

Effects of Syntactic Structure and Propositional Number on Patterns of Regional Cerebral Blood Flow

David Caplan and Nathaniel Alpert

Massachusetts General Hospital

Gloria Waters

Massachusetts General Hospital and Boston University

Abstract

■ Positron emission tomography (PET) was used to determine regional cerebral blood flow (rCBF) as a function of the syntactic form and propositional density of sentences. rCBF increased in the left pars opercularis, part of Broca's area, when subjects processed syntactically more complex sentences. There were no differences in rCBF in the perisylvian association cortex traditionally associated with language processing when subjects made plausibility judgments about sentences

with two propositions as compared to sentences with one proposition, but rCBF increased in infero-posterior brain regions. These results suggest that there is a specialization of neural tissue in Broca's area for constructing aspects of the syntactic form of sentences to determine sentence meaning. They also suggest that this specialization is separate from the brain systems that are involved in utilizing the meaning of a sentence that has been understood to accomplish a task. ■

INTRODUCTION

Sentences are the level of the language code at which the meanings of individual words are related to each other to express the propositional content of a sentence (Chomsky, 1981, 1996). The propositional content of a sentence includes information about events and states in the world, such as who is doing what to whom (thematic roles), which adjectives are associated with which nouns (attribution of modification), and other similar semantic information. Propositions can have truth values and can therefore enter into logical systems and be important in planning actions. The propositional content of a sentence enters into discourse and narrative structure, where it provides information about the topic of a discourse, what information is given and what is new, the temporal order of events, causality, and other important aspects of discourse meaning. For all these reasons, sentences and their associated propositional content are important parts of human language.

The propositional content of a sentence is determined largely by the syntactic structure of that sentence. For instance, in the sentence *The dog that scratched the cat chased the bird*, readers understand that *the dog*, and not *the cat*, is the agent of *chased*, even though the sequence of words *the cat chased the bird* occurs in the sentence. The sentence is understood this way because of the position of the words *the cat* and *the dog* in the

syntactic structure of the sentence: *the dog* is the subject of *chased* and *the cat* is the object of *scratched* and has no syntactic relationship to *chased*. Chomsky (1981, 1986, 1996) has argued that syntactic representations are structurally unlike any other human or nonhuman cognitive structure and that the human infant comes equipped to the task of language learning with a set of innate, elaborate, domain-specific syntactic schemata ("principles") that enable it to acquire knowledge of the syntax of its language. This perspective makes the neural basis for the representation and processing of syntax relevant to a set of strong, controversial claims about the nature of language and language learning. Finding that there is a (relatively) small area of the brain that supports syntactic processing has been considered to be consistent with Chomsky's views of a specialized cognitive system for language (e.g., Pinker, 1994). Finding that syntactic processing recruits a large area of the brain would be less in keeping with this model.

In contrast to assigning syntactic structure to determining sentence meaning ("sentence interpretation"), using a sentence's meaning to accomplish a task ("post-interpretive processing") cannot be a specialized cognitive function. This is partly because we can use the meaning of a sentence to accomplish a wide variety of tasks, including mapping it onto ongoing events in the world, storing it in memory, determining its plausibility, reasoning, planning actions, and others. Also, within each

of these domains, using the meaning of a sentence to accomplish a task involves complex cognitive functions. Consider using the meaning of a sentence to plan and execute an action. Suppose you hear a sentence like “Bring home two pounds of onions, radishes, a small jar of marmalade, bread, sugar, anchovies, and celery after work tonight.” Planning and executing this request requires recalling the instructions at the end of the day, searching the rows at the supermarket, and a number of other activities that require memory, spatial and motor functions, working memory, and other cognitive abilities. Although comprehending a sentence may be a specialized process, using what is comprehended cannot be.

Experimental evidence shows that factors that influence comprehension and those that influence postinterpretive processing of sentence meaning affect language tasks differently. The syntactic form of a sentence has large and easily demonstrable effects upon many measures of online sentence processing (Frazier & Clifton, 1996; MacDonald, Pearlmutter, & Seidenberg, 1994) but is poorly retained in memory shortly after a sentence has been understood (Bransford & Franks, 1971). In contrast, the effect of the number of propositions in a sentence increases as the complexity of the pictures in a sentence-picture matching task increases (Altmann, Andersen, Kempler, & MacDonald, 1996) and when the number of foils in a sentence-picture matching task increases from one to two to three (Waters, Rochon, & Caplan, in press). The effect of syntactic structure is not increased by these visual aspects of tasks (Caplan & Waters, 1995; Waters & Caplan, 1996; Waters, Caplan, & Hildebrandt, 1987; Waters, Caplan, & Rochon, 1995). Results of this sort suggest that the effect of syntactic structure arises during the process of assigning sentence meaning and dissipates rapidly, whereas that of propositional density primarily affects postinterpretive processing.

These considerations suggest that, whatever may be true of the neural basis for the operations that are involved in assigning the meaning of a sentence, those that are involved in using the meaning of a sentence to accomplish tasks are not localized in a single brain region. These operations must recruit brain regions involved in memory, spatial and motor abilities, planning, and other functions and the brain regions that serve as the interfaces between those that support comprehension and those that support these other functions. The present study investigates the neural basis for interpretive and postinterpretive operations related to sentence processing, using PET.

