Linguistic structure across time: 
ERP responses to coordinated and uncoordinated noun phrases

Ellen Lau & Chia-Hsuan Liao
University of Maryland Department of Linguistics; Neuroscience and Cognitive Science Program; Maryland Language Science Center

Abstract

Relatively little is known about how linguistic structure is neurally encoded. The current study examines a relatively subtle structural manipulation: the difference between reading a list of two noun phrases (“sunlit ponds ### green umbrellas”) and their syntactic coordination (“sunlit ponds and green umbrellas”). In two ERP experiments, the presence of the coordinator resulted in an increased anterior negativity across the entire second noun phrase, even though coordination had no direct relevance for the memory recognition task. These findings demonstrate that structural connectedness exerts strong, ongoing neural processing differences even when structured and unstructured materials are very tightly matched in sequence and content. More specifically, the results are consistent with the hypothesis that linguistic structure is automatically and actively maintained in memory across the course of a sentence; alternatively, the sustained anterior negativity may reflect computation of the more complex semantic or discourse representation associated with a longer connected structure.

Introduction

Accurate language comprehension requires encoding syntactic relationships between the words (or morphemes) of a sentence, using knowledge of the grammatical rules of the language. For example, encoding of both local (mother – loves) and non-local (loves – bowl) relationships is required in representing the 7-word phrase The red bowl that my mother loves... that serves as the syntactic and thematic subject of the upcoming sentence. Many of the broad generalizations governing these relations are well understood. We also know from previous neuroimaging work that structured sentences elicit increased neural responses compared to unstructured word lists in a number of brain regions, including left inferior frontal gyrus and left anterior and posterior temporal cortex (Mazoyer et al., 1993; Stowe et al., 1998; Friederici et al., 2000; Vandenbergh et al., 2002; Humphries et al., 2006; Rogalsky & Hickok, 2009; Fedorenko et al., 2010; Pallier et al., 2011; Bemis & Pykkänen, 2011). However, less is known about how structured linguistic information is neurally represented across time, during the short-term window in which a sentence is parsed and interpreted.

The current ERP study investigates this question using a novel comparison that manipulates structural connectedness while tightly controlling the sequence and lexical content of the critical stimuli and introducing relatively minimal differences in semantic content. We compare lists of two noun phrases, separated by a placeholder symbol (sunlit ponds ### green umbrellas) to the syntactic coordination of two noun phrases (sunlit ponds and green umbrellas). Although increasing the size of connected syntactic and semantic structure may
impact encoding processes in multiple ways, we focus our discussion here on one key question: is prior linguistic structure represented across the course of the sentence in a way that causes processing cost to increase with the size of the connected structures?

**Short-term memory and sentence comprehension**

Classic memory models can be described as tripartite (McElree, 2006), in that they assume information could be encoded in at least three different states: (1) the current focus of attention (usually capacity-limited to 1 item), (2) short-term or working memory (usually capacity-limited to 3-4 items), and (3) long-term memory. Observations of sustained delay-period neural activity in primates while information was being maintained for use in short-term memory tasks (Fuster & Alexander, 1971; Funahashi et al., 1989) have been used to support a dedicated neural mechanism for working memory representation. As classically reviewed in Caplan and Waters (1999), a long tradition of work in sentence processing has assumed a tripartite architecture and has argued that many cases of processing difficulty could be attributed to exceeding the capacity limit of the short-term memory buffer. These theories suggested some version of the idea that incomplete constituents or predicted heads were maintained in an STM buffer or ordered ‘stack’, and that sentence processing complexity was a function of the number of elements in this buffer (e.g. Yngve, 1960; Miller & Isard, 1964; Kimball, 1973; Gibson, 1998). For example, parsing of multiply-embedded sentences such as The nurse that the doctor that the lawyer defended injured died might fail because the number of predictions exceeds the capacity of the storage buffer, and processing English object relative clauses might be harder than subject relative clauses because they require maintaining more structural predictions for longer.

Neurophysiological studies have provided some support for these accounts in the form of evidence for increased neural activity when more incomplete constituents or predicted heads would be hypothesized to be maintained in working memory. In EEG, a number of studies comparing object relative clauses with subject relative clauses, or scrambled objects vs. scrambled subjects, have reported a sustained anterior negativity across the words intervening between the displaced object and its verb (e.g. King & Kutas, 1995; Fiebach, Schlesewsky & Friederici, 2002; Ueno & Kluender, 2003; Phillips et al., 2005). A number of fMRI studies have also demonstrated increased hemodynamic response for the processing of long-distance dependencies relative to controls (e.g. Fiebach et al., 2005; Santi & Grodzinsky, 2007), although the lack of time-course information makes it difficult to determine whether this increase reflects active maintenance through the dependency vs. retrieval interference at the verb.

