Running Head: Repetition Priming

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Repetition Suppression for Spoken Sentences and the Effect of Task Demands

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Abstract

We examined whether the repeated processing of spoken sentences is accompanied by reduced BOLD response (repetition suppression) in regions implicated in sentence comprehension, and whether the magnitude of such suppression depends on the task under which the sentences are comprehended or on the complexity of the sentences. We found that sentence repetition was associated with repetition suppression in temporal regions, independent of whether participants judged the sensibility of the statements or listened to the statements passively. In contrast, repetition suppression in inferior frontal regions was only found in the context of the task demanding active judgment. These results suggest that repetition suppression in temporal regions reflects facilitation of sentence comprehension processing *per se*, whereas in frontal regions it reflects, at least in part, easier execution of specific psycholinguistic judgments.

Introduction

The way that a person processes a particular sensory or motor stimulus depends critically on experience, including not only general knowledge, but also specific experience with that particular type of stimulus. Behaviorally, responses to a repeated stimulus are generally both faster and more accurate; neurobiologically, repetition can be accompanied by reduced neural activity. This reduction in neural activity, when measured using neuroimaging, is referred to as repetition suppression (RS) and may reflect the invocation of earlier processes (the "greased wheels" metaphor; see, Henson, 2003).

When processing repeated stimuli, the magnitude of RS in the fMRI BOLD response has been shown to correlate with faster behavioral performance in task execution. Such correlations have been found in the left Inferior Frontal Gyrus (IFG) for word classification tasks (Maccotta & Buckner, 2004), and in pre-frontal areas for judgments of the relative size of objects (Dobbins, Schnyer, Verfaellie, & Schacter, 2004). Recently, the strong relationship between RS and behavior has been demonstrated during a semantic classification task (Wig, Grafton, Demos, & Kelley, 2005). In that study, applying transcranial magnetic stimulation (TMS) to left frontal regions disrupted subsequent neural repetition suppression for repeated trials, and eliminated the behavioral speedup associated with task repetition. These findings indicate that RS and behavioral efficiency are closely aligned.

Repetition suppression is present for repeated processing of a variety of different types of psychological "objects." In the visual domain RS has been demonstrated for line drawings and photographs of objects (e.g., Kourtzi & Kanwisher, 2000; Vuilleumier, Henson, Driver, & Dolan, 2002), faces (e.g., Henson, Shallice, & Dolan, 2000), and written words (Fiebach, Gruber,

& Supp, 2005). In the auditory domain, repeated presentation of environmental sounds also results in RS (Bergerbest, Ghahremani, & Gabrieli, 2004).

In the present study, we capitalize on the relationship between repeated processing of cognitive objects and the appearance of RS to investigate whether repeated processing of auditorily-presented sentences results in similar RS. To the extent that sentences can be processed as "cognitive objects," their comprehension should lead to representations that could later be functionally utilized (accessed) during their repeated comprehension, thus resulting in RS. In support of this possibility, a substantial body of work in both computational modeling and experimentation argues that the comprehension of expressions and sentences is affected by prior experience (familiarity) with their structure and meaning, so that their meaning is not generated solely via semantic composition. In Bod's (1998) Data-Oriented Parsing Model, it is possible to arrive at sentence meaning by a full-form-retrieval route, and Bod (2001) presents experimental data showing that frequently heard sentences (e.g., *I like it*) are stored in memory. Other work in computational modeling (ADIOS; Solan, Horn, Ruppin, & Edelman, 2005) represents grammatical knowledge solely by marking the conditional probability that certain constructions co-occur in a given context, and operates without positing parts of speech or using predefined grammatical rules. This model makes highly accurate grammaticality judgments even after training with a minimal set of input sentences.

This computational work is consistent with experimental research showing that sentence comprehension results in both surface-structure and gist-related representations (e.g., Reyna & Kiernan, 1994). The construction of such representations explains why familiar statements can be understood more efficiently. Familiar metaphors are read faster and comprehended faster than less familiar ones (Blasko & Briihl, 1997; Blasko & Connine, 1993), and familiar idioms are understood faster when they are used as figurative expressions than when they are used literally, suggesting that their meaning might be established by direct access from a mental lexicon (Gibbs, 1985; Gibbs & Nagaoka, 1985; see also Bobrow & Bell, 1973; Swinney & Cutler, 1979). Familiarity with the meaning of a certain expression (e.g., *cave-man*) slows down its comprehension when context requires that a new meaning be generated (Gerrig, 1989). These studies suggest that frequently heard sentences could have associated meanings. Finding a neurophysiological RS effect for non-frequent sentences would support this premise, as it would reveal that there are brain regions where neural processing is sensitive to the prior comprehension of that sentence.

Although behavioral psycholinguistic research shows that repeated processing of sentences and phrases is associated with easier comprehension, there are few biological data that bear on the question. Indeed, few imaging studies have examined RS in the auditory domain at all, and there is very little information about repetition effects in language processing. To our knowledge, two studies have specifically investigated RS in the context of repeated presentation of auditory stimuli, but only one of them reported such effects in brain regions typically implicated in auditory and language processing (e.g., temporal cortex, inferior frontal gyrus). In one of those studies, Bergerbest et al. (2004) presented participants with short environmental sounds that were presented in 8 blocks, and then repeated in 8 blocks. When RS effects were examined in regions that showed above-baseline activation for the environmental sounds, the analysis revealed RS in right superior temporal gyrus (STG), bilaterally in superior temporal sulcus (STS), and in the right IFG; clusters were between 2-3 voxels in size. These results are consistent with the notion that acoustic patterns can be represented as “auditory objects,” and support the possibility that RS would be evident in repetition of semantically richer auditory stimuli.

However, in a PET study (Maguire, Frith, & Morris, 1999) in which participants were presented twice with auditory stories, reduced activity was found in the middle frontal gyrus (MFG), posterior cingulate, and precuneus, rather than in temporal cortex or IFG. In this latter study, the stories were separated by eight-minute intervals that included presentation of visual materials, which could have resulted in reduced accessibility of the previous story by the time the stories were presented again. The RS effects found in these two studies do not overlap (both studies thresholded significance at $p < .001$, uncorrected for multiple comparisons), and furthermore, Maguire et al.'s findings are not consistent with the implication of the behavioral studies, which would predict that repeated processing of auditory language stimuli would result in RS in areas implicated in language comprehension. We hoped that by using repeated auditory sentences we could determine whether an auditory stimulus leads to RS in language-associated areas, thus linking the improved comprehension found in prior behavioral research with the neural mechanisms that have been associated with language comprehension. Finding no repetition suppression in such regions (Macguire et al., 1999) or relatively limited effects (Bergerbest et al., 2004) would fail to support our hypothesis. Finding RS effects in regions sensitive to the repetition of phonological information (e.g., the inferior parietal cortex) but not in those sensitive to repetition of semantic information (e.g., posterior middle temporal gyrus, MTG) would also provide scant support for our view (cf., Gold, Balota, Kirchhoff, & Buckner, 2005).

We expected to find repetition suppression effects in areas involved in sentence comprehension; including regions important for construction of sentential meaning (semantic analysis), as well as those sensitive to phonemic or lexical stimuli. A few candidates are suggested by previous research. Repetition could result in more efficient semantic analysis and easier access to lexical items. At the sentence level, the anterior portion of the superior temporal gyrus and sulcus, especially on the left but also to a lesser extent on the right, has been shown to be active in semantic integration. Humphries, Willard, Buchsbaum, and Hickok (2001) demonstrated that when the same events were depicted by environmental sounds or by sentences, the sentence condition showed increased activation bilaterally in the anterior temporal region (including both the MTG and STG). In the left hemisphere, this activation was also evident in more posterior aspects of the temporal lobe (i.e., the temporal portion of “Wernicke's area”). The left anterior superior temporal region also shows more activity during comprehension of sensible statements vs. comprehension of scrambled sentences (Vandenberghe, Nobre, & Price, 2002).

Sentence repetition could result in easier lexical access and syntactic processing. Imaging studies have identified certain regions whose activation correlates with sentence complexity (Just & Carpenter, 1996; Keller, Carpenter, & Just, 2001). For example, Keller et al. have shown that regions including the left IFG, left MFG, as well as the left inferior parietal and STG/MTG are sensitive to variations in both the frequency of lexical items in sentences and to variations in syntactic complexity. If sentence repetition facilitates syntactic processing, we would expect that these regions may also demonstrate RS. Brain regions demonstrating sensitivity to syntactic priming could also show sensitivity to sentence repetition: The left anterior superior temporal region exhibits reduced activity during the comprehension of sentence blocks in which sentences share the same syntactic structure, as compared to the blocks where the sentences vary across syntactic structure (Noppeney & Price, 2004).

