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Effects of Tasks on BOLD Signal Responses to Sentence Contrasts: Review and Commentary

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Abstract

Functional neuroimaging studies of syntactic processing have been interpreted as identifying the neural locations of parsing and interpretive operations. However, current behavioral studies of sentence processing indicate that many operations occur simultaneously with parsing and interpretation. In this review, we point to issues that arise in discriminating the effects of these concurrent processes from those of the parser/interpreter in neural measures and to approaches that may help resolve them.

Keywords

Sentence comprehension; syntactic processing; functional neuroimaging

Introduction

Functional neuroimaging has been applied to the study of the neural basis for processes involved in sentence comprehension for over 30 years. Neurophysiological methods, mostly using EEG to obtain event-related potentials (ERPs), have identified responses that have been associated primarily with parsing and interpretation (the LAN and eLAN, a “scrambling negativity,” the P600), and others that have been associated primarily with the integration of word meanings into coherent, plausible propositions (the N400). Vascular neuroimaging methods have mainly (though not exclusively) concentrated on identifying areas of the brain that support the first of these processes (parsing and syntactically-based interpretation). Much of this research has been interpreted as providing evidence about the neural basis of parsing and interpretive processes in isolation from other operations that occur during the comprehension process. It is, however, clear from studies using behavioral measures that many cognitive operations occur at the same time as, and interact with, parsing and interpretation. We discuss these processes in more detail below, but, briefly, these operations include a) processes that assign aspects of sentential meaning asynchronously (through heuristics and combinatorial processes), b) processes that utilize non-syntactic linguistic information, such as the frequency of lexical representations and of lexical co-occurrence and plausibility of constructed meanings, to assign likely meanings of sentences;

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and c) processes that are related to task demands and task conditions, such as encoding meanings into memory in verification tasks. This review deals with interactions of these processes with parsing and interpretation, focusing on the effects of tasks.

An example of the kind of process that we are concerned with is the interaction between parsing and interpretation and perception and motor planning. A well-known example of this type of interaction occurs in experiments using “visual world” paradigms. The first such study was Tanenhaus et al. (1995), who reported that the nature of items in an array influenced looks to items when participants carried out actions in response to sentences such as “*Put the frog on the towel in the basket.*” Participants frequently looked at an unoccupied towel upon hearing the word “towel” when the visual array contained only a single frog (on a towel), but rarely did so for arrays that contained two frogs (one on a towel and one on another surface). This is consistent with the view that participants used perceptual information -- features of the array -- to determine the likely syntactic structure and thematic role of the phrase “on the towel” at the point at which the phrase was encountered (see also Tanenhaus et al., 2000; Altman and Kamide, 2007; Spivey and Grant, 2005). A complementary result was reported by Farmer et al. (2007), who described greater excursion of mouse movements towards the foil location (the towel) during comprehension of ambiguous sentences (*Put the frog on the towel in the basket*) with a single referent in the array than during comprehension of either unambiguous sentences (*Put the frog that is on the towel in the basket*) or sentences with two referents in the array, replicating the eye tracking data. The mouse movements largely occurred after the ambiguous segments had been presented. The two sets of results point to on-line interactions of both perceptual processing and motor planning with assignment and interpretation of syntactic structure.¹

Three features of the interaction of task-related processes and parsing and interpretation are important:

1. Interactions of these processes and parsing and interpretation occur incrementally.
2. Processes that occur at the same point as parsing and interpretation differ in different tasks. For instance, plausibility influences response selection directly in plausibility judgment (Garnsey et al., 1989) but not in verification. Encoding of thematic roles in a short-term memory store occurs incrementally in verification.
3. In many cases, there is a complete isomorphism between the complexity of parsing and interpretation and the complexity of the operations that occur at the same time as parsing and interpretation. For example, in English, parsing and interpretation is more complex at the embedded verb of object-extracted sentences than at any point in subject-extracted sentences, in part because more thematic roles are assigned at that point in object-extracted sentences than at any point in subject-extracted sentences, and therefore the processing loads exerted by response selection weighting on the basis of plausibility in plausibility judgment and encoding in verification are also increased at that point.

These features of the interaction of the operations and parsing and interpretation raise obvious challenges for the interpretation of neuroimaging data. How can one tell whether

¹Farmer et al. (2007) provided evidence for a true on-line interaction of perception and motor planning and parsing and interpretation, and against visual context rapidly selecting among alternatives provided by an independent parsing/interpreter, in the form of a unimodal distribution of maximal excursions of mouse movements towards the foil for ambiguous sentences with a single referent in the array, consistent with an on-line graded or probabilistic effect of visual context on parsing/interpretation and inconsistent with a serial model (which predicts a bimodal distribution). They concluded that the data support “a constraint-based account of sentence processing, in which multiple partially-active syntactic alternatives compete against one another with the help of not only syntactic, semantic, and statistical factors, but also nonlinguistic factors such as visual context (p. 570).”

the ERP or BOLD signal effect of the contrast of two sentences is due to different parsing and interpretive operations in the two sentences, or to different task-related operations in the two, if task-related operations such as encoding thematic roles in memory or assessing their plausibility occur at the same time, and vary in their processing demands in the same way, as parsing and interpretation? This question has not been widely considered. The few studies that have addressed this question show that it is a serious issue, however.

Task effects on BOLD signal correlates of sentence contrasts

The first way tasks can affect the BOLD signal associated with a sentence contrast is by requiring more processing of one type of sentence than other. An example of such an effect is found in Caplan et al. (2008b). We studied BOLD signal effects of the object/subject extraction contrast for plausible versions of both semantically unconstrained and constrained sentences with relative clauses, shown in (1), in a plausibility judgment task. Implausible foils are shown in (2).

1. a. Object extracted ("Subject-Object" -- SO) Unconstrained
 The fireman who the deputy called saved the sailor.
- b. Object extracted ("Subject-Object" -- SO) Constrained
 The policeman who the thief robbed watched the driver.
- c. Subject extracted ("Subject-Subject" -- SS) Unconstrained
 The fireman who called the deputy saved the sailor.
- d. Subject extracted ("Subject-Subject" -- SS) Constrained
 The policeman who arrested the thief watched the driver.
2. a. Object extracted ("Subject-Object" -- SO) Implausible
 The policeman who the thief arrested watched the driver
- b. Subject extracted ("Subject-Subject" -- SS) Implausible
 The policeman who robbed the thief watched the driver

Performing this task with these sentences involves five main operations, shown in Figure 1: 1. activation of thematic roles on the basis of syntactic analysis; 2. activation of thematic roles on the basis of asyntactic analyses; 3. evaluation of thematic roles for plausibility in semantic memory; 4. checking of thematic roles for whether they originated in the syntax; 5. response selection. We briefly describe and justify postulating these operations.²

The first set of operations are those that activate thematic roles syntactically. Based on an effect of structure and no effect of constraint on initial eye fixations on the relative clauses (longer first fixations on object compared to subject relative clauses), Traxler et al. (2002, 2005) argued that initial processing of the relative clause took place without consideration of

