

Parametric effects of syntactic–semantic conflict in Broca's area during sentence processing

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ABSTRACT

The hypothesized role of Broca's area in sentence processing ranges from domain-general executive function to domain-specific computation that is specific to certain syntactic structures. We examined this issue by manipulating syntactic structure and conflict between syntactic and semantic cues in a sentence processing task. Functional neuroimaging revealed that activation within several Broca's area regions of interest reflected the parametric variation in syntactic–semantic conflict. These results suggest that Broca's area supports sentence processing by mediating between multiple incompatible constraints on sentence interpretation, consistent with this area's well-known role in conflict resolution in other linguistic and non-linguistic tasks.

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1. Introduction

The role of Broca's area in sentence processing is a fundamental and controversial issue within the neurobiology of language. Many neuroimaging studies have found greater activation in this region within the left inferior frontal cortex (LIFC)¹ for some syntactic structures over others (Ben-Shachar, Hendler, Kahn, Ben-Bashat, & Grodzinsky, 2003; Caplan, Alpert, & Waters, 1998; Fiebach, Schlesewsky, Lohmann, Cramon, & Friederici, 2005; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Stromswold, Caplan, Alpert, & Rauch, 1996). Such effects have been interpreted previously as reflecting the specialization of Broca's area for syntactic computations (Ben-Shachar et al., 2003; Caplan et al., 1998). More recently, however, there has been growing interest in whether this region's well-known role in executive function – specifically, the mediation of conflict between multiple incompatible representations – might explain the observed sentence processing effects. Here, we examine this issue by manipulating conflict between syntactic and semantic cues in a sentence-processing task.

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¹ Throughout the article, we use "Broca's area" as a shorthand term to refer to the posterior portion of the left inferior frontal cortex (Brodmann areas 44/45). Note however that this region likely contains several distinct anatomical subdivisions (Amunts et al., 2010) and may not be a homogeneous area.

A plethora of evidence implicates LIFC in non-syntactic tasks requiring executive function, specifically the modulation of competition between incompatible representations (Jonides & Nee, 2006; Jonides, Smith, Marshuetz, Koeppel, & Reuter-Lorenz, 1998; Milham et al., 2001). For example, in the Stroop task, in which participants identify the font color of written color terms, increased activation in LIFC for incongruent trials – trials where font color and word meaning do not match – is taken to reflect the resolution of representational conflict (Milham et al., 2001). These findings have naturally led to the hypothesis that such conflict resolution mechanisms might also play an important role during sentence processing (Novick, Trueswell, & Thompson-Schill, 2005). Sentence comprehension is incremental and determined by multiple (sometimes competing) information sources. As such, it might involve the resolution of conflict between earlier and later interpretations, or between different sources of information such as semantics and syntax. Consistent with this proposal, recent studies have co-localized syntactic and non-syntactic conflict resolution in LIFC using neuropsychological case studies (Novick, Kan, Trueswell, & Thompson-Schill, 2009) and functional magnetic resonance imaging (fMRI) in healthy adults (January, Trueswell, & Thompson-Schill, 2009).

Under an executive function account, increased LIFC activation for non-canonical structures (e.g., passives or object-relatives) might be taken to reflect the resolution of conflict that is engendered by a preference for canonical structures within the language processing system. For example, incremental processing of an

unfolding utterance (*The boy was kick...*) might favor the default, active interpretation (that the boy was kicking something) until the syntactic structure indicates otherwise (*The boy was kicked by...*). This conflict between an earlier interpretation and the most recent sentence information could lead to increased recruitment of Broca's area (Novick et al., 2005). If this account is correct, then factors that influence the probability of a default Agent-Action-Object interpretation should also modulate LIFC activation. Consistent with this, Chen and colleagues have reported that an increase in Broca's area activation for object relative over subject relative structures was due to a subset of object relatives, specifically those where the relativized object noun was animate (e.g., *The golfer that the lightning struck survived the incident*) (Chen, West, Waters, & Caplan, 2006). In other words, non-canonical object-relative sentences led to greater LIFC activation compared to canonical subject-relative sentences if and only if the subject noun was animate and could therefore presumably bias toward a default interpretation of the subject as the agent (instead of the patient as indicated by the syntactic structure). Furthermore, activation within Broca's area is modulated by animacy even in canonical structures. Kuperberg and colleagues found increased Broca's area activation for simple active structures containing semantic-thematic violations (*At breakfast, the eggs would eat...*) compared to those that did not contain such violations (*At breakfast, the boys would eat...*) (Kuperberg, Sitnikova, & Lakshmanan, 2008). Together, these studies demonstrate that activation within Broca's area is not determined by syntactic structure alone but rather is dependent on the conflict between multiple cues to sentence interpretation.

