. The analogous operation was performed for the object-relative sentence blocks. The resultant *t*-maps across runs for a given condition were averaged as described in Constable et al. (1995). Since the average activation across an entire block of 40 s was used in the *t* test, no correction was made for slice timing effects. No normalization or linear de-trending

of raw voxel intensities, nor of the final t-maps, was performed across any of the data. T-maps and percent signal change maps were linearly interpolated from 3.125 mm in-plane voxel size, to the match the size of the anatomic images, 0.7812 mm in-plane voxel size, and median filtered [ $5 \times 5$ ], to remove spurious activations due to the multiple comparison problem. The final images had in-plane resolutions of approximately 4 mm. The anatomic images for each subject were highlighted to reveal activations with significance greater than  $P < 0.01$  as determined using a bootstrap technique (Efron and Tibshirani, 1993) and in the case of multiple subjects using a  $t$  test of the null hypothesis across subjects. Multiple subjects were coregistered based on the anatomic scans using a mutual information algorithm (Studholme et al., 2001) allowing for composite t-maps to be formed and statistical comparisons of activation (measured in terms of percent signal change) as a function of the different sentence structures or input modality. The Talairach coordinate system was defined on the reference 3D brain. Paired  $t$  tests (paired within each subject) between visual and auditory input modalities, and object-relative and subject-relative sentence types, were performed on percent signal change maps. These multi-subject comparison maps were filtered before display using a  $5 \times 5$  median filter, again to reduce the incidence of false positive activations and achieve a significance level of  $P < 0.01$ . The steps of interpolation, registration, filtering, and multisubject averaging, described above, resulted in no spuriously activated voxels arising from the multiple comparison problem when tested over 2500 times using white noise distributions. The maps illustrating the common areas of activation were created by taking the mean  $t$  value of the composite maps for each modality for those voxels that had  $P < 0.01$  in both modalities. If  $P < 0.01$  was obtained in only one input modality, the voxels were not highlighted. This logical AND operation reveals areas of common activation across the two input modalities. These data were subsequently reanalyzed using a general linear model to examine effects of task  $x$  modality  $x$  interaction.

Table 2  
Visual–auditory input modality contrast map

| ROI                            | Brodmann area | Visual–auditory input modality (positive activation) |     |     |         | Visual–auditory input modality (negative activation) |     |     |         |
|--------------------------------|---------------|--|-----|-----|---------|--|-----|-----|---------|
|                                |               | $x$  | $y$ | $z$ | Z score | $x$  | $y$ | $z$ | Z score |
| <i>Left hemisphere</i>         |               |  |     |     |         |  |     |     |         |
| Posterior parietal             | BA 40         | –58  | –55 | 7   | 2.6     |  |     |     |         |
| Temporal                       | BA 22         |  |     |     |         | –44  | –32 | 9   | 3.6     |
| Inferior frontal               | BA 44/45      | –51  | 26  | 18  | 2.2     | –40  | 20  | 18  | 2.0     |
| Superior temporal/<br>parietal | BA 39         | –42  | –74 | 23  | 2.4     |  |     |     |         |
| Premotor                       | BA 6/4        | –40  | 2   | 37  | 1.8     | 44   | 6   | 37  | 2.0     |
| Posterior cingulate            |               | –10  | –56 | 28  | 1.9     |  |     |     |         |
| Basal temporal                 |               | –40  | –40 | –11 | 2.3     |  |     |     |         |
| Hippocampus                    |               | –29  | –12 | –9  | 1.8     |  |     |     |         |
| Primary visual                 | BA 17         | –6   | –80 | –1  | 2.2     |  |     |     |         |
| <i>Right hemisphere</i>        |               |  |     |     |         |  |     |     |         |
| Posterior parietal             | BA 40         | 55   | –55 | 6   | 2.1     |  |     |     |         |
| Right temporal                 | BA 22         |  |     |     |         | 49   | –24 | 7   | 3.1     |
| Superior temporal/<br>parietal | BA 39         | 49   | –69 | 15  | 2.0     |  |     |     |         |
| Premotor                       | BA 6          |  |     |     |         | 44   | 5   | 40  | 2.0     |
| Primary visual                 | BA 17         | 4  | 79  | –2  | 2.3     |  |     |     |         |

## Results

### Modality-specific and modality-independent effects

As shown in Figs. 1a and b and Tables 1 and 2, activation for printed and spoken sentences (each in contrast to its within modality control task) was broadly distributed with spoken sentences showing a stronger right hemisphere response, especially at STG, relative to printed sentences. In Fig. 2a, modality-independent sites (i.e., sites considered activated above threshold in both modalities) are largely left lateralized and include the occipitotemporal area, MTG, STG, and several foci in IFG. With respect to (qualitative or quantitative) differences between the modalities, these are seen in a direct comparison analysis (Fig. 2b). Spoken sentences were associated with higher activation levels across large portions of STG bihemispherically and at several sites bilaterally within IFG, confirming previous studies, including one from our group (Carpentier et al., 2001) and others (Howard et al., 1992; Michael et al., 2001). For printed sentences, increases in predominantly left posterior cortex included supramarginal gyrus and angular gyrus along with the fusiform gyrus in occipitotemporal area. These print-related increases are broadly consistent with expectations from classical neurological models of reading (Geschwind, 1965). These results are summarized in Tables 1 and 2.

