Speech and Span: Working Memory Capacity Impacts the Use of Animacy but Not of World Knowledge during Spoken Sentence Comprehension

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Abstract

■ We present results from a study demonstrating that high- and low-span listeners show qualitatively different brain responses when comprehending simple active sentences. Participants listened to naturally produced sentences in three conditions in which the plausibility of thematic relations was manipulated, for instance: The dog(1)/The poet(2)/The box(3) is biting the mailman. Event-related potentials were recorded to the first noun, the verb, and the second noun in all three conditions. In (2), the thematic relations between the words in the sentence are less expected given our world knowledge, and this resulted in an N400 effect of semantic processing difficulty to the second noun for both high- and low-span subjects. In (3), the inanimate first noun cannot be the agent of the verb. Only high-span subjects showed an effect of animacy on the sentence-initial nouns, evident from a larger anterior negative shift to inanimate than animate nouns. Furthermore, to the thematically violated verbs (3), low-span subjects showed an N400, whereas high-span subjects generated a P600. We suggest that this P600 effect to the thematically violated verb may be related to processing costs resulting from a conflict between the provisional thematic roles assigned as a function of the inanimate sentence-initial noun, and the actual (animate) agent required by the verb. We further argue that low-span subjects lag behind those with high span in their use of animacy, but not real-world knowledge in the on-line computation of thematic roles in spoken language comprehension. ■

INTRODUCTION

Individuals' brains differ in the capacity to compute syntactic, semantic, and thematic relations among words in phrases, sentences, and discourses. Large individual differences in reading comprehension have been observed even among college students, and this variability has been correlated with word recognition skill, working memory capacity, domain knowledge, and characteristics of the text input (e.g., Long & Prat, 2008; Nieuwland & Van Berkum, 2006; Bornkessel, Fiebach, & Friederici, 2004; Clifton et al., 2003; Vos & Friederici, 2003; Van Petten, Weckerly, McIsaac, & Kutas, 1997; Just & Carpenter, 1992; MacDonald, Just, & Carpenter, 1992; King & Just, 1991). Much less is known about how fundamental cognitive capacities of an individual contribute to the comprehension of incoming speech. In the present study, we examine whether individual differences in working memory span influence the real-time processing of thematic relations in listening comprehension. In the next section, we will describe the sources of information that are used in thematic processing. We will then describe how working memory may be related to individual differences in thematic processing.

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Thematic Processing

Thematic role assignment (who is doing what to whom) requires the rapid integration of syntactic, semantic, and world-knowledge information. Compare, for example, the following three sentences (see also Table 1): (1) The dog is biting the mailman; (2) The poet is biting the mailman; and (3) The box is biting the mailman. All three sentences have a simple active, unambiguous structure which follows the canonical subject–verb–object (SVO) order of the English language. However, they vary in the plausibility of the conceptual relationship between the verb and the preceding subject argument. In (1), the subject noun "dog" is a perfectly legitimate agent of the verb "bite," and a dog's act of biting a mailman is a plausible event. In (2), a world-knowledge violation occurs; although a poet is capable of biting a mailman, such an event is not consistent with our common understanding of the world. In (3), an animacy violation occurs. This is because syntactic processing operations lead to an SVO structure based on the word category information (noun–verb–noun), but semantic processing operations are not consistent with this structure. This results in thematic processing problems because the subject of the sentence cannot serve as the agent of the action of the verb.[1] In this latter example, a plausible assignment of thematic roles is not possible.

Table 1. Examples of Stimuli Used in the Three Conditions of the Study

Condition	*Explanation*	*Example*
Control	No violation; condition against which world-knowledge and animacy violation conditions are compared	The **dog** is **biting** the **mailman**.
World-knowledge violation	The verb is an unlikely action of the noun in the first Noun Phrase given our knowledge of the world	The **poet** is **biting** the **mailman**.
Animacy violation	The verb is not a possible action of the noun in the first Noun Phrase	The **box** is **biting** the **mailman**.

ERPs were measured to the words in bold face in the example sentences.

Theories of language comprehension differ in their predictions of when listeners integrate these different sources of syntactic, semantic, and world-knowledge information during the interpretation of an unfolding sentence. *Modular* models predict that syntactic information will be used first to compose the structure of a sentence, followed by the integration of the lexical–semantic properties that are stored with the representations of these words in the mental lexicon (e.g., Frazier, 1987). This higher-order representation of the speech input is then further mapped onto our knowledge of the world (e.g., Fischler, Bloom, Childers, Roucos, & Perry, 1983). *Interactive models*, on the other hand, predict that there need not be a delay in the time course by which these different sources of information are used during listening comprehension (e.g., MacDonald et al., 1992). Results from many recent studies indeed suggest a very rapid influence of world-knowledge and lexical–semantic information during sentence processing. Hagoort, Hald, Bastiaansen, and Petersson (2004) have shown that there is no delay in the on-line integration of world-knowledge relative to lexical–semantic information during sentence processing. Results from many other behavioral and electrophysiological studies suggest very early effects of animacy of arguments on incremental sentence comprehension (e.g., Ferreira, 2003; MacDonald, Pearlmutter, & Seidenberg, 1994; Marslen-Wilson & Tyler, 1980; but see Markus, Bornkessel-Schlesewsky, Bisang, & Schlesewsky, 2008; Kuperberg, Kreher, Sitnikova, Caplan, & Holcomb, 2007; Kim & Osterhout, 2005; Nakano & Swaab, 2005; van Herten, Kolk, & Chwilla, 2005; Hoeks, Stowe, & Doedens, 2004; Kolk, Chwilla, van Herten, & Oor, 2003; Kuperberg, Sitnikova, Caplan, & Holcomb, 2003; Ferreira & Clifton, 1986).