The current study extends previous investigations of Broca's area's function during sentence processing in three ways. First, we manipulate syntactic structure and conflict between semantic and syntactic cues within the same experiment and ask which factor accounts better for the variation in Broca's area activation. Second, we vary conflict between semantic and syntactic cues parametrically rather than dichotomously and ask whether activation in Broca's area would also vary parametrically. Last but not least, unlike the above-mentioned studies, our manipulation of conflict between semantics and syntax relies not on animacy but on world knowledge about relations between specific entities and specific actions (e.g., cops being handcuffed versus doing the handcuffing). Many linguistic theories distinguish animacy from such semantic factors. Thus our manipulation and the concomitant pattern of neurophysiological responses may shed a different light on Broca's area function.

Participants silently read active and passive sentences [a–d]. None of the sentences were anomalous. We manipulated conflict within passive sentences [b–d] (see Sections 2 and 3 for details).

- (a) Active: *The father was calming the cranky girl.*
- (b) No-conflict Passive: *The celebrity was interviewed by a reporter.*
- (c) Neutral Passive: *The patient was interviewed by the attractive man.*
- (d) Conflict Passive: *The journalist was interviewed by the undergraduate.*

Relative to neutral passives, conflict passives were hypothesized to induce greater competition between a syntactically guided interpretation and a semantically guided one. While journalists can quite possibly be interviewees (as indicated by the syntax), they are more likely to be interviewers (as indicated by world knowledge). In contrast, no-conflict passives were hypothesized to ease processing due to the congruence of syntactic and semantic cues. Celebrities are both possible and likely interviewees. If Broca's area does not mediate the type of conflict manipulated here, we would expect activa-

tion to reflect syntactic structure alone such that all passives are equivalent and produce more activation than actives ((Conflict = Neutral = No-conflict passives) > Actives). Alternatively, if Broca's area underlies the modulation of competition between incompatible representations, activation should vary according to hypothesized conflict (Conflict > Neutral > No-conflict passives).

We tested these contrasting hypotheses in regions of interest (ROIs) in Broca's area, defined in three different ways; the effects in each case supported the conflict resolution hypothesis.

2. Methods

2.1. Subjects

Fourteen right-handed native English speakers from the Philadelphia area completed the fMRI study (18–42 years. Mean = 24.4. 8 female) and were paid \$25 for their participation. Subjects gave consent under a protocol approved by the University of Pennsylvania.

2.2. Procedure

Subjects silently read active and passive sentences and pressed buttons bimanually to indicate reading completion. Each participant completed six experimental runs of fMRI data collection. Each run contained 18 actives, 18 passives (6 each of b–d above) and 6 baseline visual search trials.

In addition to the experimental trials above, there were some sentence trials where a comprehension question followed immediately after the sentence (seven per run: four active and three passive. e.g., Sentence: *The angry fencer was stabbed by a stranger.* Question: *Was the fencer hurt?*). Subjects responded yes or no using the two outer or two inner buttons respectively on a four-button box. These comprehension test trials were included to ensure that subjects attended to the task. They were modeled separately and were not included in any of the presented contrasts.

Each run also contained six baseline visual search trials. Subjects saw a two-line display. The top line contained a single Tamil character. The bottom line contained a string of Tamil characters. Subjects were told to find the top character in the bottom string and press yes/no accordingly. This task served as a control for complex visual processing outside the domain of language. The contrast between the control and experimental trials was used to identify regions of interest for analyses (see below).

The order of trials was randomized using optseq2 (<http://surfer.nmr.mgh.harvard.edu/optseq/>). Stimuli were presented using E-prime (Schneider, Eschman, & Zuccolotto, 2002). Sentence and baseline trials lasted six seconds each. They began with a fixation cross (200 ms) followed by the stimulus. Subjects were given a maximum of 5.65 s to respond. After the response (or after 5.65 s) a blank screen was presented until the end of the trial. For sentences, we chose whole-sentence rather than word-to-word presentation because the former is more naturalistic. Trials with comprehension questions lasted nine seconds in order to accommodate the sentence stimulus as well as the question.