### Sentence complexity effects

In Fig. 3 and Table 3, areas that discriminated the more difficult object-relative from easier subject-relative sentences for both modalities are shown. These areas include most of the expected sites: IFG, MTG, STG, and occipitotemporal cortex, and includes a localized site in the angular gyrus in the left hemisphere. When the maps for the two modalities are examined separately, both IFG and STG responses are seen for each modality. Of note, while the site in the angular gyrus discriminates sentence type irrespective of modality as seen in Fig. 3a, in general, the angular gyrus effect

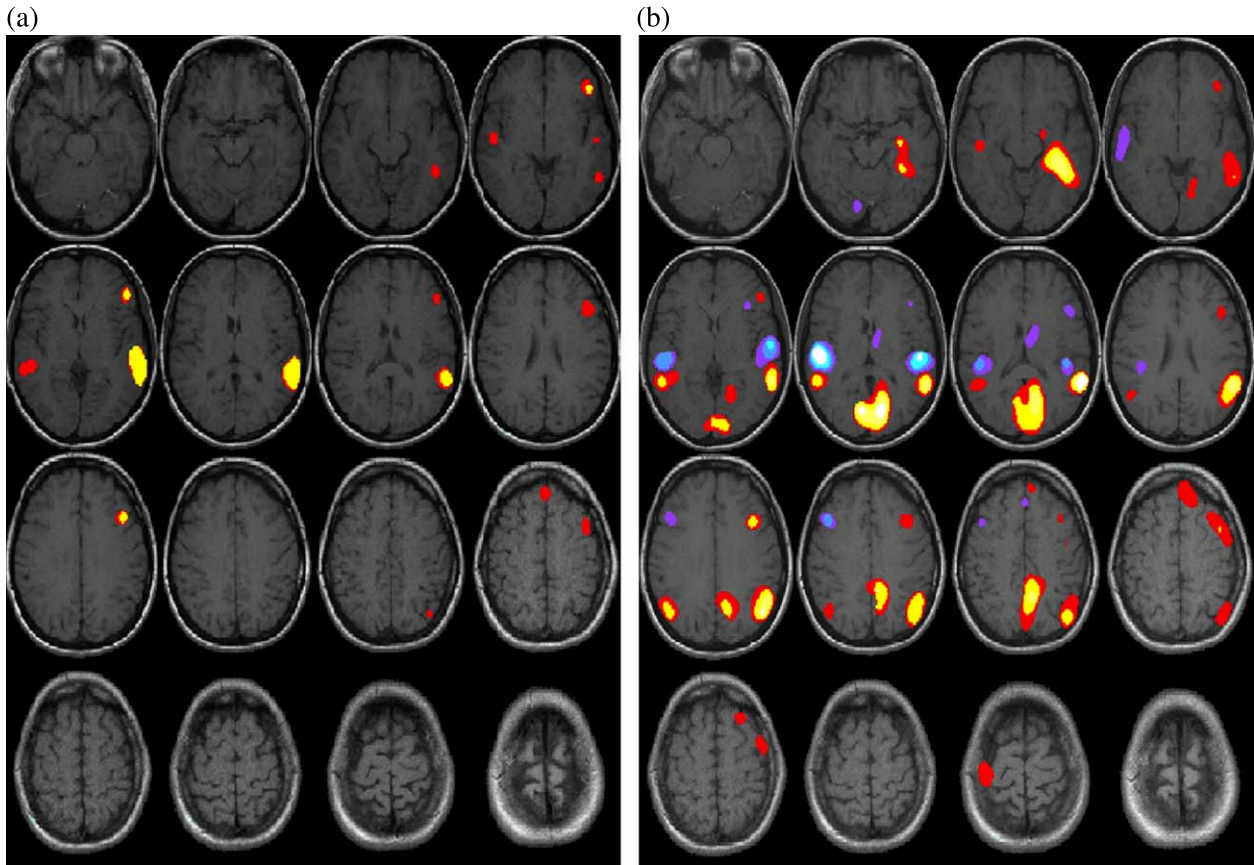


Fig. 2. Common regions (a) between visual and auditory input modalities in the primary subtractions shown in Figs. 1a and b. These common regions reflect sentence processing regions that are independent of input modality. The differences associated with modality in this primary subtraction are shown in (b), where hot colors (yellow/orange) reflect greater activation by the visual input modality, whereas cool colors (white/blue/purple) reflect regions exhibiting greater activation with the auditory input modality. Each modality activates left STG as shown in (a), but note in (b). The auditory input modality more strongly activates anterior STG regions while the visual input modality more strongly activates posterior portions of STG.