Finally, repeated sentence processing could facilitate lexical access. Auditory stem completion tasks are performed faster when the word stems can be completed with words presented previously, and this priming effect is accompanied by reduced activation in the extrastriate cortex (BA 19), independent of whether the word stems are presented in the same voice as the initially presented words (e.g., Badgaiyan, Schacter, & Alpert, 2001). Yet, imaging studies employing word-stem completion tasks rarely report priming-associated reduction in neural activity in the superior and middle temporal gyri, areas dominant in language comprehension (see Carlesimo et al, 2004, Table 3 for a review, but see Badgaiyan et al. for an exception). Bergerberst et al. (2004) have offered an explanation for this pattern; they suggest that stem completion tasks rely to a greater extent on phonological representation than on the acoustic properties of the stimulus. Similarly, repeated processing of visually presented words in the context of a lexical-decision task is accompanied by RS in posterior IFG and the occipitotemporal cortex, but is absent from more central and anterior temporal regions (Fiebach, Gruber, & Supp, 2005).

In the present study, our main goal was to examine whether brain networks implicated in sentence comprehension demonstrate RS for repeated sentences. Because different types of processing strategies can result in different mental representations for sentences (e.g., Carlson, Alejano, & Carr, 1991), we investigated whether the magnitude of neural suppression would be sensitive to the manner in which a sentence is initially processed. We hypothesized that stronger repetition suppression effects may be found for tasks demanding a more in-depth analysis of sentence content (i.e., greater "elaborative rehearsal"; Craik & Lockhart, 1972). To this end, we examined repetition effects in two tasks, with different groups of participants. In one task (Exp. 1), participants heard sentences and were instructed to press a key if a sentence was *non*sensible.

In the other task (Exp. 2), participants were instructed to listen, in the absence of an explicit task. Consequently, in both tasks participants did not perform overt external responses to the sensible sentences they heard, which enabled a direct contrast between the tasks.

We also examined whether the magnitude of suppression effects depends on the sort of sentence that is repeated. Certain brain regions demonstrate either repetition suppression or repetition enhancement (i.e., increased activity) for repeated stimuli depending on the properties of the stimulus. For instance, repeated processing of familiar faces leads to RS in the fusiform region whereas repeated processing of unfamiliar faces leads to repetition enhancement in that region (Henson, Shallice, & Dolan, 2000). Similarly, repeated lexical decisions for words leads to RS in the occipitotemporal region, whereas repeated lexical decisions for pseudowords leads to repetition enhancement in that region (Fiebach, Gruber, & Supp, 2005). These effects have been corroborated by EEG data showing a decrease in gamma power between electrode sites for repeated presentation of familiar drawings, but an increase for repetition of non-familiar ones (T. Gruber & Müller, 2005). This literature suggests that the effect of repetition on sentence comprehension could depend on the ease of initial comprehension. Simple statements could be easily and fully understood in the initial presentation, and therefore repeated presentation of such statements could lead to repetition suppression. The comprehension of more complex statements might not result in equal comprehension in the initial presentation, and thus the repeated presentation may be used to elaborate on the sentence's meaning. Repeated presentation of more complex statements could therefore result in reduced repetition suppression, or even repetition enhancement.

To summarize, we examined whether repeated presentation of sentences is accompanied by neural suppression, and in this context, we identified two parameters that could affect the extent of such suppression: The processing performed on the sentence and the sort of sentence being repeated. We manipulated processing by using specific task instructions, and sentence complexity by using sentences that either contained subordinate clauses (relative, adverbial, adjectival) or sentences that did not contain such clauses but that were otherwise equated for length (see Methods).[1]

Experiment 1 (N=14) was modeled after previous repetition priming studies in the visual and auditory domains, in which participants were actively engaged in a certain cognitive task during the initial and repeated presentation of the stimuli of interest (e.g., Bergerbest et al., 2004). Participants heard sentences and indicated whether the sentences they heard were sensible or not. They only pressed a key if the sentence was not sensible. The sensible sentences were presented twice, enabling analysis of the repetition effects for these sentences in the absence of a motor response. The nonsensible sentences were ungrammatical word sequences containing grammatical or semantic errors, and in certain cases could not be recognized as ungrammatical or meaningless until the last word. As a result, it was unlikely that participants would adopt a shallow syntactic-parsing strategy to distinguish sensible from non-sensible sentences in this task.

Experiment 2 (N=11) repeated the main part of the study in the absence of an explicit task; participants were instructed to simply listen to the sentences. The change of task was done for a number of reasons. First, explicit semantic analysis of sentences could result in more elaboration than demanded by normal conversation, especially for the initial presentation of the stimulus, which could artificially enhance RS effects. Second, although RS in the context of an active task might reflect easier sentential processing, it could also reflect easier decision-making rather than more fluent language processing *per se* (cf., Dobbins et al., 2004). To evaluate whether repetition suppression would be found in the absence of such an explicit task, we designed Experiment 2 so that participants would not have to perform any task, but simply listen to the statements presented to them. This procedure could entail shallower processing of the stimuli than in Experiment 1 because participants are not required to evaluate the sentences for sensibility, and it is devoid of a decision component. There is a clear trade-off here: Whereas sensibility decisions lead to a "deeper" but unnatural sentence processing (and decision-making) than is ecologically realistic, passive listening likely entails shallower processing, but without a concomitant meta-linguistic task (see, Small & Nusbaum, 2004). As a result, Experiment 2 served as a strong test for repetition effects, in a more ecological context.

Method

Participants

Experiment 1 included 14 participants (9 females; mean age =22.5; SD = 4.8), and Experiment 2 included 11 participants (7 females; mean age = 23; SD = 5.4). All participants were right handed as determined by the Edinburgh handedness inventory (Oldfield, 1971), had normal hearing, and normal (corrected) vision. The study was approved by the Institutional Review Board of the Biological Science Division of The University of Chicago, and all participants provided written informed consent.

Stimuli and Behavioral Procedure

In Experiment 1 the materials included 36 subordinate-clause sentences (e.g., It was my mother who baked the cupcakes), 36 sentences that did not include subordinate clauses (e.g., The sportscaster observed the events and announced his opinions) and 48 ungrammatical utterances (e.g., The army that shot the old aircraft was with; Fasten the belt and go to the orange; see *Appendix*). The subordinate-clause (SC) and non subordinate-clause (NSC) sentences were matched for the mean number of words (M=10.1, SD=1.85; M=10.1, SD=1.62), syllables (M=14.9, SD =2.5l; M=13.7, SD=2.8) and lexical frequency (M=97.6, 93.6; Kucera & Francis, 1967). During the recording of the sentences, the two types of stimuli were matched for length of pronunciation. There were 192 trials in all, as each sensible sentence was presented twice. The interval between repeated presentations ranged from one intervening trial to 180 trials (Median=50 trials; 37 excluding non grammatical trials). The trials were presented in three experimental runs of 64 trials, each containing between 20-29 sensible statements. Approximately one third of sentences were repeated in the same run, and the rest were repeated in subsequent runs. The order of trials was pseudo-randomized in advance, and was identical for all participants. Each stimulus was approximately 3 seconds long, and the interval between the onset of stimuli was 10 seconds. Participants heard the sentences and indicated whether the sentences they heard were sensible or not. They only pressed a key if the sentence was not sensible. Following the scan, participants filled out a debriefing questionnaire where they were asked about their experience during the scan, their comfort level, and whether they had any hypothesis about the purpose of the experiment.

fMRI Procedure

Scans were acquired on a 3-Tesla scanner using spiral acquisition with a standard head coil. Volumetric T1-weighted scans (120 axial slices, 1.5 x 0.938 x 0.938 mm resolution) were acquired to provide high-resolution images on which to identify anatomical landmarks and onto which functional activation maps could be superimposed. For the functional scans, thirty 5 mm spiral T2* gradient echo images were collected every 2 seconds in the axial plane (TE = 25; Flip Angle = 80). A total of 320 whole brain images were collected in each of the 3 runs.

