Predication Drives Verb Cortical Signatures

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Abstract

■ Verbs and nouns are fundamental units of language, but their neural instantiation remains poorly understood. Neuropsychological research has shown that nouns and verbs can be damaged independently of each other, and neuroimaging research has found that several brain regions respond differentially to the two word classes. However, the semantic–lexical properties of verbs and nouns that drive these effects remain unknown. Here we show that the most likely candidate is predication: a core lexical feature involved in binding constituent arguments (*boy*, *candies*) into a unified syntactic–semantic structure expressing a proposition (*the boy likes the candies*). We used functional neuroimaging to test whether the intrinsic "predication-building" function of verbs is what drives the verb–noun distinction in the brain. We first identified verb-preferring regions with a localizer experiment including verbs and nouns. Then, we examined whether these regions are sensitive to transitivity—an index measuring its tendency to select for a direct object. Transitivity is a verb-specific property lying at the core of its predication function. Neural activity in the left posterior middle temporal and inferior frontal gyri correlates with transitivity, indicating sensitivity to predication. This represents the first evidence that grammatical class preference in the brain is driven by a word's function to build predication structures. ■

INTRODUCTION

Verbs and nouns represent elemental building blocks for the grammatical rules that constrain how words can be combined into sentences (Greenberg, 1966; Robins, 1952). The grammatical distinction between nouns and verbs is of fundamental importance, because a word's grammatical category determines the types of phrases in which it appears and the morphological transformations it undergoes (*The boy likes the candies*, but not **The likes boy the candies; The boy liked the candies*, but not **The boyed like the candies*)—see Haspelmath (2012) for an overview of the debate about the extent to which the verb–noun distinction is universal across languages. There is considerable evidence showing neural differentiation between verbs and nouns. There are reports of grammatical category-specific deficits following brain damage—selective damage to either verbs or nouns (e.g., Hernández et al., 2008; Shapiro, Shelton, & Caramazza, 2000; Damasio & Tranel, 1993; Caramazza & Hillis, 1991; McCarthy & Warrington, 1985; Miceli, Silveri, Villa, & Caramazza, 1984), and functional neuroimaging studies have found regions that are particularly sensitive to a word's grammatical category (e.g., Tyler, Randall, & Stamatakis, 2008; Shapiro, Moo, & Caramazza, 2006; Perani et al., 1999). However, the precise basis for the observed neural distinction remains elusive, in part because it is not obvious that the observed noun–verb effects reflect grammatical as opposed to semantic distinctions between the two word categories. That is, the putative grammatical category effects could reflect the effect of different semantic dimensions that are correlated with grammatical category—for example, verbs prototypically refer to actions whose meanings include more motion features relative to concrete objects—rather than the effect of specifically grammatical properties.

An additional difficulty is posed by the less-than-clear picture that has emerged of the neural correlates of the verb–noun distinction. No systematic relationship has been found between type of grammatical category deficit and lesion site (see Vigliocco, Vinson, Druks, Barber, & Cappa, 2011, for a review). And although a number of functional neuroimaging studies have found verb-preferring regions, these vary across studies (see Crepaldi, Berlingeri, Paulesu, & Luzzatti, 2011, for a critical review challenging the existence of a grammatical class distinction in the brain on the basis of across-study inconsistency). Still, a number of recent fMRI studies have consistently implicated the left lateral temporal cortex (LTC), including the posterior middle temporal gyrus (pMTG), in processing verbs relative to nouns (e.g., Peelen, Romagno, & Caramazza, 2012; Romagno, Rota, Ricciardi, & Pietrini, 2012; Willms et al., 2011; Burton, Krebs-Noble, Gullapalli, & Berndt, 2009; Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008; Tyler et al., 2008; Shapiro et al., 2006; Yokoyama et al., 2006; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005) and, less consistently, different left frontal

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regions. For the latter regions, some studies have not found any effects (e.g., Peelen et al., 2012), whereas others have implicated middle frontal (e.g., Willms et al., 2011; Shapiro et al., 2006) or inferior frontal (e.g., Bedny et al., 2008) regions. The reliable observation of verb preference in LTC across recent studies suggests that this region might represent core grammatical or semantic properties of verbs. However, as already noted, the precise lexical-grammatical or semantic properties that drive the preference remain to be determined.

