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Neural Correlates of Verb Argument Structure Processing

Cynthia K. Thompson, Borna Bonakdarpour, Stephen C. Fix, Henrike K. Blumenfeld, Todd B. Parrish, Darren R. Gitelman, and M.-Marsel Mesulam

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Abstract

■ Neuroimaging and lesion studies suggest that processing of word classes, such as verbs and nouns, is associated with distinct neural mechanisms. Such studies also suggest that subcategories within these broad word class categories are differentially processed in the brain. Within the class of verbs, argument structure provides one linguistic dimension that distinguishes among verb exemplars, with some requiring more complex argument structure entries than others. This study examined the neural instantiation of verbs by argument structure complexity: one-, two-, and three-argument verbs. Stimuli of each type, along with nouns and pseudowords, were presented for lexical decision using an event-related functional magnetic resonance imaging design. Results for 14 young normal participants indicated largely overlapping activation maps for verbs and nouns, with no areas of significant activation for verbs compared to nouns, or vice versa. Pseudowords also engaged neural tissue overlapping with that for both word classes, with more widespread activation noted in visual, motor, and peri-sylvian regions. Examination of verbs by argument structure revealed activation of the supramarginal and angular gyri, limited to the left hemisphere only when verbs with two obligatory arguments were compared to verbs with a single argument. However, bilateral activation was noted when both two- and three-argument verbs were compared to one-argument verbs. These findings suggest that posterior peri-sylvian regions are engaged for processing argument structure information associated with verbs, with increasing neural tissue in the inferior parietal region associated with increasing argument structure complexity. These findings are consistent with processing accounts, which suggest that these regions are crucial for semantic integration. ■

INTRODUCTION

Research examining word class processing and production suggests that the neural networks engaged for verbs differ from those of nouns. Neuropsychological studies show that patients with anterior brain damage and concomitant Broca's aphasia often evince greater difficulty producing verbs as compared to nouns, whereas those with posterior lesions and anomic aphasia show the opposite pattern (Arevalo et al., 2007; Daniele, Guistolisi, Silveri, Colosimo, & Gianotti, 1994; Damasio & Tranel, 1993; Zingeser & Berndt, 1990; Miceli, Silveri, Nocentini, & Caramazza, 1988; Miceli, Silveri, Villi, & Caramazza, 1984). Damasio and Tranel (1993), for example, reported Patient KJ, who showed a selective action naming deficit and concomitant left frontal (premotor) lesion, whereas Patient AN, who was impaired only for noun naming, evinced a left anterior temporal lobe lesion. Neuroimaging studies have largely supported these observations. In an early study using positron emission tomography (PET), Petersen, Fox, Posner, Mintun, and Raichle (1988) found left frontal activation in normal individuals when they performed a verb generation task, whereas several researchers have found posterior activation for noun naming, including animals, tools, and familiar faces (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin, Wiggs, Underleider, & Haxby, 1996). Shapiro, Pascual-Leone, Mottaghy, Gangitano, and Caramazza (2001) also showed that suppression of the left frontal lobe using repetitive transcranial magnetic stimulation (rTMS) induced selective delays in verb, but not noun, production. Finally, neurophysiological studies using event-related potentials (ERPs) (Khader, Scherag, Streb, & Rösler, 2003; Federmeier, Segal, Lambroza, & Kutas, 2000; Pulvermüller, Lutzenberger, & Preissl, 1999) have shown that verbs and nouns evoke distinct topographies. Federmeier et al. (2000) found that verbs in their syntactic context elicited a left-lateralized anterior positivity not observed for nouns. Khader and Rösler (2004) further showed stronger desynchronization for verbs at left frontal sites when compared to nouns. These data suggest that frontal lobe networks are crucial for verb production and processing.

Other studies, however, have reported patients with lesions extending to the frontal lobe with a sparing of verb

Northwestern University

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production (De Renzi & di Pellegrino, 1995), and patients with fluent aphasic syndromes and concomitant temporoparietal lesions have been shown to have verb production deficits (Silveri, Perri, & Cappa, 2003; Berndt, Mitchum, Haendiges, & Sandson, 1997; Kohn, Lorch, & Pearson, 1989; Williams & Canter, 1987). Further, several neuroimaging studies have noted posterior brain activation for verbs, under verb generation conditions (Yokoyama et al., 2006; Davis, Meunier, & Marslen-Wilson, 2004; Herholz et al., 1996; Warburton et al., 1996; Wise et al., 1991) as well as during verb recognition tasks (Grossman et al., 2002; Perani et al., 1999). Still, other studies have found no differences in activation patterns for verbs versus nouns (Tyler, Russell, Fadili, & Moss, 2001). Tyler et al. (2001), in a PET experiment, found that both word classes activated the left inferior frontal and left inferior temporal gyri.

These mixed findings are likely related to a number of factors. Patient studies are inconclusive due to heterogeneity in lesion location. Further, these studies, as well as those which ''simulate'' lesions as in rTMS, only show that the lesioned brain sites are involved in and are capable of disrupting the language process under study. They do not fully elucidate the neural networks that underlie verb processing. PET and functional magnetic resonance imaging (fMRI) studies are more capable of revealing the interworkings of the language network. However, these studies have varied greatly in technical detail as well as in the psycholinguistic tasks used. Some have required verb production, as in verb generation (Warburton et al., 1996; Petersen et al., 1988), whereas others have examined verb processing using judgment paradigms, including lexical decision and semantic judgment. Grossman et al. (2002) used a semantic judgment task in which subjects had to decide whether the noun or the verb presented was ''pleasant'' or not. In contrast, Tyler et al. (2001) used both a lexical decision and a semantic categorization task. In the latter, subjects had to decide whether the fourth word in a series of four words presented one after another belonged to the same category as the first three words. Clearly, task-related differences may contribute to the lack of consistent findings across studies.