²We appreciate that the level of description here is not the finest grained level at which these processes have been modeled. There are many detailed models of some of these processes (in particular parsing and interpretation and response selection), many of them implemented. These models disagree about the nature of these operations, sometimes over details (Hale et al., 1987, vs Ratcliff, 2006, over particular parameters in the random walk model of response selection) and sometimes in fundamental ways (MacDonald et al. 1994, vs Frazier and Clifton, 1996, over syntax-first models of parsing). We will make reference to these more detailed analyses at some points, but this experiment was not designed to adjudicate between these disagreements. The level of detail in our model is comparable to that in much neural work. For instance, Bohland and Guenther (2006) discuss the location and interaction of components of the speech production system responsible for phonemes and phoneme sequences without tying their results to any specific model of how serial order is represented; in the work reviewed below, Gow and his colleagues (2008; 2009) do not commit to specific models of acoustic-phonetic conversion. More detailed models of the components of the system can be approached in the same way as is outlined here, once these are agreed upon.

plausibility information and was more demanding for object than subject relatives. Researchers have suggested a number of processes that could contribute to the difficulty of assigning and interpreting the object extracted structure: increased “storage” and “integration” costs (Gibson, 1998); increased confusability of preverbal NPs (Gordon et al. 2002, 2006; Lewis et al. 2006); increased distance over which a “trace” must be co-indexed (Santi and Grodzinsky, 2007); in a radically different approach, lower transitional word probabilities (MacDonald and Christianson, 2002). A feature common to all models is an increase in processing load at the relative clause verb of object-extracted sentences.

The second operation in the model is derivation of thematic roles asynchronously.³ Evidence for this process comes from Ferreira and her colleagues. Ferreira (2003) found that the error rate for assigning the agent was 45% for implausible irreversible object clefts (*It was the mouse that the cheese ate*), 36% for implausible reversible object clefts (*It was the dog that the man ate*), and 29% for symmetrical object clefts (*It was the man who the woman visited*). These observations indicate that thematic roles are assigned by asymptotic processes. Christianson et al. (2001) reported rates of endorsement of thematic roles that had to be revised in early closure sentences (e.g., endorsing *The man hunted the deer* after reading *While Bill hunted the deer lay down in the zoo*) that ranged from 11% to 51% depending upon the length of the ambiguous region, whether the probed meaning was plausible, and whether participants read the entire sentence as a whole or RSVP. These observations indicate that thematic roles that are overruled by syntactically determined revisions also persist.

One type of asymptotic process assigns thematic roles on the basis of linear relations between nouns and verbs in a clause. In English, evidence for such a process comes from studies of aphasia, where incorrect responses to tests of understanding semantically unconstrained sentences with complex syntactic forms overwhelmingly reflect the operation of heuristics based on linear order (Caplan and Hildebrandt, 1988), which we can assume are available premorbidly. Caplan and Hildebrandt's (1988) data indicate that either the immediately preverbal noun or the first noun in a sentence can be assigned the “external” thematic role assigned by the verb. The processing load associated with these heuristics increases at the same points as the load associated with syntactically based parsing and interpretation. Heuristics with these properties yield one thematic role at the embedded SS verb (*fireman called* in *The fireman who called the deputy saved the sailor*), one at the embedded object noun in SS sentences (*called deputy* in *The fireman who called the deputy saved the sailor*), and two at the embedded SO verb (*fireman called* and *deputy called* in *The fireman who the deputy called saved the sailor*).

A second type of asymptotic process assigns thematic roles to arguments that are specified in the lexical entry of a verb. Evidence for this process comes from Trueswell et al. (1994), who showed that plausibility of *the witness* as the theme of *examined* in sentences such as *The witness examined by the lawyer convinced the jury* was linearly related to eye fixation durations on *by the lawyer*. There is evidence that this “combinatorial” process applies despite clear cues that it is syntactically illegal: Just and Carpenter (1992) found that there were effects of plausibility of *the witness* as the theme of *examined* in sentences such as *The witness who was examined by the lawyer convinced the jury* on reading times for *by the lawyer*. Again, the processing load associated with this combinatorial process increases at the same points as the load associated with syntactically based parsing and interpretation. This process yields two thematic roles at the embedded verb of subject-extracted SS

³We use the term “asymptotic” to describe processes that do not construct full phrase markers, recognizing that many researchers believe that the processes we call asymptotic are, in fact, the only ones that exist (i.e., that phrase markers with more abstract and hierarchical structure do not exist). We cannot enter into the debate about this issue here.

sentences (in *The fireman who called the deputy saved the sailor*, *fireman* can be the agent or theme of *called*) and one at the relative clause-final noun (in *The fireman who called the deputy saved the sailor*, *deputy* can be the theme of *called*).⁴ In object-extracted SO sentences, four thematic roles can be assigned at the embedded verb (in *The fireman who the deputy called saved the sailor*, *fireman* and *deputy* can each be the agent or theme of *called*).

The thematic roles activated at the embedded verb and noun of SS sentences and at the embedded verb of SO sentences, and the processes that activate them, are shown in Table 1. In addition to the assignment of thematic roles individually that we have discussed to this point, nouns assigned thematic roles are related in the thematic grid of a verb. In Table 1, this is shown to occur incrementally, as soon as more than one thematic role is assigned.

The third operation in plausibility judgment is assessing the plausibility of thematic roles. There is very strong evidence that this process occurs on-line (Garnsey et al., 1989; Pearlmuter and McDonald, 1995). The evidence that the plausibility of thematic roles assigned by the combinatorial processes affects on-line processing indicates that all activated thematic roles are assessed for plausibility.

The fourth process is checking activated thematic roles for their origin in the parser/interpreter. This process is necessary in plausibility judgment because some activated thematic roles are not syntactically licensed and it is necessary to base the judgment upon the plausibility of the syntactically licensed thematic roles.⁵ The checking process must involve three stages: re-activation of the input to the parser/interpreter; re-analysis of the syntactic structure and re-assignment of at least one thematic role; comparison of this thematic role against the one being checked. The first of these processes may involve re-reading and/or rehearsal. The second involves the same parsing mechanisms as are used in the first parse (although they may only apply to the point of activating one thematic role, which suffices for the purpose of checking). The third involves comparing different sets of thematic roles, a process that has much in common operationally with the assessment of plausibility but that applies to representations in different memory stores (semantic memory in the case of assessment of plausibility, and a short-term semantic memory system (Ericsson and Kintsch, 1995) in the case of checking).

In the simplest model of plausibility judgment, activated plausible thematic roles bias the response selection process towards producing a “yes” response and activated implausible thematic roles are checked for whether they originated syntactically or asyntactically; a syntactically licensed implausible meaning triggers a “no” response. In the sentences in (1a) and (1b), all thematic roles that are activated in unconstrained sentences are plausible and thus no checking would seem to be needed in these sentences. However, based on data of Traxler et al. (2002, 2005),⁶ we assume that, though it is not mandated by task demands in plausibility judgment, the comprehension process also checks the thematic roles in unconstrained SO sentences (1a) to reconfirm which thematic roles are assigned

⁴There is no evidence that a noun that follows a verb can be taken as the external argument of that verb; thus we do not postulate that this combinatorial process assigns *deputy* as agent of *called* in *The fireman who called the deputy saved the sailor*.

