Syntactic Effects on BOLD Signal Responses to Comprehension and Verification of Sentence Meaning

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Abstract

Behavioral and BOLD signal measures were obtained while fifteen participants performed a verification task in which target sentences with more complex "subject-object (SO)" relative clause structures (e.g., *The commander who the general congratulated applauded the admiral*) and less complex "object-subject (OS)" relative clause structures (e.g., *The general congratulated the commander who applauded the admiral*) were presented and the task was to determine whether a subsequent probe sentence, presented in a simple active syntactic form, expressed a proposition in the target sentence. BOLD signal was increased for SO compared to OS sentences in association with the probe but not the initial target sentence. The results indicate that processes that occur during the retrieval and verification of sentence meaning are affected by the syntactic structure of a sentence that has been presented a short time previously, and provide information about the neural loci of these processes. The absence of sentence-type effects on BOLD signal during the initial comprehension and encoding of sentence meaning is discussed in relationship to previous work on the determinants of such effects.

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Introduction

One task that has been used to study syntactic processing using functional neuroimaging studies is sentence verification. In a typical verification task, a participant reads a "target" sentence, which is displayed for a fixed period of time, and then sees a "probe" sentence that either expresses a portion of the meaning of the target sentence or not. The task is to indicate whether the probe does or does not express the meaning of the target. The effect of processing syntactically more complex sentences on BOLD signal or PET activity has been studied by varying the syntactic structure of the target sentence, keeping the probe sentence identical for both the more and less complex version of the target. Increases in neurovascular responses associated with more complex targets have been taken as indicating areas of the brain in which the syntactic operations that differ between the more and less complex syntactic structures take place during comprehension and encoding into memory of the target sentence.

Using this task, Just et al. (1996) contrasted object-extracted relative clauses, such as (1), and subject-extracted relative clauses, such as (2),

1. The reporter who the senator attacked admitted the error. (SO)

2. The reporter who attacked the senator admitted the error. (SS)[1]

They reported increased BOLD signal activity in Broca's area and the left inferior parietal lobe and, to a lesser degree, in the right hemisphere counterparts of these areas, and concluded

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[1] In sentence (1), the "head" of relative clause (*the reporter*) is both the subject of the main clause and the object of the verb of the relative clause, and as such (1) has been called a "subject–object (SO)" structure. Sentence (2) is called a "subject- subject (SS)" structure, because the head of relative clause (*the reporter*) is the subject of the main clause and the subject of the verb of the relative clause. This nomenclature can be extended to other sentence types and is used throughout this paper.

that these brain regions supported a verbal working memory system that was utilized to a greater extent in understanding sentences such as (1) compared to (2).

Another study using verification was reported by Fiebach et al. (2001), who had participants read and answer yes/no questions about German sentences with object- *vs*. subject-extracted indirect questions (IQ). The target sentences were similar to the English sentences (3) and (4), except that in German the verb occurs at the end of the indirect question in both versions, and the syntactic structure and meaning is determined by the case markings and inflectional agreement of the nouns and verbs.

3. I asked who Mary saw in the park. (OIQ)
4. I asked who saw Mary in the park. (SIQ)

Fiebach and colleagues reported a small area of increased activation in the left anterior superior temporal sulcus for the contrast of object- and subject-extracted indirect questions, although they considered this an unreliable finding because it did not survive correction for multiple statistical comparisons.

Two other studies using the verification task were reported by Ben-Shachar et al. (2004). In the first, the authors examined Hebrew sentences with topicalized noun phrases ((5) and (6)) and sentences with inner and outer datives ((7) and (8), respectively):

5. The red book, John gave to the professor from Oxford.
6. To the professor from Oxford, John gave the red book.
7. John gave the red book to the professor from Oxford.
8. John gave the professor from Oxford the red book.

Ben-Shacher et al. found that BOLD signal increased in the left inferior frontal gyrus, the left ventral precentral sulcus, bilaterally in the superior temporal gyri in the comparison of topicalized sentences ((5) and (6)) against sentences with datives ((7) and (8)), and in the right insula and the right ventral precentral sulcus in the comparison of (7) versus (8). In the second study, Ben-Shachar and colleagues contrasted target sentences with embedded wh-questions ((9) and (10)) and sentences with embedded yes/no questions (11):

9. The waiter asked which tourist ordered the alcoholic drink in the morning.
10. The waiter asked which alcoholic drink the tourist ordered in the morning.
11. The waiter asked if the tourist ordered the alcoholic drink in the morning.

They found increased BOLD signal in the left inferior frontal gyrus, the left ventral precentral sulcus, and bilaterally in the superior temporal gyri (marginally on the right) in the comparison of wh-questions against yes/no questions, and no difference in activation for the two forms of wh-questions (those with subject-extraction (9) and those with object-extraction (10)). Basing their interpretation on Chomsky's theory of syntax, Ben-Shachar and colleagues interpreted these results as indicating that the left inferior frontal gyrus, the left ventral precentral sulcus, and both superior temporal gyri are involved in processing sentences in which one noun phrase has moved from an underlying position in which it has received a thematic role to a position in which it does not receive a thematic role. They argued that other types of syntactic movement, such as that seen in dative structures, involve different brain regions.

As noted, the authors of these studies assumed that some aspect of the initial assignment of syntactic structure and sentence meaning of the target sentences was responsible for the neurovascular effects seen in this body of work. However, the verification task involves the retrieval of the meaning of a target sentence and the matching of that meaning against the meaning of the verification probe as well as the initial comprehension and encoding of the target sentence into memory. Only Ben-Shachar and colleagues separated BOLD signal effects related to the processing of the target sentences and the probe. In the other studies, the neurovascular responses seen in the task might have occurred at the verification step.

On first consideration, the possibility that syntactic effects might arise at the stage of retrieving the meaning of the target from memory and matching it against the probe seems unlikely because it is not necessary to refer to the form of the target at the verification stage of the task. In addition, there is empirical evidence that participants do not remember the syntactic form of sentences they have seen, only their meaning (Bransford and Franks, 1971). However, both these considerations may be misleading. Many psychological processes occur in circumstances when they are not logically required. The Bransford and Franks results pertain to participants who were asked about sentences minutes, not seconds, after having read them. It is possible that syntactic form is retained for very short periods of time or can be reactivated from representations in phonological form when the meaning of a recently presented sentence is verified.

