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Shindigs, brunches, and rodeos: The neural basis of event words

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Abstract Events (e.g., “running” or “eating”) constitute a basic type within human cognition and human language. We asked whether thinking about events, as compared to other conceptual categories, depends on partially independent neural circuits. Indirect evidence for this hypothesis comes from previous studies showing elevated posterior temporal responses to verbs, which typically label events. Neural responses to verbs could, however, be driven either by their grammatical or by their semantic properties. In the present experiment, we separated the effects of grammatical class (verb vs. noun) and semantic category (event vs. object) by measuring neural responses to event nouns (e.g., “the hurricane”). Participants rated the semantic relatedness of event nouns, as well as of two categories of object nouns—animals (e.g., “the alligator”) and plants (e.g., “the acorn”)—and three categories of verbs—manner of motion (e.g., “to roll”), emission (e.g., “to sparkle”), and perception (e.g., “to gaze”). As has previously been observed, we found larger responses to verbs than to object nouns in the left posterior middle (LMTG) and superior (LSTG) temporal gyri. Crucially, we also found that the LMTG responds more to event than to object nouns. These data suggest that part of the posterior lateral temporal response to verbs is driven by their semantic properties. By contrast, a more superior region, at the junction of the temporal and parietal cortices, responded more to verbs than to all nouns, irrespective of their semantic category. We concluded that the neural mechanisms engaged when thinking about event and object categories are partially dissociable.

Keywords Event processing · Lexical access · Prefrontal cortex · Semantics

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The mind cuts the continuous stream of experience into discrete chunks we call events (Baldwin, Baird, Saylor, & Clark, 2001; Wynn, 1996). These event tokens are themselves organized into categories such as “giving” and “running.” Adults and children use these stored representations to make sense of the world and to describe it to others. Within the first year of life, infants distinguish similar-looking events, such “pushing” and “pulling” on the basis of their causal properties (Olofson & Baldwin, 2011). Before their second birthday children begin to label events such as “all gone” and “go” (Theakston, Lieven, Pine, & Rowland, 2002). Older children and adults can pick out a vast number of event categories such as “running”, “making the bed”, or “doing the dishes” (Ferretti, McRae, & Hatherell, 2001; Morris & Murphy, 1990; Rifkin, 1985; Zacks & Tversky, 2001; Zacks, Tversky, & Iyer, 2001). Knowledge about events includes typical event participants, causal relationships between participants and objects, and temporal sequences of subevents within events (McRae et al., 2005; Zacks & Tversky, 2001; Zacks et al., 2001). The conceptual category of events is marked in the syntactic structure of language. Across the world’s languages, events are predominantly labeled by verbs (e.g., “running,” “thinking”), whereas entities are labeled by nouns and properties by adjectives (e.g., Frawley, 1992; Langacker, 1987; Talmy, 1975). Events thus constitute a basic type within cognition and within the mental lexicon (Zacks & Tversky,

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2001; Zacks et al., 2001).[1] An interesting question is whether this distinction between events and other conceptual types is reflected in neurobiology. That is, are neural representations of events in any way dissociable from those of entities and properties?

Indirect evidence for distinctive neural processing of events has come from studies of verbs. As we noted above, verbs typically refer to events as opposed to entities or properties. Verbs are partially neurally dissociable from other word types. Focal brain damage can lead to a disproportionate deficit in production and comprehension of verbs, as compared to nouns (Breedin, Saffran, & Schwartz, 1998; Caramazza & Hillis, 1991; McCarthy & Warrington, 1985). Similarly, neuroimaging studies have identified brain regions that respond more to verbs than to nouns and adjectives (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008; Bedny & Thompson-Schill, 2006; Damasio et al., 2001; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). Since events are much more likely to be labeled by verbs, one possibility is that some of these neural dissociations reflect distinctive neural processing of events. In support of this interpretation, it has recently been shown that a subset of patients with verb deficits also have difficulty processing event nouns (e.g., celebration) (Collina, Marangolo, & Tabossi, 2001; Tabossi, Collina, Caporali, Pizzioli, & Basso, 2010). For example, these individuals have more trouble naming pictures of events than naming pictures of objects. One possible interpretation of these findings is that events are neurally dissociable from other categories. If so, damage to event representations would impair comprehension of event nouns and verbs, but not object nouns.

However, this straightforward interpretation of the neuropsychological findings faces a number of problems. First, a common deficit in event noun and verb comprehension could arise if verbs were obligatorily retrieved during comprehension of some event nouns. Prior neuropsychological research has focused on event nouns that are strongly linked to specific verbs—that is, verb-centered nominalizations (Tabossi et al., 2010). For example, the noun "celebration" can be morphologically derived from the verb "celebrate" by adding the ending "-ion" and means roughly the event of celebrating. It is possible that verb-centered nominalizations are understood by retrieving the lexical entry for the related verb and then deriving the noun meaning. By contrast, event nouns such as "hurricane" and "concert" are not derivable from verbs. If event noun and verb comprehension relies on a common neural mechanism for representing events, then the neurobiological association between these word classes should extend beyond verb-centered nominalizations.

