# Individual differences in rCBF correlates of syntactic processing in sentence comprehension: effects of working memory and speed of processing

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## Abstract

Positron emission tomography (PET) was used to determine the effect of working memory and speed of sentence processing on regional cerebral blood flow (rCBF) during syntactic processing in sentence comprehension. PET activity associated with making plausibility judgments about syntactically more complex subject–object (SO) sentences (e.g., *The juice that the child spilled stained the rug*) was compared to that associated with making judgments about synonymous syntactically simpler object–subject (OS) sentences (e.g., *The child spilled the juice that stained the rug*). Two groups of nine subjects differing in working memory and matched for speed of sentence processing both showed increases in rCBF in lateral posteroinferior frontal lobe bilaterally. The subjects were reclassified to form two groups of eight subjects who were matched for working memory but who differed in speed of sentence processing. Fast-performing subjects activated lateral posteroinferior frontal lobe bilaterally and slow-performing subjects showed activation of left superior temporal lobe. The results indicate that rCBF responses to syntactic comprehension tasks vary as a function of speed of sentence processing but not as a function of working memory.
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The ability to determine the semantic relationships between the words in a sentence (the sentence's propositional content) is central to normal comprehension of language. The syntactic structure of a sentence is the principal determinant of how the meanings of the words in a sentence are related to each other (Chomsky, 1965, 1981, 1986, 1995), and there is near universal agreement that, when normal language users understand sentences, they construct syntactic structures as part of this process (Frazier and Clifton, 1996; Just and Carpenter, 1992; MacDonald et al., 1994). Functional neuroimaging results using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have begun to provide evidence regarding the location of the neural tissue involved in syntactic processing in sentence comprehension.

Several functional neuroimaging studies have compared reading or understanding sentences to fixation, reading a list of words, or another type of nonsentential stimulus (e.g., Mazoyer et al., 1993; Stowe et al., 1994, 1998; Bavelier et al., 1997; Chee et al., 1999). Overall, these studies indicate that sentence comprehension involves the dominant hemisphere, and suggest that areas both within and outside the perisylvian cortex may be involved in this function. However, these experiments were not designed to isolate syntactic processing and their implications for the functional neuroanatomy of syntactic processing are therefore limited. A related approach has been to compare vascular responses to tasks that require syntactic processing against a more closely related baseline. Dapretto and Bookheimer (1999) found an increase in BOLD signal in Broca's area in a synonymity judgment task in which subjects were to say

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that sentences were the "same" if the thematic roles (agent of the verb, theme of the verb, theme of a preposition) did not differ between an active and a passive sentence (e.g., *The policeman arrested the thief, The thief was arrested by the policeman*) compared to a baseline in which active and passive sentences were evaluated for synonymous words. This study provides evidence for the involvement of Broca's area in processes that arise at the level of processing sentences. These processes include, but are not limited to, syntactic operations.

An approach that is widely used in the event-related potential (ERP) literature is to identify neural responses to particular structural abnormalities. Ni et al. (2000) used a variant of this technique—the odd-ball technique—in an fMRI study, and found that, compared to well-formed sentences, infrequently presented sentences with subject–verb agreement mismatches strongly activated the left inferior frontal lobe, with lesser activation bilaterally in the posterior language areas.

The studies that focus most narrowly on syntactic processing have contrasted sentences that differ in the complexity of the syntactic operations that are needed to assign thematic roles. Two types of structures have been contrasted— object relativized clauses (e.g., *The boy that the girl hugged held the baby*) and subject relativized clauses (e.g., *The boy that hugged the girl held the baby*). Behavioral evidence strongly indicates that the process of assigning syntactic relationships and using them to determine thematic roles is more demanding in object than in subject relativized clauses (King and Just, 1991; Caplan et al., 1994). A model of the factors that make object relativized sentences more difficult to structure and understand than subject relativized sentences was presented by Gibson (1998). This model emphasizes the larger number of words that intervene between the head noun of the relative clause and the verb in the relative clause in object relativized clauses, the larger number of integration operations that occur at the verb of the relative clause in object relativized clauses, and the fact that a new referential item occurs before the head noun of the relative clause can be related to the verb of that clause in object relativized clauses. The logic behind activation studies that contrast these sentence types is that the increased syntactic processing demands associated with object compared to subject relativized clauses would lead to increases in rCBF in neural areas where this syntactic processing is carried out.

Using PET, Stromswold et al. (1996) reported an increase in rCBF in Broca's area when eight right-handed young male subjects made plausibility judgments about written sentences with object-relativized clauses (subject object (SO) relative clauses, e.g., *The juice that the child spilled stained the rug*) compared to sentences with subject-relativized clauses (object–subject (OS) relative clauses, e.g., *The child spilled the juice that stained the rug*). Caplan et al. (1998) replicated this result in eight right-handed young females, and Caplan et al. (1999) found a similar result with auditory presentation comparing object-relativ-

ized cleft object (CO) sentences (e.g., *It was the juice that the child spilled*) with subject-relativized cleft subject (CS) sentences (e.g., *It was the child that spilled the juice*). Caplan et al. (2000) reported that the increase in rCBF in Broca's area with visually presented SO and OS sentences was not eliminated by concurrent articulation, suggesting that the role of Broca's area is not simply to rehearse the complex sentences more than the simple ones but is likely to be related to abstract aspects of syntactic processing of the more complex sentences. Using fMRI, Just et al. (1996) had subjects read simple conjoined (CON), more complex subject-relativized subject–subject (SS), and most complex object-relativized subject–object (SO) sentences, and then verify assertions about these sentences. They found that BOLD signal increased in Broca's area when the sentences contained complex relative clauses. All these studies reported increases in rCBF or BOLD signal in Broca's area in association with processing object relativized sentences in which syntactic processing associated with understanding is more demanding.