The Ben Shachar et al (2004) study raises somewhat more subtle version of this issue. These authors used a variable block design in which 1, 2 or 3 sentences with a particular syntactic form were presented in different blocks, and a verification probe was presented at the end of the block. The verification probe always questioned the meaning of the immediately preceding sentence, and BOLD signal associated with the probe was removed from the analysis. While this eliminates any sentence-type effects seen in the BOLD signal being due to operations that arise at the verification stage of the task (or greatly reduces such effects), it does not eliminate the possibility that participants maintained target sentences in a short duration memory system until the end of each block and that the BOLD signal effects arose as a result of the maintenance of syntactic representations (or their reconstruction from phonological form) in this memory system. Once again, although the most parsimonious way to accomplish the task would be for participants to dismiss the meaning of each sentence from memory as soon as a second sentence of the same type appeared, it is not clear that the participants in the study functioned in this way.

The present study was designed to investigate neurovascular effects in object- and subject-extracted relative clauses in verification tasks. We tested participants in a verification task in which each target was followed by a probe and examined the vascular response to determine whether increases in BOLD signal were associated with the initial comprehension and encoding of the target sentence or the subsequent processing of and response to the probe. We separated BOLD signal effects associated with the presentation of the target sentence from those associated with the probe.

Methods

Participants:

Fifteen participants (11 female, 4 male; mean age 21.5 years, range 18-26; all college undergraduates) took part in the research. The study was conducted with the approval of the Human Research Committee at the Massachusetts General Hospital and informed consent was obtained for all participants. All participants were right-handed, native speakers of English and naïve as to the purposes of the study. Participants were paid for their involvement.

Stimulus Materials:

The experimental items consisted of 72 pairs of synonymous SO and OS target sentences, exemplified in (12) and (13), for a total of 144 items.

(12) The fireman who the deputy called saved the sailor. (SO)

(13) The deputy called the fireman who saved the sailor. (OS)

Each matching pair of sentences had the same identical lexical items. All noun phrases were singular, common, and definite to ensure that participants would not be influenced by the referential assumptions made by the noun phrases in different ways in the two conditions. Sentences were based on scenarios. There were a total of 72 scenarios (such as the scenario involving a deputy calling a fireman who saved a sailor). Each scenario appeared once as an SO and once as an OS sentence, and the same words were used in each syntactic form of the scenario.

SO and OS sentences differ along more syntactic dimensions than some other pairs of sentences that have been used in functional neuroimaging studies, such as SO and SS sentences ((1) and (2)). SO sentences differ from OS sentences in having both object-extracted relative clauses and a center-embedded configuration of clauses and from SS sentences only in the first of these respects. While the greater number of syntactic differences between SO and OS than between SO and SS sentences may be a problem in studies intended to identify the specific syntactic operations that engender a BOLD signal response, it is an advantage for the goal of determining whether syntactic effects arise in association with the comprehension, encoding, retrieval and/or verification of sentence meaning because it increases the likelihood of finding a BOLD signal effect of syntactic structure. In addition, OS sentences can be made to be synonymous with SO sentences, which further increases the likelihood that any BOLD signal effects are due to syntactic processing compared to the comparison of SO and SS sentences, which cannot be synonymous.

Verification probe sentences were always presented as simple active sentences and either conveyed one set of thematic roles in the target sentence (e.g., either a deputy calling a fireman or a fireman saving a sailor) for the “true” condition or reversed the thematic roles played by the noun phrases around the verbs (e.g., a fireman calling a deputy, a sailor saving a deputy, a deputy saving a sailor, or a sailor saving a fireman) for the "false" condition. An equal number of true and false verification sentences were presented for each sentence type.

Procedures:

Psychological Procedures.

Each target sentence item was visually displayed in its entirety on a single line in the center of the screen. A given experimental trial consisted of a fixation cross presented for 300 msec, a 100 msec blank screen, the target sentence presented for 4 seconds, a blank screen for 1700 msec, the verification probe sentence presented for 4 seconds, and a blank screen for 1900 msec, for a total trial length of 12 seconds. The task for the participants during the experimental trial was to indicate whether the verification probe sentence conveyed a set of true or false thematic roles in the context of the target sentence. RT and accuracy were measured. A pseudo-randomized item presentation order for the event-related design was determined by a computer program developed to randomize trial types and vary the duration of inter-stimulus fixation trials for optimum efficiency in the deconvolution and estimation of the hemodynamic response (Burock et al., 1998; Dale, 1999; Dale and Buckner, 1997). Thus, randomly interspersed between each sentence trial were 0-12 second fixation trials, in increments of 2 seconds.

The 144 stimulus trials items interspersed with fixation trials were divided into 6 runs. No pair of matched SO and OS sentences were presented in the same run. Participants were allowed a short break between each run. The sentences were projected to the back of the scanner using a Sharp LCD projector and viewed by the participants as a reflection in a mirror attached to the head coil. Responses were recorded via a custom-designed, magnet compatible button box. A

Dell Inspiron 4000 computer running a proprietary software package was used to both present the stimuli and record the accuracy and reaction times.

MR Imaging Parameters.

Participants were scanned in a 3T Siemens Trio scanner (Siemens Medical Systems, Iselin, NJ) with the standard Siemens quadrature head coil, once in a structural scan set and once in a functional scan set. In the structural set, two series of high-resolution anatomical images were acquired using a T1-weighted MP-RAGE sequence (TR = 2530 msec, TE = 3.3 msec, TI = 1100 msec, and flip angle = 7°). Volumes consisted of 128 sagittal slices with an effective thickness of 1.33 mm. The in-plane resolution was 1.0 mm x 1.0 mm (256 x 256 matrix, 256 mm Field of View (FOV)).

The functional volume acquisitions utilized a T2*-weighted gradient-echo pulse sequence (TR = 2000 msec, TE = 30 msec, and flip angle = 90°). The volume was comprised of 30 transverse slices aligned along the same AC-PC plane as the registration volume. The interleaved slices were effectively 3.0 mm thick with a distance of 0.9 mm between slices. The in-plane resolution was 3.13 mm x 3.13 mm (64 x 64 matrix, 200 mm FOV). Each run consisted of 200 such volume acquisitions for a total of 6000 images. By definition, the 30 slices of a single volume took the entire TR (2 sec) to be fully acquired and a new volume was initiated every TR. An initial 8 second (4 TR equivalent) buffer of RF pulse activations, during which no stimulus items were presented and no functional volumes were acquired, was employed to ensure maximal signal during the length of the functional run.