Second, neuropsychological dissociations can arise in the absence of dissociable neural contributions in the healthy brain (Dell, Schwartz, Martin, Saffran, & Gagnon, 1997). For example, if events are more difficult to process than other conceptual categories, then damage to an undifferentiated semantic system might lead to greater deficits with events. Relatedly, patients with purported event deficits have large and heterogeneous lesions within the left frontal and temporo-parietal cortices (Collina et al., 2001; Tabossi et al., 2010). It therefore remains unclear whether any set of neural structures is particularly relevant for processing of events or instead whether general damage to the language system disproportionately affects events.

In the present study, we used neuroimaging to test the hypothesis that words that refer to events (i.e., event nouns and verbs) are processed differently from words that refer to entities (i.e., object nouns). Our primary analyses focused on a highly reliable neural signature of verb processing: elevated activity in the posterior aspect of the left middle temporal gyrus (LMTG). The LMTG response to verbs was first identified by Martin et al. (1995), who found that generating action verbs, as compared to object nouns and color adjectives, leads to higher responses in the posterior aspect of the LMTG (Martin et al., 1995). Subsequent studies extended these results to a range of tasks (e.g., semantic relatedness judgments, semantic triads), as well as a variety of languages (Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Kable, Lease-Spellmeyer, & Chatterjee, 2002; Yu, Bi, Han, Zhu, & Law, 2012; Yu, Law, Han, Zhu, & Bi, 2011). Although the initial studies focused specifically on action verbs, more recent work has demonstrated that the LMTG also responds to mental state verbs (e.g., to think) and to verbs that refer to nonagentive processes (e.g., to rust) (Bedny, Caramazza, et al., 2008; Grossman et al, 2002; Davis et al, 2004; Bedny & Thompson-Schill, 2006).

Whether the LMTG responds to verbs because they refer to events is not known. A key alternative hypothesis is that the LMTG responds to grammatical information associated with verbs, rather than semantic information associated with events (den Ouden, Fix, Parrish, & Thompson, 2009; Shetreet, Palti, Friedmann, & Hadar, 2007). For example, English verbs impose restrictions on the number and type of syntactic arguments that occur in a sentence. Verbs also have a rich inflectional morphology (i.e., "he walks"/"they walk" and "walk"/"walked"/"walking"). The LMTG could represent this grammatical information relevant to verbs (Tyler, Bright, Fletcher, & Stamatakis, 2004). In the current study we used event nouns to tease apart these semantic and grammatical hypotheses.

[1] Note that in the present article, we use the term "event" broadly to refer to a temporally situated ontological class. A further distinction is made in linguistics between events, which involve change, and states, which are homogeneous in time. The term "event," as used in the present study, subsumes both of these subtypes (Frawley, 1992).

The grammatical behavior of event nouns is in many ways similar to that of object nouns. For example, both event nouns and object nouns are commonly modified by adjectives rather then adverbs (e.g., "The loud carnival." vs. "She shouted loudly." vs. "The loud bell."). In English, both object and event nouns can be preceded by the determiners "the"/"a." The inflectional morphology of event nouns is also more similar to that of object nouns than to that of verbs ("hurricane/hurricanes," not "hurricaning/hurricaned"). By contrast, the semantics of event nouns is in some ways more similar to verbs than to entity nouns. Event nouns denote some of the same categories as verbs: namely, actions, processes or events. They tend to highlight subsets of space-time (e.g., "war") rather then subsets of space that are invariant with respect to time (e.g., "apple"). The referents of event nouns tend to be dynamic and less stable in time than the referents of object nouns (DuBois, 1987; Frawley, 1992; Givón, 1984). Adjectives such as "long" take on a temporal meaning when applied to event nouns (e.g., "a long concert"), as opposed to when applied to concrete object nouns (e.g., "a long table"). Event nouns thus provide an opportunity to dissociate the effects of grammatical and semantic properties of words on neural activity.

We reasoned that if the LMTG responds to verbs because of their grammatical properties, it should show a low response to event nouns because they lack such structural information. By contrast, if the LMTG responds to verbs because they refer to events, it might show a higher response to event nouns than to object nouns. To test these predictions, we compared event nouns to three kinds of verbs (manner of motion, emission, and perception) and two kinds of object nouns (animals and plants).

A secondary goal of the present study was to extend previously observed LMTG responses to two novel verb categories: verbs of emission and verbs of perception. The vast majority of neuroimaging studies on verbs have focused on action and manner-of-motion verb. A few have also studied mental-state verbs. If we were to find that the LMTG responds broadly to a variety of verb types, its function would be less likely to be related to any idiosyncratic feature of a particular verb class (e.g., motion information associated with manner-of-motion verbs).

Materials and Methods

Participants

A group of 18 adults (11 females, seven males) took part in the fMRI experiment (two other participants were excluded due to excessive motion). The average age of the participants was 23 years old (*SD* = 3.3, range 18 to 30). All participants were right-handed, native English speakers with no known psychiatric or neurological disabilities and not currently taking any psychoactive medications. All participants gave informed consent and were paid $30 per hour for taking part in the experiment.

