# Two Approaches to Repetition Suppression

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**Abstract:** Repetition suppression refers to the phenomenon that prior processing of stimuli (or stimulus attributes) decreases activation elicited by processing subsequent stimuli with identical attributes. We present two complementary approaches to identify regions that show repetition suppression for subsequent sentences with either identical: (1) sentence forms or (2) speakers. The first categorical approach simply compares sentences that are presented in Same and Different blocks. The second factorial approach operationally defines repetition suppression as decreased activation for the subsequent Same stimulus relative to its preceding sentence. To account for nonspecific time confounds, this approach tests for a repetition × condition (Same or Different) interaction. Surprisingly, the two approaches revealed different results: Only the categorical analysis detected sentence repetition effects in multiple regions within a bilateral frontotemporal system that has previously been implicated in sentence processing. These discrepancies might be due to the different efficiencies with which the particular contrasts were estimated or spurious differences in stimuli or attentional set that could not be entirely controlled within a single subject. Finally, we combined the two approaches in a [global null] conjunction analysis. *Hum Brain Mapp 27:411–416, 2006.* 

**Key words:** repetition suppression; fMRI adaptation; sentence processing; FIAC; conjunction analysis

## INTRODUCTION

Repetition suppression refers to the phenomenon that prior processing of stimuli (or stimulus attributes) decreases activation elicited by processing subsequent stimuli with identical attributes. Repetition suppression has frequently been interpreted as the functional MRI (fMRI) analog of neuronal response suppression, i.e., a decrease in neuronal firing rate as recorded in nonhuman primates [Desimone, 1996]. However, the underlying neuronal mechanisms as well as the relationship between the decreased BOLD activation and neuronal response suppression remain unclear [for review and discussion, see Henson and Rugg, 2003; Henson, 2003]. In fact, multiple models and theories have been advanced to explain repetition suppression: (1) It has been attributed to sharpening of the cortical stimulus representations, whereby neurons that are not essential for stimulus processing respond less for successive stimulus presentations [Wiggs and Martin, 1998]. (2) According to the fMRI adaptation approach, the number of neurons that are important for stimulus representation and processing remain constant but show reductions in their firing rates for repeated stimuli [Grill-Spector and Malach, 2001]. (3) Within neural network models, repetition suppression is thought to be mediated by synaptic changes that decrease the settling time of an attractor neural network [Becker et al., 1997; Stark and McClelland, 2000]. (4) Finally, hierarchical models of predictive coding have proposed that response suppression reflects reduced prediction error: As the brain learns to predict the stimulus attributes on successive exposures to identical stimuli, the firing rate of stimulus-evoked error units are suppressed by top-down predictions mediated by backward connections from higher-level cortical areas [Friston, 2005].

Despite the uncertainties about the underlying neural mechanisms, fMRI repetition suppression has been widely used as a tool for dissociating and mapping the processing

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stages involved in, for instance, object and word recognition. These fMRI experiments are based on the rationale that the sensitivity of a brain region to variations in stimulus attributes determines the degree of repetition suppression: The more a brain region is engaged in processing, and hence sensitive to a particular stimulus feature, the more it will adapt to stimuli that are identical with respect to this feature—even though they might vary along other dimensions. For instance, this approach has revealed that lateral occipital cortex (LOC) is sensitive to different object views but generalizes, i.e., shows invariance to size and position of an object, suggesting nonretinotopic but view-based LOC representations [Grill-Spector et al., 1999].

In this experiment the fMRI adaptation approach was applied to auditory speech processing. Speech carries information about: (1) linguistic aspects such as semantics and syntax, and (2) nonlinguistic features such as speaker identity [Belin et al., 2000, 2004; Belin and Zatorre, 2003]. Previous studies using task/attentional manipulations have suggested distinct neuronal systems specialized for processing these two types of information with left lateralized frontotemporal regions involved in linguistic processes and a right anterior temporal region engaged in processing speaker identity [von Kriegstein et al., 2003]. Manipulating speaker identity and sentence form in a 2 $\times$ 2 factorial block design, the present study employs the fMRI adaptation (i.e., repetition suppression) approach to dissociate the neural systems for processing linguistic and nonlinguistic aspects of speech.