⁵We assume a Markovian model; i.e., that, once a thematic role is activated, whether this activation occurred through the operation of the parser or via a heuristic or the combinatorial process is not available to the next stages of the comprehension process. If thematic roles were tagged as having been assigned by heuristics and combinatorial processes, results such as those reported by Ferreira et al. and Christianson et al. would not occur.

⁶Traxler et al. (2002) found that participants regressed from the main verb more often and fixated the sentence-initial noun phrase and the relative clause longer in these regressions in object extracted unconstrained sentences (1a) than in any other sentence type. Traxler et al. concluded that readers were less secure in their interpretation of the unconstrained object-extracted sentences and that the regressions to the sentence initial noun phrase supported a checking process. The assumption that this occurs in plausibility judgment can be checked by examining eye fixations, which should show increased regressions from the main verb of these sentences in that task as in verification.

syntactically (i.e., this check is intrinsic to normal processing because these sentences are hard to structure and interpret and the thematic roles assigned are highly confusable).

We assume response selection proceeds as outlined in models such as Ratcliff's random walk model (Ratcliff, 2006). In plausibility judgment, response selection is weighted incrementally as thematic roles are assigned (Garnsey et al., 1989). As noted, the simplest model for producing correct judgments in plausibility judgment maintains that plausible thematic roles directly bias the response selection process towards a "plausible" response, and if an implausible thematic role is determined to be syntactically derived, this information is conveyed to the response selection process and an "implausible" response is made.

The model maintains that these operations act in a partially parallel, feedforward fashion, as shown in Figure 1. Syntactic and asyntactic comprehension processes occur simultaneously and the thematic roles they yield are assessed for plausibility; the next step is either biasing response selection or a check for the origin of an implausible thematic role.

Figure 2 (from Caplan et al. (2008b)) shows the BOLD signal results. Effects of sentence type and constraint were found in two areas: a posterior area centered in the left middle temporal gyrus (MTG) and the left inferior frontal gyrus (IFG). In the left MTG area, BOLD signal increased for SO compared to SS sentences for both the constrained and unconstrained sentences, and for constrained SS compared to unconstrained SS sentences. In the left IFG, BOLD signal increased for SO compared to SS sentences in the unconstrained sentences only; BOLD signal in constrained SS sentences was at the same level as that associated with SO sentences.

This pattern of results can be accounted for if the left temporal area supports the assignment of syntactic structure and its use to determine thematic roles, and the left inferior frontal gyrus supports the process of comparing sets of thematic roles as part of the checking process. On this account, the left temporal area is active when the parser/interpreter is engaged, and its level of activity is a function of the load exerted on the parser/interpreter. The parser/interpreter is engaged when the sentence is initially processed for meaning, at which time the load on the parser/interpreter is higher for SO than for SS sentences regardless of constraint (Traxler et al., 2002, 2005). The parser/interpreter is engaged for a second time when the sentence is partially re-analyzed as part of the checking process, which occurs for all SO sentences and for constrained SS sentences in plausibility judgment, as described above. The result is greater BOLD signal for all SO sentences than for all SS sentences, and greater BOLD signal for constrained than for unconstrained SS sentences. The left inferior frontal area is active when two thematic roles are compared to one another. This occurs when thematic roles are checked for their origin in the syntax; that is, for all SO sentences and constrained SS sentences. The result is greater activation for SO sentences and constrained SS sentences than for unconstrained SS sentences, as observed. (For fuller discussion of the results and the model, see Caplan et al., 2008b).

The results and their analysis illustrate several important consequences of considering task effects in relation to on-line syntactic operations.

First, they show how some BOLD signal correlates of a contrast between two sentences may be due to operations that are determined by the task. If this account of the BOLD signal effects is correct, some of the BOLD signal differences between SO and SS sentences are not due to differences in parsing and interpreting these sentences, but to differences in which sentences require a check of thematic roles for their origin in the syntax, which is partially determined by the task. For instance, a different set of sentences requires this check in a verification task. In a verification task, the reader/listener can disregard implausible thematic

roles in constrained sentences (because no implausible probes are ever used) but must determine which set of thematic roles was derived syntactically in unconstrained sentences and base his/her response on that set. If the model is correct, in a verification task, SS unconstrained sentences should require more checking of thematic roles for their origin in a syntactic analysis, and there should be more BOLD signal in L MTG and L IFG for SS unconstrained sentences than for SS constrained sentences (the opposite of the pattern seen in Caplan et al., 2008b).

Second, the results show how failing to consider task demands in relation to on-line syntactic operations can lead to possible misinterpretations of functional neuroimaging results and their analysis; specifically, how it is possible for a BOLD signal effect to appear to be due to parsing/interpretation when it is in fact due to a task-induced operation. Figure 2 shows an increase in BOLD signal in L IFG for SO compared to SS unconstrained sentences. On its own, this pattern suggests a role for this area in parsing/interpretation. If the analysis outlined above is correct, however, this interpretation is incorrect: this sentence contrast effect is due to a role of this area in comparing two sets of thematic roles, not in assigning a thematic role on the basis of parsing.

“Ancillary” task-related cognitive activity and sentence type effects

A second way that tasks can affect BOLD signal associated with sentence contrasts is by inducing ancillary cognitive operations (sometimes called “strategies;” Page (2006) refers to these operations as “epiphenomenal”) that apply to different extents in different sentence types.

Results in verification tasks provide an example of this type of task effect. There have been effects of the syntactic structure of the target sentence on RTs for correct responses to probes for synonymous (or thematically very similar) object- and subject-extracted targets in the fMRI studies that have used the verification task (Just et al., 1996; Fiebach et al., 2001, 2005). This shows that the most straightforward model of how participants accomplish this task – the view that they assign the structure and meaning of the target sentence when they first read it and maintain only the meaning in short-term memory to be checked against the meaning of the probe – is wrong. If that were how the task were performed, there would be no effect of the form of a sentence on verification reaction times for correctly verified sentences (the decision would be based on a match between the memory of the meaning of the verification sentence in STM/WM and the meaning of the probe; the syntax would be “gone”). The effect of syntax on these correct responses shows that the form of the target sentence is either maintained or reconstructed from another representation (which cannot be exclusively the meaning of the sentence, because the meaning could be associated with many forms) at the point of processing the probe. One process that is likely to be used by participants is to encode the target phonologically, retain the phonological representation in short term/working memory (possibly using subvocal rehearsal), and reconstruct at least part of the syntax and meaning of the target when they see the probe. Processes such as these are likely to occur more frequently for more complex sentences. A possible basis for the results in verification, therefore, is that the areas activated when more and less demanding sentences are contrasted are related to differential use of task-related operations in different sentence types, not different demands of task-independent parsing and sentence interpretation for different sentence types.