2.3. Stimuli

Passive sentences were of the form: (noun-phrase) was (verb)-ed by (noun-phrase). Active sentences were of the form: (noun-phrase) was (verb)-ing (noun-phrase). All stimuli were matched for length. Passive and active sentences did not differ in the number of words or characters ($F < 1$; $p > .3$). Within the three types of passive sentences, none of the pair-wise comparisons were significant ($F < 2$; $p > .2$).

All passive sentences were reversible and contained two animate noun-phrases. Thirty-six verbs occurred once each in the three kinds of passives. Verbs did not repeat within a run. Active sentences contained a combination of animate and inanimate noun-phrases (27 each of animate–animate, animate–inanimate, inanimate–animate, inanimate–inanimate). Fifty-four verbs appeared once each with animate and inanimate subjects.

All sentences (including conflict passives) were constructed to be interpretable and non-anomalous. For passive sentences, syntactic–semantic conflict was manipulated using the heuristic of whether the sentential subject was more likely to be the patient rather than the agent of the verb (“yes” for no-conflict, “no” for conflict, “not particularly” for neutral passives). These intuitions were confirmed by a norming study (see below).

2.4. fMRI data acquisition and analysis

Structural and functional images were acquired using a 3T Siemens Trio scanner at the University of Pennsylvania. Functional images were acquired using an echo-planar imaging sequence (TR = 3000 ms, TE = 30 ms, flip angle = 90°, slice thickness = 3 mm). Data were analyzed using VoxBo (www.voxbo.org). Images were realigned, normalized to Montreal Neurological Institute (MNI) space, and smoothed using a 9 mm full-width half-maximum Gaussian kernel.

The general linear model was used to analyze the blood oxygen level dependent (BOLD) activity for each subject. The model contained covariates for each event type (neutral, no-conflict and conflict passives, animate- and inanimate-subject actives, baseline visual search, comprehension trials). These covariates of interest were convolved with a standard hemodynamic response function. Reading times were mean-centered for each subject and run and entered as covariates in the model. Other nuisance covariates included: scan effects, an intercept term and global signal.

First-level subject-specific models were entered into a second-level analysis treating subject as a random effect. Regions of interest (ROIs) were defined using three different methods. In the first method, we used the contrast of all sentences (actives and passives) minus baseline visual search. The resulting statistical map was thresholded at corrected $p < .05$. Suprathreshold voxels in the left inferior frontal cortex (20 voxels) and middle temporal region (39 voxels) were saved as ROIs. In the second method, we defined a spherical ROI of 27 voxels around the center of activation reported in Ben-Shachar et al. (2003). In the third method, we thresholded the contrast of no-conflict passives minus actives at uncorrected $p < .001$ (there were no suprathreshold voxels at corrected $p < .05$). Suprathreshold voxels in the left inferior frontal cortex (21 voxels) were saved as an ROI.

For each ROI, a new general linear model was calculated using the average signal in that region. The resulting parameter estimates were entered into ANOVA. The main contrasts of interest were: (1) polynomial contrast within the three types of passives and (2) pair-wise contrasts between no-conflict passives and actives, and conflict passives and actives.

3. Norming study

Twenty-four undergraduates from Swarthmore College rated sentences for course credit. All were native English speakers. None had participated in the fMRI study.

Participants answered two questions about each sentence: a. whether the sentence describes a scenario that is possible (possibility rating: yes/no), and b. how likely the scenario is (likelihood rating: scale of 1–6. 1 = highly unlikely, 6 = highly likely). In addition to the 216 sentences from the fMRI study, we constructed

two new types of sentences. Role-reversed actives ($N = 108$) were constructed by transforming passives from the fMRI study to actives such that the thematic roles assigned to the noun phrases were reversed (e.g., *The journalist was interviewed by the talk show host* → *The journalist interviewed the talk-show host*). Nonsense sentences ($N = 76$) were constructed using new verbs. Unlike the sentences used in the fMRI study, these sentences were anomalous and not easily interpretable (e.g., *The note licked its lips*). This resulted in a total of 400 sentences. Each participant was assigned to one of two lists. Each list contained 200 sentences (half of each sentence type). Order of presentation was randomized for each participant.

