

Dissociable patterns of brain activity during comprehension of rapid and syntactically complex speech: Evidence from fMRI

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Abstract

Sentence comprehension is a complex task that involves both language-specific processing components and general cognitive resources. Comprehension can be made more difficult by increasing the syntactic complexity or the presentation rate of a sentence, but it is unclear whether the same neural mechanism underlies both of these effects. In the current study, we used event-related functional magnetic resonance imaging (fMRI) to monitor neural activity while participants heard sentences containing a subject-relative or object-relative center-embedded clause presented at three different speech rates. Syntactically complex object-relative sentences activated left inferior frontal cortex across presentation rates, whereas sentences presented at a rapid rate recruited frontal brain regions such as anterior cingulate and premotor cortex, regardless of syntactic complexity. These results suggest that dissociable components of a large-scale neural network support the processing of syntactic complexity and speech presented at a rapid rate during auditory sentence processing.

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1. Introduction

Unlike reading, in which input rate can be controlled with eye movements, speech comprehension is based on a transient acoustic signal whose rate is largely controlled by the talker, not the listener. For effective comprehension auditory input must be analyzed, segmented, and processed for structure and meaning, all while new information continues to arrive. The speed at which these processes must occur is necessarily rapid, as average speaking rates can exceed 200 words per minute (wpm) even in everyday conversation (Miller, Grosjean, & Lomanto, 1984).

A number of studies have used time-compressed speech to examine the effects of presentation rate on auditory sentence comprehension. These studies typically use a computer algorithm that periodically deletes

small segments of the speech signal and then abuts the remaining segments in time. The discarded intervals are always kept to the same small size, with the rate of speech controlled by the frequency with which these segments are deleted. The resulting speech retains its normal pitch and relative prosodic features but is reproduced in less than its original speaking time (Foulke, 1971). Studies using time-compressed speech have shown that, depending on the original speaking rate and the nature of the speech materials, speech can still be understood fairly well when reduced by as much as 50%, although comprehension accuracy generally declines incrementally as speech rate is increased (Chodorow, 1979; Foulke, 1971; Wingfield, 1975; Wingfield, Tun, Koh, & Rosen, 1999).

In a previous study we showed that the added work imposed by complex syntactic structure is compounded by the processing challenge of rapid speech, producing a differentially greater effect of syntactic complexity on sentence comprehension at faster speech rates

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(Wingfield, Peelle, & Grossman, 2003). That is, syntactically complex sentences consistently produced poorer response accuracy and longer reaction times than their simpler counterparts. Faster speech rates adversely affected performance on all sentences, but differentially affected both accuracy and response latency for complex sentences. This effect was shown to be a robust one that operates on both young and older adults. Such a multiplicative effect of speech rate and syntactic complexity would be expected if the two sources of difficulty added processing costs to a shared, resource-limited processing system that acts as a general processing bottleneck (e.g., Broadbent, 1971; Kahneman, 1973). In the current study we sought to determine whether this hypothesis was supported by patterns of neural activation associated with these two difficulty manipulations.

Using functional neuroimaging techniques, significant progress has been made in identifying the regions of the brain involved in various aspects of speech comprehension. The emerging picture is one in which smaller, more generalized regions interact to form a core language processing network (for reviews, see Bookheimer, 2002; Friederici, 2002; Price, 2004). The precise location of these regions varies considerably between tasks and experiments (e.g., Kaan & Swaab, 2002), suggesting that, in addition to individual anatomical differences, activation patterns are heavily influenced by specific materials and task demands.

Identification of individual words heard in isolation is in itself a complex task that involves extensive phonological and semantic processing. Studies of auditory word processing consistently indicate portions of the superior temporal gyrus are involved in this task, although many of these regions also respond to complex non-speech sounds, suggesting they may be sensitive to physical properties of the speech stimulus, such as rapid spectral changes and amplitude modulations (Belin et al., 1998; Binder et al., 2000; Fiez et al., 1995; Griffiths, Buchel, Frackowiak, & Patterson, 1998; Price et al., 1996; Vouloumanos, Kiehl, Werker, & Liddle, 2001). In addition to the processing required to identify individual words, sentence comprehension requires segmenting the continuous speech stream to identify words (Gow & Gordon, 1995), determining syntactic structure (Mitchell, 1994), integrating meaning over this structure (Kintsch, 1994), and being sensitive to prosodic cues (Kjelgaard, Titone, & Wingfield, 1999). Each of these necessary levels of processing are important to our complete understanding of speech comprehension. However, as indicated previously, in the current study we are specifically interested in the effects of speech rate and syntactic complexity, as well as the extent to which they interact.