Cortical Surface Reconstruction.

The high-resolution anatomical MP-RAGE scans were used to construct a model of each participant's cortical surface. An average of the two structural scans was used to maximize the signal to noise ratio. The cortical reconstruction procedure involved: (1) segmentation of the cortical white matter; (2) tessellation of the estimated border between gray and white matter, providing a geometrical representation for the cortical surface of each participant; and (3) inflation of the folded surface tessellation to unfold cortical sulci, allowing visualization of cortical activation in both the gyri and sulci simultaneously (Dale et al., 1999; Fischl et al., 1999a, 2001).

For purposes of inter-participant averaging, the reconstructed surface for each participant was morphed onto an average spherical representation. This procedure optimally aligns sulcal and gyral features across participants, while minimizing metric distortion, and establishes a spherical-based co-ordinate system onto which the selective averages and variances of each participant's functional data can be resampled (Fischl et al., 1999a, 1999b).

Functional Pre-processing.

Pre-processing and statistical analysis of the functional MRI data was performed using the FreeSurfer Functional Analysis Stream (FS-FAST) developed at the Martinos Center for Biomedical Imaging, Charlestown, MA (Burock & Dale, 2000). For each participant, the acquired native functional volumes were first corrected for potential motion of the participant using the AFNI algorithm (Cox, 1996). The functional volumes were spatially smoothed using a 3-D Gaussian filter with a full-width half-max (FWHM) of 6mm. Global intensity variations across runs and participants were removed by rescaling all voxels and time points of each run such that the mean in-brain intensity was fixed at an arbitrary value of 1000. BOLD signal associated with stimuli that were responded to incorrectly was removed.

The functional images for each participant were analyzed with a General Linear Model (GLM) using a finite impulse response model (FIR) of the event-related hemodynamic response

(Burock and Dale, 2000). The FIR gives an estimate of the hemodynamic response average at each TR within a peristimulus window. The FIR does not make any assumption about the shape of the hemodynamic response. Mean offset and linear trend regressors were included to remove low-frequency drift. The autocorrelation function of the residual error, averaged across all brain voxels, was used to compute a global whitening filter in order to account for the intrinsic serial autocorrelation in fMRI noise. The GLM parameter estimates and residual error variances of each participant's functional data were resampled onto his or her inflated cortical surface and into the spherical coordinate system using the surface transforms described above. Each participant's data were then smoothed on the surface tessellation using an iterative nearest-neighbor averaging procedure equivalent to applying a two-dimensional Gaussian smoothing kernel with a FWHM of approximately 8.5 mm. Because this smoothing procedure was restricted to the cortical surface, averaging data across sulci was avoided.

Voxel-wise Analysis (or Statistical Activation Maps).

To examine the overall pattern of vascular response, contrasts of interest were first constructed at each voxel on the spherical surface across the group at each TR interval using a random effects model of the cross-participant variance of the FIR parameter estimates with a threshold of $p < .01$, uncorrected for multiple comparisons. More reliable measures of independent variables were based on contrasts that were constructed over sets of post-stimulus delays in the FIR model corresponding to the delays at which vascular responses were expected to be peaking (time windows) and that were corrected for multiple comparisons.

To correct for multiple comparisons, group statistical activation maps were constructed for contrasts of interest for each voxel for these TR intervals using a t statistic and examined for significant clusters of activated voxels on the basis of a Monte Carlo simulation (see Doherty et al., 2004, and Chen et al., in press, for examples of the use of this procedure). A volume of Gaussian distributed numbers was generated for each participant, and was processed in the same manner as the real data, including volumetric smoothing, re-sampling onto the sphere, smoothing on the spherical surface, random effects analysis, and significance map generation. A clustering program was run on these maps to extract clusters of voxels whose members each exceeded a specified threshold and whose area was equal to or greater than a specified size. This process was repeated 3500 times, allowing us to compute the likelihood of one or more clusters of a given size and voxel threshold occurring under the null hypothesis. The real data was then subjected to the same clustering procedure as applied to the simulated data using a cluster size threshold of 200 mm^2 and threshold for rejection of the null hypothesis at $p < .05$. These functional activations were displayed on a map of the average folding patterns of the cortical surface, derived using the surface-based morphing procedure (Fischl et al., 1999a, 1999b). The Talairach coordinates corresponding to the vertices within each cluster with the minimum local p-value were identified.

Results

Behavioral Results

The accuracy and RT data for correct responses are displayed in Figure 1. These data were analyzed in 2 (Syntactic Structure: SO, OS) X 2 (Response Type: Yes/ No) ANOVAs by participants (F_1) and items (F_2). There was an effect of structure in accuracy (F_1 (1, 14) = 11.8, $p < .01$; F_2 (1, 70) = 16.0, $p < .001$) and RTs (F_1 (1, 14) = 27.2, $p < .001$; F_2 (1, 35) = 31.3, $p < .001$). Participants were more accurate and faster in responding to OS than SO sentences. The effect of response was significant in the RT data only (F_1 (1, 14) = 43.3, $p < .001$; F_2 (1, 35) = 29.2, $p < .001$), as was the interaction of these factors (F_1 (1, 14) = 10.1 , $p < .01$; F_2 (1, 35) = 4.5,

$p < .05$). Responses were longer to false verification statements. This difference was only significant for OS sentences in the analysis by items.

Figure 1 here

fMRI Results

BOLD signal changes follow electrophysiological events associated with elementary sensory stimuli and simple motor functions by as little as 2 seconds, with an established response by 4-6 seconds (Bandettini, 1993; Turner et al., 1997). Thus, the hemodynamic response was collapsed across the "early" time window from 6-12 seconds after the onset of a trial, during which BOLD signal associated with processing the target sentence would be expected to peak, and during the "late" time window from 12-18 seconds after the onset of a trial, during which BOLD signal associated with processing the verification probe sentence would be expected to peak.[2] The resulting areas of significant difference in BOLD signal responses to SO and OS sentences are shown in Figures 2 - 4 and summarized in Table 1.