Here, we present two complementary analysis approaches to identify regions that show repetition suppression for subsequent sentences with identical: (1) sentence forms or (2) speakers.

The first categorical approach simply compares sentences that are presented in Same and Different blocks. This approach assumes that sentences in the Same and Different conditions were randomly selected and hence not systematically different. Activation differences can therefore only be caused by the context (i.e., Same or Different) in which they were presented.

The second factorial approach operationally defines repetition suppression as decreased activation for the subsequent Same stimulus relative to its preceding sentence. To account for nonspecific time confounds, the factorial approach tests for a repetition $\times$ condition (Same or Different) interaction. In particular, assuming an exponential decay, i.e., repetition suppression that saturates with multiple repetitions, we test for greater exponential decay for sentences in Same relative to Different blocks. In addition, we test for other time courses of adaptation such as a linear decrease and a categorical decay (i.e., Sentence 1 $>$ Sentences 2–5).

Finally, we combine the two approaches in a [global null] conjunction analysis to identify regions that show (1) decreased activation for Same relative to Different blocks and/or (2) increased exponential decay for sentences in Same relative to Different blocks. Here, a [global null] conjunction analysis, which tests for effects in either contrast under the weak constraint that both effects are positive, is sufficient. This is because both so-called congruent contrasts test for repetition suppression, i.e., the same treatment effect. The rejection of the [global null] hypothesis enables us to infer that a repetition suppression effect was significant in one or both contrasts and expressed consistently over the two contrasts (n.b., this does not mean both effects would be necessarily significant when tested alone) [Friston et al., 2005].

## MATERIALS AND METHODS

We analyzed a single subject (identified as FIAC3) from the Functional Image Analysis Contest (FIAC) dataset. For the basic description of the fMRI experiment, subjects, and data acquisition, see Dehaene-Lambertz et al. [2006].

### Data Analysis

The single-subject data were analyzed in SPM5. The functional images were realigned using the first as a reference. Using field-map echo sequences, they were unwarped to correct for static inhomogeneity of the magnetic field and movement by inhomogeneity interactions. They were co-registered with the subject's anatomical image, segmented/normalized [Ashburner and Friston, 2005], resampled to $3 \times 3 \times 4$ mm$^3$ voxels, and spatially smoothed with a Gaussian kernel of 8-mm full-width at half-maximum (FWHM). The time-series in each voxel were highpass-filtered to 1/128 Hz.

The temporal autocorrelations in the errors were estimated using a restricted maximum likelihood (ReML) and an AR(1) model and used to make the appropriate nonsphericity adjustment at the point of inference. This approach has been described previously [Friston et al., 2002a,b]. Briefly, an F-test is first used to identify voxels with potential activations. Temporal autocorrelation is then assumed identical in these voxels and is estimated using an AR(1) process with a coefficient determined using a "hyper-parameterized" Taylor series expansion about the value 0.2. These "hyperparameters" are estimated using ReML [Friston et al., 2002b]. Voxel-wise error covariance matrices, obtained by scaling the global autocorrelation estimate, are then used to estimate the regression coefficients using weighted least squares (WLS). The temporal autocorrelation estimates are also used to adjust the degrees of freedom for statistical inference, as described previously [Kiebel et al., 2003].

The fMRI experiment was modeled in an event (sentence onset)-related fashion with design matrix regressors formed by convolving each event-related stick function with a canonical hemodynamic response function [Friston et al., 1995]. The statistical model included 24 conditions in a $2 \times 2 \times 6$ factorial design with the factors: sentence (same, different), speaker (same, different), and repetition (1–6 presentations). This flexible model was selected to accommodate any nonlinear time courses of adaptation. We report the following effects:

#### *1. Categorical analysis*

(a) The main effect of sentence: Different Sentence ($D_{sen}$) $>$ Same Sentence ($S_{sen}$). (b) The main effect of speaker: Different Speaker ($D_{sp}$) $>$ Same Speaker ($S_{sp}$). (c) The interaction effect between speaker and sentence: $S_{sp}D_{sen}$-$S_{sp}S_{sen}$ > $D_{sp}D_{sen}$-$D_{sp}S_{sen}$.