**Sentence Effect: (Object Relative – Subject Relative)**

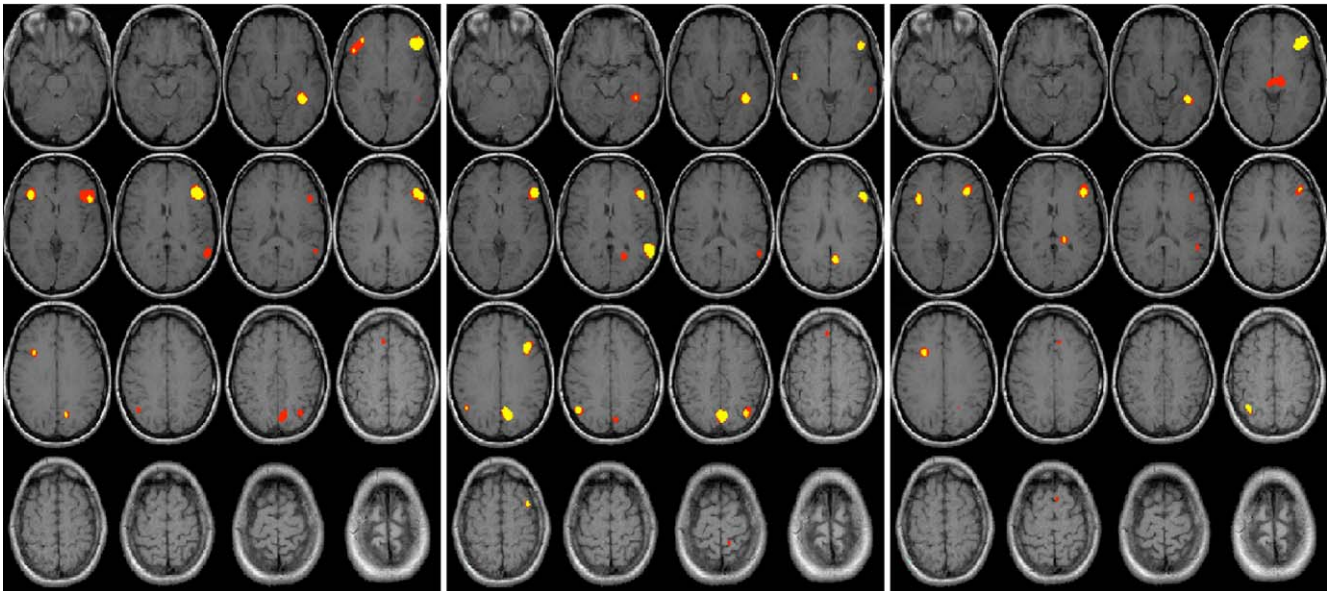


Fig. 3. (a) Combined visual and auditory sentence activity map demonstrating regions with higher activity, measured as percent signal change, for object-relative sentences compared to subject-relative sentences. Similar sentence complexity effects are observed for each input modality, (b) visual print versions, and (c) auditory spoken versions. Modality differences are also observed. For example, in (b) note posterior parietal activity associated with visual presentation, and in (c) predominantly bilateral inferior frontal activity with auditory presentation.

Table 3  
Object relative–subject relative contrast map

| Talairach coordinates      |               |  |     |    |         |
|----------------------------|---------------|--|-----|----|---------|
| ROI                        | Brodmann area | Object rel > subject rel (positive activation) |     |    | Z score |
|                            |               | x  | y   | z  |         |
| <i>Left hemisphere</i>     |               |  |     |    |         |
| Posterior parietal         | BA 40         | −51  | −58 | 3  | 2.4     |
| Inferior frontal           | BA 44/45      | −49  | 11  | 13 | 2.5     |
| Superior temporal/parietal | BA 39         | −36  | −64 | 31 | 2.1     |
| Premotor                   | BA 6/4        | −36  | 4   | 46 | 2.2     |
| Anterior cingulate         | BA 6/24       | −2   | 6   | 33 | 2.2     |
| Thalamus                   |               | −3   | −24 | 15 | 1.9     |
| <i>Right hemisphere</i>    |               |  |     |    |         |
| Inferior frontal           | BA 44/45      | 44   | 6   | 2  | 2.6     |
| Premotor                   | BA 6          | 43   | 14  | 23 | 1.9     |

appears more salient in the visual condition than in the auditory condition. Nonetheless, additional GLM analyses revealed that for each of the sites showing modality-independent sentence complexity effects in the overall map (3a), none was significantly qualified by interactions between complexity and modality. Thus, we can conclude that the major sentence effects seen across the left hemisphere in Fig. 3a, are most reasonably viewed as modality independent. Using the most conservative criterion, that the site must be similarly activated in both modalities and must show comparable effects of complexity for both modalities, the strongest candidate site appears to be BA 44/45 in left IFG.