Other brain regions have also been activated in association with tasks that require these syntactic operations. Caplan et al. (1999) found increases in rCBF in the left superior parietal lobe as well as in the left inferior frontal region. In the Just et al. (1996) study, there was an increase in BOLD signal in Wernicke's area of the left hemisphere, as well as smaller but reliable increases in rCBF in the homologous regions of the right hemisphere, when subjects were presented with the more complex SO and SS sentences compared to simpler conjoined sentences. Using event-related fMRI and a plausibility judgment task with word-by-word visual sentence presentation, Caplan et al. (2002) found increased BOLD signal in the left inferior parietal lobe in association with presentation of the relative clause in SO compared to SS sentences.

The factors that affect the localization of vascular responses to these aspects of syntactic processing have begun to be explored. Some factors appear to be related to task demands. Carpenter et al. (1999) and Reichle et al. (2000) found that superior parietal structures outside the classical language area of the brain were activated by sentence–picture matching tasks that emphasized visual processes and not by tasks that deemphasized these processes. Caplan et al. (2002) suggested that the superior temporal and inferior parietal activity seen in their report and in the Just et al. (1996) study might reflect increased demands made on the verbal short-term memory system by the tasks used in those studies (rapid serial visual presentation of long sentences at slow rates in Caplan et al., 2002, and answering questions after a target sentence in Just et al., 1996).

There may also be individual differences in localization of syntactic processing. Such individual differences are suggested by studies of the effects of lesions on syntactic processing in sentence comprehension: deficits in syntactic comprehension occur in all aphasic syndromes (Berndt et al., 1996; Caplan et al., 1985, 1997) and following lesions

throughout the perisylvian cortex (Caplan et al., 1996). Activation studies suggest that this variability may be related to subject factors. One factor that has been hypothesized to affect the neural basis for syntactic processing is a subject's working memory capacity. Some researchers have found that ERP responses to syntactic processing differ in subjects with different working memory capacities (Vos et al., 2001). Others (e.g., King and Kutas, 1995) have argued that individual differences in ERP responses to syntactic processing are due to individual differences in working memory, although the actual behavioral dimension along which subjects differed was their accuracy on the experimental task, not their working memory capacity. The possibility that individual differences in sentence processing proficiency might be related to individual differences in the location of the neural tissue involved in syntactic processing was reinforced by the finding of Caplan et al. (2003) that subjects who performed the plausibility judgment task with SO and OS sentences more slowly showed increased rCBF in posterior brain areas—the left inferior and superior parietal lobes—while subjects who performed the task more quickly activated the left inferior frontal area. These differences in the loci of rCBF effects were found in both young and older subjects (aged 70–80) and thus seem to be independent of age.

The current study was designed to further investigate the possibility that there are individual differences in the locus of rCBF effects associated with syntactic processing in sentence comprehension, and to determine whether any such differences are related to individual differences in working memory capacity and/or in sentence processing speed. We measured rCBF responses to syntactic processing, dividing subjects first into groups that differed in working memory and second into groups that differed in sentence processing proficiency. If variability in the localization of one aspect of syntactic processing is related to individual differences in working memory, subjects who differ in working memory should show different patterns of rCBF effects. If such variability is related to individual differences in sentence processing proficiency, we would expect subjects who differ in sentence processing proficiency to show different patterns of rCBF effects.

## Methods

### Assessment of working memory

Working memory capacity was tested using Alphabet Span, Backward Digit Span, Subtract 2 Span, and a modified version of the Daneman and Carpenter (1980) Reading Span. In each task, testing began at span size 2 and continued through span size 8. There were five trials at each span size. Participants were required to repeat all of the items in a trial in the correct serial order to obtain credit for the trial. For all tasks, span was defined as the longest list length at

which participants were correct on three of five trails. An additional .5 was given if two of five trials were correct at the next span size. A composite WM span measure was calculated for each participant by averaging across the four tasks. The composite measure of WM were used because it has been documented to have considerably better test–retest reliability than any one WM measure (Waters and Caplan, 2003).

### Alphabet span

Participants were required to repeat a series of monosyllablic, unrelated words after rearranging them in alphabetical order.

### Backwards digit span

Participants were required to repeat a random sequence of the numbers 1–9 in reverse order.

### Subtract 2 span

Participants were required to repeat a random sequence of digits after subtracting 2 from each.

### Sentence span

Sentence span was tested using a task we developed in our previous work (Waters and Caplan, 1996) that is based upon the Daneman and Carpenter (1980) reading span task. Participants were presented with sequences of sentences in cleft subject and subject object form and required to decide whether each sentence was acceptable or not. After seeing all of the sentences in a set, they were required to recall the final words of all of the sentences in the set.

### Assessment of syntactic processing speed

Syntactic processing speed was measured on a timed plausibility judgment task with whole sentence written presentation, using 100 cleft–object and 100 object–subject sentences.

### PET Methods

### Stimuli and procedure

The materials were those used in previous experiments (Stromswold et al., 1996; Caplan et al., 1998, 2000). Subjects were scanned during two experimental conditions. Sentences in condition 1 contained sentences with subject–object (SO) relative clauses (e.g., *The juice that the child spilled stained the rug*) and sentences in condition 2 contained sentences with object–subject (OS) relative clauses (e.g., *The child spilled the juice that stained the rug*). All 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 SO sentence *The child that the juice*

*spilled stained the rug* or the OS sentence *\*The juice spilled the child that stained the rug*). Subjects were required to read each sentence and indicate whether it was plausible or not.