Data Analysis

Functional images were interpolated to volumes with 4 mm^3 voxels, co-registered to the anatomical volumes and analyzed using multiple linear regression. Regressors were waveforms with similarity to the hemodynamic response, generated by convolving a gamma-variant function with the onset time and duration of the trials of interest. There were 4 such regressors of interest for the first and second presentations of the non subordinate-clause and subordinate-clause sentences (NSC1, SC1, NSC2, SC2), and one for the ungrammatical sentence. The remaining regressors were the mean, linear and quadratic trends, and the six motion parameters for each of the functional runs. For the analysis of temporal modulation an additional regressor was implemented, which reflected the temporal interval between presentations of the same sentence. For the second-level group analyses, functional data were converted to stereotactic coordinate space (Talairach & Tournoux, 1988), and smoothed (5 mm Gaussian full-width half-maximum filter) to decrease spatial noise and to increase the signal-to-noise ratio. Statistical analyses were performed on the resulting signal estimates as described in the text. All analyses were corrected for multiple comparisons (family-wise error, $p < .05$, corrected) on the basis of 1000 Monte Carlo simulations (Forman et al., 1995). Based on the desired alpha level, these simulations estimate the minimum volume of contiguous activation that, for a given single-voxel threshold, would not be attributable to chance. These simulations are based on the spatial intervoxel correlation and the single voxel threshold, and were implemented using AFNI's Alphasim procedure (Ward, 2000).

Experiment 2 was similar to Experiment 1, except that it did not include the ungrammatical sentences and there was no active task. Instead, participants were instructed, "listen carefully and understand sentences spoken over the headphones; you will not respond when you hear these sentences; you should only listen attentively." The interval between repeated presentations ranged from one intervening trial to 140 trials (Median=36). Because the runs did not include ungrammatical sentences, a total of 240 whole brain images were collected in each of the 3 runs (48 trials in each run), and the regressor for ungrammatical sentences was removed from the regression analysis.

Results

Experiment 1: Active Semantic Sensibility Judgment

The post-experiment debriefing questionnaires indicated that none of the participants suspected that the purpose of the study involved examining repetition. We assessed activity for the first and second presentation of the non subordinate-clause and subordinate-clause statements (henceforth; NSC1, NSC2, SC1, SC2, see *Method*). We conducted four analyses to identify: (a) regions that were more active in the initial sentence presentations vs. baseline (i.e., NSC1 + SC1 – baseline). This analysis served to verify that our procedure resulted in activation patterns similar to those in previous studies in the literature; (b) regions that showed different activation for NSC and SC sentences; (c) regions that showed different activation for first and second presentation (a repetition effect); (d) regions that showed different magnitudes of repetition effects for NSC and SC sentences (an interaction).

Compatibility with prior studies: Regions activated during sentence comprehension. To examine comparability with prior studies, we first examined those regions that were active in the NSC1 and SC1 conditions as compared to baseline (voxel threshold $p < .005$, at least 21 contiguous voxels). Consistent with previous results in auditory sentence comprehension (e.g., Mazoyer et al., 1993), we found broad activation in STG, STS and MTG (bilaterally) along their entire course, from the temporal-parietal junction posterior to the temporal pole. There was another bilateral focus of activation in the ventral premotor cortex, more on the right than the left, and a unilateral focus of activation in the primary motor cortex on the left.

The effects of repetition, sentence-type, and interaction. To assess the effects of repetition, sentence-type, and their possible interaction, we conducted a 2 (Sentence-type: NSC / SC) X 2 (Presentation: initial / repeated) voxel-wise repeated measure ANOVA on the regression coefficients from the regression analysis, with participants treated as random factors. The results of the main effect of sentence type and repetition are presented in Table 1. To interpret the main effect of Sentence-type, we created functional masks that identified regions showing at least moderate above-baseline activity for each of the two sentence types, thus assuring that the differences reflected in the main effect would be attributable to differences in activation rather than deactivation. Therefore, areas where the main effect indicated greater activity for SC sentences were masked by (SC1 > baseline AND SC2 > baseline, each $p < .05$), and areas where the main effect indicated greater activity for NSC sentences were masked comparably. Our analyses revealed increased activation for non subordinate-clause sentences in the left STG (anteriorly), but increased activation for subordinate-clause statements in the more posterior/superior part of left STG.

Our next analysis focused on the differences between the initial and repeated sentence presentations. Because our main interest was in the effects of repetition in those areas that were actively involved in language processing in both the initial and repeated trials, we constructed an *a priori* functional mask with two goals in mind. The first was to filter out (deselect) brain regions whose activity survived a relatively lax threshold only in the repeated trials, but not in the initial ones. Activity in such areas might reflect explicit or implicit memory for previously presented materials, but these processes were not the main focus this analysis (we address them in the *General Discussion*). Also note that this constraint does not preclude finding regions demonstrating greater activation in the second presentation than in the initial one. The second goal of this functional mask was to deselect brain regions whose activity in the repeated trials did not survive a lax threshold. To this end, we constructed a functional mask that included only those voxels that showed above-baseline activation in each of the four experimental conditions (i.e., a conjunctive criterion: NSC1 > baseline AND NSC2 > baseline AND SC1 > baseline AND SC2 > baseline, each $p < .05$; overall conjoint probability for voxel in mask: $p < .00001$).

Within the functional mask, the analysis of variance revealed a number of regions showing repetition suppression (individual voxel threshold, $p < .005$; at least 5 contiguous voxels; see Figure 1). As Figure 1 and Table 1 show, repetition suppression was found in right STG extending into STS (both posterior-medial portion, as well as in a more anterior-lateral portion), in posterior left MTG/STS, bilaterally in the IFG (BA 44, 47) and in the insula. Though the mask was unbiased with respect to the possibility of finding greater activity in the second presentation than in the initial one, no regions revealed this pattern, and none showed a reliable interaction between repetition and sentence type.

Figure 1 about here

Given that the analysis of the repetition effects did not reveal an interaction between sentence-type and repetition, or repetition enhancement, we conducted a more exploratory analysis of repetition effects over the entire brain volume (voxel threshold $p < .005$, at least 10 contiguous voxels). Note that RS effects in this analysis are independent of the voxel's activity vs. baseline in the first and second presentations. In this analysis (see Figure 1), reliable RS was found in several brain regions. These were found in the right caudate, bilaterally in STG/STS/MTG (mainly in STS), the cerebellum (bilaterally), left IFG (BA 44), right IFG (BA 44, 45) left superior frontal gyrus (SFG) and left precentral gyrus (PCG).

The RS effects in temporal cortex were similar to those found in our analysis based on a functional mask, and might reflect more fluent processing of the linguistic stimuli. Caudate activation in verbal tasks has been associated with phonological rehearsal (Davachi, Maril, & Wagner, 2001; O. Gruber & von Cramon, 2003), and the reduced activation might indicate that participants were rehearsing the sentences to themselves during the metalinguistic task performance; as we show later, such reductions were not found in the passive task. Repetition enhancement was found in the precuneus and angular gyrus (bilaterally), and in the left posterior cingulate gyrus. As we discuss later, activity in such areas is often associated with explicit recognition of previous items.

Experiment 2: Passive Listening

Compatibility with prior studies: Regions activated during sentence comprehension. As in the active task, we began by examining those regions that were active in the NSC1 and SC1 conditions as compared to baseline (voxel threshold $p < .005$, at least 50 contiguous voxels). This analysis revealed reliable bilateral activation across STG/STS and MTG, extending from the occipito-temporal area to the posterior part of the temporal poles. There was also reliable bilateral activity in the thalamus. These results are similar to the ones found in the active task, though they did not reveal involvement of premotor or primary motor areas.

The effects of repetition, sentence-type, and interaction. The analyses were based on the same logic as Experiment 1, and the results reported in Table 1. The main effect of Sentence-type revealed one region in left STG that was more active for non subordinate-clause statements, and another region in left STG, more posterior and superior, that was more active for subordinate-clause statements. This pattern replicates the one found in the active task. In addition, the subordinate-clause statements were associated with more activation in the right transverse temporal gyrus (TTG).

A main effect of repetition was found in one region in the posterior portion of the right MTG (256 mm^3; see Table 1, Figure 2). As in Experiment 1, no regions showed repetition enhancement, nor did any show an interaction between the sentence type and repetition.