Electrophysiological measures (event-related potentials or ERPs) can provide qualitative information about sentence processing as it unfolds in real time, without the need for an immediate behavioral response. Two ERP components have been particularly relevant to research on thematic processing: the N400 and the P600. The N400 is sensitive to semantic aspects of the input and has been related to the retrieval and integration of lexical–semantic information; its amplitude is reduced to words that match in meaning with the context (Kutas & Hillyard, 1980; for reviews, see Swaab, Ledoux, Camblin, & Boudewyn, in press; Van Berkum, in press; Kutas & Federmeier, 2000). The P600 has classically been interpreted as sensitive to syntactic aspects of the linguistic input, and its amplitude is increased to words that form a syntactically anomalous, complex, or ambiguous continuation of the preceding sentence (Kaan, Harris, Gibson, & Holcomb, 2000; Hagoort, Brown, & Groothusen, 1993; Osterhout & Holcomb, 1992). However, the current view of linguistic processes related to P600 effects has broadened based on results of recent studies where P600 effects were found in so-called thematic role violations of critical verbs in syntactically unambiguous sentences such as, “The eggs would eat toast with jam at breakfast” (e.g., Kim & Osterhout, 2005; van Herten et al., 2005; Hoeks et al., 2004; Kolk et al., 2003; Kuperberg et al., 2003). Specifically, it has been proposed that a P600 is elicited when a syntactic-based analysis of a sentence structure (e.g., S–V–O) is challenged by strong semantic relations of the words in a sentence (Kuperberg, 2007), and/or by the most plausible combination of arguments and verbs in sentences (“semantic–thematic attraction”: Kim & Osterhout, 2005; for a different view, see Bornkessel-Schlesewsky & Schlesewsky, 2008). More recently, Kuperberg et al. (2007) have shown that a semantic relation between individual words in the sentence is not required to elicit these P600 effects, as thematically violated verbs that were preceded by semantically unrelated inanimate argument NPs also showed a P600 effect (e.g., “For breakfast the eggs would plant…”). They suggested that these findings are consistent with the idea that, within English active sentences, animacy information of the argument preceding the verb is computed on-line and immediately impacts verb processing, giving rise to verb-elicited P600 effects when the verb is an anomalous continuation of the preceding context.

On the basis of these and other findings of P600s to semantic–thematic violations, Kuperberg (2007) has proposed a model of language comprehension in which two processing streams act in parallel. One, the *semantic memory-based stream*, computes semantic features and relationships among sentence components, and violations of the evolving semantic aspects of the linguistic input are primarily reflected in the N400 component. The other, the *combinatorial stream*, is sensitive to linguistic constraints, including constraints of morphosyntax and of thematic role relationships. When the two streams provide contradictory output (i.e., when the semantic interpretation output by the first stream contradicts morphosyntactic or thematic information in the sentence), continued analysis must be undertaken to resolve the inconsistency, and it is this extended analysis that is reflected in the P600 component. A somewhat different account of the P600 has been proposed by van Herten et al. (2005). These authors also emphasize the idea of conflict between multiple representations, but they additionally suggest that this conflict is detected by a monitoring process that is under executive control.

The goal of the present study is to assess individual differences in the processing of thematic information in auditorily presented simple active sentences. We do not aim to resolve the debate on the processing nature of the P600. However, based on findings with the P600 discussed above, we hypothesize that the weight of the sources of information that is taken into account in on-line sentence comprehension may vary as a function of an individual's working memory span and that this may result in different electrophysiological signatures (i.e., N400 or P600) of difficulties during thematic processing.

Individual Differences in Thematic Processing as a Function of Working Memory Span

Three important views of how working memory may influence sentence processing have been proposed. In their capacity theory, Just and Carpenter (1992) assume that language comprehension requires both storage and computation functions, which operate under a shared pool of activation resources. If a computation during sentence processing uses a lot of activation resources, then less will be available to support storage, and this will limit the amount of information that can be maintained. Thus, a low working memory capacity could lead to a decreased ability to process multiple sources of information that are required during real-time sentence comprehension. In contrast, Caplan and Waters (1999) assume *two* pools of resources: one specifically used during the assignment of syntactic structure and initial interpretation of the sentence, and the second one a general resource, not specific to language. Only this second resource is subject to individual variability and is used when language comprehenders are asked to perform an additional task such as recall or meaning judgment. Finally, MacDonald and Christiansen (2002) have suggested that individual variability is a function of experience with and exposure to language; relative to high-span readers, low-span readers have had less exposure to language and are therefore less experienced. This suggests that variability between individuals can be adjusted with practice, which is not predicted by the two other views discussed above.

Studies of the influence of working memory capacity on individual differences in sentence comprehension have typically assessed reading of complex sentences and/or syntactically ambiguous sentences (e.g., Clifton et al., 2003). Results of several ERP studies have indicated differences between high- and low-span subjects in the processing of critical words that disambiguate syntactically ambiguous sentence structures (Bornkessel et al., 2004; Vos & Friederici, 2003). An interesting qualitative difference was observed by Bornkessel et al. (2004), who found that high-span subjects showed a P600, but low-span subjects showed an N400 to the disambiguating critical words for a dispreferred continuation. The authors interpret these surprising N400 results for the low-span subjects as a reflection of integration costs because they assume that these participants were unable to suppress the syntactically dispreferred sentence structure.

Behavioral studies with syntactically ambiguous sentences suggest that low-span subjects are less able to make use of animacy information to parse sentences (Just & Carpenter, 1992). However, other studies do not find this relationship between animacy and memory span (Clifton et al., 2003). Recently, Long and Prat (2008) showed that these inconsistencies between studies could be explained if one takes into consideration the type of information that individuals use during on-line sentence comprehension, but also that these individual differences can be attenuated with practice.

The contribution of individual differences of working memory capacity on processing of syntactically *unambiguous* sentence structures has been studied as well (e.g., Van Petten et al., 1997). However, very little is known about a possible role of working memory in the processing of thematic relations in simple active naturally produced spoken sentences, presumably because the processing of simple unambiguous sentences would not seem to require a particularly large working memory capacity. However, the studies in the previous section suggest that a very dynamic interaction exists between the processing of syntactic, semantic, and world-knowledge information during on-line thematic processing, and there is some evidence that low-span individuals are less likely than high-span subjects to use animacy information during on-line language comprehension.

Present Study

In the present study, we assessed if and when low- and high-span subjects would make use of animacy information and world knowledge to assign thematic roles in simple naturally spoken syntactically unambiguous sentences. Participants were asked to listen to sentences in three conditions where the plausibility of the verb as a function of the preceding NP was manipulated as in the following example (see also Table 1): (1) The dog is biting the mailman—control condition; (2) The poet is biting the mailman—world-knowledge violation condition; (3) The box is biting the mailman—animacy violation condition.

Predictions of N400 and P600 effects for animacy violation and world-knowledge violation conditions (relative to control) as a function of span for the nouns in the first noun phrase (NP1), the verbs (V), and the nouns in the second noun phrase (NP2) are summarized in Table 2.