It is important to note that in recent years other researchers have argued in favor of bipartite memory models, in which there is no qualitative distinction between short-term and long-term memory, resulting in an architecture in which information is either (1) in the focus of attention or (2) encoded passively in long-term memory (e.g. McElree, 2006). Such models attribute observations of sustained delay-period activity either to the focus of attention or to representation-independent mechanisms such as inhibition or cognitive control (Postle, 2006). In one prominent sentence processing model of this kind, the syntactic structure for the current sentence is implemented as a set of smaller phrase chunks passively maintained in long-term memory that contain pointers to each other (e.g. Lewis & Vasishth, 2005). Incremental parsing proceeds at each new morpheme in the string by initiating cue-based
retrieval of relevant chunks of the structure from content-addressable long-term memory. Such models mainly attribute classic effects of processing complexity to retrieval interference and other factors rather than STM capacity limits (Van Dyke & Johns, 2007). One piece of supporting evidence comes from speed-accuracy tradeoff studies of dependency completion that consistently show a binary split in measurements of retrieval speed: a few elements, thought to be in the focus of attention, are retrieved rapidly, and the rest are all retrieved at the same slower speed, no matter their serial or hierarchical distance from the probe position (McElree, 2000; McElree et al., 2003; Martin & McElree, 2008). This would be predicted if items not in the focus of attention all had to be retrieved from LTM, but might not be predicted if the current sentence structure was being represented in a special STM buffer, in which case one might rather predict an ordered search of particular structural positions. The retrieval interference that might be predicted if frequent LTM retrievals are required for sentence comprehension also seems to be borne out by a number of ‘grammatical illusions’ in which an element in the wrong structural position appears to enter in a dependency with a subsequent element (Phillips, Wagers & Lau, 2011), although such effects can also be explained by a tripartite model if working memory operations are also subject to interference-based interference.

At the same time, in bipartite models the focus of attention is often thought to be neurally implemented through active maintenance (e.g. Lewis-Peacock et al., 2012), and relatively little is known so far about its capacity for representing structured material. Importantly, Wagers and McElree (2009) report a few data points from the speed-accuracy tradeoff paradigm that suggest that the focus of attention can maintain more than the single previous word-structure binding. To take one example, when making an acceptability judgment about the fit between subject and verb based on animacy properties, rapid, focus-of-attention-style response dynamics are observed both when the subject head and the verb are adjacent (the driver fainted) and when separated by an adverb (the driver evidently fainted) or a prepositional phrase (the driver of the ambulance evidently fainted). The slower rate characteristic of LTM retrieval is only observed when a relative clause intervenes (the driver who wrecked the ambulance fainted). Similarly, Wagers and Phillips (2014) present data from long-distance filler-gap processing that are consistent with some filler information being maintained in the focus of attention across intervening material. In sum, these kinds of observations indicate that even in the absence of a distinct STM/WM state, linguistic structure information could be actively maintained in the focus of attention (Wagers & McElree, 2009).

Neural evidence for active maintenance of linguistic structure

Recent neurophysiological work seems to provide important preliminary support for active maintenance of some form of structured sentence representation. In a seminal fMRI study, Pallier, Devauchelle and Dehaene (2011) introduced a novel constituency-size manipulation to look for neural evidence of active maintenance of syntactic structure. Pallier and colleagues (2011) began by adopting Smolensky and Legendre’s (2006) model of syntactic composition. In this model, syntactic structure is represented by superposition of a number of tensor products of ‘role’ and ‘filler’ vectors, where each node in the tree structure is represented by the tensor product of the role vector representing the position in the tree and the filler vector representing the content (e.g. lexical entry) in that position. They assumed
that the filler vector will have a sparse neural code such that each new filler will recruit a largely new set of neurons, and they assume that (at least for right-branching structures) the full tree has to be actively maintained across the course of the constituent being built. They also assumed that (at least for right-branching structures) these products are actively maintained across the span of a connected syntactic structure such that the longer the structure, the larger the number of active neural units. This yields the prediction that for sentences or phrases with right-branching structures, neural activity will monotonically increase across the course of the phrase, resetting only when the phrase is completed.

Pallier et al.’s manipulation was to hold constant the number of words in a trial (12) while varying the size of the connected structure chunks that they composed (an unstructured list of 12 words, a sequence of 6 unconnected two-word phrases, a sequence of 4 three-word phrases, a sequence of 3 four-word phrases, a sequence of 2 six-word phrases, and a twelve-word right-branching sentence). Although the temporal resolution of the BOLD (blood-oxygenation-level dependent) signal in fMRI is too poor to precisely resolve the increase in activity at each incoming word predicted by the model, the integrated BOLD signal across the entire trial should increase parametrically with the length of the longest constituent. As predicted by their active structure maintenance model, they found a number of left-hemisphere regions whose activity increased monotonically with the number of lexical-structure bindings that needed to be maintained as part of a connected structure across time: inferior frontal gyrus (IFG), anterior and posterior temporal cortex (pSTS), and angular gyrus. Pallier et al. also included a jabberwocky manipulation, in which the content words were replaced by meaningless pseudowords, in order to distinguish active structure maintenance effects from processes associated with conceptual combination, world knowledge, and discourse model differences in smaller and larger phrase structures. They found that IFG and pSTS continued to show constituency-size effects for these jabberwocky materials, and took this as evidence that these regions supported active maintenance of syntactic structure in particular.

Although Pallier et al.’s (2011) findings are suggestive, they are not conclusive. First, while the parametric design across a number of levels of constituent size has obvious virtues, it prevents certain kinds of stimulus control that could leave open alternative explanations. For example, the paradigm does not control lexical content across conditions, such that the proportion of function words varied across constituency size. These lexical differences, rather than structure maintenance, could have been responsible for some of the differences they observed. The randomized presentation they used also meant that participants did not know the extent to which an upcoming trial would be structured or not, so that some of the effects observed might have resulted from the degree to which a given trial was expected to be a full sentence rather than structure maintenance per se. A recent follow-up study addressed several of these concerns in a partial replication of the constituency-size manipulation using lexically-controlled materials in the 1-word, 2-word, and 6-word conditions (Matchin, Hammerly, & Lau, 2017), and notably failed to find differences between the 1-word (list) condition and the 2-word phrase condition as their model would have predicted. However, Matchin et al. (2017) did replicate their finding of increased activity for sentences vs. lists in IFG and pSTS (among other regions), even though the sentences were simple, contained only local dependencies, and were completely uniform in
structure across the experiment, and this result is consistent with active maintenance of previous or predicted structure.