Figure 2 about here

Figure 2b presents the whole-brain analysis of repetition effects in the analysis of the passive task (voxel threshold $p < .005$, at least 10 contiguous voxels). This analysis revealed repetition suppression effects in MTG/STS (bilaterally) as well as in the middle occipital gyrus (left) and right cuneus. As in Experiment 1, repetition enhancement was found in the left posterior cingulate and precuneus (medial regions not shown in Figure).

This analysis also revealed two regions that showed a repetition suppression effect for the non subordinate-clause sentences but a repetition enhancement effect for subordinate-clause sentences (i.e., an interaction effect; Figure 2c). As Figure 2c shows, the right cuneus and the right lingual gyrus / BA18 demonstrated a reliable repetition suppression effect for NSC sentences, but a reliable repetition enhancement effect for SC sentences.

Direct Contrast of the Active and Passive Tasks

The independent analyses of the active and passive tasks revealed common repetition suppression effects in the middle temporal lobes, as well as repetition enhancement effects in the cingulate and precuneus. However, there were also some differences: The active task produced reliable repetition suppression effects in IFG and left MTG, which were absent from the passive task. We carried out a direct contrast between the tasks to examine which of the differences between the tasks were statistically reliable. We combined the data from both tasks and conducted a mixed 2 (Task: active, passive) X 2 (Presentation: initial, repeated) voxel-wise ANOVA with task as a between-subjects factor and presentation as a within-subjects factor. This analysis also offered a more sensitive assessment of repetition effects due to its increased power. Because this analysis compares across two experimental tasks, we set the individual voxel threshold to $p = .01$ (Monte Carlo simulations indicated that given this threshold, a cluster should consist of at least 12 contiguous voxels). To enable maximal sensitivity in finding differences between the active task and passive task, we did not mask the results of this analysis by any functional or anatomical mask, as the application of such masks could reduce the sensitivity to finding between-task differences.

Several regions were found to be more active in the active task than in the passive one, including medial aspects of STG and cingulate gyrus bilaterally, and the right insula. The left anterior cingulate and the right transverse temporal gyrus showed stronger activity in the passive task. However, the magnitude of the main effect of Task in all the clusters reported here was rather small (maximally 0.4%).

To interpret the main effect of repetition in the ANOVA, we partitioned voxels that showed repetition suppression from those that showed repetition enhancement. We defined voxels as demonstrating repetition *suppression* when they demonstrated (a) a main effect of repetition, (b) greater % signal change in the initial than repeated presentation, and (c) an above-baseline % signal change in the first presentation (constraints *b* and *c* filter voxels showing repetition enhancement or voxels that differ only in degree of *de*activation). The results of this analysis (Figure 3) revealed much of the same pattern found in the whole-brain analyses of the repetition effects in Experiments 1 and 2 (though more extensively). In addition, it revealed repetition suppression in more anterior aspects of IFG (BA45 bilaterally), extending into BA47 in the left hemisphere, the parahippocampal gyrus (bilaterally), the temporal poles of STG (bilaterally), the right hippocampus, and the left middle occipital cortex (BA19). Repetition *enhancement* was defined whenever a voxel demonstrated reliably greater activity in the second presentation. Bilateral repetition enhancement effects were found in the angular gyrus and supramarginal gyrus as well as in the precuneus and posterior cingulate.

A number of regions showed a reliable interaction between the two factors (i.e., repetition effects in the active task (A) differed from that in the passive task (P); (A1-A2) – (P1-P2) ≠ 0; see Figure 3), but it is important to note that no such interactions were found in temporal cortex. Areas that demonstrated greater repetition suppression in the active task (i.e., (A1-A2) – (P1-P2) > 0 AND (A1 - A2) > 0) included the IFG (~ BA 44, 45) bilaterally, insula (bilaterally), left cingulate gyrus, the anterior right IFG (BA47), as well as subcortical structures. One area, the anterior cingulate gyrus (bilaterally), demonstrated a different sort of interaction effect (not shown in Figure). It demonstrated repetition enhancement in the active task, but repetition suppression in the passive task. No other interactions were reliable.

Figure 3 about here

The main finding of this analysis is that the active task did not result in greater activation in lateral aspects of STG/STS and MTG where repetition effects were found in Experiments 1 and 2, and neither was there an interaction between Task and Presentation in those regions. This null result suggests that the patterns of repetition effects in temporal areas that were described in the active and passive tasks did not differ reliably. In contrast, we did find a Task by Presentation interaction in IFG, indicating differential sensitivity to repetition in that area as a function of task. Given that repetition suppression effects in this analysis were not functionally masked, they might be found in areas that became disengaged during the repeated presentation as a result of “top-down” attentional process. In this sense, some of the areas demonstrating suppression effects (especially frontal) might not be part of a ‘core’ language network that is engaged in routine language comprehension.

Temporal Modulation of Repetition Effects in Active and Passive Tasks

In this analysis, we investigated whether the interval between the initial and repeated presentations correlated with the magnitude of the suppression effect. To the extent that repetition suppression reflects less effortful processing of sentences, we would expect that the magnitude of repetition suppression would be strongest when the repeated sentence is presented shortly after the initial one, and weaker as the temporal interval between the presentations increases. Previous studies have demonstrated such temporal modulation of suppression effects in the visual domain (Henson et al., 2000; Henson, Rylands, Ross, Vuilleumeir, & Rugg, 2004).

We conducted this analysis for both non subordinate-clause and subordinate-clause statements in both passive and active tasks. In this analysis, for each voxel we obtained a statistic that reflected the correlation between (a) the *difference in activation* between the initial and repeated presentations (Δ_{BOLD} = initial_activation – repeated_activation), and (b) the temporal interval between presentations.[2]

In general, the modulation analysis revealed two patterns, albeit with some variation between the active and passive tasks (see Table 2): Frontal and temporal regions demonstrated repetition suppression that decreased in magnitude the greater the temporal interval between presentations (this pattern was stronger in the active task). Second, regions in the left posterior cingulate and in the right cuneus demonstrated repetition enhancement that decreased in magnitude the larger the temporal interval between the presentations.

General Discussion

We examined whether repeated comprehension of spoken sentences is accompanied by decreased neural activation (repetition suppression, RS) in brain regions typically implicated in sentence comprehension, and whether the magnitude of such RS depends on the task under which the sentences are comprehended or on the complexity of these sentences. We found that sentence repetition was associated with RS in temporal regions, independent of whether participants were judging the sensibility of the statements (an active task) or were listening to them passively. In contrast, RS in inferior frontal regions was only found in the context of the task demanding active linguistic judgment. These results suggest that RS in temporal regions reflects more fluent sentence comprehension *per se*, whereas in frontal regions it reflects, at least in part, easier execution of an experimental psycholinguistic judgment.

Repetition Effects and Language Processing in the Temporal Lobe

Recent research has begun shedding light on sentence- and discourse-level processing carried out in the temporal lobe. Xu, Kemeny, Park, Frattali, and Braun (2005) demonstrated that areas in MTG show increased activation as a task advances from processing of single words, to sentences, and to complete narratives. Notably, activation in left posterior STS was found only in narrative comprehension, but not for processing of single sentences or single words. The authors suggested that activity in left STS therefore reflects "yoking a variety of cognitive processes to knowledge about the world". Similarly, Mazoyer et al. (1993) reported that certain regions in left STG and left MTG were reliably active during the comprehension of stories, but not during the comprehension of semantically anomalous sentences or single words, highlighting the importance of these regions for sentence-level processes that go beyond acoustic or lexical processing. Finally, St. George, Kutas, Martinez, and Sereno (1999) found that when a given paragraph was more easily understood (as a result of supplying its title in advance), there was decreased activity in temporal regions, perhaps indicating easier generation of a discourse-level representation. Such studies suggest that recently processed information affects processing in temporal regions, resulting in either increased activity (Mazoyer et al., 1993; Xu et al, 2005) or decreased activity (St. George et al., 1999).