Controls and counterbalances were introduced to ensure that the two conditions differed only on the syntactic dimension(s) outlined above, and to ensure that subjects did not adopt alternative strategies for judging the sentences.

1. Sentences were based on scenarios. There were a total of 144 scenarios with the same lexical items (such as the scenario involving a child staining a rug by spilling juice onto it). Each appeared once as an SO and once as an OS sentence, in different PET conditions, with the order of scenario counterbalanced across subjects. Because of this aspect of the design, differences in semantic goodness of scenarios, frequency of words, word choice, and order of presentation of scenarios could not be responsible for any differences in rCBF between the conditions.

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, and both appeared in a single block. 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 (the referential assumptions made by the noun phrases in a sentence) in different ways in the two conditions.

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 each sentence in its entirety before they could decide if it was plausible. Overall, the point at which SO sentences became implausible was earlier than the point at which OS sentences became implausible. This feature was included to eliminate the possibility that subjects could decide that an OS sentence was plausible at an earlier point than was possible in a SO sentence.

PET scans were taken as subjects read and judged the plausibility of sentences presented visually in whole sentence format on a Macintosh Powerbook G3 computer screen. The computer screen rested on a shelf approximately 12 in. from the subject's eyes. After a 300 ms fixation point, a whole sentence appeared on a single line, subtending a visual angle of 20–25°. This sentence remained on the computer screen until the subject responded. Subjects were instructed to indicate whether the sentence was plausible or not via key presses with two fingers of the left hand. Subjects were instructed to make plausibility judgments as quickly as possible without making errors. After a response, the screen was blank for 700 ms, followed first by the 300 ms fixation point, and then by the next sentence to be judged. Reaction time and error rate data were collected during PET scanning.

The two conditions were presented in blocked format, with each subject being presented each condition three times. Each block contained 48 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. 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*).

*PET imaging and analysis*

PET 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. PET data were acquired with a GE4096 scanner with 15 slices 6.5 mm thick and an 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 (FWHM), using the convolution-backprojection method with corrections for photon attenuation, dead-time loss, detector nonuniformity, and random coincidences. A head immobilization system (TRUE SCAN, Annapolis, MD) was used to restrain head rotation and flexion. Head alignment was made, relative to the canthomeatal line, using horizontal and vertical projected laser lines whose position was known with respect to the slice positions of the scanner. Each PET data acquisition condition consisted of 20 measurements, the first three with 10 s duration each and the remaining 17 with 5 s duration. Subjects were fitted with nasal cannulae through which they breathed $^{15}$O-$CO_2$ gas for 1 min during each PET condition; presentation of stimuli began 15 s earlier. After image reconstruction, additional processing was performed with the SPM99 software developed by the Wellcome Dept. of Cognitive Neurology, London, UK. Subjects' PET scans were aligned to one another to minimize the effects of head movement not constrained by the head holder. Spatial normalization was performed to transform each subject's PET scans to the MNI coordinate system (Evans et al., 1994). Talairach coordinates were approximated as recommended by Mathew Brett on his website (http://www.mrc-cbu.cam.ac.uk/Imaging/).

Statistical parametric mapping was performed using SPM99. The PET data at each voxel was normalized by the global mean. Hypothesis testing was based upon planned contrasts at each voxel. The resulting *t* values were con-

verted to $z$ scores, which were examined for significance following the principles derived from Gaussian field theory (Friston et al., 1991, 1995; Ashburner et al., 1997, 1999; Worsley et al., 1996). Random effects analysis was used to analyze the entire data set, making no a priori assumptions about the location or direction of rCBF differences. Random effects between-group analyses were used to compare rCBF differences in different subject groups. Fixed effects analysis was used to identify regions in which rCBF was greater for one sentence type than for another, making the a priori assumption that rCBF was expected to be greater for SO than for OS sentences in left perisylvian and midline frontal regions. These a priori predictions were based upon the results of deficit-lesion correlational studies and functional neuroimaging studies reviewed above. As in previous studies, we report all $z$ scores for the SO–OS contrast that were higher than $z$ scores in these predicted regions. A $z$ score was considered significant if it exceeded the $z$ score significance threshold for a region determined by Worsley et al. (1996). Normalized PET counts at each voxel were correlated with RTs for each subject on each block and the resulting $r$ values analyzed in SPM with fixed effects models. We report all resulting $z$ scores that were above the significance levels derived from Gaussian field theory in left perisylvian and midline frontal regions (based upon apriori expectations), in regions in which there were significant rCBF effects in the SO–OS contrast, and in regions in which $z$ scores were higher than $z$ scores in these areas.

### Subjects

We studied two groups of subjects ($N = 9$ in both groups) that differed on standard working memory tasks but did not differ with respect to their syntactic processing abilities. Analysis of demographic data showed that the two sets of subjects did not differ in age (mean age 21.1 and 21.8 years in the high and low working memory capacity subjects, respectively), male:female ratio (3:6 and 1:8 in the high- and low-working memory capacity subjects, respectively), or years of education (mean 14.4 and 15.1 years the high and low working memory capacity subjects, respectively). The high- and low-working memory capacity subjects differed in their composite score on standard working memory tests (mean score of 6.4 and 4.4 in the high- and low-working memory capacity subjects, respectively; $t =$ 9.2, $P < .001$).