We first analyzed the possibility ratings. These ratings can be taken to measure whether a sentence is interpretable (i.e., not semantically anomalous). The mean possibility rating for each of the 400 sentences was entered into a one-way omnibus ANOVA containing a single 8-level factor of sentence type. The overall effect of sentence type was significant [$F(7,392) = 1619.19$; $p < .001$]. Planned comparisons revealed that ratings for conflict passives ($M = .968$) did not differ from no-conflict passives ($M = .993$), neutral passives ($M = .979$) or actives ($M = .971$). All F 's < 3 ; p 's $> .1$. They did however differ significantly from those for nonsense sentences ($M = .04$, $F(1,392) = 4477.57$; $p < .001$). The contrast between conflict passives and nonsense sentences illustrates the fact that the former are quite different from the semantic–thematic violations used in some ERP and fMRI studies. In particular, successful thematic role assignment was both linguistically sanctioned and psychologically possible for the conflict passives used in the current study.

We operationalized semantic–syntactic conflict for each passive sentence by computing the difference in likelihood rating between the role-reversed active and the passive. We hypothesized that for conflict passives, semantic cues should bias towards the opposite thematic role assignments as syntax, leading to a higher likelihood rating for the role-reversed active compared to the passive (and therefore a positive conflict score). In contrast, for the no-conflict passive, semantic cues should bias towards the same thematic role assignments as syntax, leading to a higher likelihood rating for the passive compared to its role-reversed active (and therefore a negative conflict score). Neutral passives were designed to contain no strong semantic biases and were therefore expected to have conflict scores that were in between those for conflict and no-conflict passives. Statistical analysis confirmed these predictions. The conflict score for each of the 108 passive sentences was entered into a one-way ANOVA containing a 3-level factor of conflict. Polynomial contrasts revealed a significant linear trend ($F(1,105) = 294.98$; $p < .001$. Conflict–Passive Mean = 2.1, Neutral–Passive Mean = -0.6 , No-conflict–Passive Mean = -3.0).

4. Results

4.1. Behavioral results

Mean accuracy on comprehension questions and baseline visual search trials was 92% and 98% respectively, suggesting that subjects were attentive during the experiment. Average reaction times in different conditions were as follows: baseline (2390 ms), actives (2254 ms), neutral passives (2231 ms), no-conflict passives (2170 ms) and conflict passives (2259 ms). We computed the mean reaction time in each condition for each subject. Repeated-measures ANOVA of reaction times in all five conditions was not significant ($F(4,52) = 1.61$; $p > .1$). Analysis of just the four sentence reading conditions was also not significant ($F(3,39) = 1.81$; $p > .1$). Thus, time-on-task effects cannot account for any differences in activation. Further, we included reading times as covariates in all reported fMRI analyses (see Section 2).