## Discussion

The present study was conducted to examine co-varying effects of input modality, sentence complexity, and their interactions on those cortical systems that participate in language processing. Several important findings emerged. Most prominent, perhaps, is the observation that while the neural networks that serve printed and spoken sentence processing are not identical, the sites within these systems that were sensitive to parsing difficulty were largely overlapping, especially in IFG. On the view that linguistic processing operates at an abstract level, independent of input modality, we could expect such an outcome. The major language zones within the left hemisphere, IFG, STG/MTG, and the inferior parietal lobule, have all long been implicated as essential parts of the sentence-processing mechanism. Unimodal imaging studies that employed speech or print have been largely confirmatory (e.g., Caplan, 2001; Caplan et al., 2000, 2002; Just et al., 1996; Ni et al., 2000; Kang et al., 1999). A distinguishing feature of the current study is a controlled, within-subject comparison across print and speech modes. The findings lend strong support to the idea of a distributed parsing system within the dominant, left-hemisphere perisylvian cortex, reinforcing the idea that abstract linguistic processing transcends modality, cutting across differences associated with processing speech or print.

From a quantitative perspective, we note that there was considerably greater print-speech overlap than modality differences in activation patterns. The overlap is apparent in a broadly distributed left hemisphere system including frontal areas IFG and MFG, and

posterior areas MTG, STG, SMG, and angular gyrus. Modality differences in degree of activation in amplitude or area were seen in several regions. Within IFG, a few sites that were activated by either modality were reliably more active for heard sentences than for read sentences; thus, spoken sentence processing appeared to engage these common areas more vigorously than reading (Michael et al., 2001). However, several foci common to both were heightened in the print condition; thus, some degree of subspecialization is seen in IFG. In left temporal regions, activations were partially overlapping in both MTG and STG, but were centered more anteriorly for spoken sentences, with more posterior foci for print, in keeping with several findings in the recent literature (Howard et al., 1992; Michael et al., 2001; Shaywitz et al., 2001).

Sites that were uniquely activated by print or which showed relative increases of activity in the print mode were found mainly in left SMG, angular gyrus, occipitotemporal, and in the precuneus region. Thus, the classical account of left occipito-temporo-parietal involvement in print-to-language mapping (Geschwind, 1965) is reinforced by these findings. In contrast, spoken sentences showed the largest relative increases in anterior portions of STG (bilaterally) and, as noted above, across several sites within IFG that were activated to some degree by both speech and printed versions. Again, however, many sites that showed print–speech differences in degree of activation were in fact activated by both input modalities. With respect to modality differences, one potential caveat should be noted. We employed different baseline tasks for print and speech to control for large-scale sensory-level differences in the two modalities; however, as pointed out by a reviewer, these tasks could conceivably differ concerning demands placed on certain aspects of nonlinguistic processing. With respect to the modality difference, which is not the primary focus of the current study, the differing baselines could therefore be a complication. However, it should be noted that the current difference maps are quite commensurate with those of our previous study, Carpentier et al. (2001), and with that of Michael et al. (2001); in each case, different baselines were employed. In any event, we must allow for the possibility that some modality differences could, in principle, be exaggerated or suppressed with different baselines used in the two modalities. However, with respect to effects of sentence complexity, and modality-independent effects of sentence complexity, which is the core issue here, it should be noted that these analyses rely on comparisons of sentence types within each modality separately; hence, the issue of the differing baselines is of a lesser concern to these more central contrasts.<sup>2</sup>

<sup>2</sup> Nonetheless, we performed additional analyses as a check on our findings with respect to sentence complexity. The primary sentence complexity maps shown in Fig. 3 for each modality were created within each modality as follows: for (object relative–baseline) – (subject relative–baseline). Sites that showed significant effects in both modalities are indicated by the modality-independent maps (Fig. 3a). To obviate any residual concern that unspecified baseline differences between print and speech could override potential effects in the modality independent analysis, we also performed a direct subtraction of the object and subject relatives (without mediating baseline tasks). These direct contrasts, though suboptimal about temporal contiguity of on/off blocks, did reveal reliable complexity effects in each of the regions shown in Fig. 3. Direct subtraction confirms the results of mediated subtraction supporting our conclusions (e.g., for the IFG, percent difference in the direct comparison of activations of obj. rel. vs. subj. relative was  $1.4 \pm 0.1\%$ ,  $0.9 \pm 0.1\%$ , and  $1.2 \pm 0.1\%$  ( $P < 0.001$ ) for visual, auditory input, and the conjunction of modalities, respectively).