Second, the poor temporal resolution of fMRI makes it non-ideal for testing one of the critical predictions of the active maintenance hypothesis, which is that activation will increase across the course of the connected structure. EEG, MEG, or intracranial recordings can better test this prediction, and there are some interesting suggestions of this in the existing literature. Van Petten and Kutas (1991) reported a slow positive shift across the course of scrambled word lists compared to sentences in EEG, which they attributed to differences in arousal but which might also be consistent with an increased negative shift associated with structure maintenance. Bastiaansen, Magyari and Hagoort (2010) observed increasing activity in theta and beta power across the course of sentences compared to scrambled word lists in EEG, and attribute the theta increase to a ‘working memory trace’ of the input. Fedorenko et al. (2016) compare scrambled word lists and sentences in ECoG patients and find a monotonic increase in gamma power for regular sentences but not for jabberwocky sentences, and therefore attribute the increase to the representation of complex meanings. Although this prior work is suggestive, contrasting sentences with scrambled sentences is somewhat messy in temporally sensitive techniques because the distribution of word classes within the trial differs across conditions; for example, in English a verb is more likely to occur in the first position of a scrambled sentence than in a sentence.

Recent work by Ding and colleagues (Ding et al., 2016) argues that neural representation of structure across the course of the sentence can be observed with a very different constituent rate approach. Ding et al. recorded MEG while presenting syllables at a constant rate, organized such that they also formed phrase and sentence-level constituents at a constant rate (e.g. Adj-N-V-N-Adj-N-V-N…). Ding et al. observed peaks in MEG spectral power not only at the syllable rate frequency, but also at the phrasal rate and the sentence rate when the sentences were parsable by the listeners (e.g. for native speakers of the language and not for non-speakers of the language), and suggest that the increased power of the MEG response at these frequencies may index ‘the neural representation of the internally constructed hierarchical linguistic structure’. Although these data provide strong neural evidence for online syntactic structure-building, it is not clear that they speak to the question of whether maintaining the syntactic representation requires sustained neural activity across the course of the sentence, because the pattern they observe could easily reflect discrete long-term-memory encodings of structural information that are triggered at critical points in the sentence, rather than sustained activity across time (oscillatory or otherwise).

The current study

Here we used event-related potential (ERP) timecourse measures in a novel list/structure paradigm that compares noun phrase coordination to unconnected noun phrase list sequences (Figure 1). In unconnected list trials, two noun phrases are presented word-by-word, separated by a placeholder symbol (###). In coordination trials, the two noun phrases are coordinated with and. After occasional trials, participants are given a noun phrase recognition memory probe to encourage attention. The prediction of the active structure maintenance hypothesis is fairly straightforward; in the coordination condition, the second noun phrase is structurally connected to the first, and therefore the terminals of the first noun phrase need to be actively maintained, but this is not the case in the list condition. Therefore,
this hypothesis predicts a sustained difference in activity across the second noun phrase (beyond any short-lived differences associated with processing the coordinator vs. the placeholder). Any non-structural rehearsal strategies for performing the memory task should be constant across conditions.

This design has a number of virtues for testing the active maintenance hypothesis. First, the critical region—the second noun phrase—is exactly matched in physical properties and position within the trial across conditions. Second, any differences in meaning between the coordination trials and the unconnected noun phrase trials are fairly subtle. Third, encountering unconnected noun phrases is not as unusual or disruptive as encountering scrambled sentences and seems less likely to drive differences in attentional state or task strategy. Finally, this design isolates the maintenance of prior structure rather than predicted structure, as the predicted categories at the critical measurement period across the second noun phrase are the same (e.g. the prediction of a noun during the presentation of the adjective).

We included both natural (real word) and jabberwocky conditions. As discussed above, Pallier et al. (2011) were particularly interested in demonstrating evidence for the maintenance of syntactic structure, and argued that observing constituent-size effects for jabberwocky materials as well as natural materials constitutes a strong argument that the effects are syntactic in nature. Although there are some reasons to question the strength of this argument (many sentence-level semantic relations such as predicate-argument relations could be computed on a syntactically well-formed string without access to lexical semantics, and jabberwocky materials may engender less attention and therefore more shallow structural analysis than natural ones), we included this manipulation for the purpose of better comparing the results across the two designs.

**Experiment 1**

*Methods*

*Materials*

The experiment comprised a $2 \times 2$ design (structure: coordination/list × content: natural/jabberwocky). In total, 50 trials were presented in each of the 4 conditions, with each trial containing two adjective-noun sequences.

200 different adjectives and 200 different nouns were selected and combined to form 200 natural adjective-noun pairs that each formed a meaningful and plausible phrase. In order to minimize prediction of specific lexical items from the adjective to the noun, all adjectives were ‘low-constraint’; that is, in the Corpus of Contemporary American English, no single
word followed a given adjective more than 15% of the time. The noun was always presented in the plural form so that the phrase could be construed as a complete (bare) plural determiner phrase in the absence of an article. Many of the adjectives contained a common adjectival affix (e.g. -y, -al, -able, -ful, -ous, -ic). The 200 adjective-noun phrases were then randomly paired into 100 sets of two. These 100 item sets were then distributed across four lists in a Latin Square design, such that each item would appear in the coordination or no-coordination condition, and such that the phrases could appear in either order (e.g. new books ### shiny floors; shiny floors ### new books; new books and shiny floors; shiny floors and new books).