Our results support the possibility that the central portions of STG/MTG (including BA 21, 22) are part of a network that links the processing of incoming speech with recently encountered information. In the case of repeated processing of sentences, the increased availability of such knowledge as a result of prior comprehension (in a repetition context) results in reduced activity in these regions. A number of data points in our results support the interpretation that regions implicated in sentence processing are also sensitive to recently processed information. We first note that in our analyses that were constrained by a language-sensitive functional mask, we examined and found RS in areas that showed above-baseline activation in *both* the initial and repeated presentation. That is, in these regions, prior exposure modulates activation, but does not eliminate it. The data also indicate that the sensitivity to prior context was present in both the active and passive task therefore suggesting the effect is not a result of a specific comprehension strategy. We found reliable bilateral RS in STS in the active task, and in right MTG in the passive task. Temporal regions on the left did not demonstrate reliable RS in the passive task (in areas included in the functional mask), but did demonstrate a reliable correlation between the magnitude of RS and the temporal interval between the initial and repeated presentation. Such correlations were also found in right MTG (posterior) in the passive task and left MTG (posterior) in the active task. Repetition suppression in temporal regions was also found in the whole-brain analyses in Experiments 1 and 2, which were not functionally masked, and was also established in the joint analysis of both tasks. The absence of a reliable effect of RS in the left hemisphere during the passive task was unanticipated, especially since such effects were found on the right. If this finding were the only data point, it could be argued that the repetition effects in the passive task excluded left hemisphere regions known to be involved in language processing, and consequently, that these effects index cognitive processes that are not related to establishing sentence meaning. It is therefore important to note that in the passive task, left hemisphere regions did demonstrate sensitivity to recent sentence comprehension, which was evident in the modulation of the RS effects as a function of temporal interval. Thus, the left hemisphere was sensitive to prior processing, albeit more weakly so than in the right hemisphere.[3] Furthermore, the direct comparison of the active and passive tasks revealed that the magnitude of RS in temporal regions did not differ reliably between the two tasks (i.e., no reliable Task by Presentation interaction) suggesting that in those areas sentence processing was relatively independent of strategic task effects. We interpret this pattern of results as showing that MTG and STS (bilaterally) demonstrate sensitivity to prior processing of sentences during language comprehension.

It remains a question whether or not STG and MTG are involved in the actual evaluation of new versus existing information; current studies suggest they are not. Temporal regions are not sensitive to whether a statement is true or false (Hagoort, Hald, Bastiaansen, & Petersson, 2004), and it seems they are not necessary for evaluating whether a sentence validly follows from previously read sentences (cf., Goel, Buchel, Frith, & Dolan, 2000; Goel & Dolan, 2001; Goel & Dolan, 2003). Such findings are consistent with the role of temporal regions in linking incoming stimulus with prior information, but suggest they are not implicated in higher-level evaluation of that stimulus.

Our results are also consistent with those of Bergerbest et al. (2004) who reported RS in MTG for repeated environmental sounds. However, both our findings and Bergerbest et al.'s (2004) are in some contrast to studies that have examined stem-completion in the auditory domain. The majority of such studies report that when stems are completed with recently heard words (as opposed to when they are not), the decreased task difficulty is not accompanied by reduced activity in temporal regions (Badgaiyan, Schacter, & Alpert, 2001; Carlesimo et al., 2004). We concur with the hypothesis of Bergerbest et al. (2004) that the priming effects found during stem completion might reflect the relative importance of phonological representation in such tasks. Sentence comprehension, however, is more likely to depend on lexical and sentence level semantics whose processing is associated with activity in temporal regions. Indeed, even in studies carried out visually, access to lexical items is associated with reduced neural activity in temporal cortex when these items are semantically primed. For example, the processing of semantically primed words that are presented for lexical decision (e.g., primed *doctor – nurse* versus unprimed *bread – nurse*) is often accompanied by reduced neural activity in anterior parts of left MTG (Copland et al., 2003; Rossell, Price, & Nobre, 2003) and left STG (Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Rissman, Eliassen, & Blumstein, 2003). These studies are consistent with our results as they indicate that semantic priming can result in reduced activity in temporal areas.

Repetition Suppression in the Inferior Frontal Gyrus

In Experiment 1 that included an active judgment task, RS was evident bilaterally in dorsal/posterior aspects of IFG (pars opercularis; BA 44). In the right hemisphere, repetition suppression in the pars opercularis showed temporal modulation; the magnitude of repetition suppression decreased as the temporal interval between the initial and repeated presentation decreased (for non subordinate-clause statements). Temporal modulation for subordinate-clause statements was found in the border of pars opercularis and pars triangularis (BA 44/45).

The pars opercularis has been implicated in both semantic and phonological tasks though its involvement in semantic tasks might be attributed to the phonological demands of those tasks (Poldrack et al., 1999; Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000). It demonstrates more activity in phonological than semantic tasks (Devlin, Matthews, & Rushworth, 2003), and rTMS interventions indicate that it is probably necessary for phonological processing (Nixon, Lazarova, Hodinott-Hill, Gough, & Passingham, 2004). However, there is also some evidence implicating it in syntactic processes (e.g., Dapretto & Bookheimer, 1999; Fiebach, Gruber, & Supp, 2005).

A number of studies have reported reduced neural activity in the posterior portion of the IFG in the context of semantic and phonological repetition tasks involving single words or visually presented objects (Wagner et al., 2000, BA 44/6; Fiebach et al., 2005, fronto-opercular region; Henson et al., 2004, posterior IFG). However, Stowe et al. (1999) did not find repetition effects in IFG for word repetition, and neither did Badgaiyan et al. (1999, 2001) in a stem-completion task in the auditory domain. Studies of semantic priming in the context of lexical-decision are inconsistent on this point: some report priming-related suppression in IFG (e.g., Copland et al., 2003, BA 11; Matsumoto et al., 2005, BA 45 and 47), and others do not (Rissman, Eliassen, & Blumstein, 2003; Rossell, Price, & Nobre, 2003).

Theoretically, the suppression of activity in IFG as a consequence of repetition might reflect more fluent processing of syntactic or phonological properties of the stimuli, or an easier application of the decision process to that stimulus (or both). We found RS in IFG in the active task, but not in the passive task, and this difference was confirmed statistically in the direct contrast between the tasks: The statistically reliable Task by Presentation interaction effect found for IFG (BA 44, 45) suggests that RS in that area was at least in part driven by explicit task demands. Had the results reflected solely more efficient phonological or syntactic processing, we would have expected similar patterns of RS in both tasks. The possibility that RS in IFG reflects easier task execution is supported by results of a study by Wagner et al. (2000). They found that repeated presentation of lexical items was associated with RS in anterior left IFG (BA 45/47), but only when the same task was performed in the initial and repeated item presentation. When previously shown items were presented in the context of a novel task, no RS was found in these regions. In summary, repetition suppression in IFG during language comprehension might reflect (at least in part) a more fluent task execution rather than more fluent syntactic, semantic or phonological processing *per se* (see Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003, for related discussions of IFG functions; see Dobbins et al., 2004, for discussion of repetition suppression and task contexts).

Repetition Enhancement and its Modulation as a Function of Sentence Type

Repetition enhancement (greater activation in the repeated presentation) was found in a number of brain regions: In Experiment 1 this pattern was found in the precuneus and angular gyrus (bilaterally), and also in the left posterior cingulate gyrus. In Experiment 2, this pattern was found in the left posterior cingulate and left precuneus.

Repetition suppression in certain brain regions is often accompanied by repetition enhancement in others. Previous reports of repetition enhancement in the precuneus, angular gyrus or posterior cingulate have been reported for repetition of visual (Fiebach et al., 2005; Schott et al., 2005; Henson et al., 2004) and auditory stimuli (Bergerbest et al., 2004). Also, the cingulate gyrus (mainly posterior) and the cuneus have been found to show repetition enhancement that decreases as the temporal interval between presentations increases (Henson et al., 2004). Such findings support the conjecture that these areas are involved in explicit memory for or episodic recall of previously encountered stimuli. Furthermore, Schott et al. (2005) suggest these areas are implicated in explicit but not implicit priming: The authors found that whereas priming in the absence of conscious recognition was associated with decreased activity in inferior temporal and parietal areas, conscious recognition of previously studied items was associated with increased activity in the precuneus and posterior cingulate. On the basis of such findings we suggest that the repetition enhancement found in our study correlated with the explicit recognition that an item has been presented previously.

In Experiment 2, we found that the lingual gyrus exhibited bilateral repetition enhancement for the subordinate-clause statements, but repetition suppression for the non subordinate-clause statements. We suggest that this pattern reflects a learning process where simpler stimuli are rapidly consolidated into memory, whereas the more complex stimuli necessitate further processing until they are sufficiently encoded. Our results are similar to interaction effects reported by Fiebach et al. (2005). In their study, repeated processing of words resulted in repetition suppression in the lingual gyrus, but repeated processing of pseudowords resulted in repetition enhancement in that region. Such findings are also similar to those of Henson, Shallice, and Dolan (2000), who found that in the fusiform gyrus there was repetition suppression for repeated presentation of famous faces, but repetition enhancement for repeated presentation of non-famous ones. In both these studies, the interaction effects were found in the context of tasks demanding active judgments, which could imply that our failure to find the interaction effect in the context of the active task (Exp. 1) had to do with insufficient power.