Sentence complexity effects, in which more activity was evoked by object-relative sentences than subject-relative ones, were seen at most of the sites that were active in both speech and reading modes. When we apply our stringent criteria for identifying a site critical for sentence parsing (significantly active in both modalities and demonstrating significant complexity effects for both modalities), the primary site meeting this criterion is in primarily the left inferior frontal lobe, BA 44/45, or Broca's area. This region was activated equivalently by spoken and printed sentences and also showed robust differences in each modality for the harder (object relative) minus easier (subject relative) sentence comparisons. This finding reinforces previous claims both from lesion studies and neuroimaging experiments on normal subjects positing a special role for this area in syntactic processing (Friederici et al., 2000; Grodzinsky, 2000).

There is considerable variation from study to study with respect to precise localization within IFG. Some studies implicate pars opercularis (BA 44) while others suggest a strong role for parsing associated with pars triangularis (BA 45). This variation has been observed in studies that putatively assessed the same sentence variables as the present study (Caplan et al., 2000; Just et al., 1996). In Carpentier et al. (2001), we found that for most subjects BA 45 was equally active for both spoken and printed sentences while BA 44 was more strongly engaged by reading than speech. The present experiment, incorporating more complete coverage of the brain in the inventory of regions scanned and a larger sample of participants, indicates that sites within both pars opercularis and pars triangularis were implicated in each modality, and that both sites became more strongly active in sentences that make greater parsing demands. These results using multisubject composite images do not reveal subdivisions for sentence parsing within IFG.

As in frontal areas, the sites in superior and medial temporal lobe showing sentence complexity effects for print or speech overlapped considerably. In general, the zones of overlapping activity were closely adjacent to those areas differentially activated by each modality. Thus, unlike IFG, the temporal sites showed somewhat more fine-grained variation in the center of mass of the sentence effect as a function of modality; however, even here the occurrence of cross-modality overlap was striking. For example, it is noteworthy that a site in the angular gyrus showed a complexity effect for both modalities, reinforcing a recent claim by Caplan (2001) that neural networks centered in this region may play a role in syntactic analysis. The present results reinforce this contention in showing a modality-independent effect of parsing complexity. At the same time, it must also be noted that other sites within angular gyrus and SMG demonstrated complexity effects for printed sentences only. Thus, in the inferior parietal lobule, the bulk of complexity-related activity was specifically associated with the demands of reading. Complexity effects associated with posterior regions are not as consistent or as large in magnitude as those associated with anterior cortical regions. Again, applying the stringent criterion forces the conclusion that the IFG is the strongest candidate area for sentence parsing operations. It should be noted that no sites, even in anterior portions of STG, showed a complexity effect for spoken sentences alone.

As for right hemisphere activity associated with sentence processing, we noted that right frontal and temporal lobe activation was almost exclusively linked to spoken sentences, a result also seen in a previous study in our laboratory by Carpentier et al.

(2001) and in a study by Michael et al. (2001). The reason for increased right hemisphere involvement for spoken sentences, over and above that arising from auditory cortex, will need to be probed in future studies. Prosody is one obvious way that speech material differs from printed material. At the word level, pitch differences associated with stress patterns are correlated with activity in the right prefrontal cortex (Meyer et al., 2002; Zatorre et al., 1999), and at the suprasegmental level, pitch modulations that convey syntactic and semantic information also appear to involve the right hemisphere (Friederici et al., 2000). It can be said, however, that the right hemisphere response does not appear to be driven chiefly by higher-level language processing, given that sentence complexity effects were left hemisphere lateralized for the auditory as well as for the visual sentences. Thus, with Michael et al. (2001), we can conclude that abstract language processing dimensions are largely or exclusively left lateralized. Most generally, our findings implicate a unitary, left-hemisphere sentence processing circuit that cuts across speech-print differences. Moreover, modality-independent effects of sentence complexity are most apparent in BA 44/45 in IFG, but, as can be seen from the maps, several specific foci within STG, MTG, SMG, and angular gyrus are also significantly active.

Conceivably, different sites within the perisylvian circuit that show sensitivity to sentence complexity manipulations have distinct computational roles. Indeed, in a previous study from our group (Ni et al., 2000) using either syntactic or semantic "odd-ball" sentences that embedded among correct ones, we found sites among IFG (which overlap with the sentence complexity areas shown in Fig. 3a) that responded only to syntactically anomalous sentences. Similarly, at sites in STG (also overlapping with the complexity areas found in the current study), a specific response to semantic anomaly was observed. Thus, while the present results do not directly address the issue of subspecialization in sentence processing, when viewed in conjunction with Ni et al. (2000), we can speculate that anterior aspects of this left hemisphere circuit are engaged more by syntactic operations, while the posterior aspects serve in semantic and thematic processing. Overall, the present findings give evidence of a distributed perisylvian network that serves sentence parsing and interpretation and that is highly overlapping, especially in IFG, for visual and auditory sentence inputs.