There has been considerable investigation of the location of the neural tissue involved in the assignment of syntactic form and sentence meaning. Studies of brain-damaged patients indicate that the assignment of syntactic form is largely carried out by the dominant perisylvian association cortex, with possibly some contribution of the homologous contralateral cortex (Caplan, Hildebrandt, & Makris, 1996). Studies of event-

related potentials associated with syntactic processing have also been consistent with the view that syntactic operations in sentence comprehension are carried out in the dominant perisylvian association cortex (Hagoort, Brown, & Groothusen, 1993; Osterhout & Holcomb, 1992). A number of hypotheses maintain that there are more specific correlations between impairments of certain syntactic operations and lesions in particular brain locations. Swinney and his colleagues (Swinney & Zurif, 1995; Swinney, Zurif, Prather, & Love, 1996; Zurif, Swinney, Prather, Solomon, & Bushell, 1993) have reported that patients with Broca’s aphasia, whose lesions occupy Broca’s area—the pars triangularis and opercularis of the left third frontal convolution—as well as other structures (Mohr et al, 1978), have impaired performance on tasks that test the integrity of the process of relating the head of a relative clause to its position in a clause (i.e., relating *the boy* to the object of *watched* in the sentence *The boy who the coach watched impressed everyone*). Studies of event-related potentials also suggest that operations related to relative clauses in particular are associated with potentials that are maximally seen over the scalp roughly above Broca’s area (Kluender & Kutas, 1993; Neville, Nicol, Barss, Forster, & Garrett, 1991).

In contrast to studies showing localization of syntactic processing in the dominant perisylvian cortex, there is evidence from brain-damaged patients that some postinterpretive processing primarily involves other brain structures. For instance, certain aspects of inferencing appear to be affected by right-hemisphere lesions (Brownell, Potter, Bihle, & Gardner, 1986). However, in general, the literature on the location of lesions that are associated with deficits in the ability to use the meaning of sentences to accomplish tasks is sparse. There are no studies that relate pathologically large effects of propositional density to lesions in particular brain regions, for instance.

The neural systems involved in assigning sentence meaning have begun to be explored using functional neuroimaging techniques. Mazoyer et al. (1993) compared the rCBF when native speakers of French were at rest with the rCBF when they listened to stories in a foreign language (Tamil), lists of French words, a French story containing pseudowords instead of nouns, a French story containing semantic anomalies, and a story in normal French. They did not detect consistent regional activity associated with syntactic processing. They interpreted their failure to do so as evidence that the “speech processing system of the human brain . . . [involves] the coordination of a network of areas, each of which may be specialized in one aspect of speech processing, but require coherent support from the others in order to reach a high level of activation” (Mazoyer et al., 1993, p. 476). However, it is possible that the semantically anomalous and pseudoword conditions, which were designed to test syntactic and other higher-level aspects of sentence processing, did not differ in the

minimal ways necessary to isolate the neural correlates of the various components of linguistic processing above the single-word level. Bookheimer, Zeffiro, Gallard, and Theodore (1993) had subjects judge whether sentences were the same in meaning when they contained the same words but differed in word order (e.g., *The lake is west of the city; West of the city is the lake*). In three control conditions, subjects monitored sentences for a phoneme change, heard identical pairs of sentences, and rested. Based on a series of contrasts, the authors concluded that syntactic processing increased rCBF in Broca's area and in the left hippocampus. However, the syntax task involved reasoning and other operations (e.g., verbal short-term memory) that are not required in any of the baseline conditions and, conversely, the baseline conditions involved operations (such as sustaining attention in the phoneme change monitoring task) that are not found in the experimental syntax stimulation conditions.

Two additional functional neuroimaging studies, one using PET and one using functional magnetic resonance imaging (fMRI), provide more specific data regarding the localization of syntactic comprehension. Stromswold, Caplan, Alpert, and Rauch (1996) studied eight right-handed young males in a paradigm in which PET activity associated with making plausibility judgments about simpler subject-subject sentences (e.g., *The award thrilled the actress that praised the producer*) was contrasted with that associated with making judgments about the same propositions phrased in syntactically more complex subject-object forms (e.g., *The actress that the award thrilled praised the producer*). The contrast showed an increase in rCBF in the pars opercularis of Broca's area. In the second study, using fMRI, Just, Carpenter, Keller, Eddy, and Thulborn (1996) reported an increase in rCBF in both Broca's area and in Wernicke's area (the first temporal gyrus) of the left hemisphere when subjects read and answered questions about sentences in subject-object form compared to sentences in subject-subject form. These authors also reported smaller but reliable increases in rCBF in the homologous regions of the right hemisphere. Both these rCBF changes appear to be related either to syntactic processing or to some closely associated function.

These four functional neuroimaging studies involved the manipulation of syntactic form, and all found an increase in rCBF in part of Broca's area. One way to characterize the differences in these studies is in whether this was the only part of the dominant perisylvian region in which rCBF was reliably increased. This was the case in the Stromswold et al. (1996) and Bookheimer et al. (1993) studies; the Mazoyer et al. (1993) study found increased rCBF in many perisylvian areas in the comparison designed to identify syntactic processing, and the Just et al. (1996) study found two focal rCBF increases—one in Broca's area and one in Wernicke's area. These studies differ with respect to the syntactic

structures that were presented, the tasks used, the imaging techniques, and the manner of data analysis. Therefore, it is not surprising that their results do not completely converge.