We regrouped these subjects to identify eight pairs of subjects who differed with respect to syntactic processing speed, but did not differ on standard working memory tasks. The two sets of subjects did not differ in age (mean age 21.4 and 20.8 years in the high and low processing speed subjects, respectively), male:female ratio (2:6 in both sets), years of education (mean 14.9 and 14.6 years in the high- and low-proficiency subjects, respectively), or standard working memory test performance (mean working memory score of 5.4 in both sets of subjects).

## Results

### High and low capacity subjects

#### Behavioral results

There were no differences in reaction times or accuracy between the groups in the screening test by $t$ test. Fig. 1 shows the performance of the high and low working memory subjects in the PET environment.

The RT and accuracy (percent correct) data in the PET study were analyzed in a 2 (group) $\times$ 2 (sentence type) $\times$ 2 (plausibility) ANOVAs by subjects ($F_1$) and items ($F_2$). Accuracy was also described in terms of A′—a nonparametric measure similar to the parametric $d'$, designed to measure discrimination of two types of stimuli independent of response bias. The formula for A′ involves the ratio of "hits"—the proportion of correct responses to plausible sentences—and "false alarms"—the proportion of incorrect responses to implausible sentences—in each subject, and therefore does not allow for analyses over items to be performed.

In the analysis of RTs, there were main effects of sentence type ($F_1$ (1,71) = 27.3, $P < .001$; $F_2$ (1,571) = 52.4, $P < .001$) and acceptability ($F_1$ (1,71) = 6.4, $P < .05$; $F_2$ (1,571) = 4.9, $P < .05$). RTs were longer for SO than for OS sentences and for implausible than for plausible sentences. There were no effects of group, and no significant interactions. In the analyses of percent correct, there was a main effect of sentence type ($F_1$ (1,71) = 26.3, $P < .001$; $F_2$ (1,573) = 13.5, $P < .001$). There were more errors on SO than on OS sentences. In the analysis of A′ scores, there was a main effect of sentence type ($F_1$ (1,16) = 23.1, $P < .001$). As were higher for object–subject than for subject–object sentences. There were no effects of group, and no significant interactions.

#### rCBF results

Random effects analyses showed no significant effects. Table 1 and Fig. 2 show the cortical areas activated in fixed effects analyses in the comparison of SO minus OS sentences in these two groups. High and low working memory capacity subjects both activated the same areas in the left and right inferior frontal cortex, as well as midline structures. Between-groups random effects analysis showed no difference in the rCBF effects in the two groups. Correlational analyses showed significant correlations between rCBF and RTs in the high-capacity subjects in the left inferior frontal lobe (peak at −40, 44, 2; $z = 3.5$), the left anterior insula (peak at −40, 10, 4; $z = 3.77$), the left thalamus (peak at −18, −8, 12; $z = 3.87$) and the left superior temporal sulcus (peak at −58, −28, −4; $z = 4.07$). In the low-capacity subjects, there were significant correlations between rCBF and RTs in the left inferior frontal lobe (peak at −52, 48, −8; $z = 4.41$) and the right cingulate (peak at 10, 16, 42; $z = 3.36$).
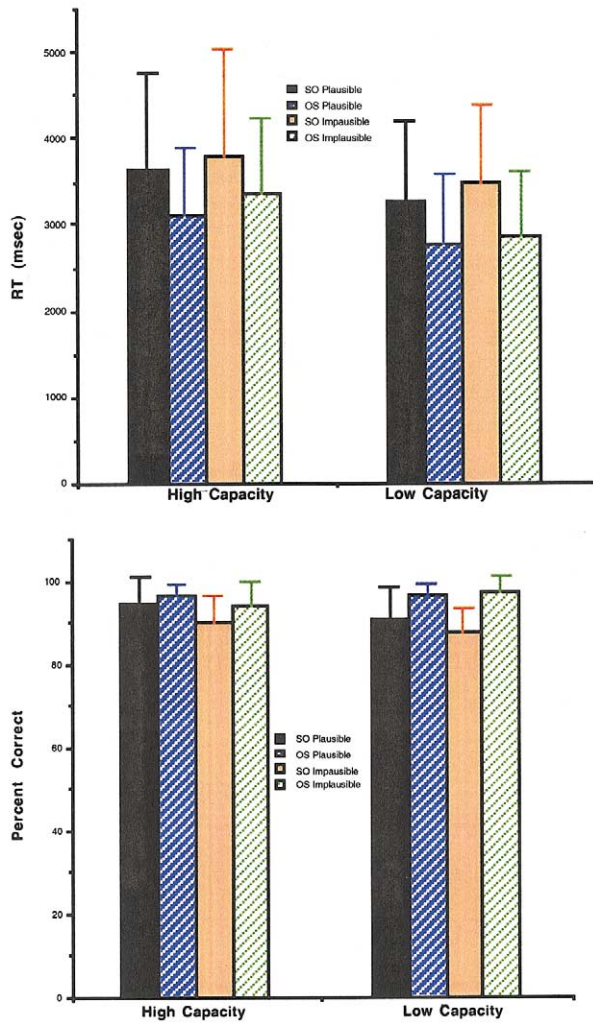
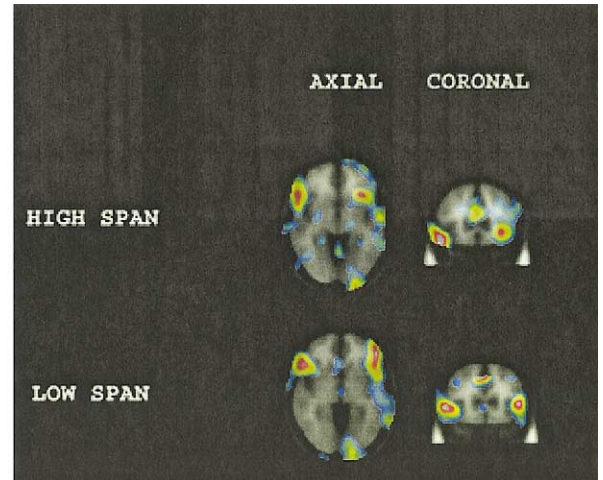Fig. 1. Reaction times and percent correct in the PET experiment for high and low working memory subjects.