In both the study of Fiebach et al. and that of Henson et al., stimuli were presented visually, and Fiebach et al. (2005) suggest that the interaction pattern is indicative of the construction of "extrastriate object representations." At this point, there are insufficient data to determine whether during repeated processing, the lingual gyrus operates solely on modality-specific or more abstract properties of stimuli; this topic could be explored in the future. Nonetheless, a number of studies have implicated the lingual gyrus in a variety of cognitive tasks that involve rehearsal, learning, or integration of currently processed stimuli with previous information, and some of these studies have employed non-visual materials. Increased activity in the lingual gyrus is found during the maintenance of famous names and faces as compared to unknown ones (Rama, Sala, Gillen, Pekar, & Courtney, 2001), and during the processing of meaningful as compared to non-meaningful sentences (Kuperberg et al., 2000). It is also active in contexts that demand logical reasoning and integration of information (Noveck, Goel, & Smith, 2004). Schott et al. (2005) reported bilateral repetition suppression in the lingual gyrus when words stems could be completed with previously learned words. Such results indicate the involvement of the lingual gyrus in learning processes, specifically, the establishment of new memories.

Conclusions, and Remaining Questions

Taken as a whole, the repetition suppression and enhancement effects, as well as their temporal modulation, indicate that participants often recognized sentences they had previously heard, and that those repeated sentences entailed less effortful processing in temporal and frontal areas. The analyses based on functional masks revealed a portion of the language network that was involved in processing both initial and repeated sentences, but less so for repeated presentations. The whole brain analyses of repetition suppression, and especially the joint analysis of both experiments, revealed broad suppression effects in areas encompassing temporal and inferior frontal regions. These results point to a novel distinction in temporal cortex between regions that are sensitive to prior processing of sentences and those that are not. Inferior frontal regions demonstrated suppression effects whose magnitude varied as a function of comprehension strategy, indicating that language processing in that region was more sensitive to task demands.

The repetition suppression effects might indicate, for example, easier processing of previously encountered syntactic structures, easier semantic integration, easier access to lexical items, easier phonological-to-lexical mapping, and/or various other processes underlying sentence comprehension. The current study was aimed to interrogate the existence of sentential repetition suppression and its sensitivity to task demands, and so we cannot categorically establish whether parts of the network showing suppression are indicative of advantageous lexical access, syntactic processing, or semantic integration.

However, previous research suggests that the suppression effects found here likely indicate more fluent processing that goes beyond lexical or syntax-based explanations alone. First, syntactic priming in itself is accompanied by more limited neural reduction in the left temporal pole (Noppeney & Price, 2004). Second, Stowe et al. (1999) found that repeated processing of printed words resulted in RS in the fusiform gyrus and the Inferior Temporal Gyrus, whereas RS in posterior aspects of MTG and STG was weaker and not reliable, in contrast to our results. Neither Noppeney and Price (2004) nor Stowe et al. reported suppression in IFG. In contrast, we found reliable pattern of suppression that extended to more posterior portions of MTG and STG, as well as in frontal regions. The possibility that RS effects found here indicate facilitated processing within the lexicon alone is also inconsistent with numerous behavioral studies showing that the more fluent processing of repeated discourse cannot be explained solely on the basis of more fluent lexical access (see, Raney, 2003 for a review). For example, Carlson, Alejano and Carr (1991 Exp. 1) had participants read paragraphs for comprehension either after reading the same paragraph or after reading its word-scrambled version. Behavioral facilitation was found only when the paragraph was read after its coherent version – no facilitation was found after reading the scrambled-word version (interestingly, facilitation was found in both cases when the instructions emphasized that participants should read the text word by word).

Our findings demonstrate that repetition suppression proves a promising method for studying the neurological basis of sentence comprehension. The repeated comprehension of sentences reveals the typical characteristics of repetition suppression found in non-sentential domains; i.e., reduced neural activity in areas implicated in task processing, enhanced neural activity in regions associated with explicit memory, and temporal modulation of these effects as a function of the interval between presentations. Conjointly, the method is sufficiently sensitive to identify regions that differ in their response to the experimental orientation task. Thus, future research could employ this method to further examine the loci of the sentential repetition effects reported here, resulting in increased understanding of systems underlying sentence comprehension.

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Appendix

Sentence	Length (seconds)
Subordinate-clause sentences	
Please shine the boots that he wore.	2.1
Was it the janitor that emptied the trash?	2.4
Please measure the fabric because he sheared it.	2.6
Furnish the loft because it has high rent.	2.8
It was the dealer that sold the convertible.	2.5
The doctor prescribed the medicine that she wanted.	3.0
Polish the lamp because it was by the vent.	2.7
Garnish the platter before it is on the ledge.	3.0
Did the plumber that I called clear the drain?	2.5
The mother wishes her son would vacuum the carpet.	2.9
The general that ordered the attack had no authority.	3.4
The guitarist played the song that went triple platinum.	3.1
Will the butler serve the sandwiches that she brought?	2.7
It was the pilot that she saw start the helicopter.	3.2
The chef that cooks at that restaurant uses exquisite knives.	3.7
It was the carousel that he found the toddlers riding.	3.1

Should the butcher grind the meat because he chopped it?	2.6
Should the family thank the fireman that saved their cat?	3.4
The engineer bought the shirt while it was in front.	3.0
The clerk straightened the shelf after the customer broke it.	3.1
The analyst opened the website because it contained the information.	3.7
The accountant did the tax forms because I paid him.	3.1
The artist composed the letter after he mailed a package.	2.9
Did the bassist listen to the track before it was recorded?	3.3
Please juice the lemon before he lays it in the bowl.	3.1
The actress that I saw win the award was the best.	2.9
The jeweler designed the ring that is in the display box.	3.2
Was it the biker that she witnessed pass the stop sign?	2.9
The player caught the ball that her teammate threw to her.	3.3
The dog that he watched run down the street bit his leg.	3.5
Should the assistant print the documents after they are in the computer?	3.7
The librarian shelved the item because I set it in the bin.	3.3
Will the critic attend the premiere because the actor is in the movie?	4.0
Will the carpenter chisel the design after he transfers it onto the dresser?	4.1
Did the patient that the pharmacist advised about the pills buy the ice pack?	4.3
Please fertilize the plant that he put by the window.	2.9

Non subordinate-clause sentences

Can the pediatrician inspect the instruments in the kit?	3.0
Did the ad talk about the new prices and the discount?	2.9
Did the broke merchant need to sell the silver rings?	3.0
Did the comedian present the monologue and smooth his hair?	2.8
Did the creative poet and the inspired writer need to impress the rich manager?	4.5
Did the lean racer need to wrap his stiff sore knee and ice his sprained ankle?	4.5
Did the quick swimmer need to wear the cap in the pool?	3.2
Did the roommate need to whine about the large apartment?	2.7
Have the handsome groom and the dazzling bride chosen the perfect chapel?	3.6
Please arrange the fresh yellow flowers and water the growing plants.	4.2
Please drive around the plastic orange cones.	3.0
Should the over-worked repairman mend the gold watch?	2.8
The agent needs to schedule the afternoon meeting	3.1
The attendant and the conductor punched the little white stubs.	3.1
The blonde host interviewed the hopeful author.	2.5
The dentist and hygienist need to examine many hospital records.	4.0
The determined runner did not miss the awaited marathon.	3.2
The elegant princess in the ballet twirled beside her strong partner.	4.3
The energetic sailor needs to anchor the boat to the dock.	3.5
The famous painter chose the bright colors from the samples.	3.3