The question of the localization of the processing involved in both comprehending sentence meaning on the basis of syntactic form and in using that meaning to accomplish tasks thus remains open. In the following two studies, we explored this question using PET. In experiment 1, we measured changes in rCBF in normal subjects that are associated with processing more versus less syntactically complex sentences. In experiment 2, we measured changes in rCBF in normal subjects that are associated with processing sentences that differ in their propositional density. For the reasons noted above, these two variables primarily increase processing load at the interpretive and postinterpretive stages of sentence processing, respectively, and therefore changes in rCBF associated with them are relevant to the question of the neural basis for these two functional capacities.

EXPERIMENT 1

Experiment 1 used two of the three conditions in the PET study by Stromswold et al (1996), and female rather than male subjects were tested.

Subjects were scanned during six blocks, each containing one of two experimental conditions. Sentences in condition 1 contained syntactically more complex center-embedded relative clauses (e.g., *The juice that the child spilled stained the rug*) and sentences in condition 2 contained syntactically simpler right-branching relative clauses (e.g., *The child spilled the juice that stained the rug*). Half the sentences in each condition were plausible and half were not. Subjects made timed plausibility judgments after each sentence. The sentences in conditions 1 and 2 were carefully constructed so as to eliminate lexical differences and other factors that could have affected subjects' processing of the sentences (see "Methods").

Results

Behavioral results

Results are shown in Table 1. Reaction times (RTs) for incorrect responses were discarded and RTs greater than three standard deviations above and below the resulting condition means for each subject were replaced by that subject's condition means. The resulting data were then analyzed in analyses of variance (ANOVAs) for the effects of block, which did not emerge as a main effect or in interaction with other variables. The data were then analyzed in 2 (syntactic structure: center-embedded vs. right-branching) \times 2 (semantic plausibility: plausible vs. implausible) ANOVAs by subjects and items. There was a main effect of sentence structure ($F_{1RT}(1, 7) = 5.3, p = 0.05$; $F_{2RT}(1, 284) = 31.6, p = .001$; $F_{1Errors}(1, 7) = 5.5,$

Table 1. Accuracy and RT Results for Right-Branching and Center-Embedded Sentences

	<i>Right-Branching</i>	<i>Center-Embedded</i>
Percentage correct	94.4%	90.5%
Mean RT (SD) in msec	2548 (1011)	2886 (1119)

$p = .05$; $F_{2\text{Errors}}(1, 284) = 12.9$, $p < 0.001$). Responses were longer and less accurate for center-embedded than right-branching sentences. No other main effects or interactions were significant.

rCBF Results

Table 2 shows the location of increases in rCBF associated with z scores of 3 or greater based on statistical parameter mapping derived by contrasting PET activity in condition 1 (center-embedded sentences) with PET counts in condition 2 (right-branching sentences). A significant increase in rCBF occurred in two medial frontal structures, the anterior cingulate gyrus and the immediately superior medial frontal gyrus, and in Broca's area, where the center of activation was in the rostral part of the pars opercularis, Brodmann's area 44 (Figure 1).

Discussion of Experiment 1

Experiment 1 replicates the results reported by Stromswold et al. (1996) fairly closely. Behaviorally, subjects took longer to make judgments about the plausibility of center-embedded sentences than right-branching sentences and made more errors on these judgments for the syntactically more complex sentence type. As in the Stromswold et al. study, rCBF increased in Broca's area for the more difficult syntactic sentences compared with the simpler ones. The exact location of the increase in rCBF within Broca's area was higher and more anterior than in the earlier study but was still centered in the pars opercularis (Brodmann's area 44). Further work will be needed to determine whether this male-female difference continues to be found systematically, independent of comprehension paradigm, modality of sentence presentation, and other experimental parameters. In the pres-

ent study, the anterior cingulate and immediately adjacent medial frontal gyrus also showed increases in rCBF in the center-embedded compared to the right-branching condition. Increased rCBF in these regions, especially the cingulate gyrus, has been seen in many activation studies and is likely to be the result of increased attention or processing resource deployment in the more demanding experimental condition (Posner, Peterson, Fox, & Raichle, 1989).

The behavioral and rCBF differences between conditions 1 and 2 are presumably due to differences in the processing associated with the center-embedded and right-branching sentences presented in those conditions. The sentences in these two conditions contained the same words and propositions and made the same referential assumptions at the discourse level, essentially ruling out differences at these linguistic levels as the sources of the behavioral and rCBF effects. The task was the same in both conditions: It required the subject to make a judgment about whether the noun phrases that occupied the subject and object positions of the main and embedded verbs were semantically compatible with their verbs. The sentences were constructed so that anomalies occurred throughout both types of sentences to ensure that subjects read the entire sentence. Performance on the sentence types used here was shown to be identical under both blocked and unblocked presentation conditions in experiments in which subjects were not being scanned (Stromswold et al., 1996), and reaction times were similar in this experiment to those in these unscanned trials and to those in the earlier PET study by Stromswold et al. (1996). It is therefore also unlikely that differences in task demands across conditions or task-specific strategies were the sources of the behavioral and rCBF effects. Because RTs were longer for the center-embedded than the right-branching sentences, it is also not possible that the rCBF differences resulted from subjects processing more stimuli in condition 1.