The first presentation of each sentence is, strictly speaking, unprimed in both the Same and Different conditions but was included in these contrasts to ensure orthogonality with the corresponding contrasts of the factorial analysis. This is important for the [global null] conjunction analysis. However, for comparative purposes we also performed the equivalent contrasts limited to the last five sentences.

### *2. Factorial analysis*

(a) The interaction of sentence effect and repetition (increased adaptation for Same > Different). (b) The interaction of speaker effect and repetition (increased adaptation for Same > Different). (c) The 3-way interaction of repetition, sentence, and speaker effect.

In particular, we tested for three different time-courses of adaptation: (i) exponential decay, (ii) linear decrease, and (iii) categorical decay (i.e., Sentence 1 > Sentences 2–5). The time courses of adaptation were entered as contrast weights in our analysis.

### *3. Conjunction analysis*

Finally, we report the conjunction analyses over the corresponding contrasts from the categorical and factorial analyses, respectively, to identify: (a) main effect of sentence (i.e., 1.a and 2.a); (b) main effect of speaker (i.e., 1.b and 2.b); (c) the interaction effect between speaker and sentence (i.e., 1.c and 2.c). Unless otherwise stated, the results are reported at $P < 0.05$ corrected for multiple comparisons in the entire brain (family-wise error rate).

## RESULTS

### 1. Categorical Analysis

(a) Sentence effect: A bilateral frontotemporal system encompassing the precentral sulci bilaterally, the right inferior frontal gyrus, and several middle temporal regions showed decreased activation for sentences that were presented in Same relative to Different sentence blocks. Nearly equivalent results were obtained when the comparison was limited to the last five sentences, i.e., the first sentence was excluded from the contrast (Table I; Fig. 1).

(b) Speaker effect: No significant effects were detected, even after constraining the search volume to a sphere (radius = 10 mm) centered on the right anterior temporal activation peak [$x = 58$, $y = 2$, $z = -8$] reported in Belin and Zatorre [2003].

(c) There was no significant sentence × speaker interaction.

### 2. Factorial Analysis

No significant effects were detected for any of the factorial contrasts.

**TABLE I. Categorical analysis: sentence effect**

| Region | Coordinates | z-score |
|---|---|---|
| R. ant. Middle temp. g. | 63, −6, −28 | 7.4 |
| L. inf. Precentral sulcus | −51, 9, 24 | 6.5 |
| L. post. middle temp. g | −69, −45, 0 | 6.1 |
| R. inf. Precentral sulcus | 48, 15, 12 | 6.1 |
| L. middle temp. g | −72, −27, 0 | 6.0 |
| R. inf. Frontal g. | 42, 36, −12 | 4.8 |

### 3. Conjunction Analysis over Congruent Contrasts from the Categorical and Factorial Analysis

(a) Sentence effect (1.a and 2.a): (i) Exponential decay: a left anterior superior temporal region and the right inferior precentral sulcus; (ii) Linear decrease: a left anterior superior temporal region; (iii) Categorical decay (i.e., Sentence 1