Fig. 2. Regional cerebral blood flow associated with syntactic processing in subjects who differ on standard working memory tests. (a) High span subjects. (b) Low span subjects.

cessing speed subjects ($t = -5.3$, $P < .001$). Fig. 3 shows the performance of the high and low processing subjects in the PET study.

Reaction times and accuracy (percent correct and A′) in the PET study were analyzed as described above.

In the analysis of RTs, there were main effects of group ($F_1$ (1,63) = 13.9, $P < .01$; $F_2$ (1,571) = 712.1, $P < .001$) and sentence type ($F_1$ (1,63) = 22.1, $P < .001$; $F_2$ (1,571) = 54.5, $P < .001$). RTs were longer in the low processing speed than in the high processing speed subjects, and longer for SO than for OS sentences. The interaction of group and sentence type was significant ($F_1$ (1,63) = 4.1, $P = .06$; $F_2$ (1,571) = 18.0, $P < .001$). Both low and high processing speed subjects had longer reaction times for the subject–object sentences than for the object–subject sentences, but the difference between reaction times for the syntactically complex and simple sentences was greater in the low processing speed subjects (817 ms) than in the high processing speed subjects (324 ms) ($F = 7.5$, $P < .01$). In the analyses of percent correct, there were main effects of sentence type ($F_1$ (1,63) = 16.2, $P < .001$; $F_2$ (1, 573) = 14.5, $P < .001$)

### High and low processing speed subjects

### Behavioral results

For the screening test, high processing subjects had shorter reaction times in making judgments than low pro-

Table 1

Areas of increased rCBF for subtraction of PET activity associated with subtracting syntactically simple object–subject sentences from syntactically complex subject–object sentences in high and low working memory capacity subjects

| Location | Max z score | MNI coordinates of peak activity {X, Y, Z} | Talairach coordinates of peak activity {X, Y, Z} |
| --- | --- | --- | --- |
| High capacity subjects | | | |
| Right inferior frontal lobe | 3.63 | 60, 38, −18 | 52, 34, −14 |
| Cingulate gyrus | 3.22 | 0, 10, 42 | −1, 6, 37 |
| Left inferior frontal lobe | 2.85 | −34, 24, −8 | −31, 20, −6 |
| | | | |
| Low capacity subjects | | | |
| Cingulate gyrus | 3.88 | 8, 20, 45 | 6, 16, 41 |
| Left inferior frontal lobe | 3.81 | −50, 38, 0 | −45, 34, 1 |
| Right inferior frontal lobe | 3.39 | 58, 24, 0 | 50, 20, 1 |
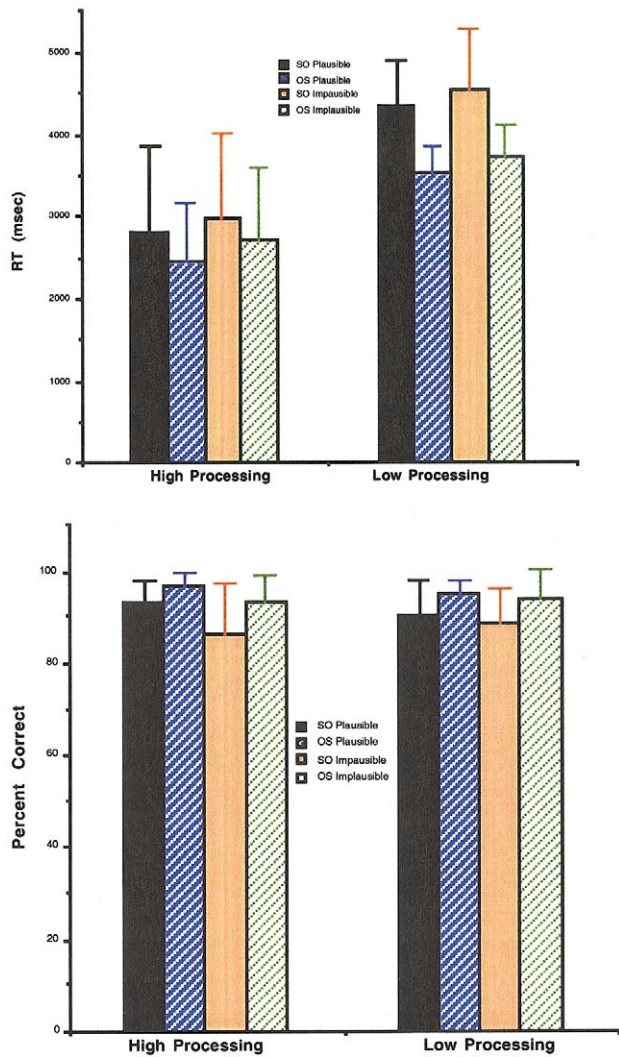
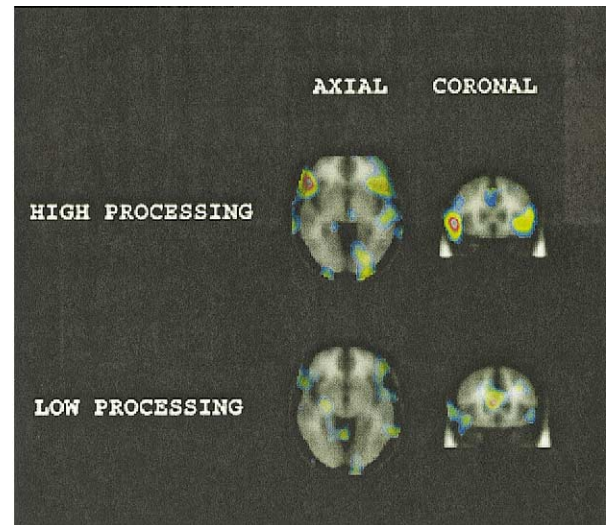Fig. 3. Reaction times and percent correct in the PET experiment for high and low processing subjects.