## Conclusions

The influence of input modality demonstrated that auditory sentence presentation was associated with pronounced activity at primary auditory cortex and across the superior temporal gyrus bilaterally, whereas printed sentences by contrast evoked major activity at several posterior sites in the left hemisphere, including the angular gyrus, supramarginal gyrus, and the fusiform gyrus in the occipitotemporal region. The intersection of these modality-dependent maps indicated modality-independent regions in the inferior frontal gyrus (IFG), strong left STG, and weak right STG. With respect to sentence complexity, object-relative sentences evoked heightened responses at several sites, including IFG, the left middle/superior temporal gyrus, left premotor and angular gyrus. It is argued that these sites that showed modulation of activity as a function of sentence type, independent of input mode, form the core of a cortical system essential to sentence parsing.

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## References

- Beauregard, M., Chertkow, H., Gold, D., Karama, S., Benhamou, J., Babins, L., Faucher, A., 1997. Word priming with brief multiple presentation technique: preservation in amnesia. *Neuropsychologia* 35 (5), 611–621.
- Binder, J.R., Swanson, S.J., Hammeke, T.A., Morris, G.L., Mueller, W.M., Fischer, M., Benbadis, S., Frost, J.A., Rao, S.M., Houghton, V.M., 1996. Determination of language dominance using functional MRI. *Neurology* 46, 978–984.
- Bookheimer, S.Y., Zeffiro, T.A., Blaxton, T., Malow, B.A., Gaillard, W.D., Sato, S., Kufta, C., Fedio, P., Theodore, W.H., 1997. A direct comparison of PET activation and electrocortical stimulation mapping for language localization. *Neurology* 48 (4), 1056–1065.
- Caplan, D., Hildebrandt, N., Makris, N., 1996. Location of lesions in stroke patients with deficits in syntactic processing in sentence comprehension. *Brain* 119 (3), 933–949.
- Caplan, D., Alpert, N., Waters, G., Olivieri, A., 2000. Activation of Broca's area by syntactic processing under conditions of concurrent articulation. *Hum. Brain Mapp.* 9, 65–71.
- Caplan, D., 2001. Functional neuroimaging studies of syntactic processing. *J. Psycholing. Res.* 30 (3), 297–320.
- Caplan, D., Vijayan, S., Kuperberg, G., West, C., Waters, G., Greve, D., Dale, A.M., 2002. Vascular responses to syntactic processing: event-related fMRI study of relative clauses. *Hum. Brain Mapp.* 15 (1), 26–38.
- Carpentier, A.C., Pugh, K.R., Westerveld, M., Studholme, C., Skrinjar, O., Thompson, J.L., Spencer, D.D., Constable, R.T., 2001. Functional MRI of language processing: dependence on input modality and temporal lobe epilepsy. *Epilepsia* 42 (10), 1241–1254.
- Chee, M.W.L., O'Craven, K.M., Bergida, R., Rosen, B.R., Savoy, R.L., 1999. Auditory and visual word processing studied with fMRI. *Hum. Brain Mapp.* 7, 15–28.
- Constable, R.T., Skudlarski, P., Gore, J.C., 1995. An ROC approach for evaluating functional brain MR imaging and postprocessing protocols. *Magn. Reson. Med.* 34, 57–64.
- Desmond, J.E., Sum, J.M., Wagner, A.D., Domb, J.B., Shear, P.K., Glover, G.H., Gabrieli, J.D., Morrell, M.J., 1995. Functional MRI measurement of language lateralization in Wada-tested patients. *Brain* 118 (Pt. 6), 1411–1419.
- Eden, G.F., Zeffiro, T.A., 1998. Neural systems affected in developmental dyslexia revealed by functional neuroimaging. *Neuron* 21 (2), 279–282.
- Efron, B., Tibshirani, R.J., 1993. *An Introduction to the Bootstrap*. Chapman & Hall, New York.
- Fiez, J.A., Peterson, S.E., 1998. Neuroimaging studies of word reading. *Proc. Natl. Acad. Sci. U. S. A.* 95 (3), 914–921.
- Fiez, J.A., Balota, D.A., Raichle, M.E., Petersen, S.E., 1999. Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading. *Neuron* 24 (1), 205–218.
- Friederici, A.D., Meyer, M., Von Cramon, Y., 2000. Syntactic, prosodic, and semantic processes in the brain: evidence from event-related neuroimaging. *J. Psychol. Res.* 30 (3), 27–250.
- Friston, K.J., Ashburner, J., Poline, J.B., Frith, C.D., Heather, J.D., Frackowiak, R.S.J., 1995. Spatial registration and normalization of images. *Hum. Brain Mapp.* 2, 165–189.