Differences in technical factors also may underlie the lack of consistent results. Studies are different, for example, in terms of how they control for statistical errors. Some studies report data that are not corrected for multiple comparisons (Perani et al. 1999). Some uncorrected activation may not appear in the final results when statistical maps are thresholded using corrections for multiple comparisons via such methods as the false discovery rate (FDR; Genovese, Lazar, & Nichols, 2002; Benjamini & Hochberg, 1995). Neuroimaging studies also have varied in the stimuli used. Tyler et al. (2001) suggested that some discrepancies across studies of word class processing may be related to inadequate control of lexical parameters such as word length, frequency, familiarity, and imageability of stimuli. The extent to which these factors have been considered in studies examining the neural instantiation of verbs and nouns is unclear. Many studies have not included this information in published reports (e.g., Grossman et al., 2002), and few have provided a list of stimuli used so that the influence of these factors on the results reported can be evaluated. Indeed, it is well known that these factors influence lexical retrieval in both normal and language-impaired individuals (Giesbrecht, Camblin, & Swaab, 2004; Kemmerer & Tranel, 2000; Wise et al., 2000; Fiez, Balota, Raichle, & Petersen, 1999; Paivio, Yuille, & Madigan, 1968). In addition, recent work has shown that verb processing is influenced by the argument structure properties, or participant roles, of verbs, which vary across verbs in terms of the number and type of arguments that they require (Levin & Rappaport Hovav, 1995; Grimshaw, 1990). For example, intransitive verbs such as *sleep* take only one argument as in: The $\text{boy}_{\text{AGENT}}$ *sleeps*. Other verbs take two arguments (e.g., the transitive verb *chase*, which requires two participants—agent and theme—as in: The $\text{boy}_{\text{AGENT}}$ *chased* the $\text{girl}_{\text{THEME}}$) and still other verbs take three arguments (e.g., the verb *put*: The $\text{boy}_{\text{AGENT}}$ *put* the $\text{book}_{\text{THEME}}$ on the $\text{shelf}_{\text{GOAL}}$).

A large range of empirical studies has demonstrated that when a particular verb is accessed for either production or comprehension, so too are its argument structure properties. For example, verb argument structure affects real-time processing of sentences in both normal and Broca's aphasic individuals (e.g., Shapiro, Gordon, Hack, & Killackey, 1993; Trueswell, Tanenhaus, & Kello, 1993; Shapiro, Brookins, Gordon, & Nagel, 1991; Shapiro & Levine, 1990; see also MacDonald, Pearlmutter, & Seidenberg, 1995), that is, all possible verb arguments are accessed in the immediate temporal vicinity of the verb during on-line sentence processing. Interestingly, Wernicke's aphasic patients with posterior brain damage do not display this performance pattern, suggesting that posterior brain sites are crucial for processing verb argument structure information.

With regard to production, several studies with Broca's aphasic patients have shown that verb production becomes more difficult as the number of arguments entailed by the verb's representation increases. This has been shown in English and across languages, including Dutch, German, Italian, and Hungarian (Kim & Thompson, 2000, 2004; De Bleser & Kauschke, 2003; Luzzatti et al., 2002; Kemmerer & Tranel, 2000; Kiss, 2000; Jonkers & Bastiaanse, 1996, 1998; Thompson, Lange, Schneider, & Shapiro, 1997; Kegl, 1995); three-argument verbs are more difficult to produce than two- or one-argument verbs and when these verbs are produced in sentence contexts, obligatory arguments often are omitted. Further, verbs with even greater argument structure complexity, namely, complement verbs such as *know*, which entail a sentential complement in their representation, present difficulty for Broca's aphasic patients

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(Thompson et al., 1997), and intransitive unaccusative verbs such as *melt*, and *amuse*-type psychological (psych) verbs, which involve complex syntactic and/or semantic computations, are more difficult to produce than intransitive unergatives such as *sleep*, and *admire*-type psych verbs which do not (Bastiaanse & van Zonneveld, 2005; Lee & Thompson, 2004; Thompson, 2003).

Few neuroimaging studies have examined verbs by type. Perani et al. (1999) studied action verbs associated with objects such as *cut*, and mental state verbs such as *believe* in a PET study, finding that both verb types (compared to nouns) activated the dorsolateral frontal and lateral temporal cortices. Grossman et al. (2002), studying similar verbs, found a different pattern. Action verbs such as *crawl* engendered greater frontal lobe activity than cognition verbs, such as *think* and *speculate*, which were associated with left posterolateral temporal activation. Neither of these studies, however, controlled the verb stimuli for argument structure properties. As discussed above, action verbs can entail one or more argument, (e.g., *crawl* is a simple one-argument verb; *cut* is an obligatory two-argument verb) and verbs such as *believe* and *think* are complement verbs, which select for either a predicate NP or complement clause (e.g., *I believe the story*, *I believe that he told a true story*). Thus, it is possible that the posterior activation found for mental state/cognition verbs reflected argument structure complexity rather than other verb properties. Unfortunately, this interpretation is not possible to confirm because stimulus lists were not included in these papers. Notably, a recent study by Ben-Shachar, Hendler, Kahn, Ben-Bashat, and Grodzinsky (2003) showed increased bilateral superior temporal sulcus (STS) activation as a function of verb argument structure complexity. However, verbs by type were not directly compared with one another. Rather, sentences containing verbs with additively greater numbers of arguments contained within matrix and embedded clauses were examined (i.e., sentences with three- vs. two-argument verbs in the matrix clause [*tell* vs. *help*] and two- vs. one-argument verbs in the embedded clause [*see* vs. *run*] were compared).

The purpose of this study was to investigate the neural correlates of verbs controlled for their argument structure properties, namely, one-, two-, and three-argument verbs, in young normal individuals using a lexical decision task. We also compared activation patterns of verbs to those of nouns. Stimuli from both word classes were carefully controlled for frequency of occurrence, familiarity, imageability, and word length. We hypothesized that posterior brain regions play an important role in processing of argument structure information associated with verbs. Thus, verbs with greater argument structure density, as compared to those of lesser density, would engender greater posterior peri-sylvian activation.

METHODS

Participants

Participants included 17 young, healthy volunteers (8 women), ages 18–27 years (M = 22). All were right-handed, based on the Edinburgh Handedness Inventory (Oldfield, 1971), with no familial left-handedness. English was the first and only language known by the participants, and the mean duration of their formal education was 16.3 years (range = 13–21 years). None of the subjects had a history of neurological/psychological disease or neurologic symptoms. Subjects signed written informed consent approved by the Institutional Review Board at Northwestern University.