Evidence that this process may underlie some of the activations reported in the literature using verification comes from our finding that the time course of the effect of object- versus subject-extraction on BOLD signal is more plausibly related to the presentation of the probe than to the presentation of the target (Caplan et al., 2008a). Figure 3 shows the areas of

syntactic effect on BOLD signal in TR intervals from 4 – 10 seconds after the onset of a target object- or subject-extracted sentence (early TR interval) and 4 – 10 seconds after the onset of the probe (late TR interval). As can be seen, the syntactic effect is associated with the probe, not the target. The effect of structure is much more likely to be due to differential rehearsal of different structures, and/or to reconstructing a structure and meaning from a partial representation held in memory, than to initial parsing and interpretation.

Effects of different tasks in which syntactic processing is “implicit” on sentence-type effects

The effects of tasks on BOLD signal correlates of sentence contrasts reviewed above occurred in tasks in which the product of the parsing and interpretation process is used to determine a response (i.e., in tasks that require comprehension). It might seem that one way to eliminate task effects would be to take the use of the products of parsing and comprehension out of the equation by using tasks in which responses do not depend on them (often called “implicit” tasks). A series of studies in our lab shows that this approach does not eliminate task effects, however.

In the first relevant study (Caplan et al., 2008b), we demonstrated that BOLD signal effects could be obtained for sentence contrasts in an implicit task, and that they differed from BOLD signal effects obtained for the same contrast in a task in which responses were based upon comprehension. We compared BOLD signal responses to the same sentences in two tasks – plausibility judgment and nonword detection -- in the same 15 participants. The contrast of plausible object- and subject-extracted sentences in which the order of animacy of nouns biased against the syntactically licensed interpretation of a sentence⁷ led to widespread increased BOLD signal in the plausibility judgment task -- in the left hemisphere, in the inferior, middle, and superior frontal gyri, the inferior and superior parietal lobe, the middle and fusiform temporal gyri, and the precentral gyrus; in the right hemisphere, in the three frontal gyri. Non-word detection showed a very different pattern of BOLD signal effects. For sentences containing only real words – the same sentences as the plausible sentences that were analyzed in the plausibility judgment task – the same contrast led to activity only in L BA 44. Behavioral results indicated that the reduction in sentence contrast effects was not due to participants not processing the sentences as sentences in the non-word detection task: the sentence type effect was significant by items; histograms of RTs by deciles showed unimodal distributions for all sentence types (confirmed by bimodality coefficients), not the bimodal distributions that would be expected if some sentences were inspected superficially for non-words and others processed deeply for meaning; and reading times for object-extracted sentences with non-words in embedded verb position were significantly longer than those for subject extracted sentences with non-words in either embedded verb or subject positions while reading times for object- and subject-extracted sentences with non-words in other positions did not differ, strongly suggesting that subjects assigned some aspects of structure and/or meaning even to the sentences with non-words. If all – or the great majority – of sentences were processed to the level of syntactic form and propositional meaning in the non-word detection task, the difference in BOLD signal between this task and plausibility judgment might be related to task demands. In plausibility judgment, but not in non-word detection, the BOLD signal sentence-type effects could have resulted from task-related processes that co-occur with parsing and interpretation -- checking propositions for their origin in syntactic processes and incremental weighting of the response selection mechanism by plausibility information that

⁷Examples are: Object extracted - incongruent noun animacy order: *The deputy that the newspaper identified chased the mugger*
Subject extracted - incongruent noun animacy order: *The newspaper identified the deputy that chased the mugger*

is activated on-line. We concluded that the BOLD signal activity in Broca's area seen in the nonword detection task reflected aspects of parsing and interpretation and other areas of BOLD signal seen in the plausibility judgment task reflected these other processes.

The products of parsing and interpretation can be used to accomplish non-word detection: a participant can conclude that a nonword is present if the sentence meaning had a lexical "gap".⁸ To address this issue, and to try to replicate these findings, we followed up this study with a study of the same sentences in a font change detection task (Caplan, in press). In this task, since all sentences are well formed and plausible, the products of comprehension cannot differentially influence response selection. As in nonword detection, behavioral results (expected interactions of syntactic and semantic variables on RTs; unimodal distribution of RTs; increased RTs when font changes occurred at points of load) indicated that participants processed the sentences to the syntactic and semantic level. A BOLD signal effect of the same sentence contrast as above led to increased activity in L inferior parietal lobe. Conjunction analysis revealed no overlap of activation in this area and the activity in the area activated in the nonword detection study, and functional connectivity analysis showed no functional relation between this activity and activity in the area activated in the nonword detection study. This result indicates that different parsing and interpretive operations and/or different ancillary operations were applied in the font change and nonword detection tasks.

The effect of the location of font changes and nonwords on RTs provides clues as to the parsing and interpretive operations that may have applied in the two tasks. In contrast to nonword detection, where, as noted above, RTs were longer for detection of nonwords that occurred at the embedded verb of object extracted sentences, in font change detection, RTs were longer when the font change occurred at the embedded subject of those sentences. We cannot think of different ancillary operations that could have applied in the two tasks to yield these RTs patterns, but there are different parsing and interpretive operations that could have produced them. The results in font change detection could reflect surprise (Levy, 2008) or assignment of generalized thematic roles (Bornkessel and Schlesewsky, 2006), both of which lead to maximal load at the embedded subject of SO sentences, and the effects in the nonword detection studies could reflect assignment of specific thematic roles, which leads to maximal load at the embedded verb of SO sentences.

To confirm these suggestions, we further investigated these sentences using head mounted eye tracking, which provides information about fixation durations in words in sentences without font changes or nonwords. These studies showed that initial fixations were almost always directed towards the words below the fixation cross – a fact that makes it very hard to interpret first fixation duration (and that indicates that fixation symbols should occur at the leftmost position of a sentence in all future work using MR). However, both total fixation time and the difference between total fixation time and first fixation time were greater on the relative clause subject of object extracted relative clauses with an incongruent order of animate and inanimate nouns than on the relative clause verb of subject extracted sentences in the font change detection study and not in the nonword detection study. Looking across all results, the relative clause subject NP of object extracted relative clauses with an incongruent order of animate and inanimate nouns was the point of greatest load in the font change study, and the embedded verb of these sentences was the point of greatest load in the nonword detection study. As noted above, this suggests different parsing and interpretive mechanisms in the two tasks.

⁸This is unlikely to be the sole basis for responses for two reasons: 1) lexical access results are a much more direct basis for response selection, and b) this strategy requires that words be accessed, which would allow participants to make nonword judgments on a lexical basis.