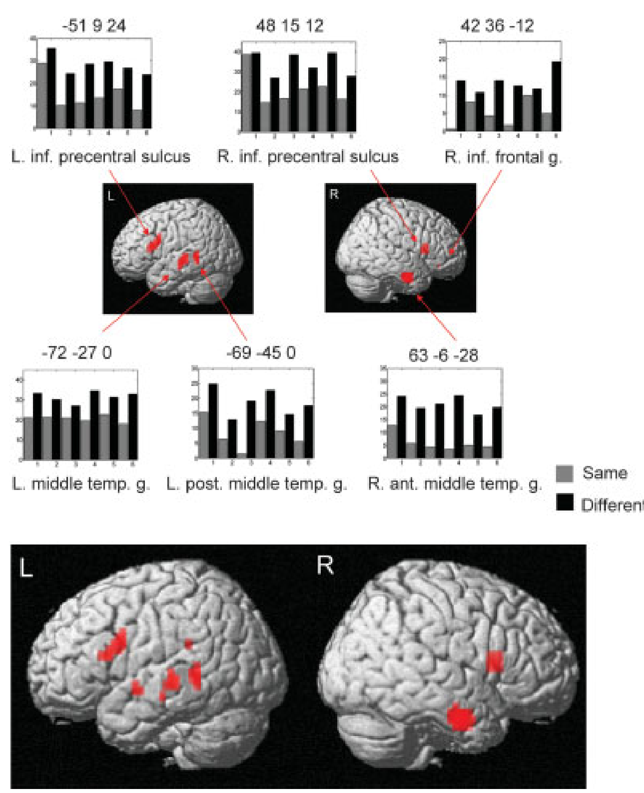


**Figure 1.**
**A:** Center: Categorical analysis: Repetition suppression effects for sentences are rendered on an averaged normalized brain. Height threshold: $P < 0.05$ corrected. Extent threshold: > 0 voxel. Surround: Parameter estimates for Sentences 1–6 relative to baseline for Different (black) and Same (gray) averaged over speaker effect. The bar graphs represent the size of the effect in adimensional units (corresponding to percent whole brain mean). **B:** Categorical analysis: Repetition suppression effects for Sentences 2–6 are rendered on an averaged normalized brain. Height threshold: $P < 0.05$ corrected. Extent threshold: > 0 voxel.

**TABLE II. Conjunction analysis: sentence and speaker effects**

| Region | Coordinates | z-score |
|---|---|---|
| Conjunction analysis: sentence effect | | |
| Exponential Decrease | | |
| L. ant. sup. temp. g. | −66, −3, −3 | 6.1 |
| R. inf. precentral sulcus | 51, 15, 12 | 5.2 |
| Linear Decrease | | |
| L. ant. sup. temp. g | −66, −3, −8 | 5.0 |
| Sentence 1 > Sentences 2-5 | | |
| L. ant. sup. Temp. g. | −66, −3, −8 | 5.4 |
| R. inf. Precentral sulcus | 51, 15, 12 | 5.3 |
| R. ant. middle temp. g. | 72, −15, −24 | 5.0 |
| Conjunction analysis: speaker effect | | |
| Sentence 1 > Sentences 2-5 | | |
| L. post. sup. Temp. g. | −54, −36, 16 | 4.9 |

> Sentences 2–5): a left anterior superior temporal and a right anterior middle temporal region and the right inferior precentral sulcus. (b) Speaker effect (1.b and 2.b): Only the categorical decay revealed a left posterior superior temporal region. (c) There was no significant sentence × speaker interaction (Table II; Fig. 2).

## Comparison of Categorical and Factorial Analysis

Surprisingly, the categorical and factorial analyses yielded different results, with the categorical analysis being more sensitive. To further investigate the differences between the two analyses, in the six regions exhibiting a main effect of sentence (in the categorical analysis), we plotted the parameter estimates + confidence intervals for (1) the sentence main effect from the categorical analysis, i.e., $D_{sen}$-$S_{sen}$ averaged over all six sentences; (2) sentence × repetition interaction using a categorical decay, i.e., $D_{sen}$-$S_{sen}$ for Sentence 1 > Sentences 2–5; (3) the simple sentence main effect, i.e., $D_{sen}$-$S_{sen}$ for Sentence 1; (4) the simple sentence main effect, $D_{sen}$-$S_{sen}$ averaged over Sentences 2–6. These plots suggest two explanations: (1) The contrast of the categorical analysis is estimated with a greater efficiency as reflected in the smaller confidence interval. (2) In some regions the difference between Same and Different sentences already emerges with the first sentence. This might be due to spurious differences in sentence stimuli or an attentional set that might not have been entirely controlled within a single subject (Fig. 3).