The syntactic contrast we chose for this experiment consisted of sentences containing a subject-relative or an object-relative subordinate embedded clause. In sen-

tences with a subject-relative clause (e.g., “Boys that help girls are caring”), the main clause (“Boys are caring”) is interrupted by the subordinate relative clause (“that help girls”). Here, the head noun phrase (“Boys”) is the subject of both the main and subordinate clauses. In sentences featuring an object-relative clause (e.g., “Boys that girls help are caring”), the relative clause not only interrupts the main clause, but the head noun phrase has two different grammatical roles: It functions as both the subject of the main clause and the object of the subordinate relative clause. This added syntactic complexity of object-relative clause sentences has been shown to produce longer processing times and more errors in comprehension than subject-relative clause sentences for both written (Cooke et al., 2002; Just & Carpenter, 1992; Vos, Gunter, Schriefers, & Friederici, 2001) and spoken (Wingfield et al., 2003) sentences.

Evidence from a number of studies associates portions of inferior frontal cortex (BA 44/45/47) and posterior superior temporal gyrus (BA 21/22) with processing syntactically complex speech. This includes studies of both written (Caplan, Alpert, Waters, & Olivieri, 2000; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Keller, Carpenter, & Just, 2001) and auditory (Caplan, Alpert, & Waters, 1998, 1999) sentence comprehension. Although there is considerable variability between studies with regard to the precise location of activation foci, there is relatively good agreement on the general areas (Kaan & Swaab, 2002). It should be noted that some recent studies have attributed portions of this inferior frontal activation to the working memory load associated with syntactically complex sentences, and not syntactic processing per se (e.g., Cooke et al., 2002; Fiebach, Schlesewsky, & Friederici, 2001).

As indicated previously, speech rate can vary considerably in everyday conversations, and artificially time-compressed speech can severely challenge language comprehension (Wingfield et al., 1999, 2003). Several studies have begun to investigate the effects of rapid presentation rate on the neural networks involved in speech comprehension. Using positron emission tomography (PET), Price et al. (1992) presented participants with single spoken words at several rates. They found a direct relationship between presentation rate and regional cerebral blood flow in the primary auditory cortices and middle regions of the superior temporal gyri. The response in the left posterior superior temporal gyrus (BA 21/22), however, demonstrated comparable amounts of activation regardless of presentation rate. Similar results have also been reported in fMRI studies with word and non-word stimuli (Binder et al., 1994; Dhankhar et al., 1997).

These findings, however, do not address the processing associated with time-compressed sentences. With such stimuli, not only do words arrive at a faster rate, but the acoustic cues themselves occur more quickly. In

addition, sentence-level operations, such as role assignment based on syntactic constraints, must be performed more quickly. Poldrack et al. (2001) used time-compressed sentences to differentiate between regions of the brain that responded to rapid acoustic signals, and those involved in comprehending rapid speech. To do so, they presented sentences that had been compressed to 60, 45, 30, and 15% of their original duration. Speech was not comprehensible at the fastest speech rate used, suggesting that activation at this fastest rate was due solely to the nature of the acoustic stimulation and not linguistic processing. Several areas showed linear changes (increases or decreases) with increasing speech rate, regardless of speech intelligibility. These included increases in the middle frontal gyrus (BA 46/10), a portion of right inferior frontal gyrus, anterior cingulate, and right striatum. Compression-related decreases were observed in the right superior temporal plane, left superior temporal cortex, and left angular gyrus region. Most interesting were the areas that exhibited convex responses—that is, activity increased with increasing speech rates until speech became unintelligible, at which point activity in these areas decreased—indicating that activity in these regions was specific to language comprehension. These included the left posterior superior temporal gyrus (BA 21/22) and several areas in the left inferior frontal gyrus (BA 44/45), as well as the right inferior frontal gyrus.

These studies indicate that speech comprehension relies on a network of highly interactive regions that are sensitive to stimulus properties and task demands. Comparisons between studies thus are very difficult. Activation in traditional language areas (i.e., left posterior superior temporal gyrus and left inferior frontal gyrus) nevertheless has been observed in response to both syntactically complex and time-compressed sentences, making these areas appealing candidates for the processing bottleneck discussed earlier. To examine whether similar brain regions are indeed involved in processing both rapid speech and complex syntax, we used event-related fMRI to examine both variables within a single experiment. This study also allowed us to address a larger question: namely, the degree to which an interaction between two variables at the behavioral level necessarily indicates a shared biological processing structure.

2. Method

2.1. Participants

Participants were 8 right-handed, neurologically normal, native English speakers, four females and four males, with ages ranging from 19 to 27 ($M = 22.6$). All participants received pure tone audiometric screening to ensure normal hearing acuity.