The implication of these results is that, although the use of tasks in which the products of the comprehension process are irrelevant to response selection (tasks in which parsing and interpretation are “implicit”) eliminates interactions between the use of the products of the comprehension process to accomplish a task and parsing and interpretation, it does not eliminate the interaction of parsing and interpretation itself and the task that participants perform. In hindsight, this is not surprising. Even if they do not affect response selection, different primary tasks are associated with different mechanisms for the deployment of attention -- both the processes whereby attention is directed towards parts of a stimulus (conceiving of attention as a spotlight; Treisman and Gelade, 1980) and the processes whereby attention is allocated to processing a stimulus dimension (conceiving of attention as a resource; Kahneman, 1973). The first of these affects parsing and interpretation by leading to different sequences of perception of the language input and thereby allowing operations to occur in different orders, and the second by allowing different amounts of processing to be applied to that input. The conclusion is that considering the effects of task on parsing and interpretation is always necessary, even in tasks in which parsing and interpretation are implicit.

We note that the absence of a task does not eliminate effects of the deployment of attention; the absence of a task simply eliminates the possibility of using any behavioral data to develop a model of the way participants processed sentences.

Issues arising from fMRI data

If concerns about tasks affecting BOLD signal effects of sentence contrasts are well-founded, they affect the interpretation of virtually every functional neuroimaging study of sentence processing, both those using ERPs and those using BOLD signal: in most, if not all, studies, it is unclear which results reflect the language processes of interest and which reflect task-related functions. The implications extend to behavioral studies. The effect of task on behavioral responses has been well recognized and much discussed in some areas, such as the different effects of lexical variables in lexical decision and naming, but, outside the visual world paradigm and mouse tracking studies, it has been discussed very little in the sentence processing literature. However, the issue arises with respect to all tasks, because of the high degree to which the processing load associated with incremental assignment of structure and meaning covaries with that associated with incremental effects of most tasks. It is hard to distinguish these effects on accuracy and reaction time, because these measures are unidimensional. Measures that afford multiple observations of processing of a given input can provide clues regarding different processes. For instance, Traxler et al. (2002, 2005) argue that initial fixations on relative clauses reflect parsing and that late fixations reflect re-analysis and checking thematic roles for their origin in the syntax (see Reichle et al., 2003, 2009, for other models of fixation effects). Neural variables can provide valuable information about these processes. As we have argued is the case in our plausibility judgment study of constrained and unconstrained object- and subject-extracted sentences (Caplan et al., 2008b), they can suggest effects of a number of processes in separate spatial locations. To verify these suggestions, and to apply this information to the question of the time course and interaction of different processes and thereby make neural data more clearly interpretable, it is necessary to measure neural activity in particular spatial locations at particular points in time on a fine-grained scale.

Approach to the Problem

As noted, the difficulty in interpreting neural and behavioral measures can be tied in part to the limitations of standard behavioral and neuroimaging techniques: the limitation of behavioral observations to a single measure, and the use of either fMRI or EEG (ERP)

measures that do not have the combined spatial and resolution necessary to directly observe the evolution of multiple representations in different brain areas and any interactions that may occur between them. Two developments have made it possible to transcend these limitations. The first is the development of multi-modal imaging techniques that provide the spatial resolution needed to track activation of multiple localized neural processes and the millisecond temporal resolution needed to identify directional causal interactions between localized processors (c.f. Dale & Sereno, 1993; Liu et al., 2002). The second is the application of Granger causality analyses (Granger, 1969) to neural data (Bernasconi & König, 1999; Liang et al., 2000; Kaminski et al., 2001; Hesse et al., 2003; Brovelli et al., 2004; Seth, 2005; Roebroeck et al., 2005; Supp et al., 2007; Dhamala, Rangarajan & Ding, 2008; Gow et al., 2008, 2009; Gow & Segawa, 2009). Granger causality is a ubiquitous tool in research and modeling in many fields, ranging from economics (Hendry & Mizon, 1999) to population ecology (Dyck et al., 2007), climate modeling (Elsner, 2007) and cardiac physiology (Faes, Nollo & Chon, 2008). Granger analysis is similar to functional connectivity analyses. However, standard functional connectivity analyses rely on correlational analyses that cannot reveal the direction of influence, and are open to misinterpretation due to spurious correlation. Granger causality is a noncorrelational approach premised on the observation that causes both precede and uniquely predict their effects, even when considered in the context of all potentially interacting variables. It is generally implemented using a statistical jackknife procedure applied to time-lagged vector autoregression analyses (Seth, 2005). It can be used to identify the direction of causal influence (including reciprocal interactions) and when applied rigorously is not subject to spurious correlation effects.

No studies exist in which Granger causality analysis has been applied to MEG responses to sentence contrasts. In the absence of such studies, we present studies of a different phenomenon that demonstrate the power of the approach, and an outline of the type of studies that could be undertaken using sentence contrasts.

MR-constrained MEG Studies of Phoneme Perception

Phoneme perception presents a problem that is similar to the one discussed above, insofar as there are unresolved questions about how different processes interact to achieve a stable representation of a phoneme. There is very strong evidence that lexical factors (e.g., whether a sequence of phonemes is a word, lexical frequency, and others) affect performance on tasks that require phonetic perception, such as decisions about whether two speech-like sounds differ, what phoneme has been presented, etc. The question is where these lexical factors exert their effects. One possibility is that they are exerted late in the course of performing such tasks. On these “bottom-up” models, phonetic processing maps acoustic parameters onto phonetic features, phonemes and syllables, and relays its output to a decision-making stage, where lexical information increases the level of activation of representations that have particular lexical properties (i.e., that are words, that are more frequent words, etc.). A second possibility (termed “top-down” or sometimes “interactive” processing) is that the mapping between phonetic features and words is a two-way process in which lexical context directly influences the assignment and grouping of phonetic features. Different simulation data support computational models of each processing strategy (c.f. McClelland & Elman, 1986; Norris et al., 2000), and neither behavioral nor imaging data have been able to decisively determine whether specific effects reflect purely bottom-up or interactive processing. We here present two studies that demonstrate that MR-constrained MEG can move towards resolving these debates. The studies also demonstrate effects of task that illustrate the points made above regarding sentence contrasts.

Granger causality analyses of lexical influences on speech perception

The first study we shall review explored the neural mechanisms that underlie lexical effects on the categorization of ambiguous speech sounds (Gow et al., 2008). The question we addressed is whether these effects reflect direct interactive lexical influence on speech perception or post-perceptual interactions at a discrete decision phase (see Norris et al., 2000 for a comprehensive review of the debate). Our work utilized the Ganong effect (Ganong, 1980), the finding that, in a /g/-/k/ continuum at the onset of tokens of *gift* and *kiss*, listeners are more likely to classify ambiguous items as /g/ in the *gift* context and as /k/ in the context of *kiss*. We replicated this behavioral finding using a five-step /s/-/•/ continuum embedded at the onset of tokens of *shampoo* and *sandal*. Subjects listened to tokens in isolation and then made a two-item forced choice (2AFC) decision about whether the initial phoneme in each token was a “s” or “sh.” Analysis of behavioral results showed a robust Ganong effect, with subjects more likely to identify mid-continuum tokens as “s” when they appeared in the *sandal* context as compared to the *shampoo* context ($p < .001$). Simultaneous MEG and EEG data were recorded during the behavioral task. These physiological data were combined with T1 structural brain images collected in a 1.5T scanner during a separate session to create high spatiotemporal resolution “MEG movies” showing estimated activation at 1 ms intervals at approximately 12,000 hypothesized dipoles corresponding to vertices in a tessellated reconstruction of the cortical surface. Analyses of these data showed a pattern of increased activation of the left posterior superior temporal gyrus (pSTG) for ambiguous tokens in the continua that showed strong Ganong effects as compared to unambiguous tokens whose interpretation was not influenced by lexical context ($p < .001$). This region is strongly associated with phonetic processing based on evidence from pathology, electrophysiology and BOLD imaging (c.f. Poeppel, 2001; Näätänen, 2001; Binder et al., 2000) and with evidence from an fMRI study of the Ganong effect by Myers & Blumstein (2008). This increased selective activation of pSTG by ambiguous tokens only became apparent 280 ms after stimulus onset. This is significant because this is more than 160 ms after the offset of the ambiguous segment, and 60 ms after the lexical contexts became discernable, suggesting the possibility of a lexical effect.