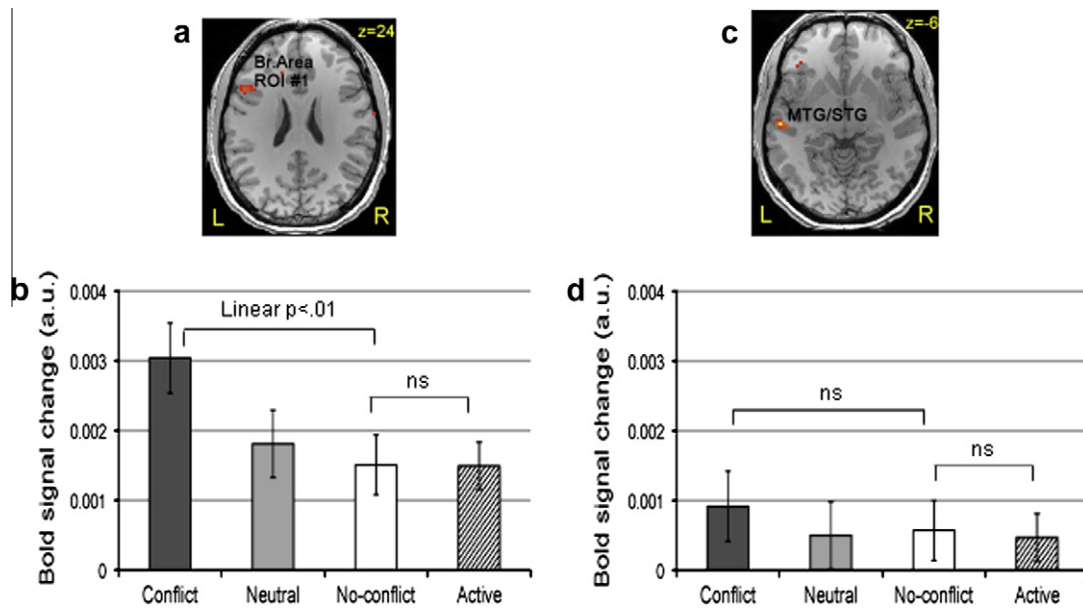


Fig. 1. ROIs derived from the contrast of all sentences minus baseline (corrected $p < .05$). (a) Broca's area. Peak Montreal Neurological Institute (MNI) coordinates: $-48, 18, 24$. (b) Hemodynamic response within (a) for different sentences. Error bars here and elsewhere represent s.e.m. (c) Middle and superior temporal gyrus. Peak MNI coordinates: $-57, -21, -6$. (d) Hemodynamic response within (c) for different sentences.

4.2. fMRI results

We report activation patterns for the active and passive sentences in three different ROIs all within Broca's area. For each ROI, the parameter estimate for each sentence type for each subject was calculated and entered into a repeated measures ANOVA. Polynomial contrasts compared the parameter estimates for the three types of passives. Pair-wise contrasts compared the parameter estimates of actives versus no-conflict or conflict passives.

The first Broca's area ROI was derived from the contrast of all sentences minus baseline visual search (corrected $p < .05$). Within this ROI (Fig. 1a), activation for the different passives followed a linear trend ($F(1,13) = 11.74$; $p < .01$, Fig. 1b). Conflict passives showed the greatest activation followed by neutral passives and then no-conflict passives. In pair-wise comparisons, no-conflict passives did not show increased activation relative to actives ($F(1,13) < 1$; $p > .9$); conflict passives did ($F(1,13) = 14$; $p < .01$). Half of our active sentences contained inanimate subjects. Such sentences can potentially give rise to conflict due to the fact that inanimate subjects are more consistent with passive than active structures. To evaluate the pair-wise results without this confound, we compared no-conflict and conflict passives to a subset of the active sentences that contained animate subjects. This showed the same pattern as with the entire set of active sentences: no-conflict passives ($\beta = 0.0015$) did not show increased activation relative to actives with animate subjects ($\beta = 0.0019$, $F(1,13) = 1.98$, $p > .1$); conflict passives ($\beta = 0.0030$) did ($F(1,13) = 7.11$, $p < .02$). The linear trend within passives was not found in a similarly derived temporal lobe ROI (Fig. 1c and d, resulting in an ROI * Conflict interaction when comparing these two regions: $F(1,13) = 9.44$; $p < .01$), suggesting that it was specific to brain regions previously implicated in executive function.

The second Broca's area ROI (Fig. 2a) comprised 27 voxels around the center of activation reported in a previous study that argued for syntactic specialization in this region (Ben-Shachar et al., 2003). As Fig. 2b shows, here too we observed a linear trend in activation for the different passives ($F(1,13) = 11.56$; $p < .01$). Again, conflict passives showed increased activation over

actives ($F(1,13) = 11.47$; $p < .01$); no-conflict passives did not ($F(1,13) < 1$; $p > .3$).²

The final Broca's area ROI (Fig. 2c) was obtained from the contrast of no-conflict passives minus actives (uncorrected $p < .001$). That is, we specifically chose voxels that may be construed as representing the syntactic difference between passives and actives. Note that this ROI is biased towards voxels where there was highest activation for no-conflict passives. As such, it is biased against finding a difference between no-conflict and conflict passives. Nevertheless we observed sensitivity within this ROI to the presence of conflict (Linear trend: $F(1,13) = 5.08$; $p < .05$. Quadratic trend: $F(1,13) = 9.84$; $p < .01$, Fig. 2d).