The sentences differ with respect to their syntactic structures and the processing associated with constructing these different structures and integrating the meanings of the lexical items in each sentence with each other based upon these structures. In both types of sentences, the head noun of the relative clause must be maintained in a short-duration memory store until the

Table 2. Areas of Increased rCBF for Subtraction of PET Activity Associated with Right-Branching Sentences from Center-Embedded Sentences

<i>Location</i>	<i>Maximum z-score</i>	<i>Number of pixels</i>	<i>Location {X, Y, Z}</i>
Medial frontal gyrus	3.8	131	10, 6, 52
Cingulate gyrus	3.5	173	-2, 6, 40
Broca's area, pars opercularis	3.0	47	-42, 18, 24



Figure 1. Reconstructed image of lateral surface of the brain showing area of maximal increase in rCBF when subjects processed syntactically more complex sentences.

verb of the relative clause is reached to be assigned its thematic role in the relative clause. In the case of the center-embedded relative clauses in condition 1, the subject of the relative clause intervenes between these two words, whereas this is not the case in the right-branching relative clauses in condition 2. In addition, the head noun of the relative clause cannot be assigned its thematic role around the main verb in condition 1 until the entire relative clause has been presented, whereas it can be assigned its thematic role around the main verb in condition 2 as soon as it (the head noun) occurs. These two features of the sentences add considerably to the memory requirements of the center-embedded sentences in condition 1 (Gibson, 1997; Just & Carpenter,

1992). These differences in assigning syntactic structure and determining the meaning of the sentences based upon their syntactic structures are strong candidates for the source of the differences in the two conditions.

It is possible that operations associated with these syntactic and interpretive operations are responsible for the rCBF effects in this experiment. One such operation is subvocal rehearsal, which could be more engaged in aid of reviewing the center-embedded than the right-branching sentences as an aid to comprehension. We have previously shown that articulatory suppression does not increase subjects' RTs for center-embedded compared to right-branching sentences in this judgment task (Waters et al., 1987), indicating that rehearsal is not

necessary for the center-embedded sentences to be understood and that the difference in RTs associated with these sentences in this task is not solely determined by increased rehearsal in the center-embedded sentences. However, the fact that rehearsal is not necessary for understanding these sentences does not entail the conclusion that it is not used or not used more to retain the form of the center-embedded than the right-branching sentences, when it *is* available. Therefore, it remains possible that the differences between conditions in experiment 1 reflect increased use of rehearsal in condition 1. This interpretation of the results of this experiment is consistent with PET results that have suggested that rehearsal activates roughly the same region as was activated in this study (Zatorre, Evans, Meyer, & Gjedde, 1992). We are currently testing this possibility by running this experiment under conditions of articulatory suppression. If the results are not affected by articulatory suppression, it is unlikely that they are due to differences in rehearsal in the two conditions.

The results of this study, like those of Stromswold et al. (1996), partially contrast with those reported by Just et al. (1996), who found increased rCBF associated with syntactically more complex sentences in Wernicke's as well as Broca's area. Just et al. used a question answering task that may have required subjects to recall a sentence for a longer time than the plausibility judgment task used here. It is possible that this difference in task demands is responsible for the wider rCBF increase in that study. It may be that the syntactic form of a sentence is retained in Wernicke's area for short periods of time, such as those that occur while subjects answer questions about a sentence.¹

EXPERIMENT 2

Experiment 2 sought to document changes in rCBF that might be associated with processing sentences that contained two, as opposed to one, proposition. Sixteen college students (eight males and eight females) were scanned in six blocks, each of which contained one of two experimental conditions. Sentences in condition 1 contained two propositions (e.g., *The magician performed the stunt that included the joke. The man that the computer bewildered consulted the expert*) and sentences in condition 2 contained one proposition (e.g., *The magician performed the stunt and the joke. It was the man that the computer bewildered*). As in experiment 1, half of the sentences in each condition were plausible and half were implausible.

Results

Behavioral Results

Results are shown in Table 3. For the analysis of RTs, incorrect responses were discarded and RTs more than 3 SDs from the mean for each condition for each subject

Table 3. Accuracy and RT Results for Sentences with One and Two Propositions

	One Proposition	Two Propositions
Percentage correct	87.5%	80.8%
Mean RT (SD) in msec	3075 (1111)	4207 (1920)

were replaced by the condition mean for that subject. Resulting RTs were analyzed by ANOVAs for the effects of block and sex, neither of which was significant or interacted with other variables. The data were then analyzed in 2 (number of propositions: one vs. two) \times 2 (semantic plausibility: plausible vs. implausible) ANOVAs by subjects and items.