Stimuli

A set of 120 written (lowercase) verbs (40 intransitive [one-argument], 40 transitive [two-argument], and 40 ditransitive [three-argument]) and 80 nouns (40 animals and 40 tools) served as experimental stimuli.[1] An additional set of 50 pseudowords was selected. Pseudowords were created by breaking one- and-two syllable words within a comparable frequency range into two pronounceable segments, and randomly recombining these segments. Any items ending in graphemes that signal grammatical morphemes for verbs or nouns (e.g., *-s*, *-ed*, *-t*, *-ing*) were eliminated on the basis of ratings from 10 monolingual English speakers. This resulted in a total of 250 stimuli (words and pseudowords). Noun and verb stimuli were matched for number of syllables (one to two syllables) and frequency of occurrence (M verb frequency = 9.5/million; SD = 16.0; M noun frequency = 9.2/million; SD = 12.9), using the CELEX lexical database (Baayen, Piepenbrock, & van Rijn, 1993) (see Table 1). In general, noun/verb homographs were avoided (e.g., *hammer*), but when used, selected verbs had a noun usage less than 25% of their total frequency and selected nouns had a verb usage of less than 25% of their total

Table 1. Frequency (Occurrences per Million in the CELEX Lexical Database) and Imageability Ratings (Based on the MRC Database) for Stimuli by Class

	Total Number	*M Frequency (SD)*	*M Imageability Score (SD)*
One-place verbs	40	9.5 (15.5)	416.6 (128.8)*
Two-place verbs	40	9.3 (15.7)	363.9 (130.2)*
Three-place verbs	40	9.7 (17.1)	341.3 (107.3)*
Total verbs	120	9.5 (16.0)	375.5 (125.8)**
Total nouns	80	9.2 (12.9)	613.4 (44.4)**
Pseudowords	50	–	–

*p = .025.

**p < .001.

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frequency (see Appendix I for a complete list of stimuli and their verb/noun usage frequencies).

Imageability ratings also were obtained using the MRC psycholinguistic database (www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). Seventy stimuli were not included in the MRC database. We therefore collected imageability ratings for these words using a questionnaire identical to that used by Paivio et al. (1968), from 10 English monolingual participants. Twenty-eight (40%) additional words found in the MRC database were included in this questionnaire, and high similarity was established between these two sets [Pearson's $r = .86$, $p < .001$; $t(55) = 1.59$, $p = .116$], suggesting that the MRC ratings and our collected ratings were highly comparable. The resulting imageability ratings for verbs were $M = 376$ ($SD = 126$) and for nouns were $M = 613$ ($SD = 44$) (see Table 1). Statistical analysis using the Wilcoxon signed ranks test[2] indicated no significant differences between verb and noun stimuli with regard to frequency ($T^+ = 1111.0$, $p = .23$); however, the noun stimuli were significantly more imageable than the verbs [$t(59) = 19.8$, $p < .001$].

Verbs were selected for their argument structure status using the Brandeis Verb Lexicon (Grimshaw & Jackendoff, 1981). In addition, we developed explicit criteria for classifying verbs (see Appendix II) and eight neurolinguists independently ranked each verb by type, with only verbs agreed upon by at least seven of the eight judges included.

Verbs of each type were matched for frequency (M frequency of one-argument verbs = 9.5/million; two-argument verbs = 9.3/million, and three-argument verbs = 9.7/million) and imageability (M imageability for one-argument verbs = 418.3, $SD = 148.5$; two-argument verbs = 354.4, $SD = 137.9$; three-argument verbs = 341, $SD = 107$). There were no significant differences between verbs by type with regard to frequency [Kruskal–Wallis one-way ANOVA: $\chi^2(2, n = 120) = 3.9$, $p = .14$] or imageability [one-way ANOVA: $F(2, 83) = 2.8$, $p = .067$].

Finally, verbs with one and two obligatory arguments were tested for reaction time (RT) using a lexical decision task with presentation by SuperLab (Cedrus, version 2.0, Phoenix, AZ) to 10 young unimpaired participants (4 men, ages 20–35 years). Participants showed faster RT for one-argument than for two-argument verbs [one-argument, $M = 599.6$ ($SD = 60.7$); two-argument, $M = 604.9$ ($SD = 59.2$)], although this difference was not statistically reliable (Wilcoxon signed rank test; $T^+ = 30$, $p = .070$).

Design and Procedures

An event-related design was used with stimuli divided into two runs, each including 125 target stimuli. A pseudo-randomized sequence was generated using the OPTSEQ program (http://surfer.nmr.mgh.harvard.edu/optseq). Words and pseudowords were visually displayed for 1200 msec followed by a 500-msec blank screen (interstimulus interval). Null events, consisting only of a fixation cross and lasting either 1700 msec or 3400 msec each, constituted 40% of the total time of each run. Stimulus runs were prepared and presented to the subjects using SuperLab on a Compaq Pentium 4 computer with visual stimuli projected by an ELP Link IV Epson projector onto a custom-designed, nonmagnetic rear-projection screen.

Participants were trained in a preparatory session using a simulated scanner located in the Aphasia and Neurolinguistics Research Laboratory at Northwestern University. Scripts similar, but not identical, to those used during scanning sessions were used. This served to familiarize subjects with the task and to screen for individuals with claustrophobia.

A 3-T Trio Siemens scanner was used to obtain both anatomical (T1-weighted) and functional scans (T2*-weighted), obtained in transaxial planes parallel to the AC–PC line. T1-weighted 3-D volumes were acquired using an MP-RAGE sequence with a TR/TE of 2100 msec/2.4 msec, flip angle of 8°, TI of 1100 msec, matrix size of 256 mm × 256 mm; FOV of 22 cm, and slice thickness of 1 mm. Functional scans were obtained in the same orientation as the anatomical scans, with a TR of 2000 msec used to acquire 32 slices 3 mm in thickness. Participants' heads were immobilized using a vacuum pillow (Vac-Fix, Bionix, Toledo, OH) with restraint calipers built into the head coil. Participants were provided with a nonmagnetic button press device which enabled recording of responses. Prior to scanning, participants were instructed to respond to visually presented letter strings by pressing one button for words and another for nonwords. Response latencies and accuracy were recorded.

Data Analysis

fMRI data were analyzed using SPM2 (Wellcome Department of Imaging Neuroscience, Institute for Neurology, University College London) running in a Matlab 6.5 environment (The MathWorks, Natick, MA). Functional scans were corrected for slice-acquisition timing and were realigned to a mean functional image. The anatomical volume was coregistered to the mean image and normalized to the MNI 152-subject template brain (ICBM, NIH P-20 project). The functional volumes were then normalized using the same transformation and were smoothed using a 10-mm (FWHM) isotropic kernel. Effects of global signal were removed from the functional time-series using the method described by Macey, Macey, Kumar, and Harper (2004).