200 jabberwocky ‘adjectives’ were created by combining a pronounceable nonword stem (e.g. blarg) with a common adjectival affix (e.g. blargful). 200 jabberwocky ‘nouns’ were created by combining a non-overlapping set of pronounceable nonword stems (e.g. kropt) with the plural –s affix (e.g. kropts). The nonwords were derived using the Wuggy package in order to match lexical and sublexical properties of the real words (Keuleers & Brysbaert, 2010). The 200 jabberwocky adjective-noun phrases were then randomly paired into 100 sets of two. These 100 item sets were then distributed across the four lists in a Latin Square design, such that each item would appear in the coordination or no-coordination condition, and such that the phrases could appear in either order.

To instantiate the memory task, we added memory probes to 10 items in each condition, for a total of 40 memory probes across the experiment (20% of trials). Half of the probes were identical to one of the previous items, requiring a ‘YES’ response, and half were not, requiring a ‘NO’ response. The ‘NO’ items were sometimes incorrect combinations of words from the previous trial (e.g. new floors) and sometimes combined one of the previous words with a new word (e.g. polished floors).

Procedure

In Experiment 1, we chose to block the structure manipulation, such that the first half of the experiment included only list trials and the second half of the experiment included only coordinate trials. We did this because we were concerned that participants would be likely to mentally insert a linguistic coordinator in the list condition if given the idea to do so by seeing the coordination conditions (note that strictly speaking, an overt coordinator is not required for linguistic coordination in English, e.g. I see birds, flowers, trees...). This would result in equal constituent size across conditions. To prevent this, in Experiment 1 the experimental materials were divided into two presentation blocks, the first of which included 100 randomly distributed natural and jabberwocky list trials, and the second of which included 100 randomly distributed natural and jabberwocky coordinated trials. A break screen appeared halfway through each block.

A practice session preceded the experimental session in which participants were presented with a number of list trials. They were told that each trial would contain two phrases and that after some trials they would be presented with a probe phrase and asked to indicate whether they had seen this phrase or not. In between the two blocks, participants were told that now ‘the two phrases would be connected, but that the task would remain the same’ and were given several practice coordination trials to illustrate.
During the experiment, participants were seated in a chair in a dimly lit room. Stimuli were visually presented on a computer monitor in white 24-point case Arial font on a black background. Each trial began with a 1500ms fixation cross. After a 200ms blank screen, the five stimuli of each trial were presented at a rate of 500ms on and 100ms off. The final word stayed on the screen for 700ms, followed by a blank screen of 300ms. After 20% of the trials, the blank screen was followed by a memory probe (e.g. suncy kads?) which remained on the screen until the participant responded.

Participants

A total of 41 students (23 females, 18-31 years old, mean age: 20) from University of Maryland participated in the current study. All the participants were native speakers of English, and none of them reported a history of neurological or psychiatric disorder or recent use of psychoactive medications. Since the duration of our critical epoch was quite long (i.e., 2000 ms), after data pre-processing, 12 participants had to be excluded from further ERP analysis due to excessive eye-blinking, muscle potentials and alpha waves during the epoch. The reported results were obtained from the remaining 29 participants (16 females, 18-23 years old, mean age: 20). All the participants were right-handed as assessed by the Edinburg Handedness Inventory (Oldfield, 1971). Written informed consent was obtained from all participants.

Analysis

We extracted epochs time-locked to the onset of the coordinator or corresponding placeholder from -100:2000ms, thus extending from the coordinator through the response to the second noun phrase. Averaged ERPs were formed off-line from these epochs, after rejecting trials free of ocular and muscular artifact, using preprocessing routines from the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes. Across the 29 participants included in the analysis, approximately 20.8% of the trials were rejected because of artifact. A 100-ms pre-stimulus baseline was subtracted from all waveforms, and a 40-Hz low-pass filter was applied to the ERPs offline. ERP data for this and the other experiment in this paper are publicly available on the first author’s website (http://ling.umd.edu/~ellenlau/public_data_archive/ERP_coordination/Lau&Liao_2017). Because we were interested in evaluating the presence of sustained activity associated with structure maintenance, we conducted analyses on mean ERP amplitudes in a broad 100-600ms time-window after the onset of each of the three words in the epoch (the coordinator, 100-600ms, the second adjective, 700-1200ms, and the second noun, 1300-1800ms). In order to quantify the topography of the effects observed, we focused on a subset of 16 electrodes (left anterior: F7, F3, FT7, FC3; right anterior: F4, F8, FC4, FT8; left posterior: TP7, CP3, P7, P3; right posterior: CP4, TP8, P4, P8) and used R (R Development Core Team, 2010) to conduct a quadrant analysis consisting of a 2 × 2 × 2 × 2 (structure × content × hemisphere × anteriority) Type III SS repeated-measures ANOVA. We report all significant main effects and interactions involving the factors of structure and content. Figures in text present ERP waveforms at selected electrodes; full ERP data from all scalp electrodes are included as supplementary figures.
As we used a block design in Experiment 1, it is possible that responses also differed prior to the coordinator or corresponding placeholder across blocks. In order to evaluate this possibility we conducted a supplementary analysis on epochs time-locked to the onset of the first adjective (at the beginning of the trial) and extending through the first noun phrase (-100ms:1200ms, and baselined these epochs to the 100ms preceding the onset of the first noun phrase.