There were significant main effects of the number of propositions ($F_{1\text{ RT}}(1, 15) = 52.7, p < 0.001$; $F_{2\text{ RT}}(1, 282) = 54.0, p < 0.001$; $F_{1\text{ error}}(1, 15) = 12.3, p = 0.003$; $F_{2\text{ error}}(1, 282) = 3.6, p = 0.05$) and plausibility ($F_{1\text{ RT}}(1, 15) = 5.6, p = 0.03$; $F_{2\text{ RT}}(1, 282) = 2.7, p < 0.1$; $F_{1\text{ error}}(1, 15) = 30.0, p < 0.001$; $F_{2\text{ error}}(1, 282) = 31.5, p < 0.001$). Sentences containing one proposition resulted in faster RTs and fewer errors than sentences containing two propositions. Plausible sentences resulted in faster RTs and fewer errors than implausible sentences. The interaction between number of propositions and plausibility was not significant, indicating that the effect of number of propositions occurred for both the plausible and implausible sentences.

rCBF Results

Table 4 shows the location of significant increases in rCBF based on statistical parameter mapping derived by contrasting PET activity in condition 1 (two propositions) and condition 2 (one proposition). A significant increase in rCBF occurred in a large contiguous posterior region that included the occipital poles and inferior temporal cortex bilaterally (Figure 2). Additional regions of activation were found bilaterally somewhat more anteriorly in the posterior and inferior temporal region. No increase in activation was found in any perisylvian structure traditionally associated with language processing.

Discussion of Experiment 2

Experiment 2 shows a very different pattern of rCBF than previously reported in any experiment in which sentence types were contrasted. Contrary to all previous studies using sentences, there was no increase in rCBF in either perisylvian cortex when PET activity associated with the one-proposition sentences was contrasted with activity associated with the two-proposition sentences. Instead, all increased activation arose in the inferior occipital lobe and the inferior and medial temporal gyri. In

Table 4. Areas of Increased rCBF for Substraction of PET Activity Associated with Right-Branching Sentences from Center-Embedded Sentences

<i>Location</i>	<i>Maximum z score</i>	<i>Number of pixels</i>	<i>Location {X, Y, Z}</i>
Occipital and inferior temporal	3.8	575	-32, -66, 0
	3.3		-22, -84, -4
Inferior temporal	3.7	54	46, -40, -4
Medial temporal	3.1	66	-52, -64, 20

addition, this increase in rCBF was bilateral, not mainly unilateral as seen in previous studies using sentences.

The anterior and middle portion of the inferior temporal gyrus on the left has been associated with aspects of lexical processing (Damasio et al., 1996). The extrastriate cortex has been associated with visual word recognition (Posner et al., 1988). However, the more

posterior part of the inferior temporal cortex and the inferior part of the occipital cortex in which most of the rCBF increase across the two conditions occurred—as well as the right-hemisphere regions in which this increase occurred in this experiment—have not been associated with language processing.