In first-level analysis, a high-pass filter of 256 sec was used to eliminate scanner drift. Conditions were modeled separately for one-place verbs, two-place verbs, three-place verbs, animals, tools, and pseudowords. For each contrast of interest, a summary activation map for

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each participant was entered into a second-level analysis. All second-level (random effects) statistics were thresholded at a voxelwise threshold of $p < .05$, corrected for multiple comparisons per FDR (Genovese et al., 2002; Benjamini & Hochberg, 1995), a correction ensuring that, on average, no more than 5% of activated voxels in each contrast were false positives. A three-voxel extent threshold was also used.

Resulting stereotactic coordinates, in MNI space, were transformed into Talairach space using a script written by Matthew Brett (www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml). Using these coordinates, the second and third authors independently determined corresponding areas of significant activation using the Talairach and Tournoux (1988) atlas. Disagreements were resolved by the first author.

RESULTS

Of 17 participants scanned, two showed excessive movement during one or more runs (defined as sudden movement greater than 0.5 mm without an immediate return to the prior position, as indicated by the SPM2 realignment output graph), and one participant failed to respond to any stimuli. Data from these participants were eliminated, leaving 14 participants for whom we report results.

Behavioral Data

Mean RTs for nouns, verbs, and verbs by argument structure are displayed in Table 2. The Wilcoxon signed-rank test showed only nearly significant RT differences between verbs ($M = 597.2$, $SD = 65.8$) and nouns ($M = 588.2$, $SD = 55.1$; $T^+ = 36$, $p = .055$). However, within the verb conditions, a Friedman ANOVA by ranks showed significant RT differences due to argument structure [$Fr(2, n = 9) = 13.6$, $p = .001$]. Follow-up pairwise tests with Bonferroni correction showed no significant difference between two- and three-argument verbs ($T^+ = 20$, $p = .77$). However, the RTs for one-argument verbs were significantly longer than those for two- and three-argument verbs ($T^+ = 45$, $p = .008$, in both cases).

Table 2. Behavioral (RT) Data for Stimuli by Type

Stimulus Type	*Mean RT, msec (SD)*
One-argument verbs	642.6 (59.5)
Two-argument verbs	598.8 (68.8)
Three-argument verbs	596.5 (63.6)
All verbs	597.2 (65.8)
All nouns	588.2 (55.1)

Main Effects

Main effects for pseudowords as compared to all real word stimuli (i.e., nouns and verbs) showed significant activation in the left and right fusiform gyri (BA 19, 37), postcentral gyri (BA 1, 2), inferior frontal (IFG; BA 44, 45), middle frontal gyri (MFG; BA 6), and cingulate gyrus (BA 32). In addition, for pseudowords, significant left hemisphere activation was seen in the following regions: the superior temporal sulcus (STS; BA 22), middle temporal sulcus (MTS; BA 37), the inferior parietal lobule (IPL; BA 40), and the cerebellum (see Figure 1 and Table 3).

The main effects for real words, both nouns and verbs, as compared to cross-fixation, are shown in Table 4 (also see Figure 2). These data indicated significant bilateral activation in occipital and fusiform regions (BA 17, 18, 19, 37), the precentral gyri (BA 6, 4), and the middle frontal gyri (MFG, BA 6 and 9). However, activation of the insula was limited to the left side for both nouns and verbs. Notably, activation in the left inferior frontal gyrus (IFG, BA 44) and central sulcus was significant for verbs, but not nouns, and that in the right IFG (BA 45 and 47) and central sulcus was significant for noun, but not verb, processing.

In the temporo-parietal region, significant activation for both nouns and verbs was seen in the right superior

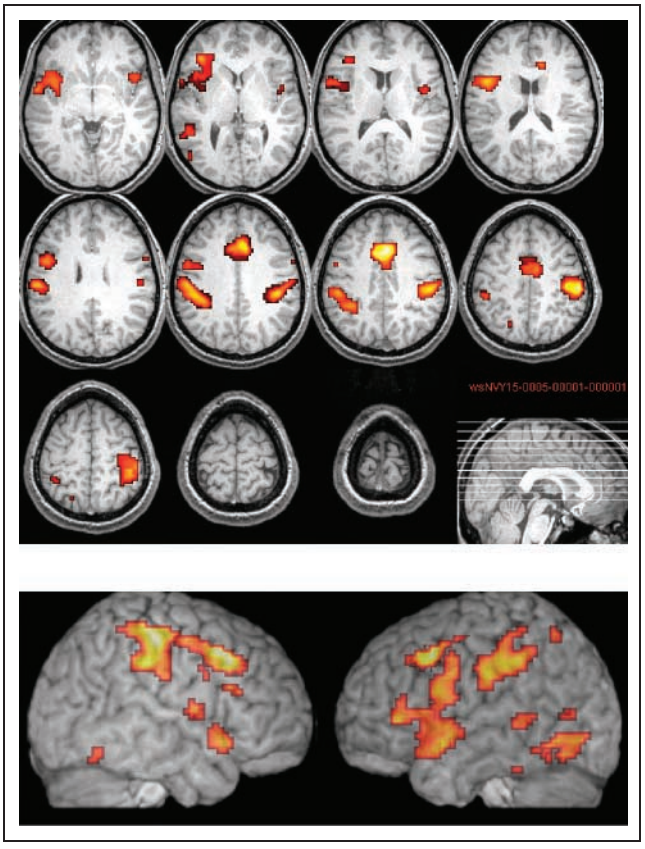

Figure 1. Activation for pseudowords minus all words. Activation is significant at a voxelwise significance level of $p < .05$ (corrected for multiple comparisons per false discovery rate) and a three-voxel extent threshold.

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Table 3. Regions of Significant Activation for All Pseudowords Minus Words

			Sterotactic Coordinates		
Location	*BA*	*Side*	*x*	*y*	*z*
IFG	44	L	−45	10	19
		R	59	7	30
	45	L	−39	32	1
MFG	6	L	−45	2	30
		R	45	0	8
Postcentral gyrus	1	L	−53	−19	31
		R	53	−21	51
		R	42	−21	51
	2	R	48	−26	57
IPL	40	L	−36	−36	38
		L	−45	−30	37
STS	21/22	L	−53	5	−10
		L	−48	−41	5
MTG		L	−56	−49	8
MTS	37	L	−50	−69	9
Cingulate	32	L	−9	14	41
		R	3	17	41
		R	9	22	35
	24/33	R	12	21	21
Fusiform	19/37	L	−39	−64	−4
		L	−48	−68	−12
	37	R	48	−62	−12
Cerebellum		L	−12	−56	−10
		L	−18	−59	−15
		L	−33	−42	−21

temporal gyrus (STG, BA 22), whereas the middle temporal gyrus (MTG, BA 37) was active only in the left hemisphere and only for verbs. In addition, the inferior parietal and superior parietal regions (IPL, BA 40, and SPL, BA 7, respectively) were engaged for both word classes, bilaterally in the IPL, but only in the left SPL. Activation also was noted in subcortical regions, including the caudate nucleus and red nucleus for verbs (right and left hemispheres, respectively), and the globus pallidus, putamen, and substantia nigra for nouns (left hemisphere only). Thalamic nuclei also were significantly activated in the right hemisphere: the medial dorsal nucleus for verbs and the ventral lateral nucleus for nouns.