The hungry diner raced through the crowded cafe.	2.8
The infant in the crib grasped the fringe on the blanket.	3.1
The lawyer and the aide at the firm fired the employee.	3.4
The maid mopped the muddy floor and scrubbed the tiles with the bleach.	3.7
The nervous pianist played the piece and finished the tiring concert.	3.7
The obsessive fan ran through the crowd in front of the band.	3.3
The sleepy passenger shoved his luggage under the seat.	3.0
The stubborn worker needed to scan the glossy color prints?	3.4
The stunning model needs to talk with the photographer.	3.2
The upset guard failed the intensive training?	2.4
The weary commuter on the train closed his eyes.	2.7
Why did the irate rebel pillage the town?	2.4
Why did the snobby realtor need to see the house?	2.5
Will the cautious editor sift through the numerous commentaries?	3.2
Will the guest hang his wool coat and his blue umbrella?	3.1
The noisy resident slammed the metal door in the screen gate.	3.2

Ungrammatical materials (Experiment 1)

The army that shot the old aircraft was with	2.8
Fasten the belt and go to the orange	2.3
The tense broker should inform his numerous trusting clients and go to the	3.9

Did the captain wishes to cook the breakfast while he did	3.0
The character took the message in his eager friend	2.5
The child unhappy wanted to win the heavy gold trophy but did not	3.8
Of the civilian that heard the talk	2.0
The young collector are the stones and the stamps	2.9
The columnist prepared the advice and the horoscope bad	3.0
The news correspondent entyped the evening telecast	3.1
The court tried down the evil English criminal	2.7
Through the seven dwarves made the enormous bed	2.8
It were the evidence that the detective thought to examine many times	3.4
The chief executive and the busy director has discussed the marketing idea	4.3
Can the explorer will draw the map and recall the stories	3.2
Father informed read the simple modern manual	2.8
Go of the forest and pick some daisies	2.4
The bitter girl and the brother despised need to sign the awaited family agreement	4.4
Will he aft and the play the prince	1.9
Hero is avoid the dangerous nuclear bomb	2.6
Herself phoned the library personnel the other day	3.0
The bright image covered massive thin screen	2.8
The ideal judge are selecting the vital moral jury	3.1
The lady accepted the money for himself	2.4

Squeeze the please ripe juicy lime before she makes drinks	3.4
The man performed herself the short skit over the bridge	3.1
The project manager compared the agenda the other	2.9
The worried that mother watched the	1.9
The nanny good held the small crying baby	2.5
Who the neighbor of closed the curtains	2.0
The married official should buy the expensive diamond necklace but he want to	4.1
The philosopher has started fewer conversations than	3.3
Religious player said the old catholic prayers	3.0
Roman poet gave great first performance	2.8
The politician wrote speech before she goes to the ceremony.	3.3
The former principal left the school after she teaches in the city	3.3
The prisoner needs to change his clothes and remain his cell	3.2
The chemistry research that the lab technician read is not	3.5
Do the sergeant apply the rule in the barrack	2.3
Who will she consider take the position and of	3.3
The starving girl wants to eat the eggs before herself.	3.1
The teacher spent the check that she clown	2.5
The opposing team lost the summer season that	2.7
The educated therapist heard troubled couple while in extensive sessions	4.6
Find the new treasurer and go to finance committee	2.8

The voter completed the poles because the candidates	3.1
The attractive waiter set three crisp cloth napkin	3.1
The struggling youth sold the van that is non	2.7

Author Note

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Footnotes

[1]We use the term *complexity* here without committing to whether it reflects syntactic-specific processes or more general differences in working memory demands; for an extended theoretical discussion of this issue see Friederici, Fiebach, Schlesewky, Bornkessel, and von Cramon (in press); for neurophysiological findings, see, e.g., Münte, Szentkuti, Wieringa, Matzke, and Johannes (1997).

[2]In this analysis, a negative correlation indicates that as the temporal interval between two sentence presentations increases, Δ_{BOLD} decreases. A negative correlation might thus reflect decreasing repetition suppression as the interval between the initial and repeated presentation increases (e.g., Δ_{BOLD} might be a large positive value when the repeated presentation is temporally close to the initial presentation, but a lower positive value when the repeated presentation is more temporally remote). However, a negative correlation could equally reflect increasing repetition enhancement over time (e.g., Δ_{BOLD} might be a small *negative* value when the initial and repeated presentations are temporally adjacent, but a large negative value when the repeated presentation is more temporally remote). Consequently, because the theoretical interpretation of a negative correlation depends on whether Δ_{BOLD} varies across positive or negative values, we masked the correlation analysis by functional masks that selected voxels demonstrating reliable repetition suppression or repetition enhancement (corresponding to positive or negative mean Δ_{BOLD} values respectively, $p < .01$, uncorrected). Thus, a negative correlation in a voxel with a positive mean Δ_{BOLD} indicates that the magnitude of repetition suppression decreased with the interval between presentations, whereas a negative correlation in a voxel with a negative mean Δ_{BOLD} indicates that the magnitude of repetition enhancement increased with the interval between presentations. The same logic applies to the interpretation of

positive correlations, as we outline in our discussion of the modulation results. In our analysis we considered only those areas that survived these masks.

[3]Recent data collected in our lab further demonstrates that the left hemisphere is sensitive to prior discourse context during passive comprehension of auditory sentences (Hasson, Nusbaum, & Small, 2006).

Tables

Table 1.

Repetition and Sentence-Type Effects in Experiments 1 and 2 (Center of Mass)

Contrast	Region	Talairach coordinates			Volume
		X	Y	Z	
	Active task				
NSC > SC					
	L. STG	-43	-21	7	1600
SC > NSC					
	L. STG	-49	-54	17	256
First > Second					
	R. STG	41	-32	3	1024
	R. STG	49	-9	-2	960
	L. MTG	-44	-40	2	640
	R. IFG	42	6	23	512
	R. Insula	30	20	4	448
	L. Insula	-32	-30	19	448
	R. TTG / STG	33	-39	10	384
	L. IFG	-41	9	22	384

	L. MTG	-57	-48	4	320
		Passive task			
NSC > SC					
	R. TTG	50	-26	10	448
	L. STG	-50	-16	7	384
SC > NSC					
	L. STG	-55	-52	21	320
First > Second					
	R. MTG	51	-45	8	256

Note. Center of mass given in Talairach coordinates. NSC = Non Subordinate-Clause Sentences. SC = Subordinate-Clause Sentences. STG = Superior Temporal Gyrus. MTG = Middle Temporal Gyrus. TTG = Transverse Temporal Gyrus. IFG = Inferior Frontal Gyrus. TTG = Transverse Temporal.

Table 2.

Modulation Effects for Non Subordinate-Clause and Subordinate-Clause Statements In Experiments 1 and 2 (Center of Mass)

Contrast	Region	Talairach coordinates			Volume
		X	Y	Z	
	Active task				
NSC:					
Decreasing Repetition Suppression					
	L. MTG	-58	-46	6	832
	R. IFG	43	3	26	640
	R. Caudate	9	6	5	512
	L. MTG / STG	-45	-41	5	384
	L. PCG	-45	-15	49	320
	R. SFG	1	4	56	320
NSC:					
Decreasing Repetition Enhancement					
	L. Cing.G	-5	-43	33	320
SC:					
Decreasing Repetition Suppression					
	L. IFG	-45	14	17	384

SC:					
Decreasing Repetition Enhancement					
	R. Cuneus	3	-75	30	576
	L. Post. Cing.G	-4	-38	21	384
	Passive task				
NSC:					
Decreasing Repetition Suppression					
	L. STG	-58	-15	4	448
	R. STG	49	-32	9	384
NSC:					
Decreasing Repetition Enhancement					
	L. Cing.G	0	-26	30	832

Note. Center of mass given in Talairach coordinates. NSC = Non Subordinate-Clause Sentences. SC = Subordinate-Clause Sentences. STG = Superior Temporal Gyrus. MTG = Middle Temporal Gyrus. TTG = Transverse Temporal Gyrus. IFG = Inferior Frontal Gyrus. TTG = Transverse Temporal. Cing.G = Cingulate Gyrus. PCG = Precentral Gyrus.

Figure Captions

Figure 1. Repetition Effects in Experiment 1.

(a) The two-colored figure partitions areas implicated in auditory comprehension (identified by a functional mask) into those demonstrating repetition suppression (yellow) and those that did not (blue). Suppression effects thresholded at $p < .05$ (corrected).

(b) Whole brain analysis of repetition suppression effects (red) and repetition enhancement effects (blue). Figure thresholded at $p < .05$ (corrected).

Figure 2. Repetition Effects in Experiment 2.

(a) The two-colored figure partitions areas implicated in auditory comprehension (identified by a functional mask) into those demonstrating repetition suppression (yellow) and those that did not (blue). Suppression effects thresholded at $p < .05$ (corrected).