Figures 2 - 4 and Table 1 here

In the early temporal interval period from 6-12 seconds after the onset of a trial, associated with the presentation of the target sentence, there were a few areas of activation in which BOLD signal was greater for OS than for SO sentences (Figure 2). In this temporal interval, there were

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[2] Simple visual inspection of the statistical activation of structure type on BOLD signal at each of the TR intervals from 0 - 22 seconds post stimulus onset confirmed this division, showing a biphasic increase BOLD signal response to SO compared to OS sentences, primarily in the left hemisphere.

also several areas in which BOLD signal was greater for sentences with probes that were false than for sentences with probes that were true (Figure 3).

In the late temporal interval period from 12-18 seconds after the onset of a trial, associated with the presentation of the probe, there were multiple areas in which BOLD signal was greater for SO than for OS sentences (Figure 4). Four of these areas were located in the perisylvian association cortex of the left hemisphere -- the inferior frontal gyrus (area 1), the middle frontal gyrus (area 2), the inferior parietal sulcus (area 3), and the middle temporal gyrus (area 4). On the medial surface of the left hemispheres, there was increased BOLD signal in the posterior parietal lobe (area 6) and superior cingulate gyrus (area 7). In the right hemisphere, two areas in the supramarginal gyrus bordering on the inferior parietal sulcus (areas 10 and 11) were activated and the middle frontal gyrus (area 12), as well as an area on the medial surface of the right superior frontal gyrus (area 13). There were also a number of areas in which BOLD signal was higher in OS than in SO sentences.

All differences in BOLD activity as a function of sentence type occurred in association with true probes (i.e., there were no significant areas of activation for SO compared to OS sentence, or *vice versa*, for false probes). As seen in Figure 4, with one exception, the areas in which there were significant sentence type effects for true probes were a subset of those in which there were significant sentence type effects for all probes. The additional area of activation for true SO compared to true OS sentences was in the left inferior temporal-occipital lobe.

There were 14 areas in which BOLD signal was higher for false probes than for true probes (Figure 5). The extent and magnitude of the areas was greater in this temporal period than in the earlier temporal period.

Discussion

The principal finding in this study is that increases in BOLD signal arose in verifying the truth of statements referring to previously presented more complex SO syntactic structures compared to less complex OS syntactic structures, and not in association with the initial presentation of the sentences. There were also greater effects for false probes than for true probes. We will first discuss the effects at the point of presentation of the probe, and then turn to the effects at the point of presentation of the target.

The effect of structure in association with the processing of the probes could be due to very delayed neurovascular effects of processing associated with the comprehension and encoding of the targets into memory. This is unlikely given the usual temporal relation of BOLD signal to stimulus presentation and given the fact that sentence type effects have been seen in BOLD signal associated with the presentation of sentences in the time frames that constitute the early TR windows used here (e.g., Caplan et al, 2001; Chen et al, in press). The syntactic effects at the point of the probe are likely to be due to processes associated with the verification of the meaning of the probe.

One possibility is that these effects are not truly syntactic, but result from participants' maintaining a rich semantic representation of the target in memory and referring to that representation during the verification stage of the task. Restrictive relative clauses imply that the item or items referred to by a noun phrase is/are selected from a larger set of items, and subject noun phrases are usually the focus of a discourse. Together, these features of discourse-level semantic representations are sufficient to distinguish SO from OS sentences that express the same thematic roles. Processing these discourse-level representations might lead to the sentence type effects found in association with the probe.

This account rests on several assumptions. One that receives strong support is that a semantic representation that includes both propositional and discourse level structures is activated in comprehension and stored in a short-duration memory system (e.g., Kintsch and van Dyke, 1978; Van Dyck and Kintsch, 1983; Ericsson and Kintsch, 1995). A second is that discourse-level semantic information influences the process of matching thematic roles in two propositions. This is another possible instance of “inefficient” or logically unnecessary processing that we must consider. The discourse information being considered here qualifies the entities to which thematic roles are assigned and thus might well be activated when thematic roles are matched. In addition, a process in which both thematic and discourse representations in different linguistic stimuli are matched is ecologically reasonable, since most instances in which a listener matches the meaning of one linguistic stimulus against that of another are ones in which the discourse-level semantic properties of both stimuli are relevant to the match. Third, the explanation rests on the assumption that the combined discourse and propositional representations of SO sentences are more complex and require more effort to process than those of OS sentences. This is likely to be the case because the focus of the discourse is the theme of the verb of the relative clause in an SO sentence; this is an unpreferred combination of semantic values that is not found in OS sentences.

Another possibility is that phonological representations are stored in memory (McCutchen and Perfetti, 1982) and used to reconstruct syntactic structure and thence propositional meaning, at least partially. Whether and how such representations might be used in the verification process is unknown. Many possibilities exist, spanning a wide range of mechanisms. At one extreme, it is possible that participants retain the phonological forms of a few words in memory and only reconstruct a small part of the syntax and meaning of the target sentence when dealing with the probe. At another extreme, they may retain the entire target sentence phonologically and reparse it entirely when they see the probe. In a similar vein, orthographic representations may be stored and used either to construct phonological representations and/or to access semantic and syntactic lexical information from which the propositional content of the target can be reconstructed. The use of phonological or orthographic representations in the verification task might occur more often for the more complex SO sentences, and reconstructing syntactic form and meaning would be more demanding for these sentences.

Finally, the syntactic structure that has been computed during comprehension of the target may be retained and used during verification. Somewhat ironically, considering that the effects found here are ones attributed to syntactic structure, syntactic representations are the representations for which there is the least evidence of retention in a short-duration memory system. Syntactic priming effects (Traxler and Pickering, 2004) do, however, demonstrate that these representations are maintained in such a system.

To summarize this aspect of the discussion, a variety of operations that might be used in the verification aspect of the verification task could lead to the syntactic effects we found at the stage of processing the probe. Some of these mechanisms involve retention or reconstruction of syntactic form, and some involve processing semantic representations associated with different syntactic forms. Different participants may approach the task in different ways and any one participant may undertake the task in different ways at different points in the experiment.