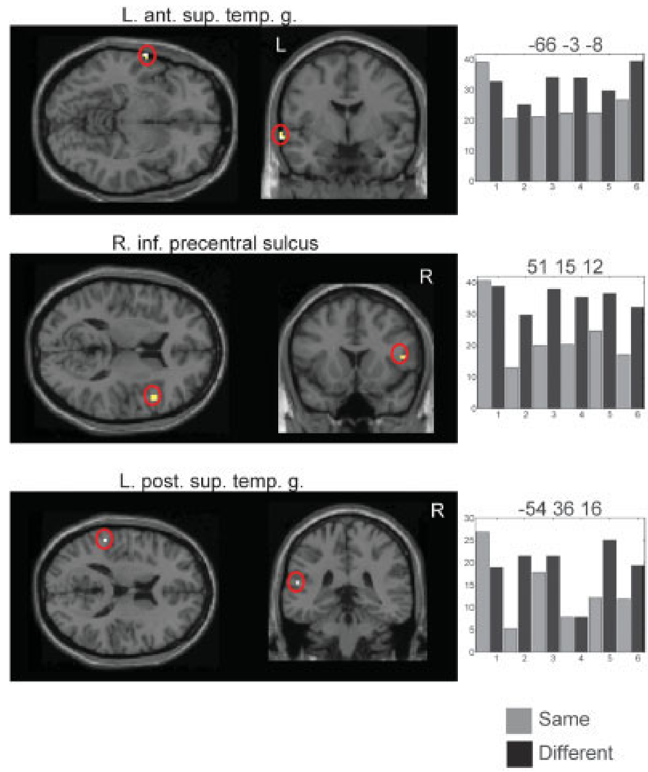


**Figure 2.**
Top and middle: Conjunction analysis – Exponential decay. Left: Repetition suppression effects for sentences are presented on axial and coronal slices of a canonical structural image. Height threshold: $P < 0.05$ corrected. Extent threshold: > 0 voxel. Right: Parameter estimates for Sentences 1–6 relative to baseline for Different (black) and Same (gray) averaged over speaker effect. The bar graphs represent the size of the effect in adimensional units (corresponding to percent whole brain mean). Bottom: Conjunction analysis – Categorical decay. Left: Repetition suppression effects for speaker are presented on axial and coronal slices of a canonical structural image. Height threshold: $P < 0.05$ corrected. Extent threshold: > 0 voxel. Right: Parameter estimates for Sentences 1–6 relative to baseline for Different (black) and Same (gray) averaged over sentence effect. The bar graphs represent the size of the effect in adimensional units (corresponding to percent whole brain mean).

## DISCUSSION

This experiment used repetition suppression to dissociate the neural systems engaged in processing linguistic (i.e., sentence identity) and nonlinguistic information (i.e., speaker identity) during auditory speech processing.

We have presented two complementary approaches, a categorical and a factorial analysis, to identify brain regions that exhibit repetition suppression. Neither of them detected a significant interaction or main effect of speaker identity, even when focusing on the right anterior temporal region that has previously been reported for processing speaker identity. However, the categorical—but not the factorial—analysis detected repetition suppression effects for sentence identity in multiple regions within a bilateral frontotemporal system that has been implicated in sentence/speech processing [Binder et al., 2000; Price et al., 2005; Scott et al., 2000; Scott and Johnsrude, 2003]. The discrepancies between the two analyses may result from the different efficiencies with which the particular contrasts were estimated: While the categorical approach compares the means of all Same and Different sentences, the factorial analysis tests for a repetition × condition interaction, which—given an exponential