2.2. Stimulus sentences

Two types of sentences were presented to participants: sentences with a subject-relative center-embedded clause structure (e.g., “Men that assist women are helpful”) and sentences with the same meaning expressed but using an object-relative clause structure (e.g., “Women that men assist are helpful”). In half of the sentences of each type a male (e.g., uncle, father, brother) was the agent of the action and in half a female (e.g., aunt, mother, sister) was the agent of the action. All of the sentences were six words in length.

The sentences were recorded by a female native speaker of American English at an average speech rate of approximately 205 words per minute (wpm) and then time-compressed using a computer-based sampling algorithm to 80, 65, and 50% of original speaking time, corresponding to 258, 321, and 410 wpm, respectively. These rates were chosen to present a processing challenge to the participants while still allowing for generally good comprehension. This was critical due to our interest in the effects of syntactic structure, which necessitated that participants understood the entire sentence: If too few words were understood, a syntactic manipulation would have had no effect on performance.

Auditory stimulus presentation in fMRI studies is constrained by the amount of noise generated by the magnet. Because of the brief nature of our stimuli, however, we were able to present the sentences in a sparse manner by transiently halting the RF pulses, and thus minimize any impact of magnet noise on listener performance.

2.3. Task procedures

Each participant heard a total of 240 sentences, 80 at 80% of original speaking time, 80 at 65% of original speaking time, and 80 at 50% of original speaking time. The sentences were presented binaurally over fiber-optic earphones. At each speech rate half of the sentences had a subject-relative clause structure and half had an object-relative clause structure, with equal numbers of each sentence type having a male or a female agent. For each participant, half of the sentences (with equal numbers of randomly ordered subject-relative and object-relative sentences and male and female agents) were presented in an ascending order of speech rates: 40 sentences at 80% of original speaking time, 40 at 65% of original speaking time, and 40 at 50% of original speaking time. When this sequence was completed, the remaining sentences were presented in reverse order, going from the fastest speech rate to the slowest speech rate. The particular sentences heard at each speech rate were varied across participants.

For each sentence, participants were instructed to press one of two keys to indicate whether a male or

female character was performing the action described in the sentence. Participants were told to respond with their keypress as quickly as possible without making careless errors. Participants were asked to make a response for each sentence; if unsure, they were asked to give their best judgment. Response accuracy and response latencies were collected for later analysis using PsyScope presentation software (Cohen, MacWhinney, Flatt, & Provost, 1993). Participants were familiarized with the sound of time-compressed speech and the gender probe by participating in a practice session prior to entering the magnet bore. Both accuracy and speed of response were recorded while imaging data were being collected. We collected imaging data in an event-related manner, allowing us to consider only correct responses in subsequent analyses.

Two baseline blocks of stimuli designed to resemble the sensory-motor features of the sentence task were also presented on each run. Stimuli for the baseline task were speech samples spoken by either a male or a female speaker that had been band-pass filtered at 250 Hz, allowing the listener to detect the gender of the speaker but not any of the segmental (phonological) information. The participant's task was to press a key as rapidly as possible to indicate the gender of the speaker. This task thus resembled the two-choice, gender-based probe of the sentences, controlling for factors such as rapid auditory input and motor response, but did not involve linguistic processing.

2.4. Acquisition of imaging data

The experiment was carried out at 1.5 T on a GE Echosped scanner using the standard clinical quadrature radiofrequency head coil. Foam padding was used to restrict head motion. Each imaging protocol began with a 10–15 min acquisition of 5-mm-thick adjacent slices for determining regional anatomy, including sagittal localizer images (TR = 500 ms, TE = 10 ms, 192×256 matrix), T2-weighted axial images (FSE, TR = 2000, TE_{eff} = 85 ms), and T1-weighted axial images of slices used for fMRI anatomic localization (TR = 600 ms, TE = 14 ms, 192×256 matrix).

Gradient echo echoplanar images were acquired for detection of alterations of blood oxygenation accompanying increased mental activity. All images were acquired with fat saturation, a rectangular FOV of 20×15 cm, flip angle of 90° , 5-mm slice thickness, an effective TE of 50 ms, and a 64×40 matrix, resulting in a voxel size of $3.75 \times 3.75 \times 5$ mm. The echoplanar acquisitions consisted of 24 contiguous axial slices covering the entire brain every 2 s. To minimize the potential confound of a degraded acoustic signal for auditory sentences during magnet pulsation, sentence stimuli were presented during a 2 s period without magnet pulsation, following which data were acquired for 2 s.