On the basis of previous findings of individual variability in reading of syntactically ambiguous sentences (e.g., Long & Prat, 2008), we predicted that high-span subjects would immediately use the animacy information of the argument in the first NP to assign thematic roles. Because inanimate subject nouns are less frequent than animate subject nouns in the English language (Bates & MacWhinney, 1989; Bock, 1986), we predicted that this might result in a processing cost in the comparison of Conditions (1) and (3) in the example above when the initial NP was heard. Previous ERP results, indeed, showed a larger N400 to inanimate than animate arguments that preceded the verb (Weckerly & Kutas, 1999). In addition, and consistent with findings of Kuperberg (2007), we predicted for high-span subjects that verbs that were preceded by inanimate arguments that violate the verb's animacy restrictions [(3) "The box is biting…"] would elicit a P600 relative to the control condition. If low-span subjects were unable to immediately use the animacy of the noun in the first NP, then no differences in processing should be found for the sentence-initial noun, and an N400 to the verbs in the animacy violation condition might result, because the meaning of "bite" is more difficult to match with "box" than with "dog." We also predicted that both high- and low-span subjects would show an N400 to the final word of the sentence in the comparison between (3) and (1) in the example above because this word would be semantically anomalous with the overall sentential context, regardless of the type of processing cost that was incurred on the preceding verb.

For the first NP in the world-knowledge manipulation (e.g., "The poet is biting the mailman"), we predicted no difference in the processing of the noun in (2) relative to (1) for either high or low-span subjects, as both were animate and perfectly matched with respect to lexical properties (see Methods section). Furthermore, because the animacy of the noun in the first NP was consistent with the present continuous tense of the verb, we predicted that high-span subjects would, in this case, show an N400 to the verbs in Condition (2) relative to Condition (1), because information in Condition (2) about the world renders the verb a less plausible continuation of the sentence ("The dog is biting…" vs. "The poet is biting…"). We predicted that the pattern of results for the low-span subjects would depend on whether or not they would make immediate use of their knowledge of the world in on-line sentence processing. If they did, their pattern of results on the verb would not differ from that of the high-span subjects. At the final word of the sentence, we predicted an N400 effect for both groups because we expected that, at this point in the sentence, the world-knowledge information would be available to both low- and high-span subjects.

Table 2. Predictions of N400 and P600 Effects for Animacy Violation and World-knowledge Violation Conditions (Relative to Control) as a Function of Span for the Nouns in the First Noun Phrase (NP1), the Verbs (V), and the Nouns in the Second Noun Phrase (NP2)

Sentence Position	*NP1*		*Verb*		*NP2*	
Span	*High*	*Low*	*High*	*Low*	*High*	*Low*
Animacy Violation–Control						
Expected result	N400	–	P600	N400	N400	N400
World-knowledge Violation–Control						
Expected result	–	–	N400	N400	N400	N400

METHODS

Subjects

Sixty-three participants took part in this study. All participants were screened for their working memory span (see below), and two groups of high- and low-span subjects were identified. Nine subjects were not included due to excessive eye movements or other artifacts in the EEG signal. Eighteen of the remaining 54 subjects were assigned to a low-span group (6 men, 12 women, age = 18–28 years, mean = 20.2 years) and 18 to a high-span group (6 men, 12 women, age = 18–32 years, mean = 22.2 years). There was no difference in age between the groups ($p = .121$). All participants were right-handed, monolingual native speakers of English with normal hearing. Participants gave informed consent before the experiment.

Assignment of individuals to high- and low-span groups was done on the basis of their scores on two working memory tasks that were administered after the experimental session: reading span (RS) and listening span (LS), which are assumed to measure both storage and computation during sentence comprehension (Daneman & Carpenter, 1980).[2] Subjects read aloud or heard groups of unrelated sentences, which were presented one at a time, and recalled the final word of each sentence once the entire group had been presented. The number of sentences in a group varied from 2 to 6, and there were five sets in each group. A participant's working memory span was calculated in two ways: (1) as the highest level at which subjects recalled the last words from three out of five sets, with a half-credit given for getting two out of five correct (working memory span [WMS]); and (2) as the total number of accurately recalled words (working memory span trials [WMST]). This measure is finer-grained than WMS. The scores between RS and LS tasks were correlated for both WMS ($r = .620$) and WMST ($r = .696$).

Based on the results of all 54 participants, the median value of the scores on the span tasks was calculated. The WMS was 3.5 for both RS and LS and the WMST was 10 for RS and 11 for LS. Individuals who had scores higher than the median for both measures were considered high span, and individuals with scores less than the median for both measures were considered low span. Subjects that were at the median span value for either of the measures were not included (18 subjects). The mean WMS was 4.5 (RS) and 4.7 (LS) for the high-span group; 2.7 (RS) and 2.8 (LS) for the low-span group. The mean WMST was 14.8 (RS) and 16 (LS) for the high-span group; 7.2 (RS) and 7.6 (LS) for the low-span group.

Materials

Simple active sentences (150) were created in which animacy and world-knowledge information was manipulated across three conditions: control, world-knowledge violation, and animacy violation (see Table 1). Each condition contained 50 sentences.

All sentences had simple active progressive syntactic structures with a third-person singular noun as the subject. The plausibility differences across the conditions were created by changing the subject noun while keeping the verb and object noun constant. In the animacy violation condition, the subject noun was always inanimate, and could not be the agent of the action. In the world-knowledge violation condition, the subject noun was an unlikely agent of the action. In order to assess the effectiveness of our manipulations, we performed a pretest with 29 undergraduate participants, who were native speakers of English; these participants were asked to rate the likelihood of occurrence for three sets of thematic relations: (1) the agent and the action (e.g., "the dog/poet/box is biting"); (2) the action and the theme (e.g., "biting the mailman"); (3) the agent, the action, and the theme (e.g., "the dog/poet/box is biting the mailman"). The order of presentation of these three sets was counterbalanced among subjects. Three blocks were created so that the verb and the second noun phrase (e.g., "is biting the mailman") were not repeated within a block, but all three plausibility conditions were equally represented in all three blocks. Order of presentation of these three blocks was counterbalanced across subjects. For each of the three sets of thematic relations, two t tests were performed to compare likelihood of the thematic relations between the control and the animacy violation conditions, and of the control and the world-knowledge violations. For the agent–action relationship, these t tests revealed that the control condition was rated as more likely than the world-knowledge violation ($t = 23.752$, $p < .0001$) and animacy violation conditions ($t = 59.470$, $p < .0001$). For the action–theme relationship, rating scores across the three conditions were identical. Finally, for the agent–action–theme relationship, the control condition was rated as more likely than the world-knowledge violation condition ($t = 43.455$, $p < .0001$) and the animacy violation condition ($t = 59.794$, $p < .0001$).