Many of the operations we have discussed are closely related to ones used in initial sentence processing. For instance, there is evidence that review processes occur during the processing of sentences (Fodor and Ferreira, 1988) and that they occur to a greater extent for object-extracted than for subject-extracted sentences (Traxler et al., 2002). The processes that underlie sensitivity to the syntactic form of a sentence during the presentation and response to the probe in this study may be the same as the review and reanalysis operations that occur during the initial presentation of a sentence. If so, the sensitivity of BOLD signal to sentence form in association with verification and not initial comprehension suggest that these operations are used to a greater extent when a sentence is reviewed and re-analyzed than when reanalysis is part of the process of initial comprehension. This may be because they are applied in a conscious deliberate fashion when participants verify a probe and in an unconscious automatic fashion during initial comprehension.

The greater BOLD signal associated with false probes is consistent with the longer RTs to those probes. Greater BOLD signal and longer RTs may occur because, on average, more checking of propositions in the probe and target sentence is likely to occur in false than in true probes. For instance, if participants randomly select one set of the thematic roles derived from the target to match against those of the probe, on half the true trials a positive match will occur after checking the first proposition, while it will always be necessary to check both propositions to determine that the probe is false. Alternatively, recognizing that one proposition does not correspond to another may lead to an “error” signal that increases the BOLD response.

Turning to the effects in the TR periods associated with the targets, the biggest effect was the presence of more BOLD activity for target sentences associated with false probes than target sentences associated with true probes. Since participants could not have known which targets were associated with which probes before the probes were presented, this effect is most likely due to the fact that the “early” TR intervals extended temporally into a period that included some BOLD signal due to processing the probe. It is also possible that subtle differences existed in the targets associated with true and false probes that affected their comprehension and/or encoding. The only syntactic effects were a few small deactivations of SO compared to OS sentences, most in primary motor and visual cortex, which are unexplained. We may speculate that they resulted from small differences in how motor responses were made or how sentences were scanned.

With respect to the main topic of this paper, the absence of an increase in BOLD signal associated with SO compared to OS sentences associated with the presentation of the targets raises questions about the existence of neurovascular effects of object- compared to subject-relativization in initial sentence comprehension. As noted above, studies using the verification that presented object- and subject-extracted constructions either did not separate effects associated with targets from those associated with the probe (e.g., Just et al. (1996) or failed to find differences between the two structures (Ben Shachar et al., 2004), or both. There are studies that have reported effects of object-compared to subject extraction in relative clauses using other experimental paradigms (e.g, plausibility judgment: Caplan et al , 1998, 1999, 2000, 2002; Stromswold et al, 1996; Waters et al, 2003; on-line gender identification: Cooke et al, 2001). However, recent studies have shown that effects previously attributed to object-relativization in plausibility judgment tasks are largely due to the goodness of thematic fit of the nouns and verbs in the stimuli, not their syntactic structure (Chen et al, in press; Caplan et al, 2005a, b, under review). The study by Cooke et al. (2001) used SO and SS sentences with different lexical items, in which proper names were found in the relative clause and common nouns as the head of the relative clause, a design that may have also introduced thematic role fit effects. Overall, the present study and the currently available evidence leave open the question of whether there are effects on BOLD signal of comprehension of object- compared to subject-relativized clauses that are not attributable to thematic role fit. There may well be such effects, but a critical view of the literature fails to unequivocally reveal them.

We conclude by considering the areas in which increases in BOLD signal occurred. Increases in BOLD signal associated with SO compared to OS sentences were seen in the perisylvian association cortex. This is consistent with most other studies of syntactic processing, as reviewed briefly in the introduction to this paper. The syntactic BOLD signal effect was not confined to this region, or to a single brain area within this region. Since many processes are likely to underlie the sentence type effect that arose in association with processing the probe, it is not surprising that this is the case. It is possible that different processes are responsible for different parts of the activation found these contrasts (for suggestions along these lines, see Ben-Shachar et al., 2004, and Keller et al., 2001). It is also possible that individual operations occur in duplicate or multifocally in these areas.

This study also gives hints as to the brain regions associated with matching of the meanings of two sentences against each other. As mentioned above, areas in which false probes produced greater BOLD signal than true probes may be ones in which matching the meaning of one proposition against that of another takes place. The possibility that these areas are ones in which a mismatch is detected remains a possibility, perhaps to be ruled out by determining where BOLD signal increases correlate with increasing numbers of propositions in the target sentence (which should not affect the mismatch signal).

To summarize, effects of the syntactic form of a target sentence were found in association with verifying the correspondence of propositional meaning of a target sentence and a probe, but not in association with the initial comprehension and encoding of the meaning of the target. This indicates that verifying whether the meaning of one proposition corresponds to that of another is a complex process involving syntactic representations, or representations correlated with syntactic form, whose nature and neural basis will require more study to be fully understood. It also raises questions about what aspects of initial syntactic processing lead to BOLD signal effects in other studies.

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Tables 1. Talairach coordinates of peak activation for the early TR interval, corresponding to the target sentence, and the late TR interval, corresponding to the verification probe sentence. Coordinates and Brodmann area locations correspond to the local minimum p-value of each area of activation. The area numbers for each contrast correspond to the area labels on the activation maps in Figures 2, 3, 4 and 5.

Early TR intervals: Effect of Syntactic Structure

	Left Hemisphere						Right Hemisphere					
Contrast	**Cluster #**	**Region**	**BA**	**Talairach (x,y,z)**	**Size (mm2)**	**p-value**	**Cluster #**	**Region**	**BA**	**Talairach (x,y,z)**	**Size (mm2)**	**p-value**
A. SO vs. OS (All Items)	1	Superior Temporal	42	(-52, -24, 10)	272	-0.000043	2	Precentral	4	(17, -16, 57)	266	-0.000022
							3	Precentral	4	(31, -11, 46)	320	-0.000193
							4	Superior Temporal	40/41/42	(49, -25, 15)	221	-0.000004
B. SO vs. OS (True Only)	1	Postcentral	1/2/3	(-47, -29, 52)	303	-0.000089	4	Middle Temporal	39	(49, -64, 12)	237	-0.000871
	2	Precentral	4	(-26, -24, 63)	219	-0.000201	5	Postcentral	3	(40, -24, 55)	787	-0.000071
	3	Occipital	18	(-18, -86, 21)	527	-0.000361	6	Precentral	4	(24, -23, 52)	315	-0.000084
							7	Precentral	4	(42, -5, 17)	485	-0.000304
							8	Precentral	4	(8, -16, 73)	203	-0.000136
C. SO vs. OS (False Only)	1	Superior Frontal	6	(-12, -14, 62)	262	-0.001355				None		