Despite these main effects and the small clusters of significant activity in the left IFG, central sulcus, and MTG seen for verbs, but not for nouns, direct comparison of the activation maps for the two word classes revealed no areas of significant activation. This was seen when verb maps were compared to that of nouns and also when noun maps were compared to that of verbs.

Verbs by Argument Structure

Comparison of activation maps for two-argument as compared to one-argument verbs showed no individual voxel that survived a whole-brain FDR correction at the chosen level of $p < .05$. Follow-up analyses were thus undertaken to examine for significant clusters using a voxelwise threshold of $p < .001$ (uncorrected for multiple comparisons) and a clusterwise threshold of $p < .05$, corrected for multiple comparisons via the theory of Gaussian random fields (cf. Aron et al., 2004). Such cluster-level correction is sensitive to different aspects of activation than the voxel-level FDR correction (i.e., larger clusters with lower peak activation; Friston, Holmes, Poline, Price, & Frith, 1996). A cluster of 67 voxels in the left angular and supramarginal gyri (BA 39, 40), with a maximum located at [−42, −52, 30] in Talairach space, was significant at the cluster level at $p < .05$, corrected for multiple comparisons (shown in blue/green in Figure 3). Further analysis of two-argument plus three-argument verbs compared to one-argument verbs showed a significant ($p < .05$, corrected for multiple comparisons) activation cluster of 78 voxels in the left angular and supramarginal gyri and a cluster of 45 voxels in the right angular and supramarginal gyri (shown in yellow/red in Figure 3). The right hemisphere activation was significant at the voxel level ($p < .001$), but at the cluster level it was not when corrected for multiple comparisons ($p = .1$).

DISCUSSION

The word processing network found in the present study is similar to that found in previous lexical decision studies (Davis et al., 2004; Tyler et al., 2001; Price, Indefrey, & van Turennout, 1999; Price, Moore, & Frackowiak, 1996). Words (both nouns and verbs) as compared to baseline cross fixation recruited overlapping neural tissue in both the left and right hemispheres, including primary visual, visual association, and fusiform areas, as well as primary sensory and motor regions. In addition, peri-sylvian regions were engaged, including the STG and STS, inferior parietal regions, and IFG. This network likely reflects early visual word processing, consistent with converging evidence that printed words engage a ventral circuit, including lateral striate and extrastriate areas (Fiez & Petersen, 1998; Frackowiak, Friston, Frith, Dolan, & Mazziotta, 1997, and others). In addition, exposure to real-word stimuli automatically invokes phonological as well as semantic processes, regardless of their grammatical or semantic class

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Table 4. Main Effects for Verbs and Nouns Compared to Cross Fixation

		Stereotactic Coordinates							
		Verb Activation				*Noun Activation*			
Location	*BA*	*Side*	*x*	*y*	*z*	*Side*	*x*	*y*	*z*
Inferior frontal gyrus	44	L	−56	7	30	R	33	20	2
	45					R	42	24	21
	47					R	33	23	−9
Central sulcus	3/4	L	−59	−16	37	R	45	−15	45
Insula		L	−30	18	5	L	−30	15	5
		L	−42	−2	8	L	−42	−5	9
Precentral gyrus	6	R	56	2	39	L	−48	3	5
		R	62	4	25	L	−50	−7	39
						L	−56	4	27
						R	36	19	27
	6/4	L	−53	−7	42				
	4					R	42	−12	53
Middle frontal gyrus	6	L	−6	5	47	L	−6	5	47
		R	6	8	47				
		R	39	−3	50				
	9					R	36	19	27
Superior temporal gyrus	22	R	53	−26	7	R	53	−34	16
	42	R	65	−23	15				
Middle temporal gyrus	37	L	−39	−61	9				
Inferior parietal lobule	40	L	−45	−33	46	L	−42	−36	40
		R	39	−41	49	L	−39	−41	52
		R	56	−20	18	L	−33	−47	52
						R	30	−65	39
Superior parietal lobule	7	L	−30	−53	52	L	−27	−68	31
						L	−30	−53	55
Cingulate gyrus	24					L	−9	7	30
Inferior occipital gyrus	17	R	15	−96	2	L	−39	−79	−11
						R	27	−90	−1
Middle occipital gyrus	18	L	−24	−90	2	L	−21	−93	2
	18	L	−27	−78	18	R	18	−96	5
Fusiform gyrus	19/37	L	−30	−73	−11	L	−36	−48	−20
		L	−39	−71	−14	R	30	−42	−18
		R	33	−82	−9				
		R	45	−74	−14				
Subcortical caudate		R	6	9	11				
		R	6	15	2				
Globus pallidus						L	−18	0	−5
Putamen						L	−27	3	−5
Substantia nigra						L	−6	−24	−9
Red nucleus		L	−3	−24	−4				
Thalamic nuclei		R (MD)	12	−17	9	R (VL)	12	−14	3

Thalamic nuclei: MD = medial dorsal; VL = ventral lateral.

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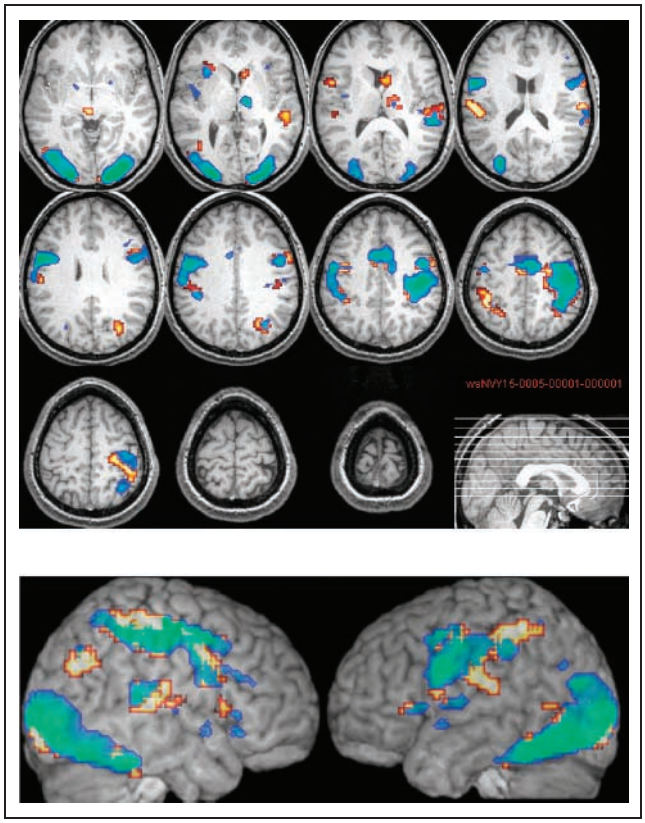