The LTC has not only been implicated in processing verbs relative to nouns but also in the conceptual representation of actions, as shown by studies that considered the relationship between lexical deficits and lesion sites (Kemmerer, Rudrauf, Manzel, & Tranel, 2012; Kalénine, Buxbaum, & Coslett, 2010; Tranel, Kemmerer, Adolphs, Damasio, & Damasio, 2003) and studies that compared the neural activity in response to action versus different types of nonaction words such as colors (Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995) or abstract words (Noppeney, Josephs, Kiebel, Friston, & Price, 2005). This pattern of results encouraged the hypothesis that differences in the type of information associated with action and object concepts were likely to be behind LTC verb-preferring responses. However, recent studies have undermined this hypothesis. Bedny et al. (Bedny, Caramazza, Pascual-Leone, & Saxe, 2012; Bedny et al., 2008) observed that LTC regions that preferentially respond to verbs relative to nouns, in both sighted and congenitally blind individuals, were not engaged in processing visual motion information associated with action concepts—for example, *think* and *cut* induced similar responses. These results show that verb preference in LTC does not reflect the representation of sensory motor properties of action concepts. Peelen et al. (2012) tested whether LTC verb preference reflects the processing of more abstract information prototypically associated with actions (rather than objects) such as the understanding of actions as dynamic events unfolding over time (which may involve visual motion information [e.g., walk] or not [e.g., watch]). However, neither of two independently defined verb-preferring LTC regions—the left STS and pMTG—responded more to verbs or nouns referring to dynamic events (e.g., *he watches*, *the accident*) relative to verbs or nouns referring to states and conditions persistent in time (e.g., *he exists*, *the aptitude*). In addition, verb-preferring responses in left STS and pMTG were not restricted to event verbs but showed equally greater activity for event and state verbs relative to event and state nouns. Crucially, Peelen et al. found greater neural activity for action relative to state verbs in a more posterior portion of the pMTG that was not verb preferring, implying that verbs and action concepts are represented in nearby but separate regions (see Watson, Cardillo, Ianni, & Chatterjee, 2013, for a meta-analysis suggesting that the pMTG may be a "hub" region for action concept processing). In short, extant results suggest that (1) the verb effect in the LTC is not driven by the representation of semantic properties associated with action concepts and (2) LTC verb-preferring regions are adjacent to more posterior LTC regions representing action concepts.

These previous studies did not provide a positive response to the question of what dimension(s) drives verb preference in left LTC but revealed a grammatical category effect that is not reducible to a number of semantic properties linked to action concepts. This led us to consider the alternative hypothesis that verb preference in the left LTC and/or the less-studied frontal regions is driven by grammatical properties linked to the specific role of verbs in sentence structure—that is, predication: binding the different components of a sentence into a unified structure expressing a meaningful proposition. Thus, for example, it is the verb "*like*" that binds the arguments "*the boy*" and "*the candies*" into "*The boy likes the candies*," a proposition stating a fact about the current state of the world. It is worth stressing that we use here the term predication to refer to this proposition-constructing role of verbs, in line with the standard semantic view of verbs as functions from entities to statements about states of the world (e.g., Heim & Kratzer, 1998). This function, incidentally, also distinguishes verbs from adjectives, which cannot, by themselves, project entities to statements. The term predication has also been applied to other concepts in the linguistic literature (e.g., by Croft, 1991, 2000, 2001)—concepts that we do not want to imply here. The fundamental predication role of verbs, distinguishing them from nouns, may be what drives verb-preferring activity in LTC. If such were the case, we should observe effects of predication in verb-preferring regions when comparing verbs differing in predicative function.

But, how does one measure the verbs' predicative function? One way is through a verb-specific property—*transitivity*—that is crucially related to their predication role. Transitive verbs (e.g., *destroy*) select for a direct object; intransitive verbs do not select for a direct object—they either do not select for any other argument besides the subject (e.g., *die*) or select for prepositional complements (e.g., *wait for Bill*). It is worth emphasizing that the transitive–intransitive opposition does not apply to other grammatical categories: Transitivity is in fact related to verb-specific morphosyntactic operations (e.g., passivization and accusative case assignment), which are in turn inherently connected to the core and unique role of verbs in forming predication. Because many verbs function as intransitive or transitive depending on the semantic context—*to sink* is intransitive in "*The ship sank*" but transitive in "*The submarine sank the ship*"—we computed a continuous transitivity score as a probabilistic gradient reflecting the ratio between the frequency of a verb's transitive uses and the frequency of the intransitive occurrences of the same verb.

Few previous studies have examined the neural correlates of verbs differing in predicative function (i.e.,