Early TR intervals: Effect of Probe Type

	Left Hemisphere						Right Hemisphere					
Contrast	**Cluster #**	**Region**	**BA**	**Talairach (x,y,z)**	**Size (mm2)**	**p-value**	**Cluster #**	**Region**	**BA**	**Talairach (x,y,z)**	**Size (mm2)**	**p-value**
A. False vs. True (All Items)	1	Inferior Frontal	45/44	(-44, 13, 21)	230	0.001282	6	Supra- marginal	40	(50, -46, 44)	360	0.001462
	2	Middle Frontal	9	(-43, 8, 38)	399	0.000175						
	3	Supra-marginal	40	(-49, -38, 36)	525	0.000031						
	4	Angular Gyrus	39/40	(-45, -49, 28)	356	0.000101						
	5	Superior Parietal	7	(-14, -57, 40)	460	0.000002						
B. False vs. True (SO Only)	1	Superior Frontal	8	(-30, 23, 44)	212	0.000571	3	Supra- marginal	40	(49, -54, 41)	687	0.000348
	2	Supra-marginal	40	(-44, -68, 39)	289	0.000577						
C. False vs. True (OS Only)	1	Inferior Frontal	47	(-56, 12, 2)	622	0.000183	5	Middle Frontal	46	(39, 27, 26)	250	0.000158
	2	Angular Gyrus	39	(-51, -50, 19)	438	0.000142						
	3	Superior Parietal	7	(-17, -50, 42)	213	0.001403						
	4	Superior Frontal	6	(-18, 6, 65)	309	0.000630						

Table 1 (cont.)

Late TR intervals: Effect of Syntactic Structure

	Left Hemisphere						Right Hemisphere					
Contrast	**Cluster #**	**Region**	**BA**	**Talairach (x,y,z)**	**Size (mm2)**	**p-value**	**Cluster #**	**Region**	**BA**	**Talairach (x,y,z)**	**Size (mm2)**	**p-value**
A. SO vs. OS (All Items)	1	Inferior Frontal	44	(-52, 13, 9)	763	0.000065	10	Supra- marginal	40	(38, -56, 40)	330	0.000237
	2	Middle Frontal	9	(-55, 8, 38)	526	0.000010	11	Supra- marginal	40	(33, -44, 42)	720	0.000179
	3	Inferior Parietal	39	(-39, -58, 29)	1277	0.000174	12	Middle Frontal	8/9	(33, 13, 32)	1236	0.000030
	4	Middle Temporal	21	(-48, -35, -1)	354	0.000003	13	Superior Frontal	8	(-1, 31, 41)	427	0.000515
	5	Superior Temporal	22	(-55, -16, 3)	399	-0.000337						
	6	Posterior Cingulate	31	(-16, -46, 40)	559	0.000290						
	7	Superior Frontal	6	(-19, 8, 57)	390	0.000830						
	8	Frontal	10	(-18, 59, 2)	232	-0.000723						
	9	Anterior Cingulate	24/32	(-9, 36, 1)	254	-0.000305						
B. SO vs. OS (True Only)	1	Inferior Frontal	45	(-40, 20, 16)	248	0.000124	8	Middle Frontal	9	(24, 40, 33)	201	0.001919
	2	Inferior Frontal	6	(-47, 1, 23)	226	0.000197	9	Occipital	18	(20, -85, -1)	309	0.001489
	3	Middle Frontal	6	(-47, 3, 44)	300	0.001007	10	Occipital	18	(17, -80, 4)	200	0.000352
	4	Supra-marginal	40	(-38, -44, 39)	229	0.000337						
	5	Middle Temporal	21	(-53, -37, -4)	562	0.000002						
	6	Occipital	18	(-24, -85, -11)	782	0.000514						
	7	Anterior Cingulate	32	(-15, 42, -1)	203	-0.001637						
C. SO vs. OS (False Only)				None						None		

Late TR intervals: Effect of Probe Type

	Left Hemisphere						Right Hemisphere					
Contrast	**Cluster #**	**Region**	**BA**	**Talairach (x,y,z)**	**Size (mm2)**	**p-value**	**Cluster #**	**Region**	**BA**	**Talairach (x,y,z)**	**Size (mm2)**	**p-value**
A. False vs. True (All Items)	1a	Inferior Frontal	44/45	(-61, 18, 6)	3489	0.000001	7	Occipital	19/40	(37, -63, 39)	792	0.000889
	1b	Middle Frontal	9	(-53, 6, 39)	500	0.000028	8	Angular Gyrus	40/39	(49, -50, 33)	222	0.000877
	2	Angular Gyrus	39/40	(-43, -52, 33)	1530	0.000001	9	Supra- marginal	40	(36, -40, 34)	250	0.000036
	3a	Superior Temporal	22	(-53, -45, 18)	2684	0.000001	10	Middle Frontal	9	(26, 36, 29)	2573	0.000005
	3b	Middle Temporal	21	(-57, -25, -3)	625	0.000005	11	Insula		(25, 25, 0)	314	0.000139
	4	Superior Parietal	7	(-11, -54, 41)	865	0.000005	12	Middle Temporal	21	(49, -15, -8)	297	0.000518
	5	Superior Frontal	6	(-14, 14, 58)	996	0.000037	13	Superior Frontal	8	(-1, 27, 49)	225	0.004227
	6	Frontal	11	(-6, 37, -23)	362	0.000001	14	Superior Parietal	7	(4, -62, 46)	542	0.000032
B. False vs. True (SO Only)	1	Inferior Frontal	44	(-58, 11, 12)	1014	0.000001	6	Superior Frontal	9	(26, 38, 31)	428	0.000695
	2	Middle Frontal	9	(-42, 6, 39)	241	0.003811						
	3	Angular Gyrus	39	(-44, -62, 28)	1199	0.000154						
	4	Superior Temporal	22	(-50, -47, 19)	352	0.000042						
	5	Superior Parietal	7	(-15, -57, 40)	414	0.000152						
C. False vs. True (OS Only)	1a	Inferior Frontal	44/45	(-59, 18, 7)	3734	0.000004	10	Supra- marginal	40/39	(34, -58, 32)	355	0.000232
	1b	Middle Frontal	6	(-44, 2, 17)	545	0.000022	11	Middle Frontal	9	(25, 36, 26)	2216	0.000008
	1c	Middle Frontal	6	(-39, 3, 46)	421	0.000021	12	Insula		(28, 20, -1)	531	0.000005
	2	Supra-marginal	40	(-42, -51, 41)	802	0.000012	13a	Occipital Lobe	17	(7, -87, 10)	251	0.000319
	3	Angular Gyrus	39/19	(-43, -68, 19)	222	0.000311	13b	Occipital Lobe	18/19	(36, -80, 0)	1969	0.000023
	4a	superior temporal	22	(-50, -50, 18)	337	0.000076	14	Hippocampus	36/20	(31, -15, -20)	204	0.000661
	4b	Middle Temporal	21	(-60, -34, -3)	2189	0.000001	15	Superior Parietal	7	(-1, -54, 43)	239	0.000005
	5	Occipital Lobe	18	(-28, -89, -8)	2057	0.000078	16	Superior Frontal	6	(-3, 7, 51)	641	0.000632
	6	Fusiform Gyrus	37	(-43, -50, -15)	200	0.000124						
	7	Superior Parietal	7	(-17, -49, 44)	293	0.002673						
	8	Superior Frontal	8	(-15, 24, 44)	1068	0.000013						
	9	Frontal Lobe	11	(-6, 38, -21)	355	0.000136						