Several factors that could have caused the increase in

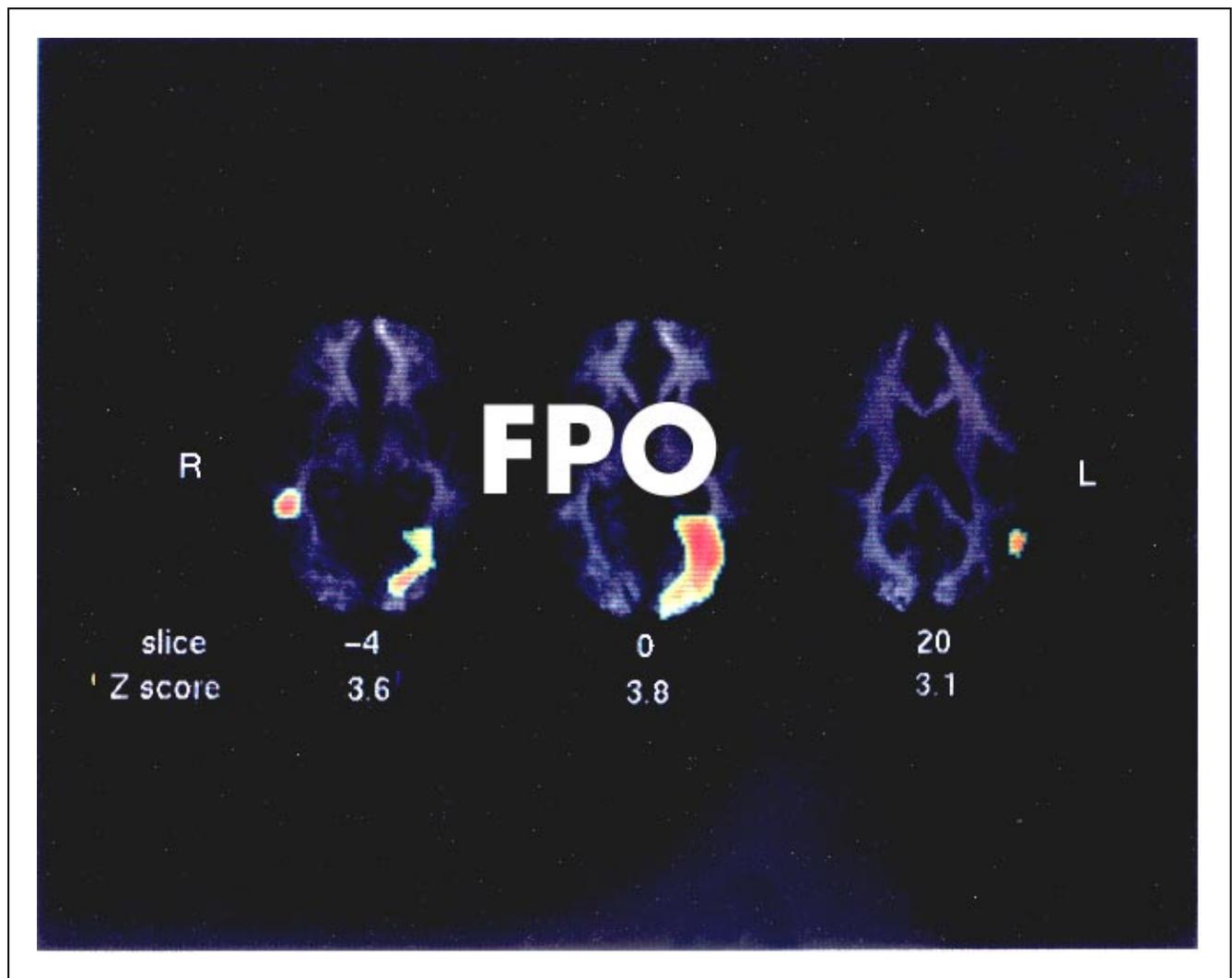


Figure 2. Reconstructed image of the brain in transverse section showing area of maximal increase in rCBF when subjects processed sentences containing two compared to one proposition.

rCBF must be considered. One is that the syntactic structure of the sentences differed in the two conditions. There are several considerations that suggest that this change in rCBF was not due to syntactic differences between the sentences in the two conditions. One is that, if it were the result of syntactic differences, one might have expected this area to also increase its rCBF in experiment 1, where the differences in syntactic processing load between the two types of sentences were certainly greater than in experiment 2. The fact that rCBF did not increase in this region in experiment 1 is therefore an argument against syntactic effects being the source of the rCBF increases in experiment 2. Second, the RTs for the two-proposition sentences in condition 1 of experiment 2 were a second longer on average than the RTs for any other condition in either experiment. This long RT is not plausibly related to assigning syntactic structure in the two proposition sentences. It could be related to the nature of the postinterpretive processing used in making the plausibility judgments about these sentences (see below).²

The major difference between the one- and two-proposition sentences is likely to be that, in the latter sentence type, a subject must check the compatibility of the nouns and verbs around each of two verbs. This requires more checking in the two- than in the one-proposition sentences, and it also increases the memory load in the two-proposition sentences. Note that this increase in memory load is different from that in experiment 1 for the center-embedded and right-branching sentences. In experiment 1, the increase in memory load was related to the need to maintain a noun phrase without a thematic role in memory while a syntactic structure was being constructed; it is therefore a memory load associated with the parsing of the sentence and/or the assigning of sentence meaning. In experiment 2, the memory load is for the propositional content of the sentence or for the outcome of the process that judges the compatibility of the nouns and verbs in the first proposition of a two-proposition sentence. Both these memory loads are associated with retaining the *products* of the comprehension process (i.e., sentence meaning) or the results of a judgment about these products, not with the *determination* of sentence meaning. The increase in rCBF seen in the comparison of conditions 1 and 2 in this experiment is most likely due to differences in some aspect of postinterpretive processing in these conditions.

Although the source of the increase in rCBF cannot be completely determined from the present experiment, one plausible account is that it is due to visual mental imagery processes that the subjects may have used to determine the plausibility of these sentences. The posterior regions of the brain activated in this experiment are areas of the brain associated with the ventral stream of visual processing (Ungerleider & Mishkin, 1982) and have been suggested to be ones involved in visual im-

agery (Kosslyn et al., 1993). If mental imagery was used, the present results suggest that it activated more cerebral tissue in the case when a judgment had to be made about two propositions compared to one.

GENERAL DISCUSSION

The results of experiment 1 reinforce the view that the pars opercularis of the left third frontal convolution plays an important role in assigning the syntactic structure of a sentence. More specifically, this region may be associated with aspects of memory storage associated with assigning one aspect of the syntactic structure of a sentence and using that structure to determine sentence meaning. The center-embedded sentences presented in condition 1 of that experiment require a subject to retain the head noun phrase of a relative clause in memory for a longer period of time than the right-branching sentences in condition 2 (see Gibson, 1997, for discussion of how this memory load can be measured). Although a role for other perisylvian cortical regions in this aspect of syntactic processing cannot be excluded, the view that Broca's area is involved in this process receives support from the present study.

The fact that increasing the number of propositions in a sentence did not lead to an increase in rCBF in the perisylvian association cortex of the brain in a plausibility judgment task, but rather in visual brain regions, raises interesting questions about the cognitive and brain systems that are taxed by the increase in propositional density of a sentence. One interpretation of this result is that syntactic structure affects the ease of assigning a meaning to a sentence—a task that recruits the language-devoted perisylvian association cortex—whereas the number of propositions in a sentence has a much smaller effect on this process and primarily complicates the process of using sentence meaning to accomplish various tasks. The brain regions that increase their rCBF as a function of the number of propositions in a sentence would, on this view, depend upon the task. We suggest that visual imagery may be activated in plausibility judgment tasks under some circumstances and that this may account for the increase rCBF found in occipital and temporal regions in experiment 2. Other tasks may activate other brain regions; for instance, it is possible that frontal regions would be more activated by a task that required enactment of two as compared with one propositions.