The delay in the hemodynamic response reflecting neural activity associated with a stimulus thus allowed collection of BOLD data corresponding to sentence processing. A separate acquisition lasting 1–2 min was needed for phase maps to correct for distortion of echoplanar images. Raw data were stored by the MRI computer on DAT tape and then processed offline.

Initial data processing was carried out with Interactive Data Language (Research Systems) on a Sun Ultra 60 workstation. Raw image data were reconstructed using a 2D FFT with a distortion correction to minimize artifact due to magnetic field inhomogeneities. Individual subject data were then prepared for analysis with statistical parametric mapping software (SPM99) developed by the Wellcome Department of Cognitive Neurology (Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997). The images in each participant's time series were registered to the initial image in the series and then aligned to a standard coordinate system. These data were scaled to equate global perfusion between participants, spatially smoothed with an 8-mm Gaussian kernel to account for small variations in the location of activation across participants, and low-pass temporal filtering controlled auto-correlation with a first-order auto-regressive method. Data for individual participants were treated as random effects, and therefore analyzed individually before being pooled. Unless otherwise stated we provide contrasts with a height threshold that is significant at least at the $p < .001$ level without correction for multiple comparisons. We used an extent threshold criterion of at least 20 voxels (Forman et al., 1995). Coordinates of activation were converted (<http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispaceshtml>) from the Montreal Neurological Institute coordinates used by SPM to Talairach coordinates (Talairach & Tournoux, 1988).

3. Results

3.1. Behavioral observations

The behavioral data were collected while participants were in the scanner performing the experimental tasks. The left panel of Fig. 1 shows the mean percent of correct gender judgments for sentences containing a subject-relative or an object-relative subordinate clause at the three speech rates tested. It can be seen that there was a trend toward greater errors on the object-relative sentences, especially at the faster speech rates. A 2 (Sentence type: subject-relative, object-relative) \times 3 (Speech rate: 80, 65, and 50% of original duration) repeated measures analysis of variance (ANOVA) performed on these data showed no main effects of sentence type, $F(1, 7) = 2.72$, n.s. ($MSE = 0.018$), or speech rate, $F(2, 14) = 2.41$, n.s. ($MSE = 0.008$). There was also no

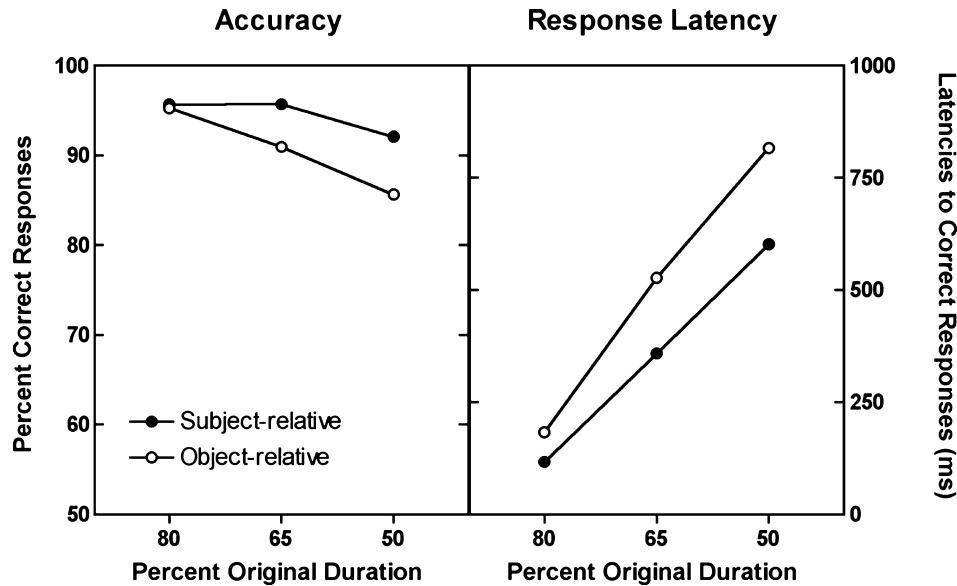


Fig. 1. Left panel: proportion of correct responses for subject-relative (filled circles) and object-relative (open circles) sentences at each of three speech rates. Right panel: latencies for these correct responses.

Speech rate \times Sentence type interaction, $F(2, 14) = 1.03$, n.s. ($MSE = 0.004$). That is, in spite of the trends towards decreasing accuracy, overall comprehension accuracy for these stimuli was good, exceeding 85% correct for object-relative sentences and 90% correct for subject-relative sentences, even at the fastest speech rate. This is in keeping with our goal of examining patterns of brain activation under conditions of processing challenge, but with generally successful comprehension performance.