Figure 2. Activation for all nouns and all verbs compared to baseline cross fixation. All nouns = blue, all verbs = yellow, overlap = green. Activation is significant at a voxelwise significance level of $p < .05$ (corrected for multiple comparisons per false discovery rate) and a three-voxel extent threshold.

(Tyler et al., 2001; Perani et al., 1999; Price, 1998). Motor and somatosensory systems also are required for word processing, for instance, for internal preparation to articulate words and perform the required button press response (Ramsay et al., 1993).

Activation for pseudowords also showed a widely distributed network which, in some areas, was more widespread than that for real words (i.e., in bilateral peri-sylvian regions as well as the cingulate gyrus). In addition, more extensive activation in visual and motor regions was noted. These findings are consistent with previous research, indicating that activation, beyond that essential for real words, is engaged for pseudoword processing, reflecting a more exhaustive lexical search as well as grapheme-to-phoneme conversion and ''no'' response generation (Xiao et al., 2005; Brunswick, McCrory, Price, Frith, & Frith, 1999; Hagoort, Brown, Indefrey, et al., 1999; Fiez & Petersen, 1998; Price, 1998; Herbster, Mintun, Nebes, & Becker, 1997; Price, Wise, & Frackowiak, 1996).

Direct comparison of our verb and noun activation maps, however, showed no regions of significant difference. This finding is in keeping with that of others. Li, Jin, and Tan (2004) and Tyler et al. (2001) found overlapping activation maps for the two word classes in English- and Chinese-speaking participants, respectively. Notably, however, we found small clusters of activation in the IFG, central sulcus, and MTL for verbs that were not seen for nouns. This result is similar to that derived by Perani et al., who also used a lexical decision task and found significant activation for verbs, but not nouns, in the IFG (BA 45 and 46) as well as posterior regions, including the MTG and SPL.

The major purpose of this study was to examine the activation patterns derived for verbs with different argument structure. Results showed that processing of two-argument verbs (i.e., transitives) compared to one-argument verbs (i.e., intransitives) was associated with activation in the IPL, including both angular and supramarginal gyri. Notably, this same heteromodal region was engaged when two- and three-argument verbs were compared to one-argument verbs; however, this analysis showed even greater left, as well as right, hemisphere activation. These subtle effects indicate that posterior brain regions are involved in verb processing and that the neural tissue required to process verbs increases as a function of argument structure complexity. Verbs with less complex argument structure do not rely as heavily on posterior brain regions. Only when argument structure complexity increases is engagement of the posterior network required.

Posterior peri-sylvian regions have been associated with verb processing in previous neuroimaging studies. For example, Ben-Shachar et al. (2003) found significant activation in the STS and Hadar, Palti, and Hendler (2002) reported STS and MTG activation associated with verbs. These regions as well as the inferior parietal region, in and around Wernicke's area (BA 22), are well known to be part of the neural network for language (Mesulam, 1990). The subtle differences across studies in activation patterns noted within this region likely reflect, at least in part, distinctions in the experimental tasks utilized to examine verb processing. Some researchers have asked participants to listen to and respond to sentences, whereas others have used semantically based tasks (Davis et al., 2004; Hadar et al., 2002). Thus, it is not surprising that the lexical decision task used in the present study yielded somewhat different areas of activation. In addition, although previous authors have attributed recruit-

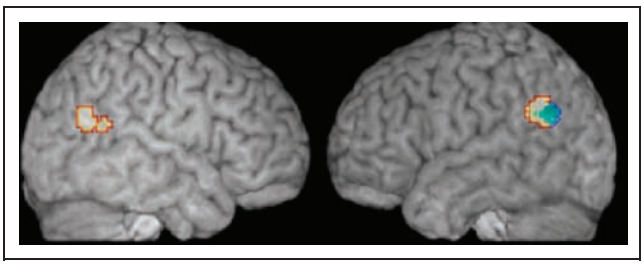

Figure 3. Activation for two-argument verbs minus one-argument verbs (blue); activation for two-argument and three-argument verbs compared to one-argument verbs (yellow).

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ment of posterior regions to processing syntactic aspects of verbs, verb argument structure complexity was not explicitly tested in these studies.

Recruitment of the posterior language network for verb argument structure processing is also in line with models of language processing (Hagoort, 2003; Levelt 1999; Bock & Levelt, 1994; Roelofs, 1992, 1993). Such models suggest that entries in the mental lexicon are associated with syntactic properties, such as grammatical class and, in the case of verbs, syntactically relevant subcategorization frames. In turn, these syntactic properties trigger argument structure assignment and phrase structure-building operations (i.e., generation of a hierarchically organized constituent structure).

Theoretical accounts of phrase structure building suggest that verb arguments guide this process. In the *Minimalist Program*, a syntactic operation, *Merge*, serves to amalgamate two categories to yield a higher-order category, and a series of Merge operations builds the syntactic structure of sentences (Chomsky, 1995, 1998; Marantz, 1995; see also Adger, 2003). Simply put, a lexical item (e.g., a verb) is selected from the lexicon and combines with other selected item to form a higher-order category. Thus, for example, the two-argument verb *chase*, subcategorized for two NPs, assigns the role of agent to the subject NP and theme is assigned to the direct object NP. Figure 4 demonstrates how this occurs in a sentence such as *The dog chased the cat*. V merges with a determiner phrase (DP) to yield V′ and the role of theme is assigned to the direct object argument, *the cat*. V′ then merges with another DP to form a verb phrase (VP), and the role of agent is assigned to the subject, *the dog*. The VP then merges with higher nodes in the syntactic tree. The number of arguments selected by the verb affects phrase structure operations: The greater the number of arguments, the more steps required to build phrase structural frames (see Lee & Thompson, 2004 for further discussion of phrase structure building operations).