- Geschwind, N., 1965. Disconnexion syndromes in animals and man. *Brain* 88, 237–294.
- Gibson, E., Pearlmutter, N.J., 2000. Distinguishing serial and parallel parsing. *J. Psycholing. Res.* 29 (2), 231–240.
- Grodzinsky, Y., 2000. The neurology of syntax: language use without Broca's area. *Behav. Brain Sci.* 23 (1), 1–71.
- Hagoort, P., Brown, C.M., 2000. ERP effects of listening to speech compared to reading: the P600/SPS to syntactic violations in spoken sentences and rapid serial visual presentation. *Neuropsychologia* 38 (11), 1531–1549.
- Hagoort, P., Indefrey, P., Brown, C., Herzog, H., Steinmetz, H., Seitz, R.J., 1999. The neural circuitry involved in reading of German words and pseudowords: a PET study. *J. Cogn. Neurosci.* 11 (4), 383–398.
- Hamburger, H., Crain, S., 1984. Acquisition of cognitive coupling. *Cognition* 17 (2), 85–136.
- Helenius, P., Salmelin, R., Service, E., Connolly, J.F., 1998. Distinct time courses of word and context comprehension in the left temporal cortex. *Brain* 121 (6), 1133–1142.
- Herbster, A.N., Mintun, M.A., Nebes, R.D., Becker, J.T., 1997. Regional cerebral blood flow during word and nonword reading. *Hum. Brain Mapp.* 5 (2), 84–92.
- Hickok, G., Poeppel, D., 2000. Toward a functional neuroanatomy of speech perception. *Trends Cogn. Sci.* 4, 131–138.
- Hodges, J.R., Patterson, K., Oxybury, S., Funnell, E., 1992. Semantic dementia: progressive fluent aphasia with temporal lobe atrophy. *Brain* 115 (6), 1783–1806.
- Howard, D., Patterson, K., Wise, R.J., Brown, W.D., Friston, K., Weiller, C., Frackowiak, R., 1992. The cortical localization of the lexicons: positron emission tomography evidence. *Brain* 115, 1769–1782.
- Just, M.A., Carpenter, P.A., Keller, T.A., Eddy, W.F., Thulborn, K.R., 1996. Brain activation modulated by sentence comprehension. *Science* 274, 114–116.
- Kang, A.M., Constable, R.T., Gore, J.C., Avrutin, S., 1999. An event-related fMRI study of implicit phrase-level syntactic and semantic processing. *NeuroImage* 10, 555–561.
- Keller, T.A., Carpenter, P.A., Just, M.A., 2001. The neural bases of sentence comprehension: a fMRI examination of syntactic and lexical processing. *Cereb. Cortex* 11, 223–237.
- Krauss, G.L., Fisher, R., Plate, C., Hart, J., Uematsu, S., Gordon, B., Lesser, R.P., 1996. Cognitive effects of resecting basal temporal language areas. *Epilepsia* 37 (5), 476–483.
- Meyer, M., Alter, K., Friederici, A.D., Lohmann, G., von Cramon, Y., 2002. fMRI reveals brain regions mediating slow prosodic modulations in spoken sentences. *Hum. Brain Mapp.* 17, 73–88.
- Michael, E.B., Keller, T.A., Carpenter, P.A., Just, M.A., 2001. fMRI investigation of sentence comprehension by eye and ear: modality fingerprints on cognitive processes. *Hum. Brain Mapp.* 13, 239–252.
- Muller, R.A., Rothermel, R.D., Behen, M.E., Muzik, O., Mangner, T.J., Chugani, H.T., 1997. Receptive and expressive language activations for sentences: a PET study. *NeuroReport* 8, 3767–3770.
- Ni, W., Shankweiler, D., Crain, S., 1996. Individual differences in working memory and eye-movement patterns in reading relative clause structures. In: Matsuoka, K., Halbert, A. (Eds.). *University of Connecticut Working Papers in Linguistics* 6.
- Ni, W., Constable, R.T., Mencl, W.E., Pugh, K.R., Fulbright, R.K., Shaywitz, B.A., Shaywitz, S.E., Gore, J.C., Shankweiler, D., 2000. An event-related neuroimaging study: distinguishing form and content in sentence processing. *J. Cogn. Neurosci.* 12 (1), 1–14.
- Paulesu, E., Frith, C.D., Frackowiak, R.S., 1993. The neural correlates of the verbal component of working memory. *Nature* 362 (6418), 342–345.
- Peterson, S.E., Fox, P.T., Posner, M.I., Mintun, M., Raichle, M.E., 1989. Positron emission tomographic studies of the processing of single words. *J. Cogn. Neurosci.* 1, 153–170.
- Pugh, K.R., Shaywitz, B.A., Shaywitz, S.E., Constable, R.T., Skudlarski, P., Fulbright, R.K., Bronen, R.A., 1996. Cerebral organization of component processes in reading. *Brain* 119, 1221–1238.
- Pugh, K.R., Shaywitz, B.A., Shaywitz, S.E., Shankweiler, D.P., Katz, L., Fletcher, J.M., Skudlarski, P., Fulbright, R.K., Constable, R.T., Bronen,