Fig. 4. Regional cerebral blood flow associated with syntactic processing in subjects who differ in syntactic processing proficiency. (a) High speed subjects. (b) Low speed subjects.

tence type ($F$ (1,14) = 18.5, $P$ < .001). As were higher for object–subject than for subject object–sentences. There were no effects of group, and no significant interactions.

*rCBF results*

Random effects analyses showed no significant effects. Table 2 and Fig. 4 show the areas of the brain activated in fixed effects analyses in the comparison of syntactically complex minus syntactically simple sentences in these two groups. The high and low processing speed subjects activated different brain regions. High processing speed subjects activated the inferior frontal cortex bilaterally, and low processing speed subjects activated left superior temporal lobe. Low-proficient subjects also activated medial structures and the right hippocampus. Between-groups random effects analysis showed no difference in the PET effects in the two groups. Correlational analyses showed significant correlations between rCBF and RTs in the high processing subjects in the left inferior frontal lobe (peak at −50, 12, 14; $z$ = 4.10) and the left superior temporal sulcus (peak at

and acceptability ($F_1$ (1,63) = 4.3, $P$ = .05; $F_2$ (1, 573) = 10.5, $P$ < .001). There were more errors on SO than on OS sentences and on implausible than on plausible sentences. In the analyses of A′ scores, there was a main effect of sen-

Table 2
Areas of increased rCBF for subtraction of PET activity associated with subtracting syntactically simple object–subject sentences from syntactically complex subject–object sentences in high and low speed subjects

| Location | Max $z$-score | MNI coordinates of peak activity {X, Y, Z} | Talairach coordinates of peak activity {X, Y, Z} |
|---|---|---|---|
| High proficiency subjects | | | |
| Right inferior frontal lobe | 4.21 | 56, 25, −4 | 48, 22, −3 |
| Left inferior frontal lobe | 3.40 | −50, 20, 0 | −45, 16, 1 |
| Low proficiency subjects | | | |
| Midline (callosum) | 3.92 | 6, 24, 10 | 4, 20, 10 |
| Right hippocampus | 3.51 | 26, −12, −16 | 22, −15, −15 |
| Left superior temporal sulcus | 3.44 | −68, −46, 8 | −61, −48, 4 |

−56, −26, −2; $z$ = 4.18). In the low capacity subject, there were significant correlations between rCBF and RTs in the left superior temporal sulcus (peak at −66, −44, 10; $z$ = 3.42).

## Discussion

The behavioral results in the PET scanner reconfirm the difficulty associated with processing subject–object sentences compared to object–subject sentences. Several features account for the difficulty of subject–object sentences. In subject–object sentences (e.g. *The juice that the child spilled stained the rug*), it is necessary to retain the head noun of the relative clause (*the juice*) over a greater number of words than in object–subject sentences (e.g., *The child spilled the juice that stained the rug*) to integrate it with the verbs of both the relative and main clauses, and there are more integrations to perform at the verb of the embedded clause in subject–object sentences than in object–subject sentences (see Gibson, 1998, for more detailed discussion of the features that render SO sentences more complex to process than OS sentences).

This study replicates previous results that found increased rCBF in the left inferior frontal lobe in association with processing the more complex subject–object sentences in this paradigm (Stromswold et al., 1996; Caplan et al., 1998, 1999, 2000). rCBF increases in this study were seen in both hemispheres, a finding that has previously been reported with sentences with similar syntactic structures (Just et al., 1996). The correlational analyses between rCBF and reaction times were consistent with the results of the analyses of variance, and with previous findings regarding vascular activity in sentence comprehension tasks. The lateral neocortical areas in which RT was correlated with rCBF are ones known to be involved in language processing and were exclusively in the left hemisphere, consistent with the finding of exclusive or greater vascular reactions in the left hemisphere in studies of sentence comprehension. Correlations were also found in the cingulate and the thalamus, regions that have been activated in previous studies using this paradigm (Caplan et al., 2000).

Because of the design of the experimental materials, the increased rCBF associated with making judgments about subject–object sentences compared to object–subject sentences is plausibly related to the differences in processing demands of the SO and OS sentences. The correlations between rCBF and RT are less clearly related to any one aspect of language processing, because many operations could have led to longer RTs in a given block of stimuli. However, two aspects of the behavioral data suggest that the correlations between rCBF and RT are also likely to be due to processing differences in these two sentence types, at least in part. First, RTs were longer for SO than for OS sentences, indicating that one source of RT differences was sentence structure. Second, ANOVAs including the factor

of block showed no effects of block and no interactions with the factor of block. This suggests that differences in stimuli within specific blocks of SO and OS sentences made only small contributions to mean RTs, compared to the effect of sentence type.[1] Both the regions that showed activation in the analysis of variance and those in which rCBF was correlated with RTs are therefore likely to be ones involved with syntactic processing, and/or ones responsible for cognitive mechanisms associated with such processing. As discussed in the introduction to this paper, these related mechanisms include short-term memory, image generation and inspection, deployment of attentional resources, and possibly others. We will consider the role of the regions identified in these analyses in relationship to the patterns of vascular activity seen in the different groups of subjects.