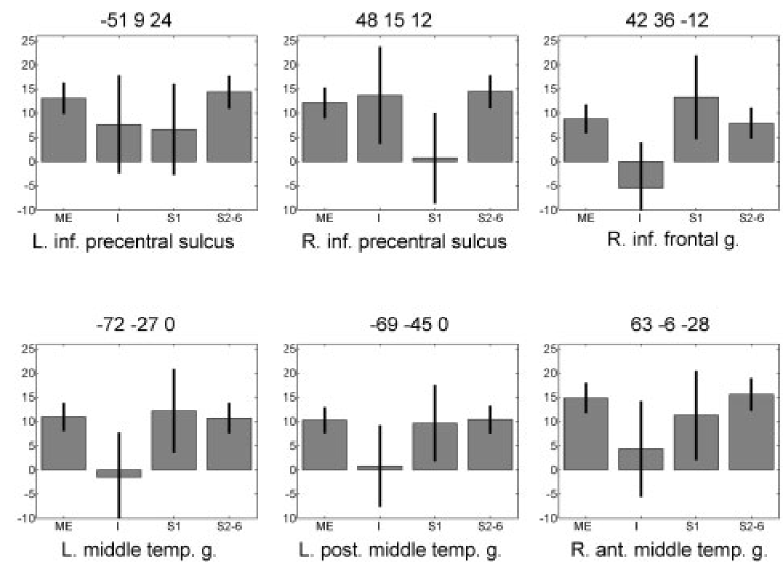


**Figure 3.**

Parameter estimates for (1) ME = the sentence main effect from the categorical analysis, i.e., $D_{sen}$-$S_{sen}$ averaged over all six sentences; (2) I = sentence × repetition interaction using a categorical decay, i.e., $D_{sen}$-$S_{sen}$ for Sentence 1 < Sentences 2–5; (3) S1 = the simple sentence main effect, i.e., $D_{sen}$-$S_{sen}$ for Sentence 1; (4) S2–6 = the simple sentence main effect, $D_{sen}$-$S_{sen}$ averaged over Sentences 2–6. The bar graphs represent the size of the effect in adimensional units (corresponding to percent whole brain mean).

or categorical decay—places particular weight on the difference between the first sentences in the Same and Different blocks. Hence, the contrast in the categorical analysis is estimated with a greater efficiency than in the factorial analysis [Friston et al., 1999; Josephs and Henson, 1999] (see also Fig. 3). A more efficient design for the factorial approach would entail fewer repetitions of the same sentence and more repetitions of different sentences. Furthermore, the factorial analysis tests for repetition suppression over multiple identical sentences within a block, while the categorical analysis compares different types of sentences that are presented in different blocks. Therefore, the categorical analysis is more susceptible to spurious differences in sentence stimuli or attentional set that might not have been entirely controlled within a single subject. Combining the two approaches in a conjunction analysis enabled us to identify left temporal regions that show a sentence effect for all three time courses of adaptation. Assuming a categorical decay, the conjunction analysis revealed a speaker effect in a left posterior superior temporal region.

Collectively, these results demonstrate that multiple frontotemporal regions are sensitive to sentence form, while generalizing over auditory surface features that might vary with speaker identity. They are consistent with a component process view, whereby several stages in speech processing can be facilitated. Thus, the repetition suppression effects for sentence form might emerge at multiple levels, ranging from phonological to syntactic processing and semantic integration at the sentential level. Previously, the fMRI adaptation approach has been used to disentangle the processing stages involved in single word recognition [for review, see Dehaene et al., 2005] by successively manipulating variables such as case (small vs. capital), font, size, position [Dehaene et al., 2004], stimulus modality (visual vs. auditory), word familiarity (word vs. pseudowords), and lexical semantics (related vs. unrelated). Similarly, a series of fMRI adaptation experiments are required to tease apart and map the different component processes involved in sentence processing. Important variables to manipulate may be sentence modality (visual vs. auditory), semantics (related vs. unrelated, sentences vs. jabberwocky sentences), phonology, and syntax. For instance, repetition suppression to identical sentences that are either spoken or written would suggest that the identified neural systems sustain modality-independent processes such as semantic or syntactic processing. Similarly, two recent fMRI studies have used the adaptation technique to disentangle and map syntactic and semantic processes involved in sentence reading by manipulating (1) syntactic structure and ambiguity, or (2) syntactic structure and semantic content in 2 × 2 factorial designs [Noppeney and Price, 2004].