We propose that anterior regions of the language network (i.e., inferior frontal gyri) are crucial for generation of structural frames associated with incoming lexical material, but that posterior regions are engaged for subsequent semantic processes (i.e., integration of syntactic and semantic information). For verbs, frontal lobe regions are involved in selecting a syntactic frame on the basis of subcategorization and selection restrictions imposed by the verb's argument structure, which in turn triggers posterior regions for integration of lexical material that satisfies these argument structure requirements. We recognize that this proposal implies a temporal relation between anterior and posterior neural tissue and that standard analysis of fMRI data does not elucidate connections between regions or "activated pathways." Further analysis of our findings using dynamic causal modeling to examine effective connectivity between these brain regions under different verb conditions may help to clarify this issue (Penny, Stephan, Mechelli, & Friston, 2004; Friston, Harrison, & Penny, 2003). However, we point out that this postulate is supported by neurophysiological (ERP) studies, indicating that syntactic structure building precedes semantic processes (Friederici, 2002). Some studies have noted left anterior negativity (LAN) and early late anterior negativity (ELAN), occurring between 100 and 500 msec, following violations of word-category constraints. Such effects have been interpreted to be syntactic in nature, functionally related to generating a syntactic structure for incoming words (Friederici, Hahne, & Mecklinger, 1996; Friederici, 1995). The electrophysiological outcome of semantic processes is a negative wave (i.e., the N400), occurring 400 msec following errors of semantic integration. Although ERP effects are not anatomically precise in that any language-related effect is associated with generators in a number of brain areas, the N400 is often largest over posterior scalp sites (Hagoort, Brown, & Osterhout, 1999). These data are in line with our findings—generating phrase structure is accomplished by anterior brain regions in association with the syntactic properties of the verb retrieved. However, satisfying the argument structure requirements of the generated structural frame engages posterior peri-sylvian areas. Verbs with greater argument structure density, therefore, require greater recruitment of posterior portions of the language network.

Patient studies provide another line of evidence. In several studies, Wernicke's aphasic subjects with posterior peri-sylvian lesions have demonstrated an inability to process aspects of argument structure information. McCann and Edwards (2002), for example, found that patients with Wernicke's aphasia did not detect argument structure violations (e.g., *John gives a car*), an ability that is spared in Broca's aphasic patients with anterior lesions (Kim & Thompson, 2000). Shapiro and Levine (1990) also found that during on-line sentence processing, Wernicke's (but not Broca's) patients showed a lack of sensitivity to argument structure. These data suggest that posterior peri-sylvian regions are necessary for verb argument structure processing.

It is possible that these findings may relate to properties of the word stimuli that we used. However, differences

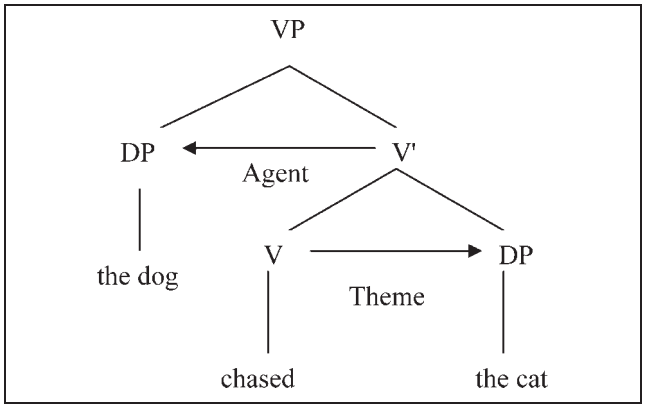

Figure 4. Schematic representation of verb phrase (VP) building.

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in word frequency cannot account for the differential activation patterns noted because the stimulus sets were matched for frequency. In the case of imageability, one-argument verbs were significantly more imageable than three-argument verbs, but not significantly different when compared to two-argument verbs. Therefore, the greater activation for two- and three-argument verbs as compared to one-argument verbs cannot be accounted for by differences in imageability.

It also is possible that our findings may be artifactual, arising from differences in RTs across our experimental conditions. Kable, Kimberg, and Chatterjee (2004) showed that longer RTs may yield confounds in the form of false positives. This possibility, however, does not account for our findings, as RTs were actually shorter for two- and three-argument verbs compared to one-argument verbs. It is unclear why this latter behavioral result emerged. As noted previously, our pilot lexical decision experiment undertaken to determine RTs (and accuracy) for verbs of varying argument structure density showed no significant difference between verb types, although one-argument verbs were slightly faster than two-argument verbs. However, because we found RT to be longest for one-argument verbs in our experimental cohort, any activation associated with verbs with two or three obligatory arguments versus verbs with one obligatory argument cannot be attributed to RT.

Considered collectively, these data suggest that verb processing involves an extensive and interactive network that overlaps with that involved in noun processing. We also found that processing of verb argument structure engages posterior regions, adjacent to Wernicke's area. Notably, the posterior brain tissue recruited to support verb processing increases as a function of argument structure density. This finding is in line with both verb processing and production patterns in agrammatic aphasic patients. Such patients, with a sparing of posterior regions, have little difficulty processing argument structure information. However, production becomes more difficult for verbs with greater argument structure complexity. This suggests that when anterior sites are lesioned, access to posteriorly represented operations also is disrupted, which affects, to a greater extent, verbs with greater argument structure complexity.

APPENDIX I. WORD STIMULI

(a) Verb Stimuli by Argument Structure

One-argument verbs

Verb	*Verb Frequency/Million*	*Noun Frequency/Million*
convulse*	0	N/A
crawl	2	N/A
cringe	0	0
dabble*	0	0
die	20	0
drool	0	0
dwindle*	0	0
fade	2	0
gargle*	0	0
glide	7	N/A
linger	1	N/A
live	56	9
loiter	0	N/A
mutate	0	N/A
perspire*	2	N/A
prosper	0	N/A
remain*	23	N/A
salivate*	0	N/A
scream	2	0
seethe	0	N/A
sit	30	N/A
sneeze	0	N/A
soar	0	N/A
stand*	29	23
stay	38	3
talk	52	40
vanish*	2	0
wait*	28	7
weep	2	N/A
writhe	0	N/A

N/A = no noun entry in CELEX.

*Stimulus repeated.