Figure Captions

Figure 1. Accuracy and RTs to probes for different conditions.

Figure 2. Areas of BOLD signal differences between SO and OS syntactic structures in the early TR interval associated with the presentation of the target sentences (6 – 12 seconds post stimulus onset). Color overlays represent p-values of the contrast such that the color threshold (red) corresponds to $p = .01$ and ceilings (yellow) at $p = .001$. Blue overlays represent areas in which BOLD signal was reduced in this contrast. Each area has a minimum area of 200 mm^2 and a false-positive $p < .05$. The number label for each area corresponds to the area number of the same contrast in Table 1.

Figure 3. Areas of BOLD signal differences between true and false response types in the early TR interval associated with the presentation of the target sentences (6 – 12 seconds post stimulus onset). Color overlays represent p-values of the contrast such that the color threshold (red) corresponds to $p = .01$ and ceilings (yellow) at $p = .001$. Blue overlays represent areas in which BOLD signal was reduced in this contrast. Each area has a minimum area of 200 mm^2 and a false-positive $p < .05$. The number label for each area corresponds to the area number of the same contrast in Table 1.

Figure 4. Areas of BOLD signal differences between SO and OS syntactic structures in the late TR interval associated with the presentation of the verification probe sentences (12 – 18 seconds post stimulus onset). Color overlays represent p-values of the contrast such that the color threshold (red) corresponds to $p = .01$ and ceilings (yellow) at $p = .001$. Blue overlays represent areas in which BOLD signal was reduced in this contrast. Each area has a minimum area of 200 mm^2 and a false-positive $p < .05$. The number label for each area corresponds to the area number of the same contrast in Table 1.

Figure 5. Areas of BOLD signal differences between true and false response types in the late TR interval associated with the presentation of the verification probe sentences (12 – 18 seconds post stimulus onset). Color overlays represent p-values of the contrast such that the color threshold (red) corresponds to $p = .01$ and ceilings (yellow) at $p = .001$. Blue overlays represent areas in which BOLD signal was reduced in this contrast. Each area has a minimum area of 200 mm^2 and a false-positive $p < .05$. The number label for each area corresponds to the area number of the same contrast in Table 1.

Figure 1

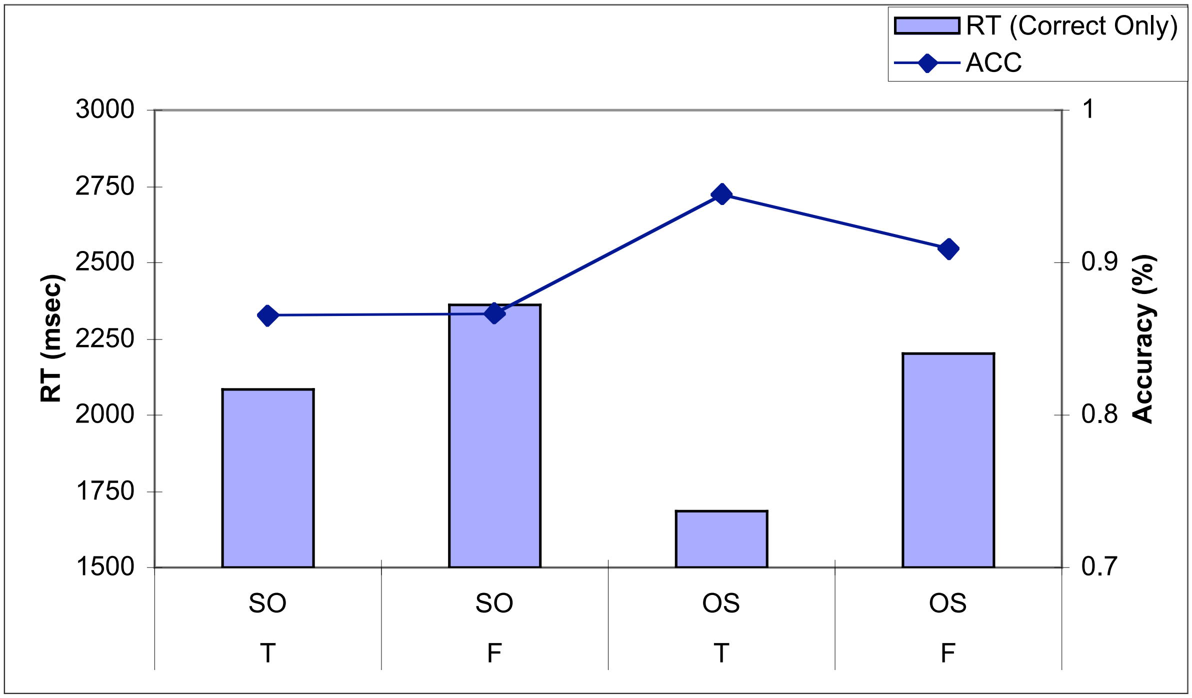
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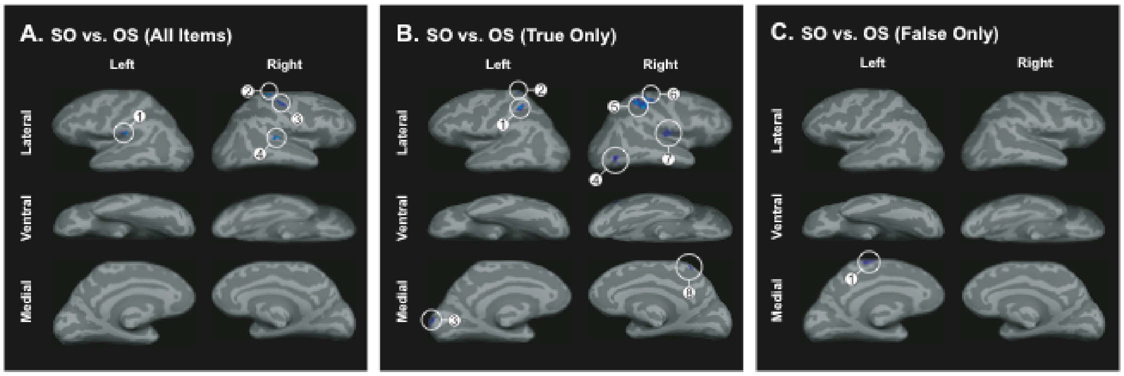
Figure 2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B. SO vs. OS (True Only)
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Ventral
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C. SO vs. OS (False Only)
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Lateral
Ventral
Medial
1