This study replicates previous studies showing individual differences in the patterns of regional cerebral blood flow associated with processing syntactic structures that make higher processing demands (Caplan et al., 2003). As in previous studies, these differences in the location of rCBF effects were associated with differences in the speed with which subjects assigned syntactic structures, and not with differences in subjects' verbal working memory as measured on standard tests of this function.

The fact that differences in the location of rCBF effects associated with syntactic processing occurred in subjects who differed in the speed with they assigned syntactic structures raises two questions: (1) what does speed of processing reflect? and (2) what do the different rCBF patterns seen in the high and low subjects tell us about the neural basis of this aspect of syntactic processing in these groups?

A behavioral finding that is relevant to the first of these questions is that the low processing speed subjects were disproportionately slow in responding to the syntactically more complex subject–object sentences. The differences in subjects' performance on the judgment task thus reflect differences in the speed with which they assigned syntactic structures and used them to determine sentence meaning, not just differences in the speed with which they read and processed sentences in general. Subjects may have differed in the speed with which they performed syntactic operations, the speed with which they related lexical items in a memory store to syntactic positions, or other aspects of sentence processing that differ in SO and OS sentences. A

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[1] More direct evidence regarding the possibility that the correlations between RTs and rCBF were due to processing syntactic structure could come from examination of correlations between RT differences on SO and OS sentences and rCBF. However, because SO and OS sentences were matched over the entire experiment, not block-by-block, only one SO–OS difference score could be obtained for each subject, leading to too few observations for such analyses to be done in this study. In addition, correlations involving difference scores are often criticized on statistical grounds and for being hard to interpret because difference scores can reflect a number of patterns of higher and lower values of the compared variables.

related possibility is that individual differences in processing speed may reflect individual differences in the size of the working memory system involved in syntactic processing, or lead to such differences. Increased difficulty in processing syntactically more complex sentences has been taken as a sign of a lower working memory availability for syntactic processing (Just and Carpenter, 1992). This study therefore is consistent with the view that variability in the size or operation of the working memory system involved in syntactic processing is related to variability in the location of rCBF activity associated with assigning such structures.

With respect to the neural basis for syntactic processing in the high and low processing speed subjects, the direct comparison of rCBF in SO and OS conditions shows different patterns of activity, and the correlational analyses show partially different regions in which rCBF was correlated with RTs, in these groups. One possibility is that these different rCBF patterns reflect high and low processing speed subjects utilizing different brain regions to assign syntactic structure—the inferior frontal lobe, particularly on the left, by high processing speed subjects and the left superior temporal area by low processing speed subjects. If this is the case, the results show that subjects' speed of syntactic processing affects the *location* of the neural substrate for syntactic processing.

However, it remains possible that high and low processing speed subjects use the same brain regions to process these sentences, and that the different patterns of rCBF reflect two differences these groups: the degree to which they use various ancillary cognitive operations to support sentence comprehension, and the way neural tissue is activated by syntactic processing in the two groups. An ancillary cognitive mechanism that may have been used to different degrees by the high and low processing speed subjects is phonological storage in verbal short-term memory, which is known to recruit left inferior parietal structures adjacent to the left superior temporal region activated in this group (Vallar and Shallice, 1990; Smith et al., 1998). If superior temporal rCBF reflects the use of STM in this task, the fact that high processing speed subjects showed a correlation between RT and rCBF in the superior temporal region suggests that they too used this system while performing the task. However, subjects who are less proficient at sentence processing could have used STM more than subjects who are more proficient at this task. Use of short-term memory may be time consuming and lead to longer response times in sentence comprehension tasks.[2]

If temporal activity reflects the use of STM in this task, where did low processing speed subjects assign syntactic structure?[3] One possibility is that all subjects utilized the inferior frontal lobes to assign syntactic structures. The absence of an rCBF effect in inferior frontal lobes in low processing speed subjects may be due to less difference in the neural activity associated with processing the SO and OS sentences. Low processing speed subjects may have generated more neural activity in the simple sentence condition (because processing these sentences is more demanding for them), less neural activity in the complex sentence condition (because they have fewer neural resources available), or both, in the inferior frontal lobes compared to high processing speed subjects. We are indebted to a reviewer of this paper for the suggestion that one possibility is that the same complexity of processing spread out over a longer period of time increases neural computational load; this, coupled with ceiling effects in slow processors, could have reduced rCBF differences between the two conditions in low processing speed subjects. If this view is correct, slow responding subjects should show activity in the inferior frontal region if baseline sentences whose processing demands are lower than those of OS sentences are compared with SO sentences, and fMRI studies may show different time courses of activity in this area in fast and slow responders. If all subjects utilized the inferior frontal lobes to assign syntactic structures and the absence of a discernable rCBF effect in slow processing speed subjects is due to any of these mechanisms, the results show that subjects' speed and proficiency in syntactic processing modulates the *response* rather than the *location* of the neural substrate involved in syntactic processing.

In contrast to the high and low processing speed subjects, subjects who differed in verbal working memory capacity as measured on standard tests of this function showed highly similar patterns of rCBF differences in the comparison of

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study involving sentences. Bookheimer et al. (1993), using fMRI, compared subjects' judgments of whether sentences were the same in meaning when they contained the same words but differed in word order with the control conditions of monitoring sentences for a phoneme change, listening to identical pairs of sentences, and resting. They reported increased BOLD signal in Broca's area and in the left hippocampus. Unfortunately, their report exists only in the form of an Abstract in which no hypothesis regarding the cognitive operation(s) responsible for the hippocampal activation is advanced.