(b) Whole brain analysis of repetition suppression. Figure thresholded at $p < .05$ (corrected). The activation reflects reliable clusters between axial slices in z-coordinates 1 to 9, with maximum intensity values projected onto an axial slice at z-coordinate 9.

(c) Regions showing Sentence-type by Repetition interaction effects. Center of activation clusters were in the right cuneus (TC: 9, -84, -4; 1856 mm^3) and right lingual gyrus (TC: 21, -92, 8; 1088 mm^3). The activation reflects reliable clusters between coronal slices in y-coordinates -75 to -92, with maximum intensity values projected onto a coronal slice at y-coordinate -79. The graph reports mean bold response in these regions for each of the experimental conditions. These regions demonstrated repetition suppression for the non subordinate-clause statements ($p < .001$), but repetition enhancement for the subordinate-clause statements ($p < .001$). Figure thresholded at $p < .05$ (corrected).

Figure 3. Combined Analysis of Repetition Effects in Active and Passive Tasks.

Dark blue: regions demonstrating a main effect of repetition suppression. Light blue: regions demonstrating a main effect of repetition suppression and greater suppression effects in the active task (an interaction effect). Red: regions demonstrating repetition enhancement. Figure thresholded at $p < .05$ (corrected).

Figure 1

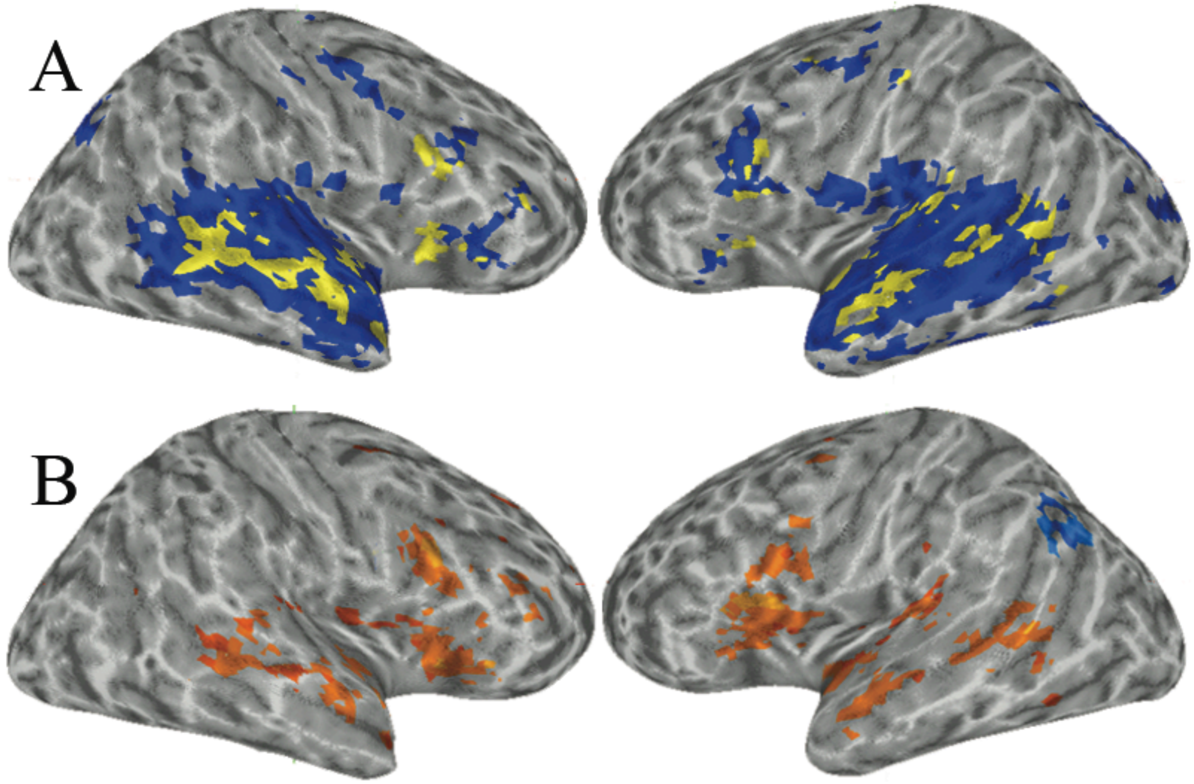

Figure 2

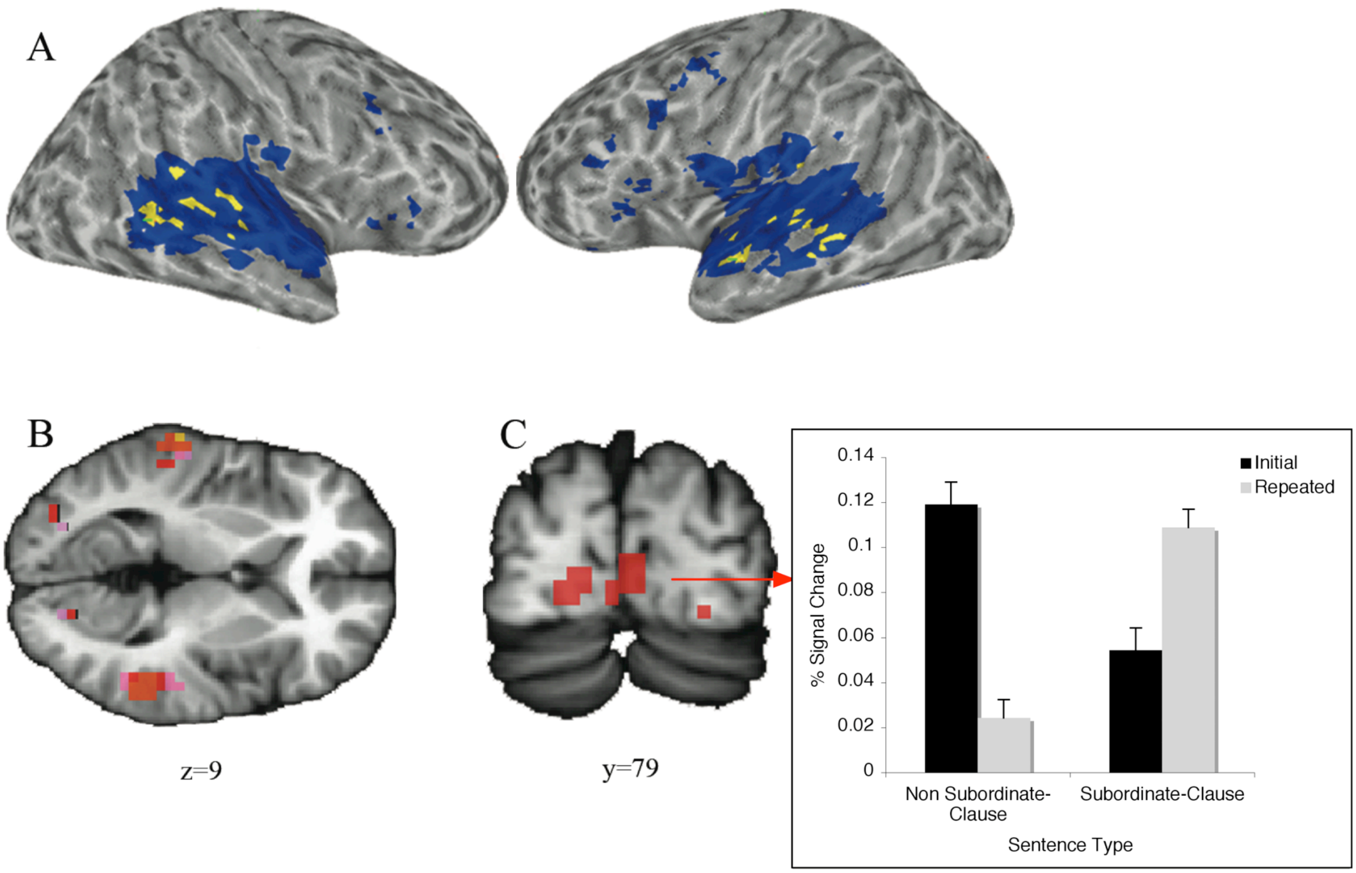
A
B
C
z=9
y=79
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
% Signal Change
Initial
Repeated
Non Subordinate-Clause
Subordinate-Clause
Sentence Type

Figure 3