We looked for patterns of causal influence in these data, using Granger causation analysis to determine whether parts of the brain modulate the left pSTG during the interval beginning at 280 ms. The first step in this process was to identify the set of all brain regions that interact with left pSTG during this period. We used evidence of increased 40 Hz gamma phase-locking to activation in the strongest vertex in the left pSTG to identify potentially causally related regions of interest (ROIs). Forty Hz phase-locking has been proposed as a mechanism for distributed binding of neural populations into transient cell assemblies during cortical processing (c.f. Gray & Singer, 1989; Gray et al., 1989; Tallon-Baudry & Bertrand, 1999; Joliet et al., 1994; Tallon-Baudry et al., 1997; Lachaux et al., 1999).⁹ Source space phase-locking relations were quantified using a spectral dynamic parametric mapping technique (Lin et al., 2004). Using an iterative thresholding processing technique, we identified 9 distinct phase-locked anatomical ROIs, all of which corresponded to well-described perisylvian language areas in both hemispheres. Granger analysis of the activation timeseries from the strongest dipole in each ROI revealed that pSTG activation between 280 and 480 ms was influenced by activation in four areas, including the left supramarginal gyrus (SMG) ($p < .001$) (Fig. 4). Analysis of the interval between 80 and 280 ms showed

⁹Recent work by Yuval-Greenberg et al. (2008) suggests that observed increases in gamma phase power associated with EEG studies of visual binding may partially reflect an ocular (non-neuronal) artifact. They note however that MEG data are not sensitive to this artifact. Melloni et al. (2008) note that this artifact may be avoided in EEG data as well through the use of non-nasal reference signals and improved spatial separation. Work controlling for this artifact has replicated the basic gamma phase binding results (c.f. Trujillo et al., 2005). In our work, source space phase analyses of integrated MEG and EEG data and a focus on non-fronto-orbital brain regions protect us from this artifact.

causation in the opposite direction, with pSTG activation influencing SMG activation. The Granger results thus provide evidence for early activation in pSTG, an area related to initial phonetic processing, affecting SMG, an area associated with activation of word forms (Sanai et al., 2008; Prabhakaran et al., 2006; Price, 1998; Orfanidou et al., 2006), and an immediately following causal influence of the SMG on pSTG activations. This provides strong evidence for the hypothesis that wordform representations directly influence phonetic processing during speech perception rather than influence a late decision-making stage of processing.

Granger causality analyses of lexical and articulatory influences on the perception of assimilation

The second study (Gow & Segawa, 2009) used the tools developed in the studies of the Ganong effect to explore how lexical and articulatory constraints influence the grouping of ambiguous phonetic cues during the perception of lawfully assimilated speech. In this work we examined English coronal place assimilation, a productive, language-specific phonological process in which the pronunciation of a word-final coronal segment (/t,d,n/) is influenced by the place of articulation of an immediately following noncoronal segment. For example, in the phrase *cone bent*, the coronal /n/ in *cone* may assimilate the labial place of the /b/ in *bent*, and end up sounding like a blend of the two sounds [n^m]. Listeners show a two-way context effect with post-assimilation context influencing the perception of the assimilated segment (Gow, 2002; 2003a, b; Gow & McMurray, 2007) and assimilated segments enhancing the perception of subsequent context (Gow, 2001; 2003a, b; Gow & McMurray, 2007). Both of these effects depend on the graded modification of acoustic-phonetic place cues caused by natural coarticulation and are not present when listeners hear stimuli that are deliberately mispronounced with assimilated phonemes (*greem beans*). Because these context effects do not depend on language-specific knowledge or exposure (Gow & Im, 2004), Gow (2003a, b) proposed a feature cue parsing model of assimilation context effects according to which simultaneous progressive and regressive context effects are the result of a perceptual mechanism that groups cues to the same feature together (a similar mechanism underlies cue trading effects). Motor theory and direct realism provide conceptually related accounts of compensation for coarticulation that place the parsing process at an articulatory level of representation (c.f. Liberman et al., 1967; Liberman and Mattingly, 1985; Fowler, 1986).

In its original form, the feature cue parsing model emphasized bottom-up grouping processes similar to the classic Gestalt rule of grouping by similarity. Gow & Segawa (2009) asked the question of whether other levels of representation, including articulatory representations, could also constrain this grouping process. We had subjects perform a 2AFC picture-matching task involving short phrases that included assimilated, nonassimilated, and misassimilated speech. A subject might hear the phrase *cone* (koⁿ_m) *bent*, and then see lateralized pictures of a bent comb, and a bent traffic cone. Behavioral data collected during the task suggested that listeners were more likely to chose the coronal interpretation of an item that had undergone labial assimilation if it was followed by a labial than if it was followed by a non-labial ($p < .05$).

We collected MEG and EEG data while subjects performed the task described above, and analyzed them as in Gow et al. (2008). As in our Ganong work, the left pSTG was the only area that showed strong activation for assimilated compared to unassimilated items during the period starting roughly 100 ms after stimulus onset. We interpret this as an indication that L pSTG is involved in phonemic processing related to assimilation. This interpretation is consistent with results of Mitterer and Blomert (2003) regarding how assimilated speech influences the magnitude of the mismatch negativity (MMN), an evoked component that

occurs in this time period and location, and that, like assimilation context effects, shows well-documented sensitivity to phonetic manipulations (Näätänen, 2001). 40 Hz phase-locking analysis of activity in pSTG 200 ms after its onset revealed a set of ROIs showing significant overlap with those found in the Ganong task.