5. Discussion

Our findings are consistent with the view that Broca's area supports sentence processing via its role in resolving conflict amongst representations. In three different Broca's area ROIs, we found that BOLD activation reflected the extent of hypothesized executive function demands. The order of activation for the different passives matched the order of conflict scores obtained in our norming study (conflict passives > neutral passives > no-conflict passives). Notably, we found sensitivity to the extent of conflict in two ROIs that were selected for being possibly structure-specific. The first of these ROIs was chosen from a previous study that argued for a syntax-specific interpretation of Broca's area function (Ben-Shachar et al., 2003). The other was selected from the current study for showing increased activation for no-conflict passives over actives. Nevertheless, we found a conflict resolution profile in these voxels while holding syntactic structure constant. These results raise the possibility that at least some of the syntax-specific effects attributed to Broca's area previously might be better explained by a broader executive

² As in the case of the first ROI, comparison of different passives to actives with animate subjects yielded the same pattern of results as the comparison to the full set of actives: no significant difference between no-conflict passives and actives ($F(1,13) = 2.46$; $p > .1$), and a significant difference between conflict passives and actives ($F(1,13) = 8.44$, $p < .02$).

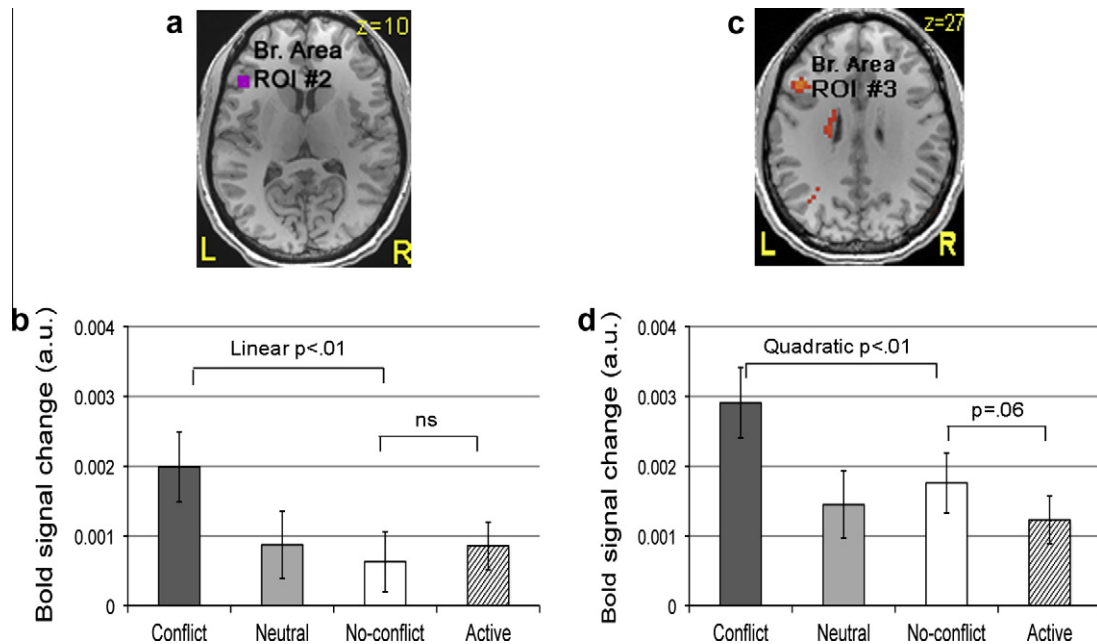


Fig. 2. (a) Broca's area ROI representing 27 voxels around MNI: $-45, 23, 10$ (Ben-Shachar et al., 2003). (b) Hemodynamic response within (a) for different sentences. (c) Broca's area ROI from the contrast of no-conflict passives minus actives (uncorrected $p < .001$). Peak MNI: $-45, 21, 27$. (d) Hemodynamic response within (c) for different sentences.

function hypothesis that takes into account multiple syntactic and non-syntactic cues to sentence interpretation.

As explained in the introduction, purely structural manipulations might also engage conflict resolution within LIFC if the language processing system has default parsing preferences that are incompatible with a non-canonical sentence structure. Such an effect of syntactic structure *per se* was weak or non-existent in the current study, however. In the whole-brain analysis, we had to employ a liberal threshold that did not correct for multiple comparisons in order to identify a small region within LIFC where no-conflict passives showed greater activation compared to actives. In the first two ROI analyses, no-conflict passives did not show increased activation relative to active sentences. The lack of an effect for no-conflict passives versus actives stands in stark contrast to the clear difference found between conflict passives and actives. These distinct patterns are consistent with the proposal that multiple cues interact during sentence interpretation. In the case of a no-conflict passive, the default preference for an active structure could be overwhelmed by a preference for the passive due to the semantic relation between the subject noun and the verb (*The celebrity was interview...*). The passive interpretation wins and is not in conflict with the presented (passive) structure, resulting in the smallest LIFC activation. In contrast, for the conflict-passive, the default preference for an active structure could be supported and enhanced by the semantic relation between the subject noun and the verb (*The journalist was interview...*). The active interpretation wins and is in conflict with the presented (passive) structure, resulting in the highest LIFC activation.