Task

Participants heard pairs of words and judged how related in meaning they were on a scale of one to four, with one being very similar and four being highly dissimilar. In a control condition, participants heard pairs of short backward speech segments and decided how similar in sound they were. Words were presented over headphones and participants indicated their responses by using both of their thumbs to press buttons on an MRI-compatible response pad. Behavioral results were obtained from 14 of the 18 participants. The participants failed to respond to a word pair on 3.79 % of trials. Word pairs were presented in blocks of five and were blocked by condition (e.g., five pairs of event nouns, followed by five pairs of animal nouns, etc.). Within condition, words were paired arbitrarily. Blocks were 18 s long (3.6 s for each word pair) and were separated by 14 s of fixation.

Stimuli

Word stimuli consisted of 50 words in each of the following categories: animal nouns (e.g., "the crocodile"), plant nouns (e.g., "the strawberry"), event nouns (e.g., "the hurricane"), emission verbs (e.g., "to clang"), manner-of-motion verbs (e.g., "to bounce"), and perception or information-gathering verbs (e.g., "to gaze") (henceforth, *perception verbs* for brevity). The word stimuli are presented in Supplementary Table S1. All verb stimuli were preceded by "to", and all noun stimuli were preceded by "the". The purpose of this was to ensure that participants retrieved the verb and noun uses of the relevant word categories. Participants heard 50 pairs per category, such that each word was heard twice during the experiment, once in each half of the study, and was paired with a different word each time.

Because verbs tend to be more difficult than nouns in similarity-judgment tasks, we intentionally selected nouns that were longer and less frequent than verbs to match the nouns and verbs as closely as possible on difficulty. Frequency ratings on the words were collected from the CELEX English Lemma Frequency Database. The average frequency of the verbs was 1.01 (*SD* = 0.55), and the average frequency of the nouns was 0.66 (*SD* = 0.58), $t(144) = 4.93$, $p < .001$. The nouns were longer than the verbs, $t(149) = 9.46$, $p < .001$: The average length of the verbs was 1.46 syllables (*SD* = 0.70), whereas the average length of the nouns was 2.33 syllables (*SD* = 0.87).

Imageability ratings were also collected, in order to better characterize the stimuli. Using the Amazon Mechanical Turk, 20 participants were asked to rate each word on how imageable it was on a scale of 1 to 7, with 7 being *most imageable*. As in previous studies, nouns (M = 5.63, SD = 1.00) were rated as being significantly more imageable than verbs (M = 4.01, SD = 1.25), $t(298) = 14.47$, $p < .0001$. Within the category of verbs, manner-of-motion and emission verbs did not differ in imageability, $t(98) = 0.74$, $p = .46$. The perception verbs (M = 3.32, SD = 1.18) were significantly less imageable than both the manner-of-motion verbs (M = 4.41, SD = 0.96), $t(98) = 6.63$, $p < .0001$, and the emission verbs (M = 4.31, SD = 1.33), $t(98) = 6.84$, $p < .0001$. Within the noun category, animals (M = 6.23, SD = 0.67) were rated as being more imageable than events (M = 4.75, SD = 0.92), $t(98) = 8.68$, $p < .0001$, and plants (M = 5.90, SD = 0.71), $t(98) = 2.40$, $p = .02$. Plants were also rated as being more imageable than events, $t(98) = 6.61$, $p < .0001$. Word frequencies, syllable lengths, and imageability ratings are listed in Table 1.

A female native English speaker recorded the stimuli at a sampling rate of 44100 Hz to produce 32-bit digital sound files. Audio files were normalized to each other in volume with respect to root-mean square (RMS) amplitude such that all files, and consequently, all categories, had approximately equal RMS (average RMS, –24.07 dBFS). All files were adjusted to have approximately equal durations (average duration, 0.76 s).

Functional magnetic resonance imaging data acquisition and analysis

Structural and functional data were collected on a 3-T Siemens scanner at the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research at the Massachusetts Institute of Technology. T1-weighted structural images were collected in 128 axial slices with 1.33-mm isotropic voxels [repetition time (TR) = 2 ms, echo time (TE) = 3.39 ms]. Functional, blood oxygenation level-dependent (BOLD) data were acquired in 3 × 3 × 4 mm voxels (TR = 2 s, TE = 30 ms) in 30 near-axial slices. The first 4 s of each run were excluded to allow for steady-state magnetization.

Data analysis was performed using SPM8 and in-house software. The data were realigned, smoothed with a 5-mm smoothing kernel, and normalized to a standard template in Montreal Neurological Institute space (ICBM152). The modified-linear model was used to analyze BOLD activity of each participant as a function of condition. Covariates of interest were convolved with a standard hemodynamic response function (HRF). Nuisance covariates included run effects, an intercept term, and global signal. Time-series data were subjected to a high-pass filter (128 Hz).