Although comprehension accuracy was generally high with these speech rates, the evidence of the greater processing challenge imposed by complex syntax and rapid speech rate can be seen in the latencies to the correct judgments. These data are shown in the right panel of Fig. 1, which plots mean latencies from the ends of the sentences to correct gender responses for sentences with a subject-relative or an object-relative subordinate clause, heard at each of the three rates tested. Participants showed an increase in response times to correct responses as speech rates increased, $F(2, 14) = 57.02$, $MSE = 21,949.30$, $p < .001$, and they took longer to respond correctly to object-relative than to subject-relative clause sentences, $F(1, 7) = 7.10$, $MSE = 37,586.23$, $p < .05$. There was a trend toward a Speech rate \times Sentence type interaction, $F(2, 14) = 2.24$, n.s. ($MSE = 10,327.66$), although with faster rates such an interaction does occur (Wingfield et al., 2003).

3.2. Imaging observations

To minimize the potential confound of differing accuracy rates on neural activation patterns, we performed imaging analyses on data collected for correct responses only. Because, as noted, response accuracy was generally

high, this resulted in only a small number of discarded trials. We conducted a 2 (Sentence type: Subject-relative, object-relative) \times 3 (Speech rate: 80, 65, and 50% of original duration) factorial analysis of the imaging data.

We first examined recruitment patterns for the subject-relative and object-relative sentences collapsed across the three speech rates. These data are summarized in Table 1, in terms of the loci and extent of peak activation associated with the main effects of the two sentence types (subject-relative, object-relative). As can be seen in Table 1, relative to the baseline condition, both subject-relative and object-relative sentences resulted in increased activation in a posterior perisylvian distribution. Object-relative sentences, compared to subject-relative sentences, resulted in marginally greater activation of left inferior frontal cortex (BA 47) and right caudate, as illustrated in the left panel of Fig. 2. We also examined activation for object-relative sentences minus subject-relative sentences at each speech rate, as summarized in Table 2. Although there was some variability between conditions, object-relative sentences resulted in increased activation in left inferior frontal gyrus (BA 44/45 or 47) at all speech rates. Uniquely at the 65% rate, the extent of this activation also included some orbital frontal regions.

We next analyzed activation associated with speech rates, collapsed across sentence type. These data are summarized in the upper part of Table 3 in terms of loci and extent of peak activation for main effects of presentation rate. These analyses revealed a wide distribution of activation patterns relative to baseline. To ascertain the portion of activation due to increasing speech rate, we contrasted speech rates with each other, shown in the middle portion of Table 3. This contrast

Table 1
Locus and extent of peak activation for main effect of syntactic frame during sentence comprehension

Condition	Activation locus (Brodmann area)	Coordinates			Z value
		x	y	z	
Subject-relative > Baseline	Left posterior parietal (7/19)	-28	-68	40	3.20
	Left globus pallidus, lentiform nucleus	-12	-4	4	3.43
	Right thalamus	8	-4	4	3.67
	Right medial frontal (25)	4	11	-11	3.21
Object-relative > Baseline	Left inferior parietal (39/19)	-32	-72	29	3.40
	Right cerebellum	12	-40	-25	3.62
Object-relative > Subject-relative	Left inferior frontal (44/45/47)*	-44	15	-7	2.83
	Right caudate*	16	23	-8	2.86
Subject-relative > Object-relative	Left frontal operculum	-28	11	-11	4.04
	Left parietal (7, 40)	-28	-44	54	3.24
	Right medial frontal (10, 32)	12	46	-9	3.66
	Right temporal-parietal operculum	32	-11	19	3.14

Note. Unless otherwise noted, contrasts listed have a height threshold that is significant at least at the $p < .001$ level without correction for multiple comparisons and an extent threshold criterion of at least 20 voxels.

* Contrast is significant at the $p < .003$ level uncorrected for multiple comparisons.