However, the complexity of sentence processing severely aggravates and adds to the interpretational problems commonly encountered in fMRI adaptation experiments. (1) Early fMRI adaptation experiments using block designs were criticized for their lack of attentional control, thus confounding repetition suppression with decreases in attention. While randomized event-related designs may have, to a large part, overcome this problem for single lexical items, this may not apply to sentence processing, as subjects can still anticipate the continuation of a repeated sentence based on its initial words even in event-related designs. (2) A recurrent issue in interpreting repetition suppression effects is its potential contamination with explicit memory retrieval. As sentence comprehension inevitably involves semantic integration, i.e., deep semantic processing irrespective of the particular task demands, sentence repetition effects will be particularly susceptible to explicit memory retrieval. (3) Repetition suppression effects have been observed at different timescales (i.e., latencies and longevities) suggesting multiple underlying neuronal mechanisms. For instance, repetition suppression effects in occipitotemporal regions have been shown for covert naming of repeated objects after a lag of several days [van Turennout et al., 2003], while left anterior temporal repetition suppression effects for semantically related stimuli is thought to be more short-lived [Neely, 1999; Rossell et al., 2003]. It may be difficult to dissociate these different repetition effects that emerge with different onsets, time-scales and -courses during the temporal evolution of a sentence. (4) Although the exact relationship between neuronal repetition suppression and behavioral priming effects is still unclear, it is often assumed that neuronal response suppression is associated with greater processing efficiency and hence behavioral facilitation as indicated by faster reaction times and increased accuracy. However, sentence reading/comprehension times as end of phrase measures may not sensitively measure behavioral facilitation effects if they are limited to particular periods and do not persist throughout the entire course of sentence comprehension. (5) Finally, the essential dimensions and categories that will enable us to dissociate the functional contributions of different neuronal elements within the sentence processing system remain to be determined. Thus, semantics and syntax have proved useful as linguistic dimensions, but this dichotomy may or may not be helpful for designing fMRI adaptation experiments to understand the neuronal organization of sentence processing.

Despite these unresolved issues and interpretational problems, repetition suppression complements task/attentional manipulations usefully to provide insights into the neural systems of sentence and speech processing.

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## REFERENCES

Ashburner J, Friston KJ (2005): Unified segmentation. Neuroimage 26:839–851.

Becker S, Moscovitch M, Behrmann M, Joordens S (1997): Long-term semantic priming: a computational account and empirical evidence. J Exp Psychol Learn Mem Cogn 23:1059–1082.

Belin P, Zatorre RJ (2003): Adaptation to speaker's voice in right anterior temporal lobe. Neuroreport 14:2105–2109.

Belin P, Zatorre RJ, Lafaille P, Ahad P, Pike B (2000): Voice-selective areas in human auditory cortex. Nature 403:309–312.

Belin P, Fecteau S, Bedard C (2004): Thinking the voice: neural correlates of voice perception. Trends Cogn Sci 8:129–135.

Binder JR, Frost JA, Hammeke TA, Bellgowan PS, Springer JA, Kaufman JN, Possing ET (2000): Human temporal lobe activation by speech and nonspeech sounds. Cereb Cortex 10:512–528.

Dehaene S, Jobert A, Naccache L, Ciuciu P, Poline JB, Le Bihan D, Cohen L (2004): Letter binding and invariant recognition of masked words: behavioral and neuroimaging evidence. Psychol Sci 15:307–313.

Dehaene S, Cohen L, Sigman M, Vinckier F (2005): The neural code for written words: a proposal. Trends Cogn Sci 9:335–341.