BOLD signal differences between conditions were evaluated through second level, random-effects analysis. In whole-brain analyses, the false positive rate was controlled at $p < .05$ (corrected) by performing Monte Carlo permutation tests on the data (using a combined voxel and cluster size threshold) (Hayasaka & Nichols, 2004; Nichols & Holmes, 2002).

Functional regions of interest (ROIs) were identified in individual subjects. LMTG ROIs were defined as in previous studies using the contrast of manner of motion verbs > animal nouns (Bedny, Caramazza, et al., 2008; Kable et al., 2005; Martin et al., 1995). In these ROIs we then compared the remaining orthogonal word conditions to each other: perception verbs, emission verbs, plant nouns, and event nouns. For the purposes of defining ROIs, statistical maps were thresholded at $p < .01$ with at least ten continuous voxels. Participants with no voxels within the LMTG at this threshold were excluded from the LMTG ROI analysis (excluded $n = 2$, participants included in ROI analysis $n = 16$). ROIs were defined as all voxels within a 10-mm sphere around the activation peak. ROI analyses were

Table 1 Behavioral table: Means and standard deviations of the behavioral data for all word categories

	Similarity Ratings	Reaction Time (ms)	Number of Syllables	Frequency	Imageability
Verbs	2.14 (1.01)	1,707 (441)	1.46 (0.70)	1.01 (0.55)	4.01 (1.25)
Emission	2.27 (1.05)	1,744 (450)	1.28 (0.45)	0.91 (0.41)	4.31 (1.33)
Manner of motion	2.08 (0.97)	1,676 (431)	1.34 (0.52)	1.10 (0.56)	4.41 (0.96)
Perception	2.05 (1.01)	1,699 (439)	1.76 (0.94)	1.21 (0.51)	3.32 (1.18)
Nouns	2.22 (0.96)	1,650 (431)	2.33 (0.87)	0.66 (0.58)	5.63 (1.00)
Animals	2.37 (0.93)	1,675 (437)	2.50 (0.79)	0.60 (0.34)	6.23 (0.67)
Events	2.08 (1.02)	1,624 (427)	2.34 (0.80)	1.15 (0.46)	4.75 (0.92)
Plants	2.20 (0.92)	1,651 (428)	2.16 (1.00)	0.83 (0.51)	5.90 (0.71)
Backward Speech	2.70 (1.00)	1,786 (404)	n/a	n/a	n/a

Standard deviations are presented in parenthesis next to the mean performed on the average of percentage signal change (PSC) relative to a rest baseline for Seconds 6–20 (the first two TRs were excluded to account for the hemodynamic lag).

Results

Behavioral results

Verbs were rated as being marginally more semantically similar to each other than nouns (verbs, M = 2.14, SD = 1.01; nouns, M = 2.22, SD = 0.96), $t(13) = 1.90$, $p = .08$. This difference was not consistent across verb and noun categories. Among verbs, emission verbs (M = 2.27, SD = 1.05) were rated as being significantly less self-similar than motion (M = 2.08, SD = 0.97), $t(13) = 3.25$, $p = .006$, and perception (M = 2.05, SD = 1.01) verbs, $t(13) = 4.03$, $p = .001$. Motion verbs and perception verbs did not differ significantly from each other, $t(13) = 0.75$, $p = .47$ (see Table 1 for similarity ratings and reaction times). Among the nouns, animals (M = 2.37, SD = 0.93) were rated as being significantly less similar to one another than were plants (M = 2.20, SD = 0.92), $t(13) = 3.17$, $p = 0.007$, and events (M = 2.08, SD = 1.02), $t(13) = 3.29$, $p = .006$. Events and plants did not differ in similarity rating, $t(13) = 1.61$, $p = 0.13$.

Participants took longer to make semantic similarity judgments for verbs (M = 1,707 ms, SD = 441 ms), as compared to nouns (M = 1,650 ms, SD = 431 ms), $t(13) = 3.07$, $p = 0.009$. However, again, this difference did not hold across verb and noun types: For example, reaction times did not differ between animal nouns (M = 1,675 ms, SD = 437 ms) and motion verbs (M = 1,676 ms, SD = 431 ms), $t(13) = 0.03$, $p = .98$. Within the category of verbs, participants took longer to respond to emission verbs (M = 1,744 ms, SD = 450 ms) than to manner-of-motion verbs (M = 1,676 ms, SD = 431 ms), $t(13) = 2.70$, $p = .02$, or perception verbs (M = 1,699 ms, SD = 439 ms), $t(13) = 2.09$, $p = .06$. Manner-of-motion verbs and perception verbs did not differ from each other, $t(13) = 1.48$, $p = .16$. Reaction times did not differ among noun types [events vs. plants, $t(13) = 0.86$, $p = .40$; events vs. animals, $t(13) = 1.49$, $p = .16$; animals vs. plants, $t(13) = 1.66$, $p = .12$]. Reaction times and similarity ratings for each word type are presented in Table 1.