Granger causality analysis of MEG activation timeseries from these ROIs (Fig 5) revealed that the dorsal premotor area (dPM) influenced phonetic pSTG activation in both assimilation conditions. The left dPM area plays a role in articulatory planning and representation, as shown in the effects of lesions (Didic et al., 1998), intraoperative surgical mapping, (Penfield & Bolchey, 1937; Ojemann et al., 1989; Duffau et al., 2003) and functional imaging (Wise et al., 1999). In both the competition and no competition conditions, bilateral pSTG activation was also influenced by left posterior middle temporal gyrus (pMTG), a region implicated in the interface between phonological and semantic representations (Hickok & Poeppel, 2004, 2007; Scott & Wise, 2004). Fig 5 also shows that, in the competition condition, where lexical information could not resolve interpretation, the pattern of Granger causality was part of a much broader network that primarily influenced the right pSTG, an area that has been suggested to be involved in phonemic processing (Hickok and Poeppel, 2004, 2007). The increased modulation of such an area in the instances where assimilation produced a competing word form is consistent with findings by Gaskell & Marslen-Wilson (1998) of stronger effects of following phonemic context on assimilations that created words. The shift to the right-hemisphere based area supporting phonemic processing may indicate increased focus on the integration of information over larger temporal epochs (Poeppel, 2003) in this condition.

Granger causality from dPM and pMTG to pSTG was not found in the Ganong experiment. We interpret the influence of dPM on pSTG as evidence for articulatory mediation of parsing the overlapping articulatory gestures that produce assimilated speech, consistent with the general predictions of motor theory's analysis-by-synthesis strategy for understanding coarticulated speech (Liberman et al., 1967; Liberman and Mattingly, 1985). The fact that dPM did not influence pSTG activation during the resolution of phonetic ambiguity in the Ganong experiment may be attributed to differences in the nature of the ambiguities in the two cases: ambiguity was the result of natural coarticulation in the assimilation study, but ambiguity in the Ganong experiment was due to artificial digital signal manipulation that cannot be reproduced by the human vocal tract. The influence of MTG of pSTG in the second study also can be attributed to task demands, namely the fact that the task involved semantic processing (picture matching) and therefore activated the ventral auditory pathway, rather than phoneme identification, a metalinguistic task that is thought to activate the dorsal auditory pathway.

Interim Summary

The studies summarized above illustrate several types of task effects on BOLD signal correlates of sentence contrasts and show how Granger causality analyses of MEG signal can reinforce models of the functions of brain regions and, by coupling these models with analyses of their causal relations at particular time points, provide insights into the mechanisms involved in psycholinguistic processes (in the examples given, phoneme perception). We next show how this approach might be applied to the problem of task effects on sentence comprehension.

Predictions for MR-constrained MEG Studies of Relative Clauses in Plausibility Judgment and Verification

To illustrate how MR-constrained MEG might be useful in exploring neural correlates of task effects on sentence contrasts, consider the sentences discussed above (1), repeated here, how they are processed in plausibility judgment and verification tasks, and the neural basis for these operations.

1. a. Object extracted Unconstrained
 The fireman who the deputy called saved the sailor.
- b. Object extracted Constrained
 The policeman who the thief robbed watched the driver.
- c. Subject extracted Unconstrained
 The fireman who called the deputy saved the sailor.
- d. Subject extracted Constrained
 The policeman who arrested the thief watched the driver.

As discussed above, a basic-level model of the processing of these sentences includes five main operations: 1. activation of thematic roles on the basis of syntactic analysis; 2. activation of thematic roles on the basis of asyntactic analyses; 3. evaluating thematic roles for plausibility in semantic memory; 4. checking thematic roles for whether they originated in the syntax; 5. response selection. There are differences in the sentences to which these operations apply in different tasks, and additional operations apply in verification.

In plausibility judgment, implausible propositions activated by heuristics and combinatorial processes in plausible constrained sentences must be checked for whether they originated syntactically or asyntactically. In verification, implausible thematic roles can be ignored, since there are no implausible target foils and verification probes are always plausible. However, in verification, as mentioned above, all thematic roles in unconstrained sentences must be checked for their origin (because all are plausible, and the task is to match the syntactically licensed set to the probe). Response selection also differs: it is affected incrementally in plausibility judgment and occurs only at the point of the probe in verification. Moreover, in verification, syntactically licensed plausible thematic roles must be encoded in a short-duration memory system; the evidence from Traxler et al. cited above suggests this occurs incrementally (and is less secure for unconstrained SO sentences). In verification, encoding plausible syntactically licensed thematic roles (and, in the case of SO unconstrained sentences, plausible asyntactically derived thematic roles) occurs at the points at which response selection is affected by plausibility in plausibility judgment.

In order to investigate this model using techniques such as those used by Gow and colleagues (2008; 2009), it is necessary to establish a working mapping between the components of this model and brain structures.

Beginning with the parsing and interpretive operations that differ in object and subject extracted sentences, there is considerable disagreement about their neural localization. The object-subject contrast has led to many patterns of activation: L IFG (Stromswold et al., 1996), Broca's area and Wernicke's area and, to a lesser degree, in their right hemisphere homologues (Just et al., 1996), bilateral inferior temporal lobe (Cooke et al., 2001), medial anterior structures (cingulate, middle frontal and superior frontal gyri) and left thalamus, left superior parietal lobe and right inferior frontal lobe (Caplan et al., 1998, 1999a, 2000;

Waters et al., 2003; Chen et al., 2006), and no effects (Indefrey et al., 2001; Ben Shachar et al., 2003; Fiebach et al., 2001, 2005); see Grodzinsky and Friederici (2006), Caplan (2006, 2007), for review. There are many possible reasons for these differences, including task effects, differences in languages and features of participants, power of the experiments, and others. Given the uncertainty about the location of many of the processes we are concerned with, we will illustrate the potential use of MEG based upon localizations that were documented in Caplan et al. (2008b), which are based upon these sentences specifically.

As discussed above and in more detail in Caplan et al. (2008b), the results in Caplan et al. (2008b) led to the conclusion that L STG/MTG supported the activation of thematic roles on the basis of syntactic analysis (this location is slightly inferior to one activated by relative clauses in several other studies (Ben Shachar et al., 2003, 2004)). The analyses in Caplan et al. (2008b) also led to the conclusion and that L IFG supported comparing sets of thematic roles, a localization consistent with other published results (Dapretto and Bookheimer, 1999; Love et al., 2006).¹⁰ Intracortical recordings of the N400 component of the ERP response to semantic anomalies and implausible sentences point to left inferior temporal lobe as the locus of assessment of the plausibility of thematic roles (Nobre and McCarthy, 1995). Encoding of thematic roles in a short-term memory system presumably involves the areas involved in episodic encoding (hippocampus) and semantic memory (ITG). Thompson-Shill and her colleagues have convincingly argued that L IFG/DLPFC is one area critically involved in response selection (Kan and Thompson-Shill, 2004; Novick et al., 2005). We return below to the area(s) that support(s) thematic role assignment though an asyntactic process.

Combining the analysis of the operations that take place in these areas with the analysis of the points in the sentence at which these operations apply leads to the predictions in Table 2 regarding processing of plausible sentences. Table 2 indicates the points in the sentence at which more processing of a particular type is expected to occur (with more plus signs), and the location of the processing. As can be seen, different operations are predicted to occur at different points in these sentences in plausibility judgment and in verification. These predictions can be tested with MR/MEG.