**Results**

*Behavioral*

Overall accuracy on the memory task was 85.4% (natural list: 91.0%; natural coordination: 92.0%; jabberwocky list: 80.0%; jabberwocky coordination: 78.6%). A 2 × 2 repeated measure ANOVA revealed a main effect of content (F(1, 28) = 37.1, MSE = 4346, p < .01) reflecting lower accuracy in the jabberwocky conditions. There was no main effect of structure (F(1, 28) = .006, MSE = .86, p > .2), and no interaction between structure and content (F(1,28) = .476, MSE = 42.24, p > .2).

*ERPs*

Visual inspection of the grand-average ERPs time-locked to the coordinator position indicates that responses were more negative throughout the epoch for the coordination condition relative to the non-coordination condition. Topographically, the distribution of this effect shifted across the epoch: at the coordinator position, coordination resulted in an increased posterior negativity in both natural and jabberwocky conditions, while during the subsequent noun phrase, coordination resulted in a sustained increased anterior negativity that was mainly present in the natural conditions (Figures 2 and 3).

Statistical analysis confirmed these observations. In the 100-600ms time-window corresponding to 100ms post-onset of the coordinator position, an omnibus quadrant
ANOVA revealed a significant main effect of coordination \( (F(1,28) = 18.7, \text{MSE} = 6.4, p < .01) \) and a significant interaction between coordination and anteriority \( (F(1,28) = 10.3, \text{MSE} = .61, p < .01) \), as well as a main effect of content \( (F(1,28) = 5.3, \text{MSE} = 2.94, p < .01) \) and an interaction between content, hemisphere, and anteriority \( (F(1,28) = 5.2, \text{MSE} = .11, p < .05) \). The interaction between coordination and anteriority was driven by a larger coordination effect in posterior channels \( (1.2 \mu V) \) than in anterior channels \( (.8 \mu V) \). These effects are likely to reflect differential early visual processes and lexical access and grammatical analysis of the coordinator \((\text{and})\) relative to the placeholder \( (###) \) in both natural and jabberwocky trials; the central-posterior distribution is similar to N400 effects of lexical-conceptual processing.

In the 700-1200ms time-window corresponding to 100ms post-onset of the adjective of the second noun phrase, we again observed a main effect of coordination \( (F(1,28) = 7.9, \text{MSE} = 8.4, p < .05) \) and a significant interaction between coordination and anteriority \( (F(1,28) = 6.8, \text{MSE} = 1.0, p < .05) \), but this time the interaction was driven by a larger coordination effect in anterior electrodes \( (1.0 \mu V) \) than in posterior electrodes \( (.5 \mu V) \). We also observed a marginally significant interaction between coordination and content \( (F(1,28) = 3.3, \text{MSE} = 5.39, p = .08) \), driven by a larger coordination effect in natural \( (1.1 \mu V) \) than jabberwocky \( (.4 \mu V) \). There was also a significant interaction between language and hemisphere \( (F(1,28) = 7.5, \text{MSE} = .85, p < .05) \), driven by more positive responses to jabberwocky in the left hemisphere and more positive responses to natural text in the right hemisphere.

The pattern was similar in the 1300-1800ms time-window corresponding to 100ms post-onset of the noun of the second noun phrase. Here we observed a marginal main effect of coordination \( (F(1,28) = 3.4, \text{MSE} = 8.4, p = .08) \) and again a significant interaction between
coordination and anteriority \((F(1,28) = 5.6, \text{MSE} = 1.57, p < .05)\), again driven by a larger coordination effect in anterior electrodes \((.8 \mu V)\) than posterior electrodes \((.2 \mu V)\). Although the effect appeared larger in English conditions, the interaction between coordination and content only trended towards significance \((F(1,28) = 2.7, \text{MSE} = 7.5, p = .1)\).

Because Experiment 1 used a block design, such that participants knew in advance that trials in the first block were list trials and trials in the second block were coordination trials, one potential concern is that the results we observe during the second noun phrase were ongoing effects from the first noun phrase, or due to artifactual baseline shifts. Supplementary Figure 3 illustrates the ERP for the first noun phrase. Although an increased posterior negativity is visible for coordination trials during the first adjective, the responses re-converge and are tightly matched prior to the onset of the coordinator or placeholder.

**Discussion**

In Experiment 1, we presented participants with an initial block of intermixed natural and jabberwocky trials comprising two separate noun phrases, and a subsequent block of intermixed natural and jabberwocky trials comprising two coordinated noun phrases. Unsurprisingly, we observed differential activity at the coordinator \((\text{and})\) relative to the control stimulus \((###)\) presented in the list condition, which took the form of an increased posterior negativity for the coordinator between \(~100-600\text{ms}\). However, in the natural conditions we also observed downstream effects of coordination on the processing of the second noun phrase, which manifested as a sustained increased anterior negativity throughout the second noun phrase in the coordination condition relative to the list condition.

These results appear consistent with an active maintenance account in which prior structure must be actively maintained across the course of a connected phrase. According to such an account, the increased anterior negativity that we observed during the second noun phrase in coordination trials would reflect the activity of the neural assembly encoding the structural position of the first noun phrase in the coordinated NP—in other words, the neural activity required to maintain the binding of the lexical terminals in the first noun phrase to positions in a relational syntactic structure representation. The distribution and polarity of the effect are consistent with the interpretation that it reflects short-term memory processes for encoding structure, because sustained anterior negativities have been previously associated with short-term memory maintenance of phonological information (Ruchkin et al., 1990; 1992) and syntactic predictions (King & Kutas, 1995; Fiebach et al., 2002; Phillips et al., 2005).