Dehaene-Lambertz G, Dehaene S, Anton JL, Campagne A, Ciuciu P, Dehaene GP, Denghien I, Jobert A, LeBihan D, Sigman M, Pallier C, Poline JB (2006): Functional segregation of cortical language areas by sentence repetition. Hum Brain Mapp 27:360–371.

Desimone R (1996): Neural mechanisms for visual memory and their role in attention. Proc Natl Acad Sci U S A 93:13494–13499.

Friston K (2005): A theory of cortical responses. Philos Trans R Soc Lond B Biol Sci 360:815–836.

Friston KJ, Holmes A, Worsley KJ, Poline JB, Frith CD, Frackowiak R (1995): Statistical parametric mapping: a general linear approach. Hum Brain Mapp 2:189–210.

Friston KJ, Zarahn E, Josephs O, Henson RN, Dale AM (1999): Stochastic designs in event-related fMRI. Neuroimage 10:607–619.

Friston KJ, Glaser DE, Henson RN, Kiebel S, Phillips C, Ashburner J (2002a): Classical and Bayesian inference in neuroimaging: applications. Neuroimage 16:484–512.

Friston KJ, Penny W, Phillips C, Kiebel S, Hinton G, Ashburner J (2002b): Classical and Bayesian inference in neuroimaging: theory. Neuroimage 16:465–483.

Friston KJ, Penny WD, Glaser DE (2005): Conjunction revisited. Neuroimage 25:661–667.

Grill-Spector K, Kushnir T, Edelman S, Avidan G, Itzchak Y, Malach R (1999): Differential processing of objects under various viewing conditions in the human lateral occipital complex. Neuron 24:187–203.

Grill-Spector K, Malach R (2001): fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol (Amst) 107:293–321.

Henson RN (2003): Neuroimaging studies of priming. Prog Neurobiol 70:53–81.

Henson RN, Rugg MD (2003): Neural response suppression, haemodynamic repetition effects, and behavioural priming. Neuropsychologia 41:263–270.

Josephs O, Henson RN (1999): Event-related functional magnetic resonance imaging: modelling, inference and optimization. Philos Trans R Soc Lond B Biol Sci 354:1215–1228.

Kiebel SJ, Glaser DE, Friston KJ (2003): A heuristic for the degrees of freedom of statistics based on multiple variance parameters. Neuroimage 20:591–600.

Neely JH (1999): Semantic priming effects in visual word recognition: a selective review of current findings and theories. In: Besner D, Humphreys GW, editors. Basic processes in reading: visual word recognition. Hillsdale, NJ: Lawrence Erlbaum.

Noppeney U, Price C (2004): An fMRI study of syntactic adaptation. J Cogn Neurosci 16:702–713.

Price C, Thierry G, Griffiths T (2005): Speech-specific auditory processing: where is it? Trends Cogn Sci 9:271–276.

Rossell SL, Price CJ, Nobre AC (2003): The anatomy and time course of semantic priming investigated by fMRI and ERPs. Neuropsychologia 41:550–564.

Scott SK, Johnsrude IS (2003): The neuroanatomical and functional organization of speech perception. Trends Neurosci 26:100–107.

Scott SK, Blank CC, Rosen S, Wise RJ (2000): Identification of a pathway for intelligible speech in the left temporal lobe. Brain 123(Pt 12):2400–2406.

Stark CE, McClelland JL (2000): Repetition priming of words, pseudowords, and nonwords. J Exp Psychol Learn Mem Cogn 26:945–972.

van Turennout M, Bielamowicz L, Martin A (2003): Modulation of neural activity during object naming: effects of time and practice. Cereb Cortex 13:381–391.

von Kriegstein K, Eger E, Kleinschmidt A, Giraud AL (2003): Modulation of neural responses to speech by directing attention to voices or verbal content. Brain Res Cogn Brain Res 17:48–55.

Wiggs CL, Martin A (1998): Properties and mechanisms of perceptual priming. Curr Opin Neurobiol 8:227–233.