In summary, this study provides evidence for a distinction in the neural tissue that increases its blood flow in sentence comprehension as a function of syntactic complexity versus the number of propositions in a sentence. This pattern is compatible with the existence of partially distinct neural systems underlying the construction of syntactic form and its use in the determination of sentence meaning and the use of that meaning to accomplish a task.

METHODS

Experiment 1

Subjects

Eight native, monolingual English-speaking female college students, mean age 25.5 years (range: 21 to 31), mean years of education 16.5 (range: 16 to 20) participated. All were strongly right-handed and had no first-degree left-handed relatives. All had normal vision and hearing and no positive neurological or psychiatric history.

Conditions

Subjects were scanned during two experimental conditions. Sentences in condition 1 contained center-embedded relative clauses (e.g., *The juice that the child spilled stained the rug*) and sentences in condition 2 contained right-branching relative clauses (e.g., *The child spilled the juice that stained the rug*). The sentences contained verbs that required that a noun in either subject or object position be either animate or inanimate. Half of the sentences in each condition were semantically plausible sentences that obeyed this restriction, and half were semantically implausible sentences that violated this restriction (e.g., the center-embedded sentence **The child that the juice spilled stained the rug* or the right-branching sentence **The juice stained the rug that spilled the child*).

In both condition 1 and condition 2, in order to decide whether a sentence is acceptable, a subject must parse and interpret the sentence. Right-branching and center-embedded sentences were chosen as stimuli in this experiment because results from previous psycholinguistic research indicate that normal subjects reliably make more errors and take longer to process sentences that contain center-embedded relative clauses than sentences that contain right-branching relative clauses (e.g., Caplan, Hildebrandt, & Waters, 1994; King & Just, 1991; Waters et al., 1987). This is thought to result from the memory load associated with holding the matrix subject noun phrase (NP) in a parsing buffer until it is assigned a thematic role (Berwick & Weinberg, 1984) or with the combination of this memory load and the operation of structuring the relative clause (Just & Carpenter, 1992).

Stimulus Design

A number of controls and counterbalances were introduced to ensure that the three conditions differed only on the dimension(s) outlined above and to ensure that subjects did not adopt alternative strategies for judging the sentences. The following factors were controlled for in the design of the stimuli and the experiment.

1. Sentences were based on scenarios. There were a total of 144 scenarios (such as the scenario involving a

child staining a rug by spilling juice onto it) and each scenario appeared in each condition equally often across subjects. Because each scenario appeared in each condition equally often, differences in semantic goodness of scenarios, frequency of words, word choice, etc., could not be responsible for any differences in rCBF between the conditions. No verb appeared in more than one scenario and no subject judged any scenario more than twice.

2. The animacy of subject and object noun phrases and the plausibility of the sentences were systematically varied within block by sentence type. Thus, for example, the semantically plausible sentence *The patient that the drug cured thanked the doctor* and the semantically implausible sentence **The girl that the miniskirt wore horrified the nun* both contained an animate noun phrase, followed by an inanimate noun phrase, followed by an animate noun phrase. Animacy type, acceptability, and sentence type were counterbalanced within subjects. This feature of the design was included to ensure that subjects could not make plausibility judgments on the basis of the sequence of animacy of the nouns.

3. All noun phrases were singular, common, and definite. This feature of the design was included to ensure that subjects would not be influenced by discourse effects.

4. Sentences became implausible at various points in the relative clauses and the main clauses. This feature was included to ensure that subjects had to read the sentences in their entirety before they could decide if they were plausible. Overall, the point at which center-embedded sentences became implausible was earlier than the point at which right-branching sentences became implausible. This feature was included to eliminate the possibility that the advantage enjoyed by right-branching sentences was attributable to right-branching sentences becoming implausible at an earlier point than center-embedded sentences.

Behavioral Testing Procedure

PET scans were taken as subjects read and judged the goodness of sentences presented visually in whole sentence format on a Macintosh Classic II computer screen. The computer screen rested on a shelf approximately 12 in from the subject's eyes. After a 300-msec fixation point, a whole sentence appeared on a single line, subtending a visual angle of 20 to 25°. This sentence remained on the computer screen until the subject responded via keypresses with two fingers of the left hand. After a response, the screen was blank for 700 msec, followed first by the 300-msec fixation point and then by the next sentence to be judged. Reaction time and error rate data were collected during PET scanning and subjects were told to make acceptability judgments as quickly as possible without making errors.

At the beginning of the experiment, subjects were

given six practice trials judging simple active sentences for semantic plausibility (e.g., *The child licks the lollipop*, **The lollipop licks the child*). The two conditions were presented in blocked format, with each subject being presented each condition three times. Each block contained 24 items. The order of presentation of blocks was counterbalanced across subjects in order to eliminate any effect of order of presentation on behavioral or PET data.