fMRI results

Does the LMTG respond to emission, motion and perception verbs? Consistent with prior findings with other verb types, BOLD signal was higher in the LMTG ROI for verbs (emission and perception verbs) than for the object nouns (plants) [PSC difference = 0.35, paired t test, $t(15) = 7.42$, $p < .0001$] (Kable et al., 2005; Kable et al., 2002). As in prior studies, the percentage of signal change (PSC) for object nouns did not different from that for backward speech [$t(15) = -0.28$, $p = .78$] (see Fig. 1). Consistent with the ROI analyses, whole-brain analyses revealed that the LMTG responds more to verbs (emission, motion, or perception) than to object nouns (plants or animals) (PSC difference = 0.38, $p < .05$, corrected). The posterior temporal responses to verbs extended superiorly into the superior temporal gyrus and the inferior parietal lobule (see Table 2 for a complete list of activations).

Because reaction times were slower to verbs than to nouns, we conducted follow-up analyses to investigate whether LMTG activity is modulated by grammatical class and semantic class, or instead by judgment difficulty. If LMTG activity is modulated by difficulty, and not word type, then word type differences should disappear once reaction time is matched across conditions. Using whole-brain analyses we compared motion verbs to animal nouns, which were matched on reaction times. Across the entire brain, only the LMTG showed a reliably higher response to motion verbs than to animal nouns. These results suggest that LMTG responses to verbs persist when verbs are matched to nouns on reaction times.

Does the LMTG respond to the semantic category of events or the grammatical category of verbs? For the critical category of event nouns, the response of the LMTG ROI was reliably higher than for the independent object noun condition (plants; PSC difference = 0.24), $t(15) = 5.55$, $p < .0001$, although the LMTG response to event nouns was still somewhat lower than the response to verbs (both perception and emission; PSC difference = 0.11), $t(15) = 2.85$, $p = .01$. Note that reaction times were similar for plant and event nouns; thus, greater responses to event nouns were unlikely to result from general task difficulty. In whole-brain analysis, event nouns also produced a larger response in the LMTG than object (plant) nouns. In addition to the LMTG, the event noun > object noun contrast revealed greater BOLD signal in anterior aspects of the left middle temporal gyrus as well as the left superior frontal gyrus (see Fig. 1 and Table 2 for details). These findings demonstrate that the comprehension of event and object nouns engages partially nonoverlapping cortical systems.

In whole-brain analyses, the event noun > object noun effect was distributed along the middle and inferior temporal gyri (Fig. 1). By contrast, the all verbs > object nouns effect extended into the superior temporal gyrus and the inferior parietal cortex. We next looked for brain regions that were more responsive to verbs than to event nouns using whole-brain analyses. Although no regions survived the corrected level of significance ($p < .05$), at a more lenient threshold of $p < .1$ (corrected), we observed a

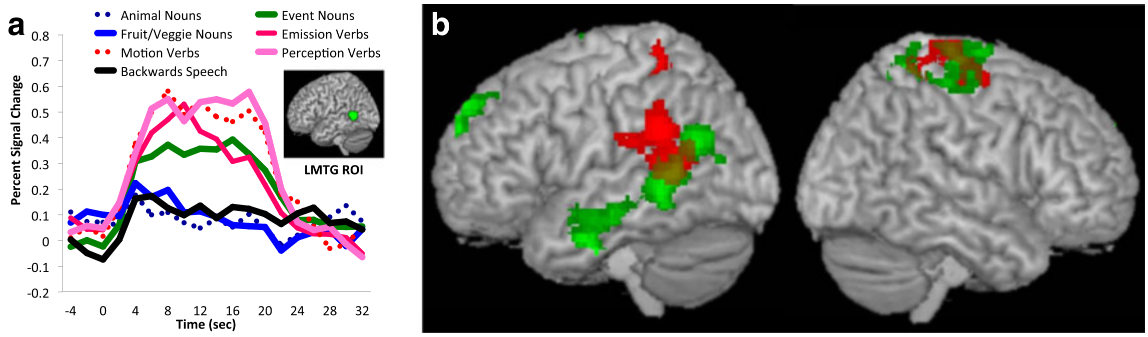

Fig. 1 Responses to event nouns and verbs. (A) Percentages of signal change in the left middle temporal gyrus (LMTG). (B) Results of the whole-brain analyses for event nouns>object nouns (green/light) and verbs>object nouns (red/dark). The results are thresholded at $p<.05$ (corrected for multiple comparisons) and displayed on a normalized template brain. For a complete list of whole-brain activity, see Table 2

larger response to verbs in the left inferior parietal lobule (LIPL), as well as the left inferior frontal gyrus (LIFG; see Fig. S2). These findings suggest a distinct spatial distribution of neural responses to events (concentrated on the LMTG) as opposed to verbs (in the IPL and the LIFG).