- R.A., Lacadie, C., Gore, J.C., 1997. Predicting reading performance from neuroimaging profiles: the cerebral basis of phonological effects in printed word identification. *J. Exp. Psychol. Hum. Percept. Perform.* 23 (2), 299–318.
- Pugh, K.R., Mencl, W.E., Shaywitz, S.E., Shaywitz, B.A., Fulbright, R., Constable, R.T., Skudlarski, P., Marchione, K.E., Jenner, A.R., Fletcher, J.M., Liberman, A.M., Shankweiler, D.P., Katz, L., Lacadie, C., Gore, J.C., 2000. The angular gyrus in developmental dyslexia: task-specific differences in functional connectivity within posterior cortex. *Psychol. Sci.* 11 (1), 51–56.
- Pugh, K.R., Mencl, W.E., Jenner, A.J., Katz, L., Lee, J.R., Shaywitz, S.E., Shaywitz, B.A., 2001. Neurobiological studies of reading and reading disability. *J. Commun. Dis.* 34, 479–492.
- Roeltgen, D.P., Heilman, K.M., 1984. Lexical agraphia. Further support for the two-system hypothesis of linguistic agraphia. *Brain* 107 (Pt. 3), 811–827.
- Schmolck, H., Stefanacci, L., Squire, L.R., 2000. Detection and explanation of sentence ambiguity are unaffected by hippocampal lesions but are impaired by larger temporal lobe lesions. *Hippocampus* 10 (6), 759–770.
- Shallice, T., 1987. Impairments in semantic processing: multiple dissociations. In: Colheart, M., Sartori, F., Job, R. (Eds.), *The Cognitive Neuropsychology of Language*. Erlbaum, London, pp. 111–127.
- Shaywitz, S.E., Shaywitz, B.A., Pugh, K.R., Fulbright, R.K., Constable, R.T., Skudlarski, P., Fletcher, J., Liberman, J., Shankweiler, D.P., Katz, L., Marchione, K., Lacadie, C., Mencl, E., Gore, J.C., 1998. Functional disruption in the organization of the brain for reading in dyslexia. *Proc. Natl. Acad. Sci.* 95 (5), 2636–2641.
- Shaywitz, B.A., Shaywitz, S.E., Pugh, K., Fulbright, R.K., Skudlarski, P., Mencl, W.E., Constable, R.T., Marchione, K.E., Fletcher, J.M., Lacadie, C., Gore, J.C., 2001. The functional neural architecture of components of attention in language processing tasks. *NeuroImage* 13 (4), 601–612.
- Simos, P.G., Papanicolaou, A.C., Breier, J.I., 1999. Localization of language-specific cortex using MEG and intraoperative stimulation mapping. *J. Neurosurg.* 91, 787–796.
- Springer, J.A., Binder, J.R., Hammeke, T.A., Swanson, S.J., Frost, J.A., Bellgowan, P.S.F., Brewer, C.C., Perry, H.M., Morris, G.L., Mueller, W.M., 1999. Language dominance in neurologically normal and epilepsy subjects: a functional MRI study. *Brain* 122, 2033–2045.
- Studholme, C., Constable, R.T., Duncan, J.S., 2001. Accurate alignment of functional EPI data to anatomical MRI physics based distortion model. *IEEE Trans. Med. Imag.* 19 (11), 1115–1127.
- Tagamets, M.A., Novick, J.M., Chalmers, M.L., Friedman, R.B., 2000. A parametric approach to orthographic processing in the brain: an fMRI study. *J. Cogn. Neurosci.* 12 (2), 281–297.
- Warburton, E., Wise, R.J., Price, C.J., Weiller, C., Hadar, U., Ramsay, S., Frackowiak, R.S., 1996. Noun and verb retrieval by normal subjects. *Stud. PET, Brain* 119 (Pt. 1), 159–179.
- Wise, R.J.S., Scott, S.K., Blank, S.C., Mummery, C.J., Murphy, K., Warburton, E.A., 2001. Separate neural subsystems within ‘Wernicke’s area’. *Brain* 124, 83–95.
- Zatorre, R.J., Mondor, T.A., Evans, A.C., 1999. Auditory attention to space and frequency activates similar cerebral systems. *NeuroImage* 10 (5), 544–554.