The coordination effect seemed to be largely absent in the jabberwocky conditions. Following the logic of Pallier et al. (2011), this could indicate that the sustained anterior negativity observed in the natural conditions relates to the encoding of semantic rather than syntactic structural representations. However, another possibility is that the short adjective-noun phrases used here did not contain enough functional content to encourage participants to assign a syntactic structure to them in the jabberwocky conditions. We review these possibilities in more detail in the General Discussion.

Experiment 2 was designed to determine whether the sustained anterior negativity would also be observed in a randomized design in which coordination and list trials were intermixed. We used a block design in Experiment 1 because we were concerned that randomizing might
result in participants applying syntactic coordination to the list trials, in the absence of an overt coordinator. However, block designs often raise concerns that state-level differences other than the one intended, such as attention or fatigue, might be driving the effects of interest. Although it was not clear to us that such a plausible alternative account existed in the current case, if it turned out that the structural effect was robust to the randomized design then we would be able to fully rule out this possibility. Experiment 2 also provided us an opportunity to replicate the novel effect that we observed in Experiment 1.

**Experiment 2**

*Methods*

*Materials*

Experimental materials were identical to those used in Experiment 1.

*Procedure*

Experimental procedure was identical to that used in Experiment 1 except that the list and coordination trials (of both types) were randomly interleaved rather than blocked.

*Participants*

A total of 22 students (12 females, 19-26 years of age, mean age: 21) from University of Maryland participated in the current study. All the participants were native speakers of English, and none of them reported a history of neurological or psychiatric disorder or recent use of psychoactive medications. Five participants had to be excluded from further ERP analysis due to excessive eye-blinking, muscle potentials and alpha waves during the epoch. The reported results were obtained from the remaining 17 participants (10 females, 19-26 years old, mean age: 21). All the participants were right-handed as assessed by the Edinburg Handedness Inventory (Oldfield, 1971). Written informed consent was obtained from all participants.

*Analysis*

The analysis procedure was the same as that used in Experiment 1, except that in Experiment 2 we did not carry out supplementary analyses on the response to the first noun phrase, since in this randomized design coordination and list trials were indistinguishable until the coordinator or placeholder was encountered.

*Results*

*Behavioral*

Overall accuracy on the memory task was 85.3% (natural list: 90.0%; natural coordination: 92.4%; jabberwocky list: 78.2%; jabberwocky coordination: 80.6%). A 2 x 2 repeated measure ANOVA revealed a main effect of content (F(1,16) = 11.6, MSE = 2352.9, p < .01), reflecting lower accuracy in the jabberwocky conditions. There was no main effect of structure (F(1, 16) = 1.2, MSE = 94.1, p = .28), and no interaction between structure and content (F(1,28) = 0, MSE = 1, p > .2).
**ERPs**

Visual inspection of the ERPs indicated that the results were qualitatively similar to Experiment 1, although slightly smaller in magnitude (Figures 3 and 4). In the 100-600ms time-window (post-coordinator-onset), an omnibus quadrant ANOVA revealed a significant main effect of coordination ($F(1,16) = 15.4$, $MSE = 4.9$, $p < .01$), a significant interaction between coordination and hemisphere ($F(1,16) = 7.7$, $MSE = .64$, $p < .01$), and a significant 3-way interaction between coordination, hemisphere, and anteriority ($F(1,16) = 11.0$, $MSE = .18$, $p < .01$). The interaction between coordination and content also approached significance ($F(1,16) = 3.5$, $MSE = .51$, $p = .08$), reflecting a larger difference between coordinator and placeholder in the natural condition. The interaction between content, hemisphere, and anteriority was also marginally significant ($F(1,16) = 4.1$, $MSE = .09$, $p = .06$).

In the 700-1200ms time-window at the adjective, we observed a marginal main effect of coordination ($F(1,16) = 4.5$, $MSE = 7.5$, $p = .05$), a significant interaction between coordination and content ($F(1,16) = 5.7$, $MSE = 5.4$, $p < .05$), and a significant interaction between coordination and hemisphere ($F(1,16) = 7.3$, $MSE = .8$, $p < .05$). As in Experiment 1, the interaction between coordination and content was driven by a large coordination effect in natural materials (1.4 $\mu$V) with little difference between jabberwocky conditions (.03 $\mu$V). In the subsequent 1300-1800ms time-window at the noun, we again observed a significant interaction between coordination and content ($F(1,16) = 4.7$, $MSE = 5.6$, $p < .05$) and a marginal interaction between coordination and anteriority ($F(1,16) = 3.2$, $MSE = 1.2$, $p = .09$).
Discussion

Experiment 2 was a replication of Experiment 1, this time randomizing rather than blocking presentation of list and coordination trials. Despite the change in presentation, we observed essentially the same results as in Experiment 1: coordination resulted in a sustained anterior negativity across the course of the second noun phrase in natural conditions. Little difference between coordination and list trials was observed in jabberwocky conditions. These results provide further support for the effects of structure observed in Experiment 1.

It is interesting to note that in both experiments, the difference in the ERPs at the coordinator and the placeholder (###) position itself was numerically larger in the natural condition than in the jabberwocky condition, an interaction which was marginally significant in Experiment 2. Some speculative explanations for this trend which could be pursued in future work are (a) early part of the structure maintenance cost; (b) simple attentional differences between jabberwocky and natural stimuli; (c) additional predictive processing for the content or structure of the upcoming noun phrase in the coordination case.