Discussion

Previous studies had identified a brain region along the posterior aspect of the LMTG that is active during lexical semantic tasks and responds more to verbs than to object nouns and adjectives (Kable et al., 2005; Kable et al., 2002;

Table 2 Results of whole-brain random-effects analyses $p<.05$ (corrected)

			Voxel Peak t				
k	w	p_{combo}		x	y	z	Brain Area (Brodmann Area)
Motion Verbs>Animal Nouns							
164	4.97	.027	5.76	–62	–52	8	Left superior/Middle temporal gyrus (22)
Event Nouns>Plant Nouns							
227	7.03	.004	6.30	–12	54	42	Left superior/Middle frontal gyri (9/10)
1,813	7.32	.003	6.11	–44	–60	24	Left posterior middle temporal gyrus (39)
			5.90	–54	–12	–34	Left inferior temporal gyrus (20)
			5.34	–54	–50	4	Left middle temporal gyrus (21)
Verbs>Nouns							
285	3.96	.070	5.36	–50	10	4	Left superior/Middle temp. gyri (22/38)
1,177	5.25	.021	5.27	–60	–42	28	Left inferior parietal lobule (40)
			4.19	–48	–40	16	Left insula (13)
			4.09	–50	–54	16	Left superior temporal gyrus (22)
Event Nouns>Object Nouns							
238	8.82	.001	6.74	–12	54	42	Left superior frontal gyrus (9/10)
1,704	7.12	.004	6.06	–56	–48	4	Left middle temporal gyrus (21/39)
			5.77	–54	–12	–34	Left inferior temporal gyrus (20)
983	6.47	.006	5.80	18	–54	64	Left superior parietal lobule (7)
			4.99	36	–22	70	Right precentral gyrus (6/4)
Verbs>Object Nouns							
276	3.76	.083	5.22	–22	–44	60	Left superior parietal lobule (40)
			4.30	–20	–42	68	Left postcentral gyrus (3/4)
1,441	5.73	.013	5.17	–60	–42	28	Left inferior parietal lobule (40)
			5.15	–50	–46	30	Left supramarginal gyrus (40)
			5.06	–60	–52	8	Left superior/Middle temporal gyrus (22)
721	4.49	.042	4.88	22	–32	62	Right postcentral gyrus (3)

Martin et al., 1995). This brain region responds not only to action verbs, such as “to run,” but also to mental state verbs, such as “to think”; bodily function verbs, such as “to bleed”; and change-of-state verbs, such as “to rust” (Bedny, Caramazza, et al., 2008). The present study extended these findings to verbs of emission (e.g., “to sparkle”), perception (e.g., “to see”), and manner of motion (e.g., “to roll”). Along with the prior evidence, the present findings suggest that the LMTG responds to a wide variety of verb types. Thus, the LMTG does not appear to be selective for a particular semantic subclass of verbs (e.g., motion verbs or mental state verbs). These data raise two possible hypotheses regarding LMTG function. First, the LMTG might not represent semantic information at all, but could instead represent grammatical information relevant to verbs. Alternatively, the LMTG might process information relevant to a broad semantic class that is shared across verb categories but distinct from object nouns—that is, events. The key finding of the present article favors the semantic hypothesis: we found that the LMTG responds more to event nouns, such as “hurricane,” than to object nouns, such as “cactus”.

The present findings are consistent with prior neuropsychological investigations reporting that some patients who have difficulty producing and understanding verbs also have difficulties with event nouns (Collina et al., 2001; Tabossi et al., 2010). Why might verbs and event nouns depend on similar neural machinery? As we noted in the introduction, one possibility is that event nouns are understood by deriving their meaning online from verbs. This account seems an implausible explanation of the present findings. The majority of event nouns in the present study did not share a lexical root with verbs (e.g., “rodeo” and “concert”; see Table S1). The subset of our event noun stimuli that did share a root with a verb (e.g., “the wedding” vs. “to wed”) were more frequently used as nouns, and the verb meaning was often obscure (e.g., “to burgle” and “to adventure,” both having CELEX frequencies of 0). The three exceptions to this were the words “the robbery” (“to rob”), “the speech” (“to speak”), and “the exam” (“to examine”). However, the meanings of “speech” and “exam” cannot be derived from their associated verbs (e.g., examining a photograph does not constitute an exam). We therefore think that it is unlikely that participants understood the event nouns used in the present experiment by deriving their meanings from the related verbs. Despite this, we found similar neural responses to event nouns and verbs. Our findings suggest that event nouns and verbs rely on similar neural representations.

Neural responses to event words

An intriguing possibility is that the LMTG responds to event words (verbs and nouns) because they elicit retrieval of event concepts (Du Bois, 1987; Ferretti et al., 2001; Givón, 1984; Higginbotham, Pianesi, & Varzi, 2000; Morris & Murphy, 1990; Rifkin, 1985; Tversky, Zacks, Morrison, & Hard, 2011). Previous behavioral studies have shown that reading and hearing verbs leads to retrieval of rich information about events. For example, the verb “to skate” primes typical skating locations (“arena”) and the verb “arresting” primes typical agents of arresting events (“cop”; Ferretti et al., 2001). Subtle features of the way a verb is used in a sentence influence which aspects of an event concept are retrieved. For example, information about event location is more likely to be retrieved for “was skating” (imperfective aspect) than for “had skated” (perfective aspect) (Ferretti, Kutas, & McRae, 2007; Ferretti et al., 2001). These studies suggest that words are potent cues to event concepts. The LMTG might respond to event nouns and verbs because they refer to category-specific semantic information that is relevant to events.