To summarize, we do not argue that differences in syntactic structure cannot result in activation differences within LIFC. Rather, we stress that such activation differences must be interpreted in the context of the interactive nature of sentence interpretation and LIFC's broader executive functions. Our results show that LIFC activation varies parametrically with syntactic-semantic conflict while holding syntactic structure constant. An experimental design that equates syntactic-semantic conflict while varying syntactic structure might well find an effect of the latter, assuming

that there is increased conflict during the processing of less canonical compared to more canonical sentences.

Our interpretation of Broca's area function as mediating between different cues – only some of which are syntactic – is consistent with other recent proposals. Chen et al. (2006) concluded that the main determinant of BOLD responses while processing object relative clauses was the ease of thematic role assignment as a function of animacy and syntactic structure. Similarly, Kuperberg et al. (2008) interpreted LIFC activation in terms of semantic-thematic processing to determine whether the agent indicated by the syntax could in fact perform the action indicated by the verb, particularly when that agent was inanimate. These proposals are consistent with our own proposal that Broca's area helps resolve conflict when different cues point towards different interpretations. We have described the plausible underlying mechanism as executive function whereas the above-mentioned authors have described it in terms of thematic role assignment. The current study cannot completely disambiguate between these explanations (conflict in this study was induced by syntactic and world knowledge leading to alternate interpretations). Future research should clarify whether the distinction between the thematic integration and executive function accounts is simply one of domain-specificity (e.g., thematic integration is conflict resolution specifically applied to thematic role assignment) or whether the two proposed processes are fundamentally different (e.g., thematic integration is a core thematic role assignment process that evaluates which entities can be assigned which roles).

Our study does not speak at all to the domain-specificity of executive function within different parts of LIFC (but see e.g., January et al. (2009) and Novick et al. (2009) for co-localization of syntactic and non-syntactic conflict resolution in Broca's area). However, two aspects of our study do bear upon the question of whether the thematic integration that is proposed to be supported by Broca's area is a thematic role assignment process that is quite different from executive function. First, our conflict sentence stimuli were interpretable and did not violate any semantic constraints on thematic role assignment. Thus, unlike the case for the stimuli used in Kuperberg et al. (2008) (e.g., ...at breakfast, the eggs would

eat. . .), there was no requirement to evaluate whether the agent of the sentence *could* perform the action described by the verb. Rather, what varied was the relative likelihood that the subject was the agent versus the patient of the action. Second, the likelihood of the subject being the agent versus the patient was dependent not on animacy (unlike stimuli in Chen et al. (2006) and Kuperberg et al. (2008)), but on world knowledge of the relations between specific entities and specific actions. Some linguistic theories accord a role for generalizable semantic features in thematic role assignment (e.g., Dowty, 1991) – many of which correlate with animacy (e.g., volition, sentience). But we know of no linguistic theory that includes world knowledge about particular actions in core thematic role assignment processes. Thus, we would suggest that our particular manipulation of syntactic–semantic conflict and the resulting effects in Broca's area are more consistent with a conflict resolution than a thematic processing account.

The distinction between animacy and real-world semantic constraints is explicit under a neuroanatomical model proposed by Bornkessel-Schlesewsky and colleagues. Under this account, animacy is an important cue for computing “prominence” or what goes before what (Bornkessel-Schlesewsky & Schlesewsky, 2008). This prominence computation process is assumed to be distinct from plausibility processing that takes into account real-world semantic constraints (Bornkessel-Schlesewsky & Schlesewsky, 2008). The former may be localized to posterior LIFC and the latter to more anterior LIFC (BA 44 versus BA 45/47) (Bornkessel-Schlesewsky & Schlesewsky, 2008; Newman, Ikuta, & Burns, 2010). In the current study, both noun-phrases in the passive sentences were animate. The relevant manipulation was arguably plausibility based on world knowledge. The ROIs where we detected effects are near BA 44/45. It remains to be determined whether the broad executive functions ascribed to the LIFC region can be fractionated into different sub-components.