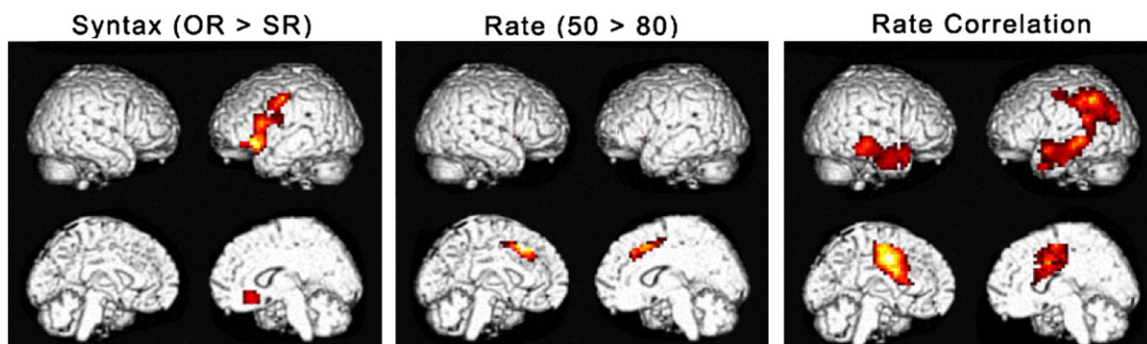


Fig. 2. Areas of increased activation for object-relative compared to subject-relative sentences collapsed across all speech rates (left panel) and areas of increased activation at the fastest speech rate (50% of original duration) compared to the slowest rate (80% of original duration) collapsed across sentence type (middle panel), as well as regions where brain activation showed a significant correlation with speech rate (right panel). Note that inferior frontal regions shown in the left panel are only marginally significant (see text and Table 1).

Table 2
Locus and extent of peak activation for interaction effect between syntactic frame (object-relative minus subject-relative) and presentation rate during sentence comprehension

Condition	Activation locus (Brodmann area)	Coordinates			Z Value
		x	y	z	
80% Original	Left premotor and inferior frontal (4/6, 44/45)	-51	-3	15	3.25
	Left inferior parietal lobule (40)	-44	-11	19	3.18
	Left inferior occipital (18, 19)	-24	-70	-3	3.73
65% Original	Left inferior frontal (47)	-36	7	-10	3.13
	Right lateral temporal	51	-62	3	3.61
	Right caudate	12	19	-8	3.39
50% Original	Left inferior frontal (45)	-55	20	10	3.15
	Left inferior frontal (44)	-48	8	14	3.10

Note. Contrasts listed have a height threshold that is significant at least at the $p < .001$ level without correction for multiple comparisons and an extent threshold criterion of at least 20 voxels.

between rates demonstrates activation in brain regions such as anterior cingulate, premotor, and striatal regions. The middle panel of Fig. 2 illustrates the distri-

bution of activation associated with sentences at 50% of their original duration compared to those compressed to 80% of their original duration. Increased activation was

Table 3

Locus and extent of peak activation for main effect of presentation rate during sentence comprehension and correlations with presentation rate

Condition	Activation locus (Brodmann area)	Coordinates			Z value
		x	y	z	
80 > Baseline	Left frontal (6)	-28	-13	49	3.35
	Left temporal (42)	-63	-30	16	3.10
	Left posterior temporal (39)	-32	-76	33	3.71
	Left thalamus	0	-19	8	3.47
	Right frontal (44)	55	12	7	3.77
65 > Baseline	Left posterior parietal (19/39/40)	-28	-68	40	3.58
	Left inferior parietal (19/39)	-28	-76	26	3.10
	Left inferior temporal (20)	-51	-36	-15	3.42
	Left posterior parietal (7)	-16	-64	40	3.13
	Right thalamus	12	-23	-2	3.77
	Right subthalamic nucleus	12	-8	-3	3.60
	Cerebellum	0	-36	-12	3.55
50 > Baseline	Left striatum	-12	7	-7	4.03
	Left parahippocampal gyrus (30)	-20	-39	2	3.40
	Right inferior frontal (44)	55	8	7	4.13
	Right ventral frontal (25)	4	7	-10	3.56
50 > 80	Left anterior cingulate (32)	-8	21	39	3.90
	Left anterior cingulate (32)	-16	10	47	3.14
	Right anterior cingulate (32/8)	4	22	43	3.47
65 > 80	Left striatum	-12	8	-4	3.20
	Right caudate	8	8	0	4.20
50 > 65	Left premotor (6)	-32	10	44	3.15
	Right premotor (6)	4	-20	56	3.15
Rate correlation	Left anterior cingulate (24)	-8	-2	37	3.90
	Left lateral temporal (21)	-59	3	-14	4.06
	Left inferior parietal (39/40)	-36	-48	47	4.47
	Right lateral temporal (21)	55	-27	-5	3.29
	Right lateral temporal (21)	51	-1	-23	3.10
	Right superior temporal (38)	36	19	-18	3.16
	Right cerebellum, pons	16	-32	-25	3.41

Note. Contrasts listed have a height threshold that is significant at least at the $p < .001$ level without correction for multiple comparisons and an extent threshold criterion of at least 20 voxels. 80 = 80% of original sentence duration; 65 = 65% of original sentence duration; 50 = 50% of original sentence duration.

seen in the anterior cingulate and medial frontal regions bilaterally.