PET Procedures

Image Collection

A General Electric Scanditronix PC4096 15 slice whole body tomograph was used in its stationary mode to acquire PET data in contiguous slices with center-to-center distance of 6.5 mm (axial field equal to 97.5 mm) and axial resolution of 6.0 mm full width half maximum (FWHM), with a Hanning-weighted reconstruction filter set to yield 8.0-mm in-plane spatial resolution. The studies were carried out in the MGH PET imaging suite, which has been designed to provide for control of ambient light, temperature, and noise level. Subjects' heads were restrained in a custom-molded thermoplastic face mask and aligned relative to the cantho-meatal line, using horizontal and vertical projected laser lines. Subjects inhaled $^{15}\text{O-CO}_2$ gas by nasal cannulae within a face mask for 90 sec, reaching terminal count rates of 100,000 to 200,000 events per second. Previous work in our laboratory has demonstrated that the integrated counts over inhalation periods up to 90 sec are a linear function over the flow range 0 to 130 ml/min/100g (unpublished data).

Image Reconstruction

Each PET data acquisition run consisted of 20 measurements, the first 3 with 10-sec duration and the remaining 17 with 5-sec duration each. Scans 4 through 16 were summed after reconstruction to form images of relative blood flow. To minimize the effect of head movement during the experiment, the summed images from each subject were realigned using the first scan as the reference. Realignment parameters (translation and rotation) were determined using a least-squares fitting technique (Alpert, Berdichevsky, Levin, Morris, & Faschman, 1996). Spatial normalization to the coordinate system of Talairach and Tournoux (1988) was performed by deforming the contour of the 10-mm parasagittal PET slice to match the corresponding slice of the reference brain (Alpert, Berdichevsky, Weise, Tang, & Rauch, 1993).

Statistical Analyses

Following spatial normalization, scans were filtered with a two-dimensional gaussian filter, FWHM set to 20 mm. Statistical analysis followed the theory of statistical para-

metric mapping (Friston et al., 1995; Friston, Frith, Liddle, & Frackowiak, 1991; Worsley, Evans, Marrett, & Neelin, 1992). Data were analyzed with SPM95 (from the Wellcome Dept. of Cognitive Neurology, London, UK). The PET data at each voxel was normalized by the global mean and fit to a linear statistical model with cognitive state (i.e., scan condition) considered as a main effect. Hypothesis testing was performed using the method of planned contrasts at each voxel. A z threshold of 3.00 was chosen as reliable, which is a compromise between the higher thresholds provided by the theory of gaussian fields that assume no a priori knowledge regarding the anatomic localization of activations and simple statistical theories that do not consider the spatial correlations inherent in PET and other neuroimaging techniques.

Experiment 2

Subjects

Sixteen native, monolingual English-speaking college students, 8 males and 8 females, mean age 26.7 years (range: 22 to 30), mean years of education 16.9 (range: 12 to 20) participated. All were strongly right-handed and had no first degree left-handed relatives. All had normal vision and hearing, and no positive neurological or psychiatric history.

Conditions

Subjects were scanned during two experimental conditions. Sentences in condition 1 contained two propositions (e.g., *The magician performed the stunt that included the joke. The man that the computer bewildered consulted the expert.*) and sentences in condition 2 contained one proposition (e.g., *The magician performed the stunt and the joke. It was the man that the computer bewildered.*). As in experiment 1, the sentences contained verbs that required that a noun in either subject or object position be either animate or inanimate. Half of the sentences in each condition were semantically plausible sentences that obeyed this restriction and half were semantically implausible sentences that violated this restriction (e.g., one proposition: **The stunt performed the magician and the joke.* **It was the computer that the man bewildered;* two propositions: **The stunt performed the magician that included the joke.* **The computer that the man bewildered consulted the expert.*).

Stimulus and Experimental Design

Controls and counterbalances similar to those used in experiment 1 were introduced to ensure that the two conditions differed primarily on the dimension(s) outlined above and to ensure that subjects did not adopt alternative strategies for judging the sentences. Sen-

tences were based on scenarios, with each scenario appearing in each condition equally often. The animacy of subject and object noun phrases and the plausibility of the sentences were systematically varied within block by sentence type. All noun phrases were singular, common, and definite. Sentences became implausible at various points in the sentence to ensure that subjects had to read a sentence in its entirety before they could decide that it was plausible. The two conditions were presented in blocked format, with each subject being presented each condition three times. Each block contained 24 sentences. The order of presentation of blocks was counterbalanced across subjects in order to eliminate any effect of order of presentation on behavioral or PET data.

Behavioral Testing and PET Procedures and Analyses

The same testing and PET procedures and analyses as used in experiment 1 were used in this experiment.

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Reprint requests should be sent to David Caplan, Neuropsychology Laboratory, Vincent Burnham 827, Massachusetts General Hospital, Fruit Street, Boston, MA, 02114 or via e-mail: Caplan@helix.mgh.harvard.edu.

Notes

1. Just et al. (1996) may have presented both the target sentence and the statement to be verified on the screen at the same time. If so, subjects may have read the verification statement first and then searched the target sentence for information as to whether it is correct. In this case, the rCBF changes may largely reflect task-specific processing strategies.
2. The longer RTs in experiment 2 combined with a fixed intersimulus interval (ISI) lead to a longer “duty cycle”—the amount of time from stimulus to stimulus occupied by processing—in this experiment than in experiment 1. An anonymous referee has asked whether this could have affected the rCBF results. It is possible that the duty cycle could have increased the rCBF differences across the two conditions in experiment 2. It is unlikely that this would have affected the location of the rCBF differences across these conditions.

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