To summarize, we found parametric variation in activation within Broca's area that paralleled the variation in semantic–syntactic conflict, while syntactic structure was held constant. These results are compatible with a role for Broca's area in mediating conflict between representations. A vast literature on monkey and human executive function implicates this region in selection under competition (Petrides, 2005). While further sub-specialization within the region remains a possibility, the kinds of operations imputed to these areas is already constrained by available evidence.

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References

- Amunts, K., Lenzen, M., Friederici, A. D., Schleicher, A., Morosan, P., Palomero-Gallagher, N., et al. (2010). Broca's region: Novel organizational principles and multiple receptor mapping. *PLoS Biology*, 8(9), e1000489.
- Ben-Shachar, M., Hendler, T., Kahn, I., Ben-Bashat, D., & Grodzinsky, Y. (2003). The neural reality of syntactic transformations: Evidence from functional magnetic resonance imaging. *Psychological Science*, 14(5), 433–440.
- Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2008). An alternative perspective on semantic P600 effects in language comprehension. *Brain Research Reviews*, 59(1), 55–73.
- Caplan, D., Alpert, N., & Waters, G. (1998). Effects of syntactic structure and propositional number on patterns of regional cerebral blood flow. *Journal of Cognitive Neuroscience*, 10(4), 541–552.
- Chen, E., West, W. C., Waters, G., & Caplan, D. (2006). Determinants of BOLD signal correlates of processing object-extracted relative clauses. *Cortex*, 42(4), 591–604.
- Dowty, D. (1991). Thematic proto-roles and argument selection. *Language*, 67, 547–619.
- Fiebach, C. J., Schlesewsky, M., Lohmann, G., Cramon, D. Y. v., & Friederici, A. D. (2005). Revisiting the role of Broca's area in sentence processing: Syntactic integration vs. syntactic working memory. *Human Brain Mapping*, 24, 79–91.
- January, D., Trueswell, J. C., & Thompson-Schill, S. L. (2009). Co-localization of stroop and syntactic ambiguity resolution in Broca's area: Implications for the neural basis of sentence processing. *Journal of Cognitive Neuroscience*, 21(12), 2434–2444.
- Jonides, J., & Nee, D. E. (2006). Brain mechanisms of proactive interference in working memory. *Neuroscience*, 139(1), 181–193.
- Jonides, J., Smith, E. E., Marshuetz, C., Koeppe, R. A., & Reuter-Lorenz, P. A. (1998). Inhibition in verbal working memory revealed by brain activation. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 8410–8413.
- Just, M. A., Carpenter, P. A., Keller, T. A., Eddy, W. F., & Thulborn, K. R. (1996). Brain activation modulated by sentence comprehension. *Science*, 274, 114–116.
- Kuperberg, G. R., Sitnikova, T., & Lakshmanan, B. M. (2008). Neuroanatomical distinctions within the semantic system during sentence comprehension: Evidence from functional magnetic resonance imaging. *NeuroImage*, 40, 367–388.
- Milham, M. P., Banich, M. T., Webb, A., Barad, V., Cohen, N. J., Wszalek, T., et al. (2001). The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Cognitive Brain Research*, 12, 467–473.
- Newman, S. D., Ikuta, T., & Burns, T. (2010). The effect of semantic relatedness on syntactic analysis: An fMRI study. *Brain and Language*, 113(2), 51–58.
- Novick, J. M., Kan, I. P., Trueswell, J. C., & Thompson-Schill, S. L. (2009). A case for conflict across multiple domains: Memory and language impairments following damage to ventrolateral prefrontal cortex. *Cognitive Neuropsychology*, 26(6), 527–567.
- Novick, J. M., Trueswell, J. C., & Thompson-Schill, S. L. (2005). Cognitive control and parsing: Reexamining the role of Broca's area in sentence comprehension. *Cognitive, Affective, & Behavioral Neuroscience*, 5(3), 263–281.
- Petrides, M. (2005). Lateral prefrontal cortex: Architectonic and functional organization. *Philosophical transactions of the Royal Society B*, 360, 781–795.
- Schneider, W., Eschman, A., & Zuccolotto, A. (2002). *E-prime reference guide*. Pittsburgh: Psychology Software Tools, Inc.
- Stromswold, K., Caplan, D., Alpert, N., & Rauch, S. (1996). Localization of syntactic comprehension by positron emission tomography. *Brain and Language*, 52, 452–473.