Beyond the difference scores shown in the middle part of Table 3, we also conducted a correlation analysis to determine which areas varied significantly with increasing speech rate. This analysis was accomplished by rerunning the model in SPM99 and assigning a regressor to each scan based on the stimulus rate (80, 65, and 50%). Due to the nature of the jitter design, null events were assigned an arbitrary value of 100 and then modeled out using a secondary set of regressors that identified which scans were stimuli (a value of 1) and which were null events (a value of 0). The results from this correlation analysis are summarized in the lower portion of Table 3 and illustrated in the right panel of Fig. 2. Changes in speech rate were associated with bilateral increases in anterior cingulate cortex (BA 24) and lateral temporal cortex (BA 21/22), as well left parietal cortex (BA 39/40).

4. Discussion

Our results suggest a dissociation between the primary neural areas activated by complex syntax and those activated by increasing the rate of speech input. Specifically, activation in inferior frontal cortex was associated with successful comprehension of object-relative sentences compared to subject-relative sentences. There was no relationship between these areas and increasing speech rate. Rather, the challenge of comprehending rapidly presented sentences was associated with increasing activation centered in the anterior cingulate, supplemented by the striatum, premotor cortex, and portions of temporal cortex. Although at a behavioral level it would appear that the added demands of complex syntax and rapid speech are competing for a single resource, these neuroimaging findings are more consistent with the hypothesis that these two sources of processing demand are dissociable.

Numerous studies using both written and spoken materials have associated activity in the left inferior frontal cortex with the processing of syntactically complex sentences (e.g., Caplan et al., 1998, 1999; Just et al., 1996; Keller et al., 2001). In the current study, we also found activity in this region for object relative sentences at the fastest rate of speech used. If the commonly observed activity in BA 44/45 is indeed related to the increased working memory demands of syntactically complex sentences (e.g., Cooke et al., 2002; Fiebach et al., 2001), it would follow that shorter sentences, such as the six-word sentences used in the current study, require this information to be retained for a shorter period of time, and thus might require less inferior frontal activity. The current results indicate, however, that short object-relative sentences are sufficiently complex enough to elicit a response in this inferior frontal region.

In contrast to the predominantly inferior frontal activation observed with syntactically complex sentences, contrasts of speech rates associated faster speech rates with activity in the anterior cingulate. Anterior cingulate activation has rarely been associated with grammatical aspects of sentence comprehension in functional neuroimaging studies (Grossman et al., 2003), although ischemia in this region has been thought to disrupt sentence comprehension by interfering with task-related factors such as attention (Alexander & Schmitt, 1980; Luria & Tsvetkova, 1967; Masdeu, Schoene, & Funkenstein, 1978). Indeed, functional neuroimaging studies of healthy adults tend to associate anterior cingulate recruitment with attention, response selection, error detection, and other goal-oriented behaviors (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter, Botvinick, & Cohen, 1999; Devinsky, Morrell, & Vogt, 1995).

Of potential relevance to the current study is a study by Barch et al. (1997) in which increasing task difficulty, but not increased working memory demands, resulted in greater activation of the anterior cingulate. Participants monitored a series of visually presented letters for the presence of a probe (e.g., “B”), responding only when it followed a particular cue (e.g., “F”). Memory demand was increased by lengthening the delay between the cue and probe, whereas overall task difficulty was increased by degrading the perceptual quality of the stimulus. Increasing working memory demands led to increased activity in dorsolateral prefrontal cortex, left inferior frontal cortex, and part of the left parietal cortex. However, a different set of regions—most notably the anterior cingulate—were activated by increasing perceptual difficulty.

Although the Barch et al. (1997) study was carried out with a visual working memory task, the paradigm has much in common with the theoretical motivation of the current experiment. Time compressing speech increases comprehension difficulty on several levels. First,

the stimulus itself is degraded by the loss of information which may challenge the listener’s perceptual recognition of each word in the sentence (Heiman, Leo, & Leighbody, 1986). Second, at the sentence or discourse level, words must be integrated into a larger meaning. At this level, a large effect of time compression is the loss of processing time that would normally be available to the listener for integrative purposes (Chodorow, 1979; Foulke, 1971; Wingfield et al., 1999). In the present study, participants’ comprehension accuracy remained high in all conditions, and latencies to correct responses increased with increasing speech rate. This suggests that, although stimulus perception was generally accurate, successful comprehension required greater effort at faster rates of speech. This is analogous to the Barch et al. (1997) study in which task difficulty was increased by degrading a visual stimulus, with comprehension accuracy remaining high. The increased activation of the anterior cingulate is likely a result of the greater attention and effort required because of the degraded stimulus information and processing time pressure present in time-compressed speech.