General Discussion

We conducted two ERP experiments designed to investigate the hypothesis that sustained neural activity plays a role in encoding linguistic structure across the course of a phrase or sentence. We looked for evidence of increased activity while processing a second noun phrase that was syntactically coordinated with a previous noun phrase, relative to a case in which the second noun phrase was just the second element in an uncoordinated list. In both experiments we found a sustained increased anterior negativity across the second noun phrase for coordinated trials when natural materials were used.

Active maintenance of syntactic structure
As reviewed in the introduction, Pallier et al. (2011), following from Smolensky and Legendre’s (2006) computational model of syntactic structure encoding, proposed that each new terminal added to a current connected syntactic representation increases the amount of neural activity required to maintain the entire representation. Pallier et al.’s (2011) account predicted that neural activity associated with syntactic structure encoding should thus increase monotonically across the course of the largest syntactic constituent, but the poor temporal resolution of fMRI data made it difficult to precisely evaluate the timing of the increased activity that they observed. The results of the current ERP study showed a sustained difference between structured and unstructured conditions with the temporal profile predicted by this hypothesis. In the list condition, there was no syntactic connection between the first noun phrase and the second noun phrase, and therefore after the first noun phrase the syntactic ‘buffer’ would be cleared and structural encoding would restart on the second noun phrase. In the coordination condition, the coordinator indicated that both noun phrases belong to a single connected syntactic representation. Therefore, as the second noun phrase was processed, the size of the syntactic representation being maintained increased, which would result in increased neural activity during this period relative to the list condition.

The difference between conditions during the second noun phrase took the form of a negativity with a focus at anterior electrodes. This is somewhat consistent with the broader ERP literature, where it has long been suggested that sustained anterior negativities reflect working memory processes in sentence comprehension (Kluender & Kutas, 1993ab; Munte et al., 1998; Fiebach et al., 2002; Ueno & Kluender, 2003; Phillips et al., 2005). However, these studies focused on different operations than simply encoding prior structure; many examined the hypothesis that syntactic predictions are actively maintained in working memory, such as the ‘filler’ in wh-filler gap constructions, while Munte et al. suggested that the interpretation of temporally reversed clauses (before x, y) required extra working memory processing. Therefore much more work is needed to determine whether these effects in fact reflect a common process, and to develop a theory of what exactly that process could be. Some promising initial steps in this direction are evident in new results from Nelson and colleagues (2017), who obtained direct intracranial recordings from patients reading sentences of various lengths and structures; they report that high gamma power was sensitive to the number of syntactic nodes that still belong to an incomplete constituent (maintenance of prior structure, modulo compression of finished sub-phrases).

Pallier et al. (2011) and Nelson et al. (2017) report constituency-size effects for syntax in left inferior frontal and left posterior superior temporal cortices. Indeed, a very long and storied literature has associated left inferior frontal cortex with working memory and integration processes, with much debate over whether these processes are language- or syntax-specific (Caplan & Waters, 1999; Fiebach et al., 2005; Hagoort, 2005; Fedorenko et al., 2011). Other work has suggested that posterior temporal cortex might serve in short-term memory mechanisms akin to the classic phonological loop, in which phonological or lexical representations in posterior temporal cortex are cyclically reactivated in order to maintain them in short-term memory (Hickok & Poeppel, 2008; Buchsbaum & D’Esposito, 2008; Hickok, 2009). Some fMRI studies that used long-distance dependency paradigms of the kind that elicited sustained anterior negativities in EEG reported increased activity in inferior frontal cortex (e.g. Fiebach et al., 2005; Santi & Grodzinsky 2007) but others have not (Matchin et al., 2014), and several recent studies have associated this activity with resolution
of interference rather than active maintenance of syntactic structure (Glaser et al., 2013; Santi et al., 2015). Although the poor spatial resolution of EEG would make it difficult to precisely determine the source of the anterior negativity in the current study, future work with MEG will provide better estimates.

We note that an interesting ambiguity related to electrophysiological response differences that sustain over a long time period is whether or not they reflect the temporal properties of response differences on single trials. The Pallier et al. (2011) model suggests that individual units encoding structure sustain their activity across the full duration of the constituents in which they participate. However, another possibility akin to a phonological loop mechanism is that the full structure is passively encoded, but that sub-constituents of the structure are strategically reactivated periodically such that they will be highly accessible for future computation. On this view, individual units encoding structure do not sustain their activity across a single trial, but rather demonstrate randomly distributed short ‘bursts’ of activity across the trial. If these bursts are randomly distributed in time, then when multiple trials are averaged to create the ERP, there would appear to be a sustained increase in activity across the trial. Recent work with single-unit recordings during working memory tasks in animals suggests that this ‘burst-y’ mechanism could be responsible for some of the classic active maintenance effects (Meyers et al., 2008). However, the high signal-to-noise ratio in ERP recordings will likely make it more challenging to disambiguate these possibilities in the language case.

A different question raised by evidence for active maintenance of linguistic structure is whether these mechanisms result in better memory for the sub-elements of the structure. In the current study, we did not observe significantly better memory recognition performance for phrases when they were coordinated rather than separated by a placeholder, although there was a trend in this direction in Experiment 2 when a randomized presentation was used. However, this study was not designed to test behavioral effects of structure and therefore we only collected memory recognition responses on a small number (10%) of trials. Examining more systematically the possible effects of active structure maintenance on memory for sub-parts of the structure will be an interesting direction for future work.