All sentences were randomized for recording purposes and read by a female native speaker of American English with natural intonation and at a normal speaking rate. The sentences were digitally recorded using a Schoeps MK2 microphone and Sound Devices USBPre A/D (44,100 Hz, 16 bit). The recorded sentences were then segmented into two parts: the subject noun phrase (e.g., "The dog") and the verb phrase (e.g., "is biting the mailman"). Each segment was saved as a separate audio file. The same verb phrase audio file was spliced with the subject noun phrase files in each of the three conditions, with a 100-msec interval of silence between the subject noun and the verb. Thus, three different subject noun phrases were followed by the exact same verb phrase for each triplet set of stimuli. Each sentence file sounded natural because the splices were edited at zero crossing points, and thus were not detectable.

Subject nouns did not differ across conditions in terms of lexical frequency ($F < 1$; mean = 23.86), number of syllables ($F < 1$; mean = 2.5), acoustic duration [$F(2, 98) = 1.660$, $p = .195$; mean = 974 msec], or imageability [control (C): 583.37; world-knowledge violation (W): 555.79; animacy violation (A): 557.32; p values of 3 pairwise comparisons: $p > .10$ (C vs. W); $p > .20$ (C vs. A); $p > .90$ (W vs. A)].

Filler sentences (110) were constructed that differed from the experimental items in their syntactic structures and in their lexicality (pseudowords, 30 items). These filler sentences were included to mitigate subjects developing theories and strategies about the purpose of the study. All filler sentences with real words contained adjectives or adverbs. Forty-six of the real word fillers started with an inanimate noun, half were in past tense, and/or in passive voice, and/or incorrect; the violations were at different positions in the filler sentences. To further avoid predictability as a function of the animacy of the first noun, half of the correct real word filler sentences began with an inanimate noun and half of the incorrect real word filler sentences began with an animate noun.

Procedure

Participants were comfortably seated in a dimly lit, electrically shielded booth. The stimuli were presented via a computer using Presentation (www.neurobs.com) through Sennheiser HD 265 linear closed-ear headphones. Participants were asked to listen to the sentences for comprehension. Each trial began with a white fixation cross (1000 msec) on a video screen situated 100 cm in front of the participant. The fixation cross remained visible during the auditory presentation of the stimuli (3064 msec on average, ranging from 2447 to 4004 msec), and for an additional 2000 msec after the offset of the sentence. The white cross was then replaced by a green cross that was presented for 3000 msec, unless a true/false comprehension question followed the stimulus (12% of all stimuli), in which case the green cross remained on the screen until the participants had pressed a "yes" or "no" button to answer the question. These probe questions were recorded in a male voice to make them maximally distinct from the experimental stimuli. In all other respects, the recording parameters were the same as for the test and filler stimuli.

Participants were asked to refrain from blinking for the duration of the white fixation cross. Condition-specific stimulus codes were sent out at the onset of the critical words and these codes were used for later off-line averaging of the EEG. Visual and auditory inspection of the speech signal was used to determine the onsets of the critical words in the experimental sentences.

EEG Recording

EEG was recorded from 29 tin electrodes, mounted in an elastic cap (Electro-Cap International, Eaton, OH; see Figure 1). The right mastoid electrode was used as the recording reference. The left mastoid was also recorded for later off-line algebraic re-referencing. The EEG signal was amplified with band-pass cutoffs at 0.01 and 30 Hz, and digitized on-line at a sampling rate of 250 Hz (Neuroscan Synamp I). EEG was digitized continuously along with accompanying stimulus codes used for subsequent averaging. Impedances were kept below 5 kΩ.

Prior to off-line averaging, all single-trial waveforms were screened for amplifier blocking, muscle artifacts, horizontal eye movements, and blinks over epochs of 1200 msec, starting 200 msec before the onset of the critical words. This led to an average rejection rate of 42.9% of the trials. Average ERPs were computed over artifact-free trials for subject nouns, verbs, and object nouns in the control, world-knowledge violation, and animacy violation conditions. All ERPs were filtered off-line with a Gaussian low-pass filter with a 25-Hz half-amplitude cutoff.

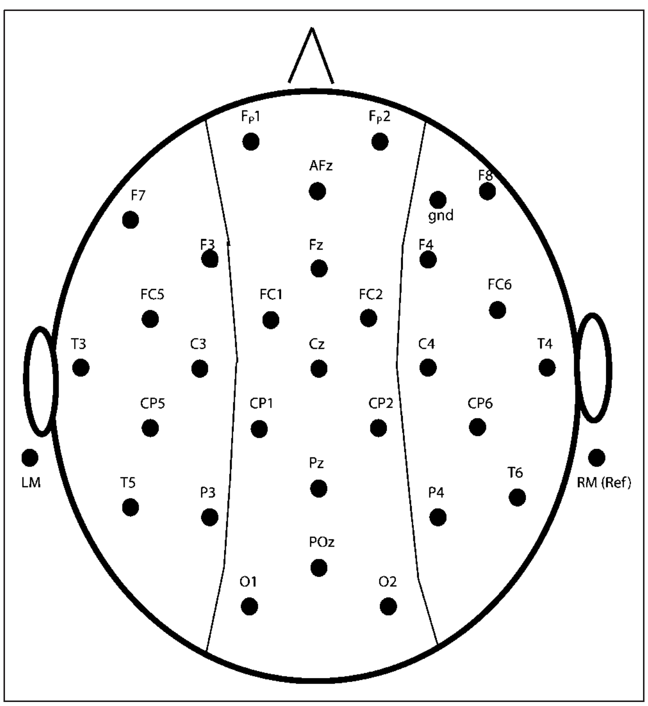

Figure 1. Electrode configuration.

RESULTS

Behavioral Data

The average percent correct for responses to the comprehension probes was 95.2%, and this was not different between groups (high span = 96.0%; low span = 94.4%; $p = .15$).

EEG Data

ERP data were analyzed using repeated measures analyses of variance (ANOVAs) performed on the mean amplitude of the ERPs to the critical words for each of the 29 electrode sites separately in the N400 (300–600 msec) and P600 (600–900 msec) time windows (relative to a 100 msec prestimulus baseline). Separate ANOVAs were performed for each of the time windows and for each of the thematic manipulations (i.e., 300–600 msec: world-knowledge violation vs. control; animacy violation vs. control; and the same two comparisons for 600–900 msec). These ANOVAs were performed for the subject nouns, the verbs, and the object nouns, respectively.

All ANOVAs included the factors group (high span vs. low span), plausibility[3] (world-knowledge violation, control; animacy violation, control), and electrode site (29 levels).[4] The factors plausibility and electrode site were nested under group. Table 3 displays the *F* values for these analyses in both time windows. Only statistically significant (or marginally significant) results are reported.

When interactions with group occurred, follow-up analyses were performed for high-span and low-span subjects separately.

Figure 2 shows the grand-average ERPs for control, world-knowledge violation, and animacy violation conditions, time locked to the onset of the noun in NP1, the verb, and the noun in NP2, at Fz, Cz, and Pz electrode locations, for high-span (top) and low-span (bottom) subjects, respectively.

300–600 msec Time Window (N400)

Animacy violation vs. control. At the *subject noun*, interactions of Plausibility × Electrode site [$F(28, 952) = 4.02$, $p = .0018$], and of plausibility, electrode site, and group [$F(28, 952) = 2.64$, $p < .025$] were found. Follow-up ANOVAs for high- and low-span subjects separately did not show a main effect of plausibility for either high or low-span subjects [high: $F(1, 17) = 1.48$; $p = .24$; low: $F(1, 17) = 1.34$, $p = .26$], but for the high-span subjects, the interaction of Plausibility × Electrode was significant. Further analyses to pinpoint the topographic distribution of this effect for the high-span subjects showed a significant main effect of plausibility over 12 anterior sites [i.e.,

Table 3. *F* Values for the Effects of Animacy Violation and World-knowledge Violation

		Animacy Violation vs. Control			*World-knowledge Violation vs. Control*		
	Time Window	*Subject Noun*	*Verb*	*Object Noun*	*Subject Noun*	*Verb*	*Object Noun*
300–600 msec							
F(1, 34)	G	–	–	–	–	–	–
	P	–	–	6.00**	–	3.38*	11.81***
	P × G	–	6.97**	–	–	–	–
F(28, 952)	P × E	4.02****	–	–	–	–	6.06****
	P × G × E	2.64**	–	–	–	–	–
600–900 msec							
F(1, 34)	G	–	–	–	–	–	–
	P	–	–	3.29*	–	–	7.46***
	P × G	4.07*	13.94****	–	–	–	–
F(28, 952)	P × E	3.83****	–	–	–	2.11*	3.96***
	P × G × E	3.82****	2.18*	–	–	–	–

P = plausibility; G = group; E = electrode.

*$p < .08$.

**$p < .05$.

***$p < .01$.

****$p < .001$.

Fp1, Fp2, F3, F4, FC1, FC2, FC5, FC6, AFz, Fz; $F(1, 17) = 5.25, p = .0035$], but not over 11 centro-parietal sites (i.e., C3, C4, CP5, CP6, CP1, CP2, P3, P4, Cz, Pz; $F < 1$). This can be seen in Figure 3 (top left); high-span subjects' ERPs to the inanimate nouns were more negative than to the animate nouns at anterior electrode sites. This anterior distribution is not typical for the canonical N400 effect, which has a centro-parietal distribution.

At this point in the sentence, the only difference between these conditions is in the animacy of the subject noun: In the animacy violation condition, the subject nouns were inanimate, whereas in the control condition, the subject nouns were animate (and these words did not differ on lexical properties; see Methods section). At the *verb*, a Plausibility × Group interaction was found [$F(1, 34) = 6.97, p = .0124$]. Follow-up analyses showed a significant N400 effect for the low-span [$F(1, 17) = 5.4, p = .033$], but not for the high-span subjects [$F(1, 17) = 1.5, p = .24$] (see Figure 2 and bottom panel of Figure 3). At the *object noun* (see Figure 2), an N400 effect of plausibility was found [$F(1, 34) = 6.00, p = .0196$], but there was no interaction of Plausibility × Group.

World-knowledge violation vs. control. In the comparison between control and world-knowledge violation conditions (see Figure 2), no significant differences were obtained at the *subject noun*. A marginal N400 effect of plausibility was found at the *verb* [$F(1, 34) = 3.38, p = .0747$], and this effect was significant at the *object noun* [$F(1, 34) = 11.81, p = .0016$], where there was also an interaction between plausibility and electrode site, indicating the typical centro-parietal distribution of the N400 effect [$F(28, 952) = 6.06, p < .001$]. Importantly, none of the comparisons showed a significant interaction of any of the factors with group, indicating that high- and low-span subjects showed the same pattern of results for the less plausible scenario in the world-knowledge violation condition.

600–900 msec Time Window (P600)

Animacy violation vs. control. In this time window, a marginal interaction of Plausibility × Group to the *subject noun* was found [$F(1, 34) = 4.07, p = .0517$]. Both the interactions of Plausibility × Electrode [$F(28, 952) = 3.83, p < .001$], and Plausibility × Group × Electrode [$F(28, 952) = 3.82, p < .001$] were significant. Follow-up analyses for the high- and low-span subjects separately showed no main effects of plausibility in either group [high: $F(1, 17) = 1.23, p = .28$; low: $F(1, 17) = 3.07, p = .10$], but a significant interaction of Plausibility × Electrode site was found for the high-span subjects [$F(128, 476) = 4.78, p = .002$]. This is most likely the continuation of the frontally distributed animacy effect that was observed for the high but not the low-span subjects in the 300–600 msec time window, that is, a more negative ERP to the inanimate than animate subject nouns (see Figure 3, top left). At the *verb*, there was a significant interaction of plausibility with group [$F(1, 34) = 13.94$, $p = .0009$]. In this time window, the high-span group showed a larger positive deflection to the animacy violation than to the control condition [$F(1, 17) = 6.85$, $p = .018$], whereas the low-span group showed the reverse, a larger negative deflection to the animacy violation than to the control condition [$F(1, 17) = 6.63$, $p = .02$] (see Figure 3, bottom). Finally, at the object noun, the effect of plausibility was marginal in this time window [$F(1, 34) = 3.29$, $p = .0786$].

World-knowledge violation vs. control. No significant effects of plausibility were found at the *subject noun*. At the *verb*, there was also no main effect of plausibility, but a marginal interaction of Plausibility × Electrode site [$F(28, 952) = 2.11$, $p = .0674$], indicating a trend to a posteriorly distributed N400 effect. A significant effect of plausibility was obtained for the *object noun*, where the world-knowledge violation condition elicited a larger negative shift than control [$F(1, 34) = 7.46$, $p = .0099$]. This effect was maximal over central and posterior electrode sites [Plausibility × Electrode site: $F(28, 952) = 3.96$, $p = .002$]. Again, just like for the analyses of the world-knowledge violation manipulation in the N400 time window, none of the factors interacted significantly with group, indicating that the high- and low-span subjects showed the same pattern of results for violations of world knowledge.

Correlation Analyses

Two regression analyses were performed to further examine the relation between working memory span and the plausibility effects at the verb in the animacy violation relative to the control condition for the mean amplitudes (per subject) of the P600 and the N400, respectively. Figure 4 shows that lower working memory scores were correlated

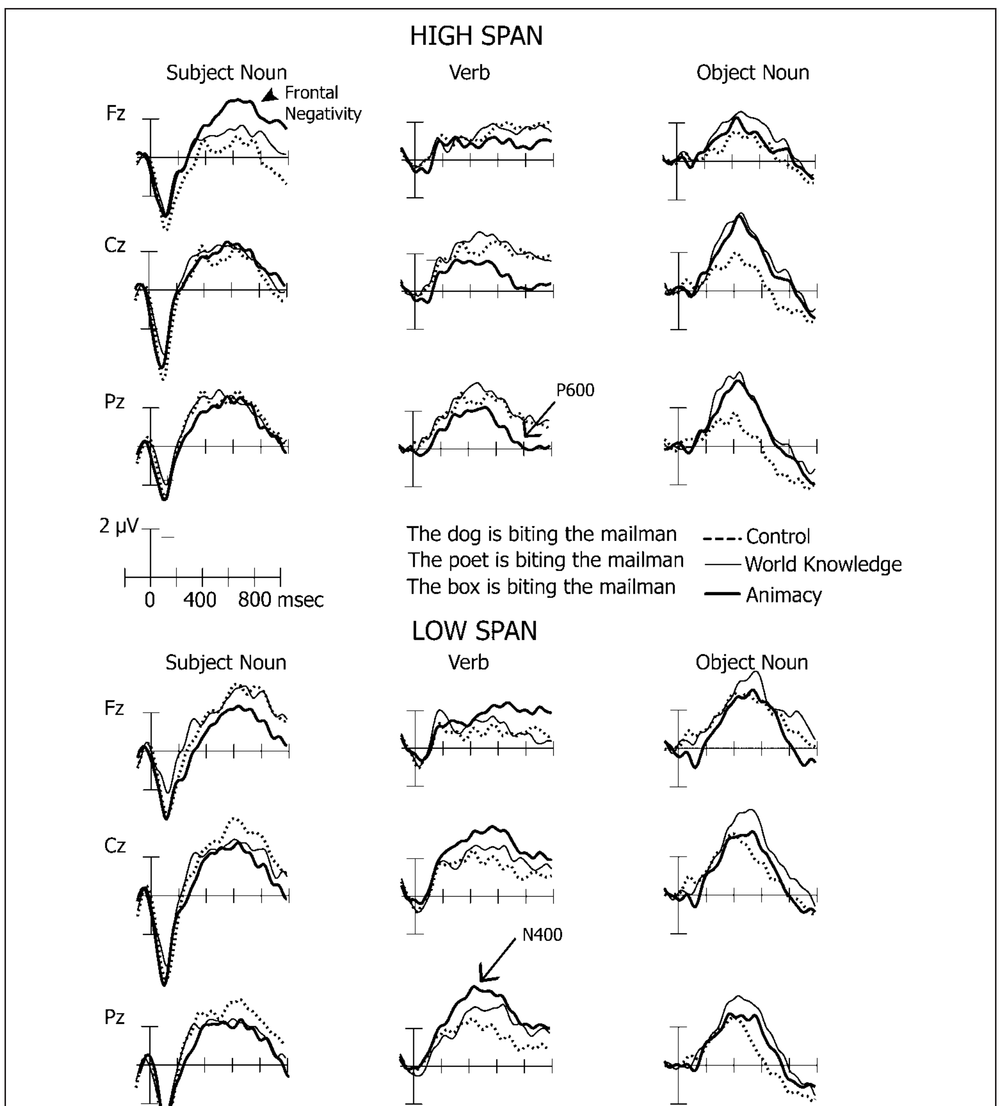

Figure 2. ERP results for the high-span subjects (top) and low-span subjects (bottom) are shown for three midline electrode sites (Fz, Cz, and Pz), for the subject nouns (left column), verbs (middle column), and object nouns (right column) in the control condition (dotted line), world-violation condition (thin solid line), and animacy violation condition (thick solid line).

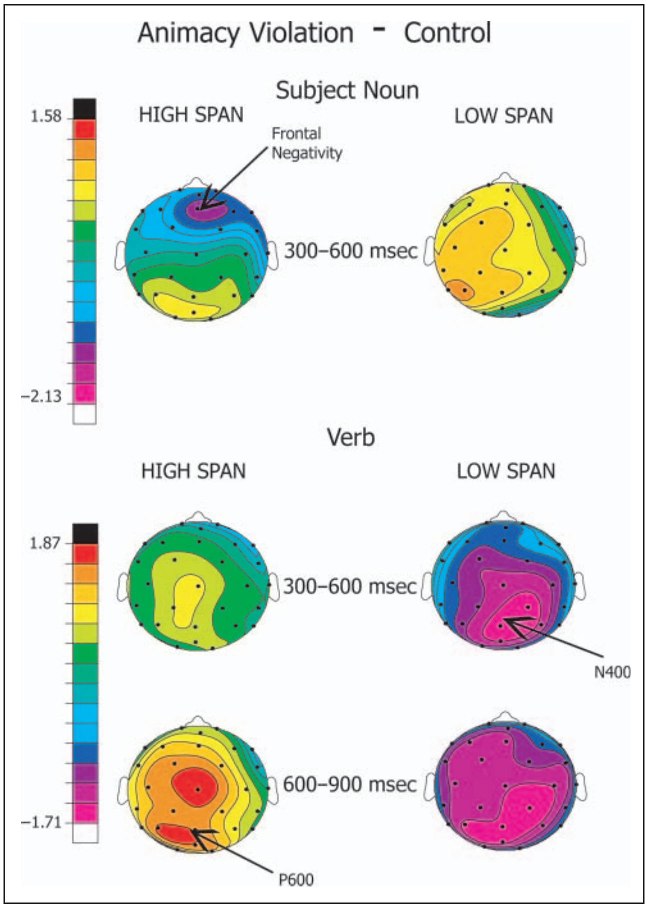

Figure 3. Topographic distribution is shown for the mean amplitude of the difference between the animacy violation and control conditions, for the 300–600 msec time window both for subject nouns (top) and verbs (bottom) and for the 600–900 msec time window for the verbs.

with greater N400 effects (r = .507, p < .01), and higher working memory scores were correlated with a greater P600 effect (r = .368, p < .05).

DISCUSSION

The goal of this study was to establish whether individual differences in working memory capacity, as assessed by reading and listening span, affected real-time processing of thematic relations in spoken simple active English sentences. We observed striking qualitative differences in the on-line use of animacy but not world-knowledge information during thematic processing between high- and low-span listeners.

As predicted, in the comparison between the *control* and *animacy violation* conditions (e.g., "The dog/box is biting the mailman"), high-span but not low-span subjects showed evidence of a processing cost to the sentence-initial, inanimate nouns. This was evident from a sustained anterior negativity that was larger to inanimate than animate nouns. An effect of animacy on sentence-initial nouns of difficult object relative sentences was also found in a study by Weckerly and Kutas (1999). These authors reported a larger amplitude N400 to inanimate than animate sentence-initial nouns. Although they did not comment on the topographic distribution of this effect of animacy, it also appeared more frontally distributed than the centro-parietal distribution that is typically found for the classical N400 effect (see their Figure 1, p. 565). Differences in the scalp topographic distribution of ERP effects suggest that these effects are generated by (partially) nonoverlapping neuronal sources, and this may indicate that the ERP effect of animacy and the classical N400 effect are sensitive to different processes during on-line comprehension. We suggest that the ERP animacy effect obtained in the high-span subjects may indicate that they, in contrast to low-span subjects, have the working memory capacity to use this animacy information to assign provisional thematic roles in sentences immediately upon hearing the sentence-initial noun. Two pieces of information are in favor of such an explanation. First, sentence-initial inanimate nouns do not often serve as agents or subjects of English sentences (Bates & MacWhinney, 1989; Bock, 1986), and high-span subjects were sensitive to this irregularity. This may have signaled the parser that a canonical SVO sentence should be suppressed in favor of a (more costly) noncanonical sentence structure. Second, sustained anterior negativities have been related to higher processing loads as a function of working memory requirements during sentence processing (e.g., Münte et al., 1998;

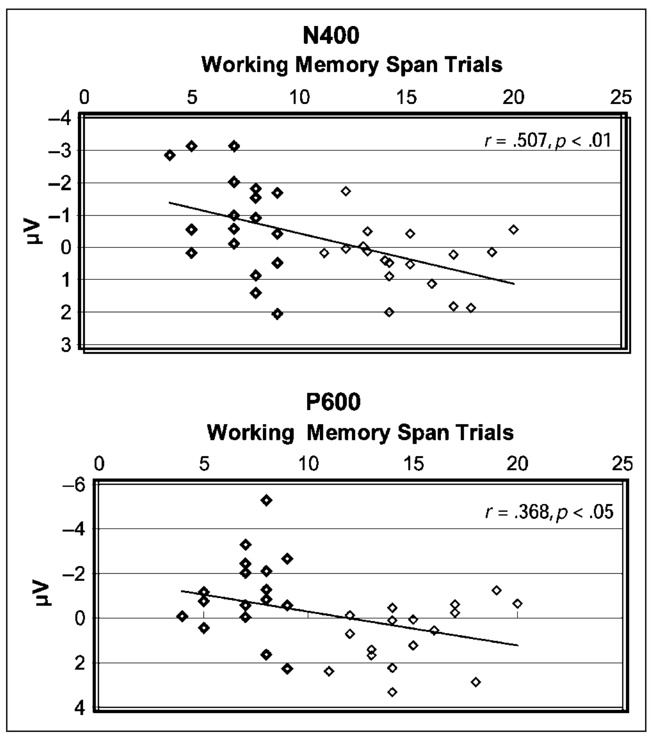

Figure 4. Results of the regression analyses for the mean amplitude of the N400 (top) and the P600 (bottom) effects on the verb in the animacy violation condition (relative to control) as a function of working memory span scores for each individual in the low-span (bold diamonds) and high-span groups. The amplitude (μV) and the correct number of trials in the span tasks are displayed on the vertical axis and horizontal axis, respectively.

King & Kutas, 1995), and our ERP effect of animacy also had an anterior distribution. Thus, the sustained anterior negativity found in sentence-initial inanimate nouns may reflect that more working memory resources were required for the on-line use of this information in sentence processing. Future studies are needed to test the validity of this latter assumption.

These differences in the sensitivity to the animacy of the sentence-initial noun led to qualitative differences in the nature of the costs that were incurred by high- and low-span individuals during the processing of the verb in the animacy violation condition (e.g., "The box is biting…"); An N400 was found for the low-span and a P600 for the high-span subjects (see Figures 2 and 3). Further, a regression analysis (Figure 4) showed that the size of the N400 and P600 effects was correlated with an individual's working memory span; lower working memory scores were correlated with greater N400 effects and higher working memory scores were correlated with greater P600 effects.

These results can be interpreted within Kuperberg's (2007) proposal that sentence processing relies on two parallel streams of information, one for semantic (based on word meanings) and one for combinatorial (based on syntactic and thematic information) information in sentence comprehension. The N400 effect that was elicited to the verbs in the animacy violation condition in the low-span subjects of this study suggests that these subjects' initial processing costs occurred as a function of lexical–semantic integration difficulty because "box" and "biting" are not semantically related. Findings of a study by Van Petten et al. (1997) also suggest a special role of lexical–semantic relations between words during sentence processing in low-span subjects but not high-span subjects. Independent of working memory span, differences in the influence of lexical association on comprehension are observed as a function of the context in which these associations occur. Robust effects of lexical association are found in isolated sentences, but these effects are delayed in the context of a discourse (Camblin, Gordon, & Swaab, 2007; Ledoux, Camblin, Swaab, & Gordon, 2006). The results of Camblin et al., together with the results of the present study, suggest that the time course of the influence of lexical–semantic information on real-time language comprehension is not fixed, and may vary as a function of language context, and as a function of working memory span. In addition, absence of an effect of animacy in the low-span subjects suggests that not all sources of semantic information are treated equally in spoken sentence comprehension; that is, these subjects immediately used lexical–semantic but not animacy information during on-line sentence processing. High-span subjects, on the other hand, were immediately sensitive to the animacy information available at the verb-preceding initial argument, and this affected the combinatorial stream at an earlier point in time, which resulted in a cost reflected by the P600 to the verbs. This latter finding of a P600 to animacy violations in high-span subjects is also interesting because it is the first time this has been observed during spoken language comprehension. Furthermore, the P600 effect in high-span subjects was obtained in the absence of a meta-linguistic judgment task, showing that the P600 is not a purely task-driven effect.

The differences that were found as a function of working memory capacity in the on-line use of lexical–semantic relations and animacy information in sentences were fairly short-lived: Both high- and low-span subjects showed an N400 to the object nouns in the comparison of the animacy violation and control conditions. This last result, in conjunction with the high accuracy on the true/false questions for both groups, indicates that both high- and low-span subjects had used the thematic information in the sentences to arrive at the correct higher-order representation of the whole sentence context. This was to be expected because the low-span participants in this study were college students who are very likely not impaired in understanding simple active spoken sentences. In fact, Long and Prat (2008) have shown that low skilled readers, who do not show evidence of on-line use of animacy information in processing of syntactically ambiguous sentences, do build appropriate message-level memory representation of sentences. The results of our study further indicate that low-span subjects, similar to high-span subjects, have processed the animacy information during on-line processing of the noun in the second NP. Further, because we did not find any evidence of a P600 effect during the processing of the animacy violations in the low-span subjects, the context of one experiment is apparently not enough to find the effects of training that Long and Prat observed with multiple exposures.

Interestingly, in the comparison between *world-knowledge violation* and *control* conditions ("The poet/dog is biting the mailman"), no differences were found between high- and low-span subjects. In this case, the verb was a possible but less plausible action of the agent, and both high- and low-span subjects showed a marginally significant N400 effect to verbs and an N400 to the object nouns. This shows that there is no difference as a function of working memory capacity in the on-line use of knowledge of the world during sentence comprehension. This difference in the influence of world-knowledge and animacy information during real-time sentence comprehension in low-span subjects may be explained in terms of differences in the way in which these types of information are retrieved and integrated. It has been shown that manipulations of world knowledge and lexical semantic knowledge result in N400 effects with the same latency and topographic distribution, suggesting that these sources of semantic information can be retrieved and integrated at the same moment in time during on-line sentence comprehension (e.g., Hagoort et al., 2004). However, animacy information may serve a special role in thematic processing during language comprehension. Retrieval and integration of the thematic combinatorial information related to the animacy of the subject noun may therefore require more processing resources than retrieval of lexical–semantic and world-knowledge information.

The differences in the real-time use of animacy information in sentence processing by high- and low-span subjects suggest that working memory capacity indeed influences the processing of spoken simple active sentences. We cannot determine on the basis of our present study whether this is due to individual variability in a general capacity for storage and maintenance of information in sentences (Just & Carpenter, 1992), or from variability in the capacity of a separate domain-independent processing resource that is not related to real-time sentence processing, but instead reflects processing as a function of the off-line task (Caplan & Waters, 1999). However, we suggest that some aspects of the design and results of the present study argue against this latter interpretation. In our study, the task of the subjects was to listen for comprehension, and to answer a true/false comprehension question to only 12% of all sentences. This task did not encourage metalinguistic judgments, nor did it encourage subjects to engage in response-related strategies when processing the sentences, as no speeded response was required to the comprehension questions. In addition, the inclusion of filler sentences with various structures likely prevented subjects to engage in "off-line" strategies to predict which sentences would be correct or not. Further, the available evidence of the role of the P600 in language comprehension suggests that this ERP component signals a processing cost as a function of a conflict in on-line (or monitoring of) combinatorial sentence processing operations. Thus, our observation in high-span subjects of a P600 to verbs that were preceded by an anomalous inanimate argument suggests that it was on-line combinatorial sentence processing that was affected most in this group, which argues against a strong role of strategic differences between groups in our results.

Although the results of the present study seem less consistent with the operation of a domain-general, task-dependent processing resource during thematic processing, they do not exclude the account of Macdonald and Christiansen (2002), because it may well be the case that training with, and more exposure to, the consequences of the (in)animacy of the verb-preceding argument for thematic role assignment would lead low-span subjects to use this information earlier during sentence processing (Long & Prat, 2008).

The results of this ERP study cannot determine the neural circuitry of the thematic processing differences found for low- and high-span subjects. However, a recent neuroimaging study that compared processing of noun–verb ambiguities in lists of words relative to sentences showed activation of posterior areas of the (left) temporal lobes during retrieval of lexical information, but activation of left inferior frontal cortex during sentence integration processes (i.e., unification; Snijders et al., 2009). Presumably, these latter processes need more computational resources and require more working memory capacity than access and retrieval of individual word meanings. Consistent with these neuroimaging results, our work with aphasic patients with lesions that include the inferior frontal gyrus has shown delayed contextual integration of lexical–semantic and thematic information in sentences and discourses, but intact semantic priming in lists of words (Nakano & Swaab, 2005; Nakano & Blumstein, 2004; Swaab, Brown, & Hagoort, 1998; Hagoort, Brown, & Swaab, 1996). In line with these findings, we suggest that high-span subjects perhaps engage prefrontal language areas more efficiently than low-span subjects during integration of the thematic roles of words in sentence contexts.

Conclusions and Future Directions

To conclude, the results of the present study suggest that variability in working memory span influences the way in which listeners make use of animacy information, but not of world-knowledge information of the verb-preceding-argument in simple active sentences during thematic processing. In contrast to low-span subjects, high-span subjects are immediately sensitive to animacy information as is evident from the processing costs on the sentence-initial noun itself and from the combinatorial costs incurred on the processing of verbs that violate the theme that is dictated by inanimate nouns. Future studies that take into account individual working memory span and the processing effects of animacy of arguments on thematic processing in sentences are needed to further determine the exact nature of the relation between these factors. The current data suggest differential timing of semantic and thematic combinatorial processing during listening comprehension depending on the amount of working memory at hand.

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Notes

1. A verb such as "to bite" requires an animate subject as the agent of the action, unless used in a metaphorical sense, (e.g., "The sun is very hot today and really bites my skin").
2. It has been argued that the reading span task does not measure working memory for syntactic processing (e.g., Waters & Caplan, 2004). But it has not been disputed that this task is related to individual differences in language comprehension. Furthermore, Waters and Caplan (2003) have shown that the use of more than one working memory span task (as in our study) increases test–retest reliability of these measures when measured over items.

3. In order to be consistent, we use plausibility to label this factor for the subject nouns as well, even though at this point in the sentence there is no world-knowledge or animacy violation.
4. In order to avoid Type I errors due to violations of the assumption of equal variances between conditions, the Greenhouse–Geisser (1959) correction was applied for effects involving more than one degree of freedom. The corrected *p* values are reported.

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