In addition to the anterior cingulate, we found activity in several perisylvian areas to be positively correlated with faster speech rates. Previous studies have reported activations in and around the superior temporal sulci for both words (e.g., Vouloumanos et al., 2001) and complex nonlinguistic auditory stimuli (Belin et al., 1998; Binder et al., 2000; Griffiths et al., 1998). Thus, the activation observed around the superior temporal sulci in the current study is likely a result of physical characteristics of the stimuli (i.e., rapid spectral modulations) and not necessarily language specific. This is unlikely to be true for the activation seen in posterior superior temporal gyrus (BA 21/22). As noted previously, Poldrack et al. (2001) reported that activity in BA 21/22 was dependent on the intelligibility of sentences, and thus attributed it to linguistic processing rather than strictly auditory processing. There is nothing in the current data that indicates otherwise, and therefore it is reasonable to attribute this activity in the current study to increased language processing demands.

We also observed compression-related increases in the left angular gyrus and neighboring posterior inferior parietal cortex. Activity in this region has not been previously reported in studies of rapidly modulating nonlinguistic stimuli (e.g., Belin et al., 1998; Fiez et al., 1995; Griffiths et al., 1998). Because a wide variety of non-linguistic tasks have failed to elicit responses in this area, we think it likely that this activity is due to linguistic processing. Interestingly, Poldrack et al. (2001) report compression-related decreases in a similar region. Further investigation is warranted to determine the potential role of these areas in processing time-compressed sentences.

An important difference between the current study and that of Poldrack et al. is that we did not replicate

their finding of compression-related increases in the inferior frontal gyrus. One possible explanation is the difference in speech rates used: the rates in the current study (80, 65, and 50% of original speaking time) were significantly slower than those used by Poldrack et al. (60, 45, 30, and 15% of original speaking time). Poldrack et al. attribute the inferior frontal activity they observed to the processing of rapidly modulating acoustic signals. It is possible that this activation is only seen with signals that modulate more quickly than in the present study. This could be due to the physical properties of the stimuli—i.e., rapid frequency and/or amplitude shifts—or due to the extra cognitive burden associated with time-compressed speech. In the latter case, inferior frontal regions may play a “compensatory” role, in that they are only activated under cases of extreme task difficulty. This issue cannot be resolved fully based on the current data, but will be important for future studies using time-compressed stimuli. Most important for the current study is the fact that, under conditions that suggest a multiplicative behavioral effect of complex syntax and time-compressed speech, inferior frontal activation is not associated with increasing speech rates.

There is some suggestion in our data of increased involvement of the striatum at more rapid speech rates, a finding also noted in previous studies of rapid temporal processing in both non-linguistic (Rao, Mayer, & Harrington, 2001) and language-oriented (Poldrack et al., 2001) tasks. This finding is of particular interest because of the declines in sentence processing observed in non-demented individuals with Parkinson’s disease. This disease results in the interruption of a frontal-striatal loop, and difficulty with sentence comprehension in these patients has been associated limited information processing speed (Grossman et al., 2000; Grossman, Lee, Morris, Stern, & Hurtig, 2002). An fMRI study of sentence comprehension in Parkinson’s disease showed that these patients have significantly less activation of the striatum relative to age-matched healthy subjects during sentence comprehension (Grossman et al., 2003). Striatal activation has also been observed in working memory tasks for letters as part of a frontal-striatal-thalamic loop involved in short-term maintenance (Braver et al., 1997; Rypma, Prabhakaran, Desmond, Glover, & Gabrieli, 1999) and in non-verbal measures requiring resources that support planning (Dagher et al., 2001; Owen et al., 1998). Further research is needed to determine what activation of the caudate is specific to the processing of rapid linguistic input.

In the context of other studies that have separately examined time-compressed speech and syntactic processing, the current results may indicate some degree of overlap between the processing regions associated with these two sources of difficulty. Given both the widespread finding of language-related activity in both inferior frontal and superior temporal regions, it would be sur-

prising if these areas were not affected in some way by both speech rate and syntactic manipulations. However, it is significant that we observed no overlap with the current stimuli and procedure, even though these methods have elicited a reliable behavioral interaction (Wingfield et al., 2003). The dynamic nature of cortical processing (Friston & Price, 2001) and the variability with regard to specific activation foci across experimental conditions indicate that neural regions involved in linguistic processing are highly sensitive to task demands. Taken as a whole, however, the current results point to primarily distinct regions supporting rapid speech and complex syntax, despite the multiplicative behavioral effect.

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