Dissociating syntactic and semantic encoding

Although the sustained anterior negativity observed here could reflect sustained activity encoding syntactic structure, an alternative possibility is that this effect resulted from differences in semantic encoding. Dissociating syntactic from semantic structure-building neural processes is well-known to be challenging because the complexity of the compositional semantic representation is obviously highly correlated with the complexity of the syntactic representation (see Pylkkänen, Brennan, & Bemis, 2011 for more discussion). Pallier et al. (2011) used constituency-size effects in jabberwocky materials in an attempt to dissociate syntactic and semantic encoding, arguing that regions demonstrating constituency-size effects for materials lacking lexical semantics must be involved in syntactic encoding. In the current ERP experiments, we failed to observe robust effects of structure in jabberwocky conditions. Therefore, one possible conclusion is that the sustained anterior negativity observed in the natural conditions reflects semantic rather than syntactic processes.
Semantic accounts of the structural effects observed here could fall into two categories. On the one hand, one could assume an active structure maintenance account functionally parallel to the Pallier et al. (2011) proposal, but specified for semantic rather than syntactic representations. In other words, the sustained anterior negativity would reflect the binding of lexical-semantic information to some structured semantic object (e.g. logical form, or a propositional representation) and the maintenance of this binding as this object is constructed across the course of the phrase. Pallier et al. suggested this kind of account for their observation that anterior temporal cortex regions showed constituency-size effects in natural but not jabberwocky materials. Similarly, in ECoG patients Fedorenko et al. (2016) found a monotonic increase in gamma power across the course of regular sentences but not for jabberwocky sentences, and attributed this increase to the representation of complex meanings.

Alternatively, the sustained anterior negativity might rather be attributed to other semantic processes that might differ as a function of syntactic context, such as conceptual integration and discourse representation. For example, Pallier et al. (2011) speculated that linguistic input might only be integrated into the discourse when it forms complete sentences, and suggested that this might explain why a temporoparietal region showed increases only for conditions with longer phrases. In the current study it is not immediately obvious what additional conceptual or discourse processes differ between noun phrase lists and coordinated noun phrases, but several colleagues have noted their informal intuition that the presence of the coordinator might make one more likely to attempt to imagine a scenario in which both of the noun phrases would be discussed together, or to visualize them together. We are not aware of previous work associating anterior negativities with these kinds of processes in particular, but several studies suggest that anterior negativities are associated with ‘frame-shifting’ or reinterpretation as required for processing figurative language (e.g. Coulson & Kutas, 2001; Wlotko & Federmeier, 2011). Future studies might explore the latter kind of alternative account by systematically varying the imageability and conceptual association between the two noun phrases and evaluating whether there is any impact on the sustained anterior negativity for structure.

At the same time, one could maintain that the sustained anterior negativity indeed reflects the encoding of syntactic structure, and explain the absence of structural effects in the jabberwocky conditions as a result of the limited functional cues to structure. In the structures used in the current experiment, the only functional cues in the jabberwocky condition were the use of frequent adjectival endings (suncy) to cue that the first word was an adjective, the use of the plural –s to cue that the second word was a noun (kads), and the coordinator itself. However, these limited cues may not have been as effective at inducing parsing of jabberwocky as cases in which less ambiguous functional cues appear earlier in the string (e.g. in the suncy kads). Future work could straightforwardly explore this possibility by testing materials with additional functional material (e.g. the suncy kads and the whisy cawregrols).
Conclusion

We reported two ERP experiments that investigated neural mechanisms for encoding linguistic structure by measuring the impact of coordination on the neural response to the coordinated elements. We found that processing a noun phrase as part of a larger connected coordinate structure is associated with a differential neural response—a sustained anterior negativity—throughout the noun phrase, relative to the unstructured comparison case. Although much work remains to be done to distinguish alternative accounts of the underlying mechanisms, these results crucially show that structural connectedness exerts strong, ongoing effects on neural activity even when the properties of structured and unstructured materials are very tightly controlled.

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Figure Captions

Figure 1. Illustration of the design, contrasting lists of two noun phrases with structurally connected coordinate phrases.

Figure 2. Scalp maps and event-related potentials time-locked to the coordinator (and) or the placeholder (###) at selected frontal and posterior electrode sites for natural list and natural coordination conditions in Experiment 1. Scalp maps illustrate the mean difference between coordination and list conditions across a 100-600ms time-window following presentation of each word.

Figure 3. Scalp maps and event-related potentials time-locked to the coordinator (and) or the placeholder (###) at selected frontal and posterior electrode sites for jabberwocky list and jabberwocky coordination conditions in Experiment 1. Scalp maps illustrate the mean difference between coordination and list conditions across a 100-600ms time-window following presentation of each word.

Figure 4. Scalp maps and event-related potentials time-locked to the coordinator (and) or the placeholder (###) at selected frontal and posterior electrode sites for natural list and natural coordination conditions in Experiment 2. Scalp maps illustrate the mean difference between coordination and list conditions across a 100-600ms time-window following presentation of each word.

Figure 5. Scalp maps and event-related potentials time-locked to the coordinator (and) or the placeholder (###) at selected frontal and posterior electrode sites for jabberwocky list and jabberwocky coordination conditions in Experiment 2. Scalp maps illustrate the mean difference between coordination and list conditions across a 100-600ms time-window following presentation of each word.
References