[3] We note that the behavioral data provide evidence that all the subjects, fast and slow performers alike, did in fact assign complex syntactic structures in this task. Nonlinguistic mechanisms such as verbal short-term memory and mental imagery can only help retain the form of the presented sentence or its interpretation in an accessible state; they cannot generate the meaning of a sentence. Neither simple heuristics (Townsend and Bever, 2001) nor nonsyntactic association mechanisms (MacDonald and Christiansen, 2001; Rohde and Plaut, 1999) achieve good comprehension of SO sentences (see Caplan and Waters, 2001, for discussion). Given the high rate of correct responses to these structures in all groups of subjects, we would argue that all subjects must have used a syntactic analysis to determine sentence meaning. Where did this analysis take place in the low processing speed subjects, if not in the left superior temporal lobe?

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[2] The activation of the right hippocampal gyrus in these subjects is less easily explicable. A reviewer suggested that it might be due to the use of visual imagery, which we have previously suggested may have been responsible for inferior temporal activation seen in a different subtraction (Caplan et al., 1998). However, the activity seen here is considerably more medial than that seen in the previous study, and is not in unimodal visual association cortex in the inferior temporal lobe. We note that hippocampal activation has been previously reported in one functional neuroimaging

SO and OS conditions. Both groups also showed correlations between rCBF and RTs in the left inferior frontal lobe. If we accept that the inferior frontal lobe, particularly on the left, is the likely location of the syntactic operations that are performed in the comprehension of these sentences, these results suggest that working memory capacity, as measured on standard tests, does not affect the location or the utilization of the neural substrate of these operations.[4]

As noted in the introduction to this paper, some researchers have reported ERP differences in sentence processing tasks in subjects with high and low working memory (e.g., Vos et al., 2001). Differences were also found between the high and low capacity subjects in the pattern of correlations of rCBF with RTs found in this study. High capacity subjects showed these correlations in a larger set of left hemisphere regions (the insula, thalamus, and superior temporal sulcus), and low capacity subjects showed a correlation in a midline structure likely to be more involved in regulating attention (the cingulate). These differences are consistent with the view that there are differences in the neural processes that occur in relation to syntactic processing in high and low capacity subjects.

These results can, however, be reconciled with the claim that working memory capacity does not affect the neural substrate for purely syntactic operations. We have suggested that the working memory system involved in initial syntactic processing is distinct from the one that underlies performance on standard tests of working memory, and that the latter system is involved in review and reanalysis processes when initial (first-pass) processing fails (Caplan and Waters, 1999, 2002). The results of this study and those in the ERP literature are consistent with this view. The ERP differences that have been documented in high and low working memory subjects have occurred in the P600, which is thought to reflect processes involved in the reanalysis of ambiguous sentences that were initially misinterpreted (Friederici, 1999) and in the recognition that a sentence is syntactically anomalous (Osterhout and Holcomb, 1992, 1993, 1995). The P600 is not a purely syntactic ERP component. It occurs in relation to musical "anomalies" (Patel et al., 1998) and may be related to the P300 that is generally associated with unexpected events (Coulson et al., 1998a,b; for discussion, see Osterhout and Hagoort, 1999; Osterhout et al., 1996). Differences in the P600 in high and low capacity subjects may reflect differences in their abilities to

recognize anomalies and to reanalyze structures in general. The differences found in this study in high and low capacity subjects are consistent with this view. They occurred in the left superior temporal lobe, which we have suggested may reflect the use of STM in review processes in the task used here, and in the thalamus and cingulate, which we have suggested are involved in deployment of attention (see Posner et al., 1987, 1988; Cabeza and Nyberg, 2000, for discussion). The high and low capacity subjects showed similar patterns of neural activity in the left inferior frontal region, which is most clearly related to the syntactic processing required in this task.

In summary, the present research documents individual differences in the location of rCBF increases that are associated with one aspect of syntactic processing. When rCBF was compared across sentences that differed in their syntactic complexity and were matched for other linguistic features, subjects who performed the sentence comprehension task slowly and whose reaction times were significantly longer on the more complex sentences activated superior left temporal structures, while subjects who performed quickly and who were less affected by syntactic complexity activated inferior frontal regions. There were no differences in rCBF patterns in these comparisons in subjects who differed in working memory capacity. These results suggest that the region that supports syntactic processing either varies or is differentially activated by syntactic processing in subjects who differ in the speed, and possibly the overall proficiency, with which they carry out this process, but not in subjects who differ their overall working memory capacity. Other features of the results (correlations between rCBF and performance) point to differences in neural activity associated with aspects of sentence processing in individuals who differ in either speed of processing or working memory. These differences could be due to differences in review and reanalysis processes and in the extent of use of ancillary cognitive mechanisms in sentence comprehension tasks in these groups.

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[4] There were differences in the exact location in the left frontal area of peak correlation between rCBF and RT in the high and low capacity groups. The peak correlation was more ventral in the low capacity subjects (centered in Brodman area 47) and more posterior in the high capacity subjects (with peaks in area 45 and the insula). These differences may provide a clue that the neural substrate for syntactic processing does differ in these groups of subjects. However, they are not greater than differences in the location of rCBF and BOLD effects within the left frontal lobe found across published studies of syntactic processing that have been taken to reflect activation of the same region. Further study is needed to understand their functional significance.

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