The event concepts hypothesis of LMTG function is related to a previous proposal: that the LMTG contributes to the representations of actions (Kable et al., 2005; Kable et al., 2002; Kemmerer & Gonzalez Castillo, 2010; Kemmerer, Rudrauf, Manzel, & Tranel, 2012, Martin et al., 1995; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003). However, a number of key differences distinguish the action hypothesis from the event hypothesis. Events are a broader and more abstract category than actions. Although actions, as conceived of in this literature, necessarily involve motion (e.g., “to run”), events do not (e.g., “to think”). Also, actions require an agent, whereas events can be agentless (e.g., “rusting” and “melting”). The hypothesis that the LMTG represents events rather than actions also implies that its representations are more abstract than has previously been proposed. For example, one proposal is that the LMTG stores imagistic representations of typical motion patterns relevant to actions (e.g., Kemmerer et al., 2012). By contrast, according to the event hypothesis, the LMTG stores information such as temporal sequence of subevents and causal relationships among objects and agents within an event (Baldwin, Andersson, Saffran, & Meyer, 2008; Morris & Murphy, 1990; Rifkin, 1985; Tversky et al., 2011). If the event hypothesis is on the right track, we might also expect the LMTG to be specifically sensitive to information about time. A distinguishing feature of events is their inherently temporal nature (Langacker, 1987). Relative to entities and properties, event categories are more unstable in time and are more likely to pick out subsets of time (Givón, 1984).

If the LMTG responds to event concepts, a further question is whether it is selective only for those event concepts that are accessible through language, or perhaps even more narrowly, only those event concepts that are labeled by single words. Whether the LMTG is involved in retrieving nonlexicalized event concepts, such as “making the bed” and “shopping for clothing,” is not known. A related question is whether LMTG representations can also be accessed through nonverbal stimuli, such as audio or video clips. Future research will be required in order to delineate the spectrum of verbal and nonverbal stimuli that elicit LMTG responses.

An alternative to the idea that the LMTG stores conceptual representations of events in general is that it specifically stores aspects of event concepts that are relevant to language structure (Pustejovsky, 1991). For example, whether or not an event entails completion ("arriving" [telic] vs. "walking" [atelic]) predicts the way in which the word for that event is used in a sentence. One can say "She arrived at 5 pm," but not "She arrived for a long time." Some evidence has indicated that the LMTG is sensitive to syntactically relevant properties of event words (Romagno, Rota, Ricciardi, & Pietrini, 2012). By contrast, there are semantic properties of events that have no consequences for language structure. Although surgeries typically include a physician and trials typically include a judge, this semantic distinction has little consequence for predicting the syntactic behavior of the words "surgery" and "trial." Whether the LMTG is also sensitive to such syntactically irrelevant semantic information is not known.

Some alternative explanations

The LMTG responds to abstract words Although we argue that the LMTG contributes to event semantics, several alternative explanations remain open. First, since both event nouns and verbs are more abstract than object nouns, the LMTG could respond to abstract words generally, rather than to temporally situated words in particular. The abstractness hypothesis cannot be ruled out on the basis of the present findings. However, several considerations weigh in against the possibility that LMTG responses are driven by abstractness per se.

The abstractness/concreteness dimension generalizes over a wide variety of lexical types. Abstract words include function words (e.g., "if"), abstract entities (e.g., "idea"), concrete but general entities (e.g., "thing"), and properties (e.g., "smart"), as well as events (e.g., "wedding"). Similarly, concrete words include a wide range of ontological classes such as actions (e.g., "to run"), objects (e.g., "the cat"), and properties (e.g., "red"). Neither abstract nor concrete words form a coherent class. It is therefore perhaps unsurprising that neuroimaging studies have failed to identify a consistent "abstractness" response in the LMTG, or elsewhere in the brain. Most relevant for the present question, only a small fraction of previous studies of abstract words find responses in the LMTG, suggesting that the LMTG responds to a subclass of abstract words rather than to abstract words in general (Binder, Westbury, McKiernan, Possing, & Medler, 2005; Noppeney & Price, 2004; Pexman, Hargreaves, Edwards, Henry, & Goodyear, 2007; Rodriguez-Ferreiro, Gennari, Davies, & Cuetos, 2011; Sabsevitz, Medler, Seidenberg, & Binder, 2005; Wang, Conder, Blitzer, & Shinkareva, 2010).