transitive vs. intransitive). None of those studies, however, posed the question of whether predication would be encoded in verb-specific regions, but simply aimed at examining whether different types of verbs (e.g., intransitive vs. transitive) showed different neural correlates anywhere in the brain. Unfortunately, extant results paint a complicated picture about the possibility that verb-specific LTC and frontal regions encode predication. In two studies, Assadollahi et al. (Assadollahi, Meinzer, Flaisch, Obleser, & Rockstroh, 2009; Assadollahi & Rockstroh, 2008) report mixed results. In a study using magnetoencephalography (Assadollahi & Rockstroh, 2008), they found larger effects for intransitive than transitive verbs in left MTG and left inferior IFG (infIFG). In a later study using fMRI (Assadollahi et al., 2009), they found greater activation for intransitive than transitive verbs in the left inferior temporal fusiform gyrus and in the right infIFG. An equally complicated picture emerges from the fMRI studies by Thompson and colleagues (Thompson, Bonakdarpour, & Fix, 2010; den Ouden, Fix, Parrish, & Thompson, 2009; Thompson et al., 2007), who report predication effects in both directions (intransitive > transitive and transitive > intransitive) in a wide range of brain regions. In one study (Thompson et al., 2007), they observed greater neural activity in the left supramarginal and angular gyri for transitive relative to intransitive verbs. In a follow-up study (Thompson et al., 2010) using the same task and materials, they observed similar results but this time restricted to the angular gyrus. In a different study, Meltzer-Asscher, Schuchard, den Ouden, and Thomphon (2013) observed greater neural activity in the bilateral angular and supramarginal gyri, as well as in the right posterior superior temporal gyrus (STG), the right MTG, and the right middle and superior frontal gyri for verbs that can act as transitive or intransitive versus verbs that must exclusively act as intransitive. However, in an fMRI study using an overt action picture naming task (den Ouden et al., 2009), they found a wide range of regions that respond differentially to intransitive and transitive verbs, in both directions: transitive > intransitive and intransitive > transitive. Larger intransitive relative to transitive verb effects were reported for the right hemisphere in the thalamus, precentral gyrus, and STS (encompassing Heschl's gyrus and insula) and for left hemisphere in STG extending into Heschl's gyrus; larger transitive relative to intransitive verbs were reported in bilateral fusiform gyrus, middle occipital gyrus (extending into inferior occipital gyrus in the left hemisphere), pMTG and angular and supramarginal gyri, and the precuneus, as well as left hemisphere activation in the postcentral and precentral gyri, middle frontal gyrus (MFG), and infIFG. And, finally, in an fMRI study using written Hebrew sentences on which participants performed a semantic judgment task, Shetreet, Palti, Friedmann, and Hadar (2007, Experiment 1) examined whether the neural activity correlated with the number of components that each verb type could bind, which

included unergative (binding no components), transitive (two components), and ditransitive (three components) verbs. The results showed greater neural activity as a function of the number of components in brain regions typically not associated with language processing—the right precuneus and right anterior cingulate. In contrast, in Experiment 2, they found that the neural activity in brain regions more typically associated with language—left STG and IFG—increased with the number of different types of complements that a verb can take (e.g., "discover" can take a direct object [e.g., John discovered <the killer>$_{DO}$] but also a propositional phrase [e.g., John discovered that <the killer was there>$_{PP}$]).

At least part of the inconsistency across these studies in terms of brain regions involved in transitivity effects may derive from undercontrolled linguistic confounds. For example, verb-specific properties related to the goal of the actions (e.g., telicity or subject agentivity) may account for Thompson et al.'s (2007, 2010) results, because the supramarginal and angular gyri have been implicated in the neural representation of action goals (e.g., Oosterhof, Tipper, & Downing, 2012; Spunt, Satpute, & Lieberman, 2011; Desmurget et al., 2009; Hamilton & Grafton, 2006, 2008; Lestou, Pollick, & Kourtzi, 2008; Majdandzić et al., 2007; Sirigu et al., 2004). Similarly, the predication effects in a number of the regions reported by den Ouden et al. (2009) may be attributed to visual complexity confounds in their naming task (e.g., occipital cortex). In contrast, the inconsistency across and within studies in the direction of the transitivity effects may reflect the encoding of different processes associated with the predication function. For example, the greater neural activity for transitive relative to intransitive verbs may reflect the processing of verb syntactic frame complexity—that is, the set of slots representing the different arguments that a particular verb can bind in a sentence (e.g., subject, direct object), with transitive verbs being more complex than intransitive verbs. It is unclear, however, whether this greater complexity could also be attributed to other dimensions (e.g., telicity, subject agentivity) that have been undercontrolled in previous studies. Alternatively, the opposite direction of the effect—greater activity for intransitive relative to transitive verbs—could index processes reflecting the prototypicality of a verb's syntactic frame, with transitive verbs being more prototypical than intransitive verbs, and therefore easier to process. Note that these are tentative interpretations and that it is still unknown why transitivity effects have been observed in both directions. Nevertheless, what it is relevant for the purpose of our study is that (in)transitivity effects, regardless of their direction, are related to the verbs' binding role of arguments. Therefore, in this study, we measure (in)transitivity as an index of sensitivity to predication without regard to the direction of the effects.

To test the hypothesis that predication drives neural verb preference, we first performed a localizer experiment

that included separate verb and noun conditions to localize verb-specific regions reported in earlier studies. Then, we sought transitivity effects in those regions by means of an experiment that included verbs varying in the transitivity index. If verb-preferring LTC and/or frontal regions respond to predication, we would expect activity in those regions to correlate (positively or negatively) with the probabilistic gradient of transitivity after controlling for relevant intrinsic properties of words (length, frequency, imageability, number of senses) and difficulty of word processing (through RT). We also controlled for other verb-specific dimensions that might be correlated with transitivity and that could contribute to determining the syntