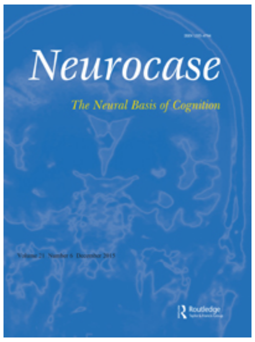

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Neural bases of event knowledge and syntax integration in comprehension of complex sentences

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Comprehension of complex sentences is necessarily supported by both syntactic and semantic knowledge, but what linguistic factors trigger a readers' reliance on a specific system? This functional neuroimaging study orthogonally manipulated argument plausibility and verb event type to investigate cortical bases of the semantic effect on argument comprehension during reading. The data suggest that telic verbs facilitate online processing by means of consolidating the event schemas in episodic memory and by easing the computation of syntactico-thematic hierarchies in the left inferior frontal gyrus. The results demonstrate that syntax–semantics integration relies on trade-offs among a distributed network of regions for maximum comprehension efficiency.

Keywords: verb; argument; working memory; strategy; syntax

Recent behavioral research shows that readers dynamically combine information about real-world events with linguistic information from multiple language modules and use it for online sentence comprehension and dynamic prediction of likely incoming words (Bicknell, Elman, Hare, McRae, & Kutas, 2010; Matsuki et al., 2011). Less is known, however, about the neural network interactions underlying information integration during language comprehension. This functional neuroimaging (fMRI) study orthogonally manipulated argument plausibility and verbal event structure to investigate the neural bases of integrating semantic and syntactic information with event schemas during reading.

Verbal event structure refers to both frame semantics and the syntactic combinability of the verb. Semantically, telic verbs define changes of state (such as *fall* and *awaken*), while atelic verbs denote homogenous actions (such as *read* and *worship*).[1] Thus, only telic verbs describe events as having a natural end point or boundary. The event boundary denoted by the verb, or telicity, is cross-linguistically attested as a grammatically relevant semantic feature – it affects the syntactic structure of the sentence in such typologically distinct languages as Russian, Dutch, Icelandic, and Bengali (Ramchand, 1997; Ramchand, 2008a; Svenonius, 2002; Van Hout, 2001) and has been considered a semantic primitive in multiple cross-linguistic verb typologies (Dowty, 1979; Jackendoff, 1991; Pustejovsky, 1991; Ramchand, 2008a; Van Hout, 2001; Van Valin, 2007; Vendler, 1967; Verkuyl, 1972). Multiple psycholinguistic studies have also shown that verbal event structure is instrumental to language processing and language acquisition; it is critically important for tense and aspect development in native (L1) and second-language (L2) English, Japanese, and Russian (Folli & Harley, 2006; Kaku, Liceras, & Kazanina, 2008; Slabakova, 2005). Children with specific language impairments (SLI) have difficulty using completion cues pertaining to verbal event structure (Leonard & Deevy, 2010). Behaviorally, telic verbs appear to facilitate online syntactic processing and thematic role assignment during reading (Friedmann, Taranto, Shapiro, & Swinney, 2008; O'Bryan, 2003). Evoked response potential investigations show that the arguments of atelic verbs require additional attentional resources during processing, as compared to the arguments of telic verbs (Malaia, Wilbur, & Weber-Fox, 2009, 2013). According to Ramchand (2008b), telic verbs structurally project the resultant phrase in the syntax, generating a more complex event structure with the resultee position for the internal argument, which could make for an easier argument integration downstream.

In addition to facilitating internal argument integration, telic verbs provide a conceptual boundary to the events they denote. Event segmentation theory (Zacks, Speer, Swallow, Braver, & Reynolds, 2007) proposes that perception of an event boundary leads to consolidation of event features maintained in working memory (WM) using an abstract event schema from long-term (episodic) memory. Neuroimaging studies of human perception of events show that perceived event boundaries – whether derived from visual segmentation of a natural scene, or conceptual, as inferred from linguistic narratives – trigger the update of WM and episodic memory reference (Swallow, Zacks, & Abrams, 2009). WM update is typically associated with several network effects: increases in activation of the

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dorsolateral prefrontal cortex (DLPFC), corresponding to the executive component of WM updating process, and in decreases in precuneus/posterior cingulate (PCC) activation, corresponding to consolidation of information in the WM buffer and (episodic) memory reference (Malaia, Ranaweera, Wilbur, & Talavage, 2012; Yarkoni, Speer, & Zacks, 2008). The present study manipulated verbal event structure to investigate the interaction of syntactic processing of different verb types with episodic memory use during comprehension. We hypothesized that verbal telicity[2] would facilitate event schema retrieval from episodic memory, leading to an increased activation of the DLPFC, but a decreased activation of the PCC during sentence comprehension.

Based on prior behavioral and electroencephalograpy (EEG) studies, we also expected telicity to contribute to semantic analysis triggering syntactic computation. Multiple neuroimaging studies have attested the role of Brodmann area (BA) 47 in processing syntactic complexity (Lee & Newman, 2010; Newman, Ikuta, & Burns, 2010; Newman, Just, Keller, Roth, & Carpenter, 2003), as well as semantic processing (see Binder, Desai, Graves, & Conant, 2009, for meta-analysis), while the PCC has been associated with episodic memory, as well as its use for event boundary processing, including a linguistic boundary (Malaia, Wilbur, & Weber-Fox, 2012; Yarkoni et al., 2008).

The second manipulated variable was the animacy of the first noun in the sentences. Noun animacy is a key semantic feature that contributes to thematic role assignment at the sentence level in multiple languages (Folli & Harley, 2008). From the event knowledge (semantic/pragmatic) viewpoint, inanimate nouns are also unlikely to be used as sentence agents – the first argument encountered in a sentence of subject–verb–object (SVO word order) languages, such as English, is typically assumed to be the agent of the main verb and the subject of the sentence (Kuperberg, Kreher, Sitnikova, Caplan, & Holcomb, 2007; Townsend & Bever, 2001; Weckerly & Kutas, 1999). EEG research shows argument animacy affects neural computation of thematic roles and immediately impacts the processing of the following verb (Kuperberg et al., 2007; Weckerly & Kutas, 1999). Neuroimaging data show that argument semantic–thematic animacy violations are processed similarly to morphosyntactic inflectional violations, activating a distributed network of language-processing regions, including BA 44 and BA 46/9 bilaterally (Kuperberg, Sitnikova, & Lakshmanan, 2008).

The objective of the present study was to investigate the neural bases of event-type (semantic) knowledge and syntactic integration during reading and their interaction with episodic memory. To ensure the need for WM update and episodic memory reference during reading, we used complex sentences with reduced relative clauses (RRCs) as stimuli (e.g., *The lawyer escorted by the governor arrived on time*). The characteristic feature of RRCs is that they create a so-called "garden-path" in comprehension, requiring the participants to revise the original representation of the event and argument structure in order to understand the entire sentence (Clifton et al., 2003; Ferreira and Clifton, 1986). Use of such complex stimuli followed by comprehension probes ensured high WM load during reading (Malaia et al., 2009). Further, we orthogonally manipulated verbal event types in the relative clause as well as the animacy of the first argument in the sentence; thus, although all the stimuli sentences were meaningful, half of them violated semantic–pragmatic expectations of argument animacy.

Based on the linguistic theory of event structure (Ramchand, 2008b), we hypothesized that verbal telicity would facilitate syntactic processing during reading, while the animacy of the first argument would modulate the difficulty of thematic role reassignment during reading and post hoc sentence processing. Figure 1 provides a schematic representation of the hypothesized linguistic reanalysis during garden-path recovery.

The event structure of telic verbs syntactically projects the presence of an internal object argument. The atelic verb template (Figure 1b) does not activate the syntactic position for the object. When the second argument is encountered, the syntactic structure projected by the telic verbs facilitates reassignment of the patient thematic role to the first argument; this process is easier if the first argument is inanimate, i.e., it is lower on the animacy hierarchy[3] vis-à-vis the newly interpreted agent. Thus, we hypothesized that telic stimuli will facilitate syntactic analysis in RRCs by priming the thematic role of the patient during sentence reading. Thematic priming by telic verbs was expected to lighten the processing load in the left inferior frontal gyrus (IFG), i.e., higher IFG activation would be seen for atelic conditions in comparison with telic ones. We also predicted that argument animacy, important for thematic role computation during syntactic processing, would modulate activation in the same region. Since the second noun in the stimuli was always animate, we predicted that reanalysis of thematic role assignment should be easier for the sentences with an inanimate argument first, since the reassignment of thematic roles would allow the argument order to conform to the animacy hierarchy.

Prior neuroimaging research indicated that significant differences in activation exist between the online sentence processing and sentence reanalysis during the question probe (post hoc processing) (Newman, Lee, & Ratliff, 2009; Newman et al., 2010). Post hoc processing appears to elicit more activation in regions related to WM, likely due to the need to activate the representation of the sentence created during the online processing phase. We compared activations during reading and probe responses

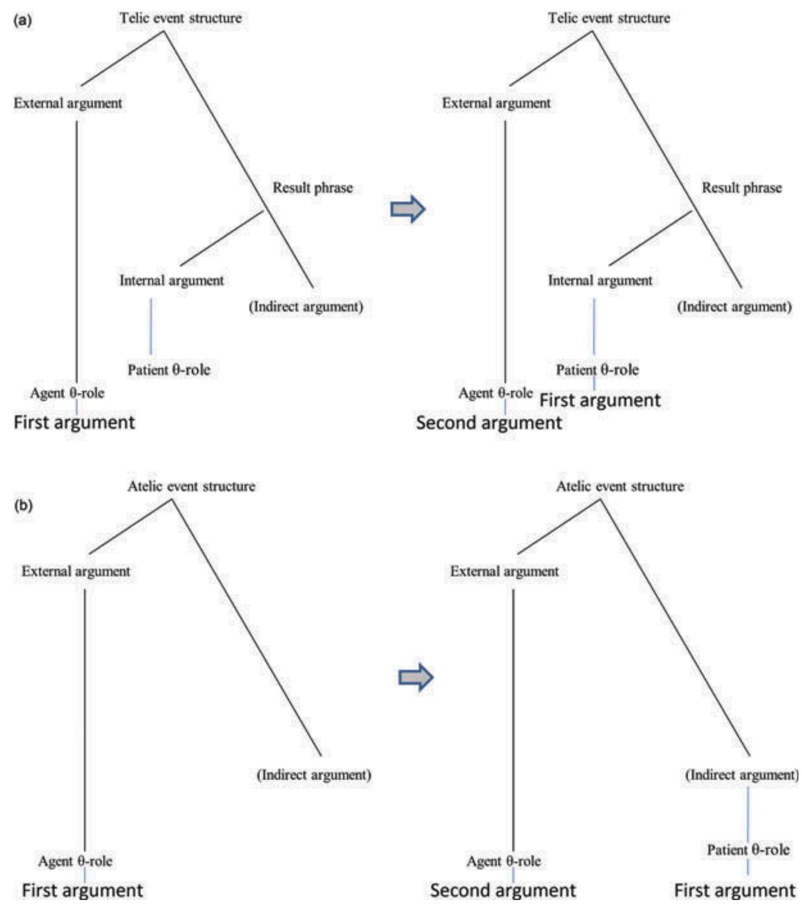

Figure 1. (a) A schematic representation of changes in the argument structure of telic verbs during garden-path recovery in RRCs. (b) A schematic representation of changes in the argument structure of atelic verbs during garden-path recovery in RRCs.

and analyzed the online and post hoc portions of the data separately to assess the effect of verbal event types and argument plausibility on creating and referencing the mental representation of each sentence during the two phases.

1. Methods

1.1. *Participants*

Seventeen healthy volunteers (5 male, aged 18–31 years, mean = 23.9, SD = 4.4) took part in the study. They had normal or corrected-to-normal visual acuity, no language impairment, and no psychiatric or neurological history. All participants were native speakers of English, which was their sole native language. All participants were right-handed (as assessed by Oldfield, 1971, inventory). Written informed consent was obtained from all participants. Indiana University Institutional Review Board approved the experimental protocol. Participants underwent a training session prior to scanning. During the training session, a description of the task was provided, and practice trials were completed.

1.2. *Materials and procedure*

Stimulus sentences with RRCs were constructed using 30 items from each of the following groups: animate nouns, inanimate nouns, telic verbs, and atelic verbs. Transitive verbs (30 telic and 30 atelic) were chosen based on Levin's (1993) work and cross-referenced with examples of allowable usage from multiple dictionary sources. The telic verbs chosen described complete (non-gradient[4]) change, and no semelfactives[5] or reciprocal verbs[6] were used. Telic and atelic verbs and animate and inanimate nouns used as the first argument in the sentences were compared for frequency using SubtLexUS American Word Frequencies (Brysbaert & New, 2009). Frequency and lengths of target verbs and nouns did not differ across conditions ($p > 0.05$). Noun–verb co-occurrences have been assessed using point-wise mutual information measures (Recchia & Jones, 2009); neither animacy nor telicity was a significant factor in noun–verb co-occurrence ($p > 0.05$). Each verb and each noun appeared in two different sentences, for a total of 120 stimulus sentences. The stimulus set for this study was constructed as a 2 × 2 paradigm, contrasting verbal event structure (telicity) and the animacy of the first argument in garden-path, inducing object RRCs (see Appendix for the list of stimuli).

The rest of the lexical material in the sentences was identical, and the second argument was animate in all conditions. 80 simple control sentences were included (e.g., “The uniformed policeman stopped the driver at a crossing”), which were constructed using a different set of verbs and nouns in order to ameliorate an effect of repetition; the simple sentences also had a 50/50 distribution of animate/inanimate subject nouns. Participants were visually presented with stimuli and filler sentences in a word-by-word manner (500 ms per word), followed by a 6-second visual fixation, and a comprehension probe, which was presented for 4 s. The study employed a single-trial event-related design, in which each trial was treated as an event block (Kruggel & von Cramon, 1999; Newman et al., 2009). A trial could be divided into two phases: a sentence reading phase and a responding to a comprehension probe phase. The probe (comprehension question) required the participant to correctly assign thematic roles in the preceding sentence in order to answer it correctly, e.g., the sentence “The client entertained by the administrator was successful.” was followed by the question “Was the client entertained?” The participants were asked to respond to probes as accurately as possible. Half of the correct responses were positive, half were negative; the sentence–probe pairs were pseudo-randomized within each block such that no correct answer was repeated more than 2 times in a row and that agent or patient thematic roles were queried no more than 2 times in a row; the hand assigned to “yes” response was counterbalanced among the participants. A slow event-related design was used, with a pseudo-random interval (6, 8, or 10 s) following each sentence–probe combination. The stimuli were divided into four 12-minute runs. Each run contained 50 sentences, and two 30-second fixation periods (one at the beginning and one at the end of the run) that served as a common baseline.

1.2.1. *Data acquisition and analysis*

The fMRI images were acquired on a 3-T Siemens TRIO scanner with a 32-channel radio frequency coil located in the Imaging Research Facility at Indiana University, IN, USA. The functional images were acquired in 30 3.8-mm-thick oblique axial slices using the following parameters: TR = 2,000 ms, TE = 25 ms, flip angle = 70°, voxel size = 1.5 × 1.5 × 3.8, no gap. High-resolution structural images were also acquired using Siemens MPRAGE sequence (160 3DMPRAGE oblique axial images, TR = 2,000 ms, TE = 3.34 ms, flip angle = 7°, 256 × 256 FOV, resulting in 1 mm^3 voxels).

Images were corrected for slice acquisition timing, motion-corrected, spatially normalized to a standard EPI template (Evans et al., 1993), and smoothed with a 6-mm Gaussian kernel to decrease spatial noise. Statistical analysis was performed on individual and group data by using the general linear model and Gaussian random field theory in SPM8. The onset of each event (first word in the comprehension stimuli; probe question presentation) was convolved with a canonical hemodynamic response function and motion estimates were entered as regressors into the model. For the random effects analysis on group data, two-level analyses of variance (ANOVAs) were performed on contrast images to examine main effects (telicity, animacy, and telic × atelic interaction). The resultant voxel-wise statistical maps were then thresholded for significance by using a cluster-size algorithm that protects against an inflation of the false-positive rate with multiple comparisons. The results are reported at an uncorrected intensity threshold of $p < 0.001$ for the extent threshold of kappa = 14 voxels. A Monte Carlo simulation (AlphaSim, AFNI) of the brain volume in the present study indicated that these thresholds correspond to a whole-brain false-positive rate of less than 0.05, corrected for multiple comparisons.

Contrast images for stimuli with animate and inanimate first arguments and telic and atelic verbs in relative clauses were obtained for each individual subject separately for sentence reading and probe response epochs, and the images were entered in the group-level analysis for the 2 × 2 (argument animacy × verbal telicity) factorial analysis separately during reading and probe response.

Additionally, a region-of-interest (ROI) analysis was performed on the two areas that were predicted to be affected by the manipulations of stimuli parameters by the a priori hypothesis: left BA 47 and PCC. The ROI centroids were determined by the sentence minus fixation and the probe minus fixation contrasts with family-wise error (FEW) correction ($p < 0.05$). The functional ROIs were defined as spheres with a 10-mm radius, with center MNI coordinates of (−48, 52, 6) for the left BA 47 and of (6, −40, 44) for the PCC.

Using the MarsBar toolbox, averaged beta-weights of all the voxels within the spherical ROIs were extracted for each individual normalized imaging dataset and sorted by experimental conditions (e.g., animate telic sentence). With these values, a three-way repeated measures ANOVA (verb type × argument type × phase) was conducted to test the main effects and interactions between the three factors for each ROI.

2. Results

2.1. *Behavioral results*

Behavioral data from one participant were not collected due to equipment malfunction. The remaining participants ($N = 16$) performed the probe task with high accuracy ($M = 88.4\%$, SD = 6.42%). A three-way repeated

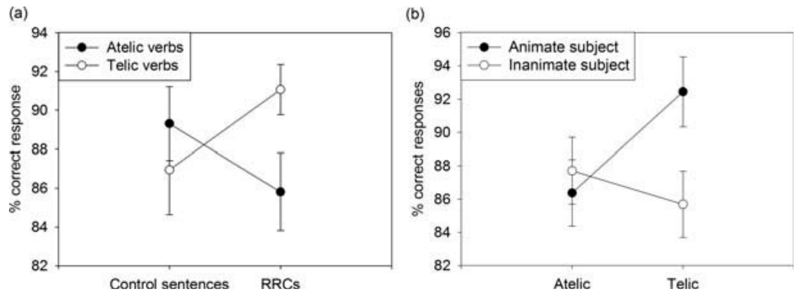

Figure 2. The telicity effect on response accuracy in relation to: (a) sentence type and (b) argument animacy. Error bars denote standard error.

measures ANOVA (verb type × argument type × sentence type) revealed significant interactions of telicity × animacy ($F(1, 15) = 7.111$, $p < 0.018$, $e_p^2 = 0.337$) and sentence type (reduced, filler) × telicity ($F(1, 15) = 6.198$, $p < 0.026$, $e_p^2 = 0.307$), such that verbal telicity facilitated more accurate responses in sentences with an animate first argument, as well as in stimuli with RRCs (see Figure 2).

2.2. ***Neuroimaging results***

2.2.1. *Whole-brain analysis*

2.2.1.1. *Online sentence comprehension.* Neuroimaging analysis was performed only on volumes collected during sentences with correct responses (those that have been understood correctly by the participants). The summary of cortical areas activated during online sentence is presented in Table 1; activation regions were identified using the xjView toolbox for SPM (http://www.alivelearn.net/xjview).

2.2.1.1.1. Main effect of telicity. The whole-brain group analysis revealed a significantly higher activation of the IFG bilaterally (BA 47/45 on the left, BA 46 on the right) when reading sentences with atelic verbs, as well as a higher activation of the cerebellum, insula, putamen, middle frontal gyrus (BA 6), and the temporal pole (BA 22) in the right hemisphere. No region showed a higher activation in telic, as opposed to the atelic condition.

2.2.1.1.2. Main effect of animacy. Sentences with an animate first argument elicited stronger activation in the left supramarginal gyrus (SMG, BA 40) and precentral gyrus. Sentences with an inanimate first argument elicited a stronger activation in the right cerebellum.

2.2.1.1.3. Telicity × animacy interaction. An interaction between telicity and animacy effects during reading was observed in the left precuneus/PCC (BA 23/31), occipital (BA 19), and medial frontal gyrus (MFG, BA 11). The right IFG (BA 47), inferior parietal lobe (IPL, BA 40), middle temporal gyrus (MTG, BA 21), parahippocampal gyrus, and superior frontal gyrus (SFG) also showed interactive effects of telicity and animacy; the temporal pole (BA 38) and SFG (BA 8/10) showed interactive effects bilaterally.

All single comparisons between conditions are detailed in Table 1; Animate telic minus animate atelic contrast did not show any clusters at or above significance levels.

2.2.1.2. *Post hoc sentence processing.* The summary of cortical areas activated during offline sentence comprehension is presented in Table 2.

2.2.1.2.1. Main effect of telicity. Probes to sentences with atelic verbs elicited a higher activation in the left IFG (BA 47/13), left postcentral gyrus, right cerebellum, and supplementary motor area (SMA). No region showed higher activation in the telic, as opposed to the atelic condition.

2.2.1.2.2. Main effect of animacy. Probes to sentences with an inanimate first argument elicited higher activation in the IFG, SFG, and superior temporal gyrus (STG) bilaterally, as well as the left MFG (BA 10) and right cerebellum, fusiform gyrus, basal ganglia, and occipito-temporal junction (BA 19/37). No region showed higher activation in an animate, as opposed to an inanimate condition.

2.2.1.2.3. Telicity × animacy interaction. An interaction between telicity and animacy effects during post hoc sentence processing was observed in the left precuneus (BA 7), right middle frontal gyrus, MFG, and the occipital lobe (BA 18/19) bilaterally.

All single comparisons between conditions are detailed in Table 2.

2.2.1.3. *Online comprehension vs. reanalysis for probe response.* The summary of cortical activation in the probe minus sentence and sentence minus probe contrasts is summarized in Table 3. Figure 3 shows activation maps for probe minus sentence and sentence minus probe contrasts for reduced relative sentences.

Table 1. Cortical areas activated during online sentence comprehension.

	Left hemisphere				Right hemisphere			
Anatomical region	BA	Cluster size	*t*-Value	Coordinates (*x, y, z*)	BA	Cluster size	*t*-Value	Coordinates (*x, y, z*)
Interaction (telicity × animacy)								
Temporal pole	38	28	5.08	−34, 22, −26	38	26	5.21	48, 16, −28
Lentiform nucleus						34	4.74	28, −8, −8
						22	5.34	6, 2, −4
Inferior frontal gyrus					47	18	4.79	54, 22, 2
Inferior parietal lobe					40	30	5.43	30, −44, 56
Middle temporal gyrus					21	23	5.04	60, −22, −8
Occipital gyrus	19	24	4.58	−42, −70, −8				
Parahippocampal gyrus						14	4.56	20, −2, −16
Medial frontal gyrus	11	31	6.69	−10, 52, −12				
Posterior cingulate/precuneus	23/31	24	4.56	−4, −68, 14				
Superior frontal gyrus	8/10	232	7.76	−12, 46, 50	8	15	4.95	16, 50, −8
					10	45	5.17	12, 62, 18
Atelic minus telic								
Cerebellum						38	5.17	12, −44, −24
Insula					13	24	6.11	38, −16, 2
Inferior temporal lobe	36/37	14	4.93	−36, −36, −14				
Middle temporal gyrus					27	23	5.82	52, −44, 4
Superior temporal gyrus					22	17	4.78	40, −44, 16
Inferior frontal gyrus/insula	47/13	14	5.02	−32, 20, 0				
	45	34	6.06	−32, 28, 20	46	18	5.04	34, 36, 14
Middle frontal gyrus	8	23	4.66	−24, 16, 42				
Telic minus atelic								
n/s								
Animate minus inanimate								
Precentral gyrus	4	16	4.64	−38, −4, 26				
Supramarginal gyrus	40	21	5.55	−42, −44, 32				
Inanimate minus animate								
Cerebellum						26	6.34	12, −52, −8
Animate atelic vs. animate Telic								
Middle temporal gyrus	21	27	4.89	−46, 6, −36				
Temporal pole	38	20	5.68	−36, 24, −24				
Animate telic vs. animate atelic								
n/s								
Inanimate telic vs. inanimate atelic								
Inferior frontal gyrus	47/13	21	5.11	−32, 22, 2				
Cerebellum						29	7.60	24, −50, −30
Inanimate atelic vs. inanimate telic								
Inferior occipital gyrus	18/19	39	5.61	−24, −76, −16				
Cerebellum		26	6.59	−20, −36, −14		18	5.28	26, −76, −20
						20	6.13	14, −46, −22
Inferior temporal gyrus	37	29	4.71	−56, −54, −18	37	136	7.46	46, −66, −2
Middle temporal gyrus					22	16	5.53	54, −34, 2
Superior temporal gyrus					13/22	79	6.84	26, −10, −8
					13/22	18	5.53	40, −44, 18
Inferior frontal gyrus					47	16	4.74	52, 22, 4
					45/46/47	27	5.78	54, 44, 2
					46	28	4.94	46, 30, 10
Middle frontal gyrus	10/46	21	5.75	−22, 14, 42				
	46	37	5.37	−40, 34, 22	10	15	4.40	36, 40, 24
	8/9	40	5.32	−42, 32, 36				
Superior frontal gyrus	6/8/9	78	5.04	−4, 48, 46				
PCC/precuneus	31	16	4.55	−10, −70, 14	23	22	5.38	8, −60, 14
					7	16	4.87	20, −46, 52
Parahippocampal gyrus					36	22	5.62	20, −2, −18

Notes: For each cluster, the peak location is given in MNI coordinates, accompanied by location in terms of BA and sulcal/gyral locus; *t*-values represent the peak voxel activation within each cluster. Clusters achieving $p < 0.001$, uncorrected, are reported and thresholded at $k = 14$ voxels (120 mm^3). n/s, not significant.

Table 2. Cortical areas activated during post hoc sentence processing.

	Left hemisphere				Right hemisphere			
Anatomical region	BA	Cluster size	*t*-Value	Coordinates (*x*, *y*, *z*)	BA	Cluster size	*t*-Value	Coordinates (*x*, *y*, *z*)
Interactions (telic × atelic)								
Middle frontal gyrus					11	27	4.99	28, 42, −18
Precuneus/posterior cingulate	7	24	5.81	−10, −70, 38				
Medial frontal gyrus					8	34	5.33	2, 34, 44,
Occipital lobe	18/19	30	5.29	−28, −80, −4				
	18/19	16	4.51	−34, −88, −2	18/19	19	4.83	22, −96, −2
Atelic minus telic								
Supplementary motor area (bilateral)	6	35	4.51	−8, 14, 60				
Postcentral gyrus	3/4	30	4.82	−26, −34, 46				
Inferior frontal gyrus/insula	47/13	49	5.46	−42, 16, −2				
Cerebellum						21	7.19	20, −64, −22
Telic minus atelic								
n/s								
Inanimate minus animate								
Superior temporal gyrus	38	18	4.63	−32, 12, −26	40	17	5.72	58, −24, 14
	42	26	6.15	−62, −34, 18				
Superior frontal gyrus	9	26	4.66	−2, 54, 38	9/10	30	5.01	16, 62, 32
Middle/inferior frontal gyrus	11/47	42	5.57	−32, 42, −12	47	16	5.88	32, 16, 26
	9	16	4.77	−30, 32, 32				
Medial frontal gyrus	10	50	6.66	−10, 44, −10				
	10	51	5.64	−6, 58, −8				
	10	54	5.92	−14, 42, 14				
Basal ganglia		21	7.11	−18, 12, −6				
Fusiform gyrus					37	76	7.91	36, −48, −18
Cerebellum						22	5.88	6, −36, −16
Occipito-temporal junction					19/37	14	4.85	48, −72, 8
Animate minus inanimate								
n/s								
Animate telic > Animate atelic								
Precuneus	7	37	6.26	−22, −54, 66				
Animate atelic > Animate telic								
Inferior frontal gyrus	13/47	77	5.47	−32, 22, −2				
Middle temporal Gyrus	37	24	5.25	−48, −44, −12				
Inanimate telic > inanimate atelic								
Parahippocampal gyrus		21	4.81	−28, 0, −14				
Middle/inferior frontal gyrus	45/46	22	5.29	−30, 28, 28				
Supramarginal gyrus					40	23	5.45	62, −38, 42
Inanimate atelic > Inanimate telic								
Middle occipital gyrus	18	41	7.11	−24, −80, 10	17	22	5.13	20, −90, −10
Parahippocampal gyrus	36	17	5.05	−28, −32, −8				
Precuneus	7	53	5.01	−20, −66, 34				
Anterior cingulate					32	23	7.52	14, 36, −4

Notes: For each cluster, the peak location is given in MNI coordinates, accompanied by location in terms of BA and sulcal/gyral locus; *t*-values represent the peak voxel activation within each cluster. Clusters achieving $p < 0.001$, uncorrected, are reported and thresholded at $k = 14$ voxels (120 mm^3). n/s, not significant.

2.2.1.3.1. Probe minus sentence. Cortical areas which were more active during the probe phase included a large cluster, subsuming PCC and portions of the left and right occipital gyri, bilateral activations of BA 47/insular region, precuneus, the SFG and middle frontal gyrus, left MFG, two distinct clusters in inferior parietal gyrus, including SMG, anterior cingulate, and cerebellum.

2.2.1.3.2. Sentence minus probe. Cortical areas more active during the sentence phase included the left IFG (BA 47), fusiform gyrus, precuneus, SMA, portions of MTG and STG, and the MFG.

Two regions (left BA 47 and precuneus/PCC) were explored further by extracting the contrast estimates (beta-weights) for each participant. As shown in Figure 4, noun animacy and verbal telicity of the

Table 3. Brain activation clusters significantly different during sentence reading vs. probe response.

	Left hemisphere				Right hemisphere			
Anatomical region	BA	Cluster size	*t*-Value	Coordinates (*x, y, z*)	BA	Cluster size	*t*-Value	Coordinates (*x, y, z*)
Probe minus sentence								
Posterior cingulate/occipital gyrus					23/17/18	2,058	6.38	20, −72, −16
Posterior cerebellum						64	5.41	30, −72, −32
Precuneus	7	123	6.33	−8, −60, 48	7	58	6.33	2, −72, 44
Parahippocampal/fusiform gyrus	36/37	76	5.23	−30, −50, −10				
Inferior frontal gyrus/insula	47/13	63	5.30	−34, 14, −8	47/13	95	7.18	30, 16, −8
	13	635	9.59	−44, −6, 10	44/45	172	6.23	58, 20, 4
Superior frontal gyrus					6/8	66	5.68	4, 28, 60
Middle frontal gyrus	10	191	6.05	−28, 50, −4				
	9	338	5.98	−28, 14, 36				
Anterior cingulate	24	57	5.16	0, 10, 32				
Inferior parietal lobe	40	573	7.37	−58, −34, 38				
	40	298	7.72	−52, −58, 36				
Caudate						65	6.06	18, −8, 24
Sentence minus probe								
Postcentral/precentral gyri	3/4	431	6.07	−50, −14, 50,				
Supplementary motor area	6	111	6.23	−4, 2, 58				
Superior temporal gyrus	22	325	6.66	−44, −54, 14				
Middle temporal gyrus	21	83	5.35	−54, −12, −16				
Medial frontal gyrus	11	387	6.35	−2, 50, 14				

Notes: For each cluster, the peak location is given in MNI coordinates, accompanied by location in terms of BA and sulcal/gyral locus; *t*-values represent the peak voxel activation within each cluster. Clusters achieving $p < 0.001$, uncorrected, are reported and thresholded at $k = 14$ voxels (120 mm^3).

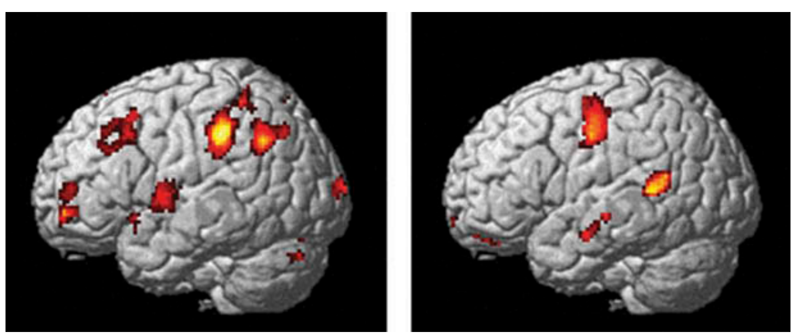

Figure 3. Activation maps. The left figure depicts the probe minus sentence contrast; the right figure depicts the sentence minus probe contrast. [To view this figure in color, please see the online version of this Journal.]

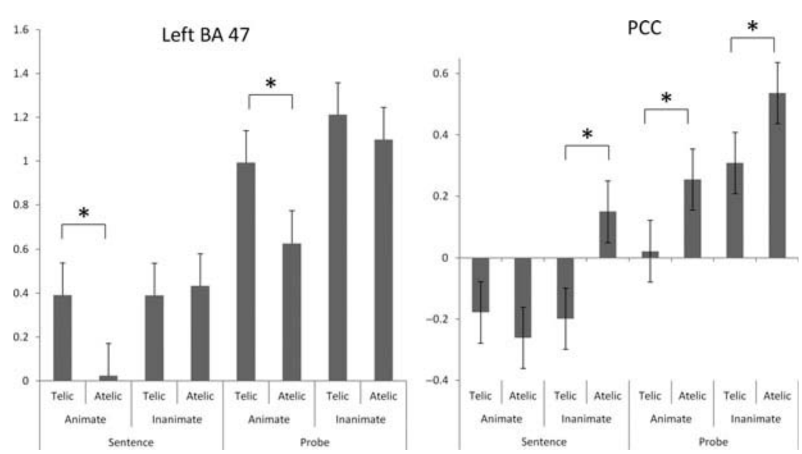

Figure 4. The bar graphs show the contrast estimates (β-weights), which demonstrate the differential response in the left BA 47 across conditions. Error bars denote standard error.

stimuli had different effects on these regions during the probe phase. The effect of telicity was observed in the animate condition in BA 47, showing increased activation. The effect of telicity was also present in the PCC in both animate and inanimate conditions in the form of decreased activation. In the PCC, inanimate first conditions showed an overall higher level of activation, as compared to animate conditions. The higher PCC activation for atelic conditions is consistent with the noted role of the PCC in the default network, whereby it is deactivation, rather than activation, that is indicative of stimulus response in this region.

3. Discussion

The aim of the current study was to investigate the neural bases of integration of syntactic analysis and event knowledge during reading. The results demonstrate that verbal event types and the argument's plausibility affect neural processing in distributed, partially overlapping networks both during online comprehension and during the probe (postprocessing). We discuss each aspect of the results in detail.

3.1. *Neural substrates of thematic role reanalysis*

The present results demonstrate that both sentence plausibility and verbal event type contribute to syntactic integration and thematic role reanalysis. The interaction of the two variables observed in BA 47 was due to the fact that the animate atelic condition elicited significantly less activation in the region, as compared to other conditions. Constructionist approaches to event structure (Ramchand, 2008b) suggest that telic verbs activate a richer event structure (see Figure 1a), likely requiring additional processing. Similarly, higher processing efforts are likely expended on the coercion of an inanimate (implausible) argument into the agent position during garden-path processing in RRCs (see Figure 1b). This interaction was observed in BA 45/47 and implicates it in thematic role assignment. These results agree with prior investigations of animacy hierarchy processing in the left IFG (Bornkessel, Zysset, Friederici, von Cramon, & Schlesewsky, 2005; Grewe et al., 2005), indicating a role of the IFG (as well as posterior superior temporal regions) in thematic role assignment. In the area supporting syntactic computation (BA 47), the response to the inanimate argument was that of higher processing load (in agreement with Kuperberg et al., 2008). Higher activation of the PCC by inanimate first sentences, however, indicated that they were less likely to trigger event segmentation. Verbal telicity appears to facilitate syntactic processing by activating a more complex syntactic representation in the WM and by priming the patient thematic role. Inanimate arguments are more likely to be assigned the patient role based on event knowledge. Thus, conditions with an inanimate first argument, and/or telic verb, require preassignment of WM resources for the expected patient argument. The reliance on both semantic and syntactic cues as they become available during reading might allow for the distribution of cognitive load for faster processing and more economical use of metabolic resources. Future studies correlating individual WM capacity and linguistic proficiency are needed to investigate this possibility.

3.2. *Memory effects during online syntactic comprehension and post hoc reanalysis*

Prior studies have demonstrated network-level processing differences between online sentence processing and post hoc syntactic analysis during response to probe questions (Meltzer & Braun, 2011; Newman et al., 2010). Specifically, Newman et al. (2010) suggested that sentence comprehension vs. probe processing involves different memory resources, with post hoc reanalysis involving temporal cortex and basal ganglia more extensively. In the present study, we observed extensive PCC, inferior parietal, superior temporal, and insular involvement in post hoc processing vs. sentence reading, indicating that offline processing likely relied on both working and episodic memory resources. The regions demonstrating significant activation in the present study have been previously linked to the WM system: the IPL is thought to be involved in phonological maintenance (Awh et al., 1996; Fiez, 1997; Newman & Twieg, 2001), while the posterior portion of the IFG in the anterior insula has also been linked to verbal rehearsal (Awh et al., 1996). Extensive activation of the PCC during post hoc processing might also be related to referencing of the situation schemas (constructed during the sentence reading phase) in episodic memory.

Lack of the predicted DLPFC activation in response to telic verbs suggests the possibility that the cognitive load and WM update during reading did not differ sufficiently during processing of relative clauses with telic vs. atelic verbs. Given the complexity of the stimuli, the variability between telic and atelic conditions was likely subsumed by variability of individual participant response, both in activation and in precise timing of peak load processing (cf. Malaia et al., 2009; Newman, Malaia, Seo, & Cheng, 2013).

Animacy and telicity also appeared to affect the extent of activation in online vs. post hoc processing. Online, animate (more semantically plausible) conditions evoked more extensive activation (including the SMG) than inanimate; this pattern was reversed during offline processing. The same was true for atelic stimuli – online, atelic stimuli also evoked more activation than telic stimuli. Prior studies have shown that when conflicting thematic role cues are present, online comprehension appears to rely on a more detailed syntactic parsing of sentences in the left IFG and STG (Friederici, Rüschemeyer, Hahne, & Fiebach, 2003; Pallier, Devauchelle, & Dehaene, 2011). The results of the present study suggest that extensive online processing might help create a richer representation of the sentence in WM, which is then easier to access during post hoc processing.

Although in the present study the number of participants was not sufficient for the analysis between correlations in WM capacity and neural activation, a study of a larger sample of participants reading complex sentences (Newman et al., 2013) indicated that WM capacity has a correlation with deactivation of the PCC/precuneus during sentence reading. As the PCC is a part of default-mode network (Raichle et al., 2001), the decrease in its activation relative to baseline likely indicates that high WMC readers have the executive resources to generate event representation during reading, using the PCC. PCC deactivation is observed due to readers engaging it within the event representation network, rather than within the default-mode network (Newman et al., 2013). WM capacity also correlated with BA 45 activation during the probe, likely due to the involvement of this region in postretrieval selection process (Nee & Brown, 2012).

3.3. *Relevance of findings to existing theories of sentence comprehension*

The representation of language processing as dynamically combining world knowledge and linguistic and extralinguistic incoming information, as recently attested in multiple studies (Bicknell et al., 2010; Ferretti, Kutas, & McRae, 2007; Hare, Tanenhaus, & McRae, 2007; Matsuki et al., 2011), requires the consideration of interaction between language processing and both WM and long-term memory. In the present study, we investigated the interaction of verbal event structure, linked to the retrieval of event schemas from episodic memory, and argument thematic plausibility, which affects online thematic role assignment. Prior studies have linked PCC deactivation to the retrieval of event schemata from episodic memory during real-world event segmentation (Zacks & Swallow, 2007) and language comprehension (Yarkoni et al., 2008). During sentence processing, only inanimate atelic stimuli elicited PCC activation. The gradient of PCC activation during probe response appears related to the effort involved in event boundary retrieval from the event schema (from the least effort in animate telic condition, to the maximal effort in an inanimate atelic condition).

Although our results did not show WM-related activation during processing of telic stimuli, atelic stimuli elicited activation of BA 46 during online processing. This region has previously been implicated in the manipulation of information already contained in WM (Fellinger, Gruber, Zauner, Freunberger, & Klimesch, 2012; Grodzinsky & Friederici, 2006). This indicates that a higher WM load is induced by sentence processing in the absence of a boundary. The presence of a telic verb in the sentence, on the other hand, appears to trigger event schema creation/recall, thereby reducing the WM load.[7] This picture of the interplay of neural activations is not easily reconcilable with linear accounts of interface processing, but rather it supports dynamic memory-based theories of sentence comprehension (Hare, Jones, Thomson, Kelly, & McRae, 2009; Jackendoff, 2007) and dynamic anticipatory processing of hierarchical sequential events using contextual control (Koechlin & Summerfield, 2007).

The role of BA 47 during comprehension of the present data has an alternative interpretation under constraint satisfaction theories (MacDonald, Pearlmutter, & Seidenberg, 1994; McRae, Spivey–Knowlton, & Tanenhaus, 1998). These theories suggest that multiple sentence interpretations are maintained in parallel, and the likelihood of each interpretation is calculated constantly using multiple cues (including animacy, etc.). Under this viewpoint, the observation that a combination of animate and atelic cues lead to a drastic decrease in BA 47 activation would suggest that the *combined* cue frequency (i.e., argument animacy as well as verbal telicity) is taken into account at each time. If the opposite was true – i.e., frequency counts underwent sequential filtering for each cue – then an inanimate subject should lead to decreased activation for low-frequency stimuli, which was not the case.

Overall, the subtle, but significant upregulation and downregulation of activity in the PCC and left IFG correlated with the telicity of the verbs and argument animacy in the sentences indicating formation of transient neural networks, which participate in the task of binding the semantic and syntactic information in memory. Newman et al. (2013) identified a semantic network, involving the MTG, anterior IFG, and IPL, and an event representation network comprising the PCC, BA 44/45, and IPL, both of which arise during different stages of reading in order to allow the reader to use long-term memory stores to generate an online representation of the meaning of the stimulus sentence. Transient increases in the coherence of activation within such networks of brain regions are the basis of binding information across linguistic modules (syntax and semantics) and of representing meaning in short-term memory.

4. Conclusion

The data in the present study demonstrate that verbal telicity facilitates online processing, likely triggering the reference to event schemas in episodic memory. The linguistic feature of telicity appears to act as the early computational trigger for the process of binding at the syntax–

semantics interface. Thus, the neurological evidence supports the nanosyntactic approaches to sentence and event structure computation (Ramchand, 2008b; Starke, 2010) and demonstrates a neurological implementation for the binding mechanism at the interface of semantics and syntax (Jackendoff, 2007; Malaia, 2014).

The present results indicate that processing of event and argument structure during sentence comprehension relies on integration of syntactic and event knowledge in a distributed network, including both language processing and working and episodic memory regions. It has been previously suggested that semantic and syntactic comprehension processes draw on a shared infrastructure of cortical resources (Keller, Carpenter, & Just, 2001); the present results extend this proposal by suggesting that episodic memory referencing mechanisms are used by the language-processing system in order to facilitate online processing.

Disclosure statement

No potential conflict of interest was reported by the authors.

Notes

1. Widely used tests for predicate telicity include modification with "in an hour"-type adverbials (Borik, 2006; Dowty, 1979; Verkuyl, 1972), conjunction test (Verkuyl, 1972), and progressive entailment test (Borik, 2006; De Swart, 1998; Dowty, 1979).
2. In English, telicity characterizes not the verb per se, but rather the verbal phrase (VP); for example, a lack of quantification of the object can render the VP atelic regardless of verb type (cf. *She ate the fish* (telic). vs. *She eats fish* (atelic).). In the present study, the sentence frames (object quantification, etc.) were consistent across all stimuli, such that the typical (telic or atelic) interpretation of the verb applied to the entire VP.
3. Arguments higher on the animacy hierarchy map onto the highest available thematic role.
4. Verbs of gradient change can describe partial attainment of the end-state, as in *The sun warmed the ground in April*, where only comparison with an initial state is implied, but not a specific end state (ground temperature).
5. Semelfactive verbs denote punctual events, such as "blink," or "knock."
6. Reciprocal verbs allow each of the arguments/participants to occupy the role of both agent and patient, e.g., *Jack and Jill married (each other).*
7. Prior research also suggests that individual WM capacity can influence the choice of processing strategy for object relative sentences (Malaia et al., 2009) and that the comprehension strategy chosen is correlated with PCC activation during sentence processing (Newman et al., 2013). The present study did not have enough participants to investigate the relationship between sentence processing strategy and WM capacity.

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Appendix. Stimulus sentences in each category.

Animate, telic
The witness seized by the agent was in danger.
The painter glimpsed by the visitor was very original.
The candidate abandoned by the panel had some drawbacks.
The mailman dispatched by the secretary arrived too late.
The lady found by the boy was quite unusual.
The defendant designated by the lawyer turned out unreliable.
The singer heard by the crowd was very popular.
The lawyer sent by the governor arrived too late.
The speaker proposed by the colleague satisfied all requirements.
The thief identified by the victim was in custody.
The specialist requested by the surgeon had finally arrived.
The contestant selected by the judge did not win.
The prisoner grabbed by the guard was closely watched.
The killer captured by the policeman scared the public.
The detective hired by the lawyer refused to comment.
The accountant rescued by the custodian was finally safe.
The programmer alerted by the supervisor launched system check.
The dancer joined by the host surprised the guests.
The author lost by the publisher became famous quickly.
The mother pinched by the toddler was very soft.
The racer caught by the competitor disappeared from view.
The secretary appointed by the boss impressed the customer.
The solider disarmed by the officer stayed in barracks.
The engineer tenured by the manager was very productive.
The producer struck by the musician stayed completely silent.
The client mentioned by the administrator was extremely successful.
The teenager injured by the mentor left good impression.
The doctor brought by the driver arrived on time.
The analyst audited by the consultant remained highly rated.
The journalist released by the editor arrived at night.

Inanimate, telic
The mansion seized by the agent was in danger.
The painting glimpsed by the visitor was very original.
The alternative abandoned by the panel had some drawbacks.
The letter dispatched by the secretary arrived too late.
The necklace found by the boy was quite unusual.
The data designated by the lawyer turned out unreliable.
The song heard by the crowd was very popular.
The package sent by the governor arrived too late.
The solution proposed by the colleague satisfied all requirements.
The jewelry identified by the victim was in custody.
The equipment requested by the surgeon had finally arrived.
The recipe selected by the judge did not win.
The gold grabbed by the guard was closely watched.
The evidence captured by the policeman scared the public.
The company hired by the lawyer refused to comment.
The money rescued by the custodian was finally safe.
The program alerted by the supervisor launched system check.
The performance joined by the host surprised the guests.
The short list lost by the publisher became famous quickly.
The toy pinched by the toddler was very soft.
The car caught by the competitor disappeared from view.
The deadline appointed by the boss impressed the customer.
The tank disarmed by the officer stayed in barracks.
The division tenured by the manager was very productive.
The string struck by the musician stayed completely silent.
The idea mentioned by the administrator was extremely successful.
The reputation injured by the mentor left good impression.
The parcel brought by the driver arrived on time.
The department audited by the consultant remained highly rated.
The bulletin released by the editor arrived at night.

(*continued*)

Appendix. (*Continued*).

Animate, atelic
The witness protected by the agent was in danger.
The painter ridiculed by the visitor was very original.
The candidate considered by the panel had some drawbacks.
The mailman accompanied by the secretary arrived too late.
The lady described by the boy was quite unusual.
The defendant examined by the lawyer turned out unreliable.
The singer supported by the crowd was very popular.
The lawyer escorted by the governor arrived too late.
The speaker embraced by the colleague satisfied all requirements.
The thief scrutinized by the victim was in custody.
The specialist hosted by the surgeon had finally arrived.
The contestant kept by the judge did not win.
The prisoner chaperoned by the guard was closely watched.
The killer tugged by the policeman scared the public.
The detective instructed by the lawyer refused to comment.
The accountant guarded by the custodian was finally safe.
The programmer employed by the supervisor launched system check.
The dancer ushered by the host surprised the guests.
The author dominated by the publisher became famous quickly.
The mother nuzzled by the toddler was very soft.
The racer followed by the competitor disappeared from view.
The secretary encouraged by the boss impressed the customer.
The solider inspected by the officer stayed in barracks.
The engineer counseled by the manager was very productive.
The producer pulled by the musician stayed completely silent.
The client entertained by the administrator was extremely successful.
The teenager fostered by the mentor left good impression.
The doctor ferried by the driver arrived on time.
The analyst advised by the consultant remained highly rated.
The journalist held by the editor arrived at night.

Inanimate, atelic
The mansion protected by the agent was in danger.
The painting ridiculed by the visitor was very original.
The alternative considered by the panel had some drawbacks.
The letter accompanied by the secretary arrived too late.
The necklace described by the boy was quite unusual.
The data examined by the lawyer turned out unreliable.
The song supported by the crowd was very popular.
The package escorted by the governor arrived too late.
The solution embraced by the colleague satisfied all requirements.
The jewelry scrutinized by the victim was in custody.
The equipment hosted by the surgeon had finally arrived.
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The reputation fostered by the mentor left good impression.
The parcel ferried by the driver arrived on time.
The department advised by the consultant remained highly rated.
The bulletin held by the editor arrived at night.