Figure 3

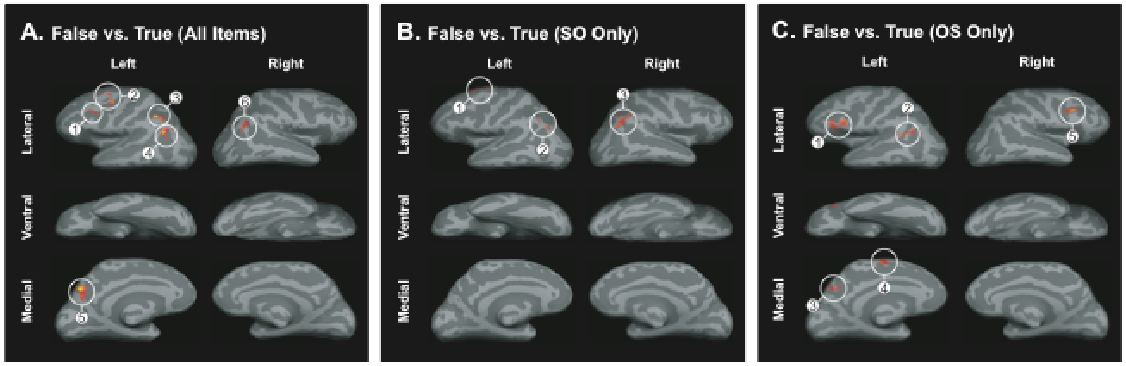
A. False vs. True (All Items)
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Figure 4

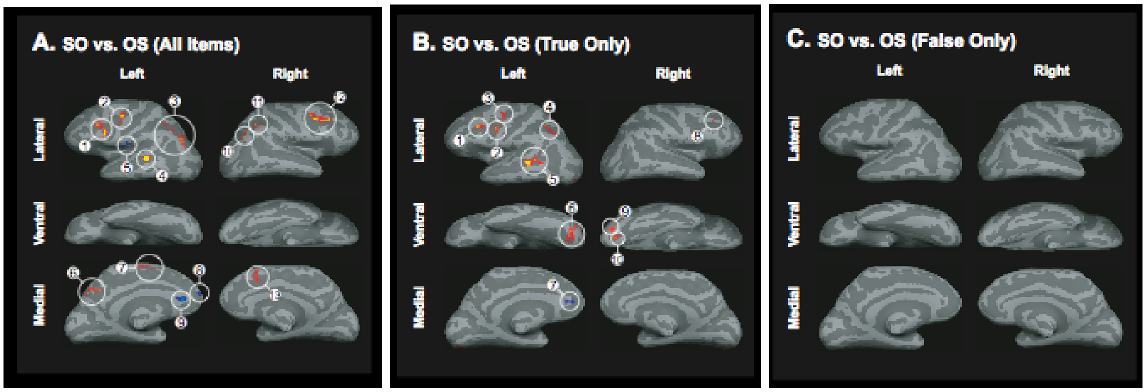
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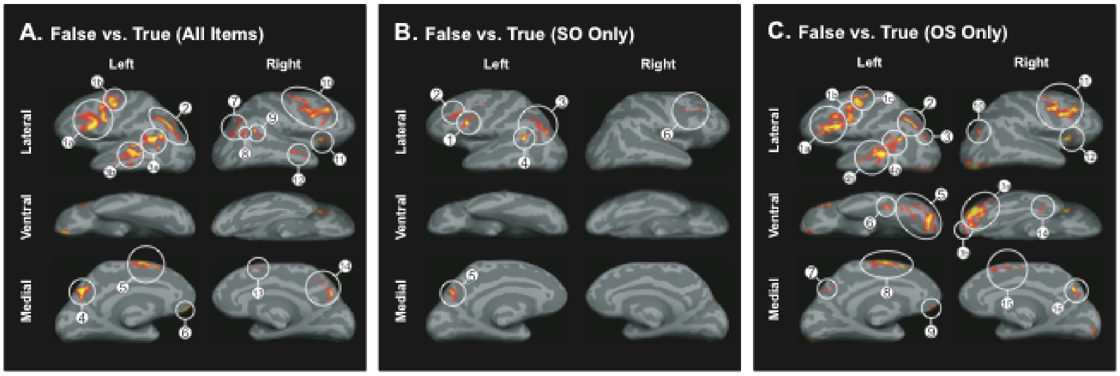
Figure 5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