In addition to these predictions about the points in these sentences at which these areas are expected to be activated by these operations, the model predicts patterns of Granger causality among these regions. At each point at which thematic roles are assigned, the model predicts parallel activation of L STG/MTG and the area(s) in which thematic roles are assigned asyntactically (this area is not specified in Table 1), and immediately ensuing Granger causality effects of the activity in these areas on L ITG. The L ITG activity would then be expected to show Granger causality effects on L IFG (part of the checking process), at the points in the relative clauses in the sentence types in the two tasks discussed above, which are indicated in Table 2. As discussed, we predict there would be a second activation of L IFG at the end of unconstrained SO sentences; this second check is not triggered by the output of plausibility assessment, and therefore would not be Granger-caused by L ITG activity. In plausibility judgment, the L DLPFC response selection region becomes active at the points shown, and receives input (is Granger-causally influenced by) L ITG in both constrained and unconstrained sentences (recall that plausible thematic roles, which occur in both constrained and unconstrained sentences, bias towards “plausible” responses).¹¹ In verification, the areas involved in encoding (presumably, L hippocampus and ITG) become

¹⁰Dapretto and Bookheimer (1999) had found that making synonymy judgments about sentences with different syntactic forms activated L IFG. Love et al. (2006) found that a thematic role verification task produced more BOLD signal in Broca’s area than two tasks that did not require semantic processing (there were no effects of syntactic structure in any task). Both these results are consistent with comparing sets of thematic roles occurring in L IFG.

active following thematic role assignment. The simplest model maintains that when more than one set of plausible thematic roles is activated (as occurs in unconstrained sentences), the origin of thematic roles is checked and syntactically licensed thematic roles are encoded. This predicts Granger-causality from L IFG to L hippocampus and ITG at the encounter with the relative clause verb in SO sentences and with the relative clause noun and verb in SS sentences in unconstrained sentences. When only one set of plausible thematic roles is activated (as occurs in constrained sentences), it is encoded; this predicts Granger-causality from L ITG to L hippocampus at these points in constrained sentences.

An issue we have so far avoided is the neural basis for asyntactic assignment of thematic roles. To our knowledge, there is no work on this question. The proposed experiment can shed light on the area(s) of the brain that support this process. The model predicts that the area(s) of the brain in which this process(es) occur(s) will a) show increased activity at the same time as L STG/MTG does (because asyntactic and syntactic thematic role assignment occur at the same time), b) Granger cause activity in L ITG at the same time as L STG/MTG does (because these thematic roles are assessed for plausibility), but c) would not be activated during the checking process. Areas with these properties are candidates for these processes. In verification, the Granger causality pattern that applies to the areas involved in encoding thematic roles in a short-term memory system can also be sought in the data, and the same discovery process could be applied to verify the hypothesis that these areas occupy hippocampus and inferior temporal lobe.

Conclusions

The effects of task on assigning and interpreting syntactic structures have been demonstrated in online behavioral measures for visual arrays and plausibility. These effects affect BOLD signal correlates of sentence contrasts in several ways:

- by directly influencing parsing and interpretation as occurs with behavioral measures (e.g., by arrays in visual world tasks influencing prepositional attachment);
- by leading to increases in processing load that are isomorphic to the load exerted by parsing and interpretation (e.g., by plausibility assessments affecting response selection or encoding occurring at the same points and exerting the same relative load as parsing and interpretation);
- by leading to differential activation of processing operations that are required for task performance in different sentences in different tasks (e.g. different patterns of checking thematic roles for their origin in syntactic processes in different tasks);
- by inducing differential utilization of ancillary cognitive processes (e.g., by differential rehearsal of sentence types in verification)
- by leading to different patterns of attention to input and availability of attentional resources (e.g., by requiring more visual inspection, as would occur if more pictures were present in an array in a sentence-picture matching task).

These task effects may appear as activation related to sentence contrasts in different areas of the brain. It may be possible for multidimensional neuroimaging techniques with sufficient temporal and spatial resolution to go beyond one-dimensional behavioral measures of

¹¹L DLPFC should also be Granger-causally influenced by L IFG in implausible sentences (because implausible thematic roles affect response selection if they are syntactically derived). The predictions for implausible sentences are not shown in Table 1 for reasons of expository simplicity.

performance such as accuracy rates and RTs to dissociate these effects from the effects of parsing and interpretation themselves.

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Figure 1.
Model of operations involved in performing plausibility judgment task

Figure 2. BOLD signal activity in left inferior frontal and left middle temporal areas as a function of syntactic structure and semantic constraint in plausibility judgment (from Caplan et al., 2008b).

Figure 3.
BOLD signal activity related to sentence type contrast in early and late TR periods in verification (from Caplan et al., 2008a).

Figure 4. Granger causality during a 200 msec interval in trials that produce a Ganong effect. Red arrow indicates influence of supramarginal gyrus on superior temporal gyrus (from Gow et al., 2008)

Figure 5. Granger influences on bilateral superior temporal sulcus for trials in which assimilation does not produce competition (A) and trials on which it does produce competition (B) (from Gow and Segawa, 2009)

Table 1

Thematic roles activated in subject and object relative clauses, and the mechanisms whereby they are activated. S: syntactic analysis and interpretation; H: linear heuristic; C: combinatorial process

Subject subject	The fireman	who called	the deputy	saved the sailor
Parse		fireman call	call deputy	
Linear Heuristic		fireman call	fireman call	
Argument- based combiation		fireman call call fireman	call deputy	
Full set			fireman call deputy deputy call fireman	
Total		4	5	
Subject Object	The fireman	who the deputy	called	saved the sailor
Parse			deputy call call fireman	
Linear Heuristic			fireman call deputy call	
Argument- based combiation			deputy call call deputy fireman call call fireman	
Full set			fireman call deputy deputy call fireman	
Total			10	

Table 2

Expected areas and time points of increased MEG activity in example of experiment. V₁ = verb of relative clause; N₂ = noun in relative clause; END = end of sentence.

Operation	Plausibility Judgment									
	Parsing/Interpretation		Asyntactic processing		Plausibility Assessment		Check of thematic roles		Response Selection	
Location	L STG/MTG				L ITG		L IFG		L DLPFC	
Time Point	V ₁	N ₂	V ₁	N ₂	V ₁	N ₂	V ₁	N ₂	V ₁	N ₂
SO Unconstrained	++		++		++			+	++	
SO Constrained	++		++		++				++	
SS Unconstrained	+	+	+	+	+	+			+	+
SS Constrained	+	+	+	+	+	+	+		+	+
Verification										
Operation	Parsing/Interpretation		Asyntactic processing		Plausibility Assessment		Check of thematic roles		Encoding	
Location	L STG/MTG				L ITG		L IFG		L HIP, ITG	
Time Point	V ₁	N ₂	V ₁	N ₂	V ₁	N ₂	V ₁	N ₂	V ₁	N ₂
SO Unconstrained	++		++		++		++		++	
SO Constrained	++		++		++				++	
SS Unconstrained	+	+	+	+	+	+	+	+	+	+
SS Constrained	+	+	+	+	+	+			+	+