Two-argument verbs

Verb	*Verb Frequency/Million*	*Noun Frequency/Million*
achieve	11	N/A
adopt	5	N/A
betray	2	N/A
carve*	1	N/A
collect	7	N/A
consume	2	N/A
criticize	2	N/A

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Two-argument verbs (*continued*)

Verb	*Verb Frequency/Million*	*Noun Frequency/Million*
cut	19	N/A
destroy	11	N/A
earn*	5	N/A
eat	35	N/A
elect*	1	N/A
endure	3	N/A
erase*	0	N/A
explore	3	N/A
hold	33	29
imitate	1	N/A
include	14	N/A
injure*	0	N/A
inspect	2	N/A
join*	17	N/A
kill*	19	3
locate	2	N/A
meet	89	13
pursue	4	N/A
resist	7	N/A
seize*	3	N/A
spend	21	N/A
stir*	4	2
tickle*	0	0

N/A = no noun entry in CELEX.

*Stimulus repeated.

Three-argument verbs

Verb	*Verb Frequency/Million*	*Noun Frequency/Million*
assign*	1	N/A
bake*	1	N/A
bestow*	0	N/A
borrow*	4	N/A
bring	46	N/A
build	17	N/A
buy	31	0
deliver*	4	N/A
devote*	0	N/A
donate*	0	N/A

Three-argument verbs (*continued*)

Verb	*Verb Frequency/Million*	*Noun Frequency/Million*
entrust*	0	N/A
insert*	1	1
invite	3	2
leave	59	10
lend*	3	N/A
owe	3	N/A
pour	6	N/A
provide*	30	N/A
put	74	N/A
repay*	1	N/A
sell	13	1
send	20	N/A
sew*	1	N/A
smuggle*	0	N/A
teach	11	N/A
throw	11	7

N/A = no noun entries available.

*Stimulus repeated.

(b) Nouns

Animals	*Noun Frequency/Million*	*Verb Frequency/Million*
bear	13	6
chicken	31	0
cow	23	0
deer	6	N/A
dog	71	1
duck	4	0
frog	4	N/A
giraffe	1	N/A
goat	12	N/A
hippo	1	N/A
kangaroo	1	N/A
leopard	7	N/A
lion	8	N/A
lizard	2	N/A
monkey	9	N/A
moose	0	N/A
ostrich	2	N/A

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(b) Nouns (*continued*)

Animals	*Noun Frequency/Million*	*Verb Frequency/Million*
owl	3	N/A
panda	0	N/A
parrot	3	0
pigeon	2	N/A
rabbit	11	0
rooster	1	N/A
shark	15	N/A
sheep	21	N/A
spider	4	N/A
squirrel	4	N/A
tiger	5	N/A
whale	0	0
wolf	6	0

N/A = no verb entries available.

*Stimulus repeated.

Tools	*Noun Frequency/ Million*	*Verb Frequency/ Million*
broom*	7	1
chisel	2	0
clamp	1	0
crowbar	1	N/A
drill*	6	1
funnel	2	0
hammer*	9	1
hatchet	0	N/A
key	73	0
knife	38	0
ladle	1	0
mallet	2	N/A
mixer	2	N/A
needle*	10	1
pencil	16	0
pliers	2	N/A
rake	1	0
ratchet	1	N/A
razor	0	N/A
rope	33	0

(b) Nouns (*continued*)

Tools	*Noun Frequency/ Million*	*Verb Frequency/ Million*
scalpel	1	N/A
scissors*	5	0
screwdriver*	3	N/A
shovel	3	0
sieve*	2	0
spoon	12	0
stapler	0	N/A
straw*	23	0
sword*	14	N/A
wrench*	3	0

N/A = no verb entries available.

*Stimulus repeated.

APPENDIX II. CLASSIFICATION OF VERBS BY ARGUMENT STRUCTURE

One-argument Verbs

These select only one external argument (typically agent), for example, *sleep*; and usually cannot be followed by a noun phrase (NP). For example, **The bear sleeps the woods* is ungrammatical. However, they can be followed by a prepositional phrase (PP), for example, *The bear sleeps in the woods*. Further, these verbs cannot be passivized (e.g., **The bear was slept by* ___ is ungrammatical).

Two-argument Verbs

These select two arguments, one external and one internal (typically agent, theme), for instance, *chase*. They can be passivized, for example, *the girl was chased by Zack*, and (if obligatory) they cannot be followed by a PP, for example, **Zack chased around the garage* is ungrammatical.

Three-argument Verbs

These select three arguments (typically agent, theme, goal), for example, *put*. Three-argument verbs must pass two of the three following tests:

(1) The ''obligatoriness'' test. Examines whether the PP is obligatory. For example, in *John put the movie in the VCR*, the PP (*in the VCR*) is obligatory and cannot be omitted from the syntax (e.g., **John put the movie*). Thus, the verb *put* qualified as a three-place verb. This is in contrast with the verb *eat* as in *John ate the cake in the kitchen*. The PP (*in the*

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kitchen) can be omitted, disqualifying *eat* as a three-argument verb.

(2) The ''do so'' substitution test. For example, in the sentence *John will rent the car in Chicago, and Bill will do so in New York*, the PP (*in Chicago*) can be substituted (with *in New York*) in the ''do so'' clause and, therefore, the PP is not an argument; rather, it is considered an adjunct clause. Thus, *rent* does not qualify as a three-argument verb. However, the verb *put* is a three-argument verb because in **John will put the car in the garage and Bill will do so in the parking lot*, substitution of the PP results in an ungrammatical sentence.

(3) The ''order test.'' If a PP cannot be moved to the right of an adjunct, it is a selected argument. For example, moving the PP *in the garage* in *John will put the car in the garage on Tuesday* to the right of the adjunct (*on Tuesday*) results in an ungrammatical sentence: **John will put the car on Tuesday in the garage*. In contrast, such movement does not render sentences with the verb *rent* ungrammatical; that is, both *John will rent the car in Chicago on Tuesday* and *John will rent the car on Tuesday in Chicago* are grammatical. Thus, *put*, but not *rent*, qualifies as a three-argument verb.

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Reprint requests should be sent to Cynthia K. Thompson, Department of Communication Sciences and Disorders, and Neurology, Northwestern University, 2240 Campus Drive, Evanston, IL 60208, or via e-mail: ckthom@northwestern.edu.

Notes

1. A pilot event-related lexical decision study using 44 nouns (1200 msec), 28 pseudowords (1200 msec), and 30% null events (ITI = 300 msec) indicated a minimum of 40 stimuli required per condition for signal detection. Thus, some stimuli were repeated in each condition to reach this number (see Appendix I).
2. Nonparametric statistics were used to compare frequencies across word classes, because word frequencies are not normally distributed (Baayen, 2001).

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