On the other hand, the LMTG could still respond to a semantic subclass of words that is less general than all abstract words, but broader or different from events. Some evidence for this possibility has come from a study by Peelen, Romagno, and Caramazza (2012). These authors observed greater responses in the LMTG to verbs than to nouns. However, they also observed no difference between responses to event nouns (e.g., "the wedding") and state nouns (e.g., "the prestige"; Peelen et al., 2012). These data suggest that the LMTG may respond not only to events, but also to state nouns that are not inherently temporal. Future studies comparing verbs and event nouns to other types of abstract nouns and adjectives would provide more precise insights into the contribution of the LMTG to word comprehension. Whatever the selectivity profile of the LMTG, the present findings demonstrate that its response is modulated not only by grammatical class, but also by semantic properties of nouns.

LMTG represents relational words Another possibility is that the LMTG contributes to representing the conceptual category of relations. Relative to other word types, verbs are far more likely to highlight relationships between entities (Gentner, 1978). For example, the verb "to give" relates the giver, the thing given, and the recipient. Whether giving has occurred depends on whether an event satisfies this relational structure. By contrast, object nouns like "the apple" pick out types of entities on the basis of their stable and inherent features. Thus, the LMTG could respond more to verbs than to entity nouns because verbs refer to relations. This hypothesis, however, fails to explain why the LMTG responds to event nouns such as "hurricane" more than to entity nouns such as "dog," since neither is explicitly relational. The present data therefore suggest that the LMTG does not specifically represent relational knowledge. On the other hand, relational information is a key aspect of event knowledge, and it is possible that the LMTG represents relational information among other types of event-relevant information.

The LMTG responds to the grammatical properties of verbs Could the LMTG still respond to the grammatical properties of verbs, despite the observed responses to event nouns? We argued above that the event nouns used in the present study could not be understood by deriving their meanings from verbs. Nonetheless, perhaps verbs and their associated grammatical information are automatically retrieved during event noun comprehension. This could occur for two reasons. One possibility is that all event nouns automatically elicit the retrieval of verbs. For example, hearing the word "seminar" might automatically partially activate verbs such as "talk" and "listen." If this hypothesis is correct, the LMTG should also respond to other words that strongly prime verbs (e.g., nouns that are typical thematic role fillers for specific events; McRae, Hare, Elman, & Ferretti, 2005). A second possibility is that the task and stimuli used in the present experiment biased participants to retrieve verbs when hearing event nouns. We attempted to mitigate this concern in a number of ways. First, all event nouns were preceded by the determiner "the," which is a strong cue to the occurrence of a noun. Second, we avoided event nouns that are homophonous with verbs ("the run"/"to run"). Most of the event nouns in the present study did not share a root with any verbs, and the subset of event nouns that did were more commonly used as nouns. Thus, it seems unlikely that the present task and stimuli caused participants to automatically retrieve verbs when hearing event nouns.

One more piece of evidence weighs in against the verb retrieval hypothesis. We found that the LMTG's response profile dissociates from those of other regions that respond to verbs per se. Left inferior frontal and inferior parietal areas respond more to verbs than to event nouns, but unlike the LMTG, these areas did not respond more to event nouns than to object nouns. This response pattern is more consistent with sensitivity to grammatical class. A similar pattern of response in prefrontal and parietal areas has been reported in a number of previous studies of verbs (e.g., Bedny & Thompson-Schill, 2006; Perani et al., 1999; Shapiro, Moo, & Caramazza, 2006; Willms et al., 2011). The contributions of these brain areas to verb processing remain debated. One class of hypotheses posits that these regions store linguistic information associated with verbs, such as syntactic frames or morphological rules (e.g., Shapiro et al., 2006; Tyler, Randall, & Stamatakis, 2008). By contrast, others have argued that that prefrontal and parietal responses reflect greater need for domain-general processes during verb retrieval (Thompson-Schill, Bedny, & Goldberg, 2005). Irrespective of which of these hypotheses accounts for verb responses, the present findings suggest that responses to event words are partially distinguishable from those to verbs per se.

Processing explanations of LMTG responses to event words Above we considered the neural dissociation between event words and object words in relation to qualitative differences in conceptual content (temporal vs. atemporal, concrete vs. abstract, and relational vs. nonrelational). An alternative class of explanations appeals to processing differences between event and object words (Tyler et al., 2004). For example, if event words are more difficult to retrieve and if the LMTG supports word retrieval in general, higher LMTG responses could be related to retrieval difficulty. Such quantitative differences could lead to larger LMTG responses, even in the context of a semantic system that is not differentiated along knowledge domains. The behavioral data from the present experiment provide evidence against one version of this hypothesis. Since neural differences between event and entity words persist even when semantic judgments are equally difficult (i.e., no difference in reaction times between event noun and object noun categories), general task difficulty is unlikely to account for the present results. It remains possible, however, that the meanings of event words are inherently more difficult to retrieve in a way that was not captured by the current task. A challenge for future research will be to identify specific processing demands that are different for event words, as compared to object and property words.

In summary, we found that in addition to responding to a wide variety of verbs, the LMTG responds to event nouns. On the basis of these findings, we hypothesized that the LMTG is driven by semantic properties of event words, rather than by syntactic properties of verbs. In future research, it will be important to identify the specific properties of event words that lead to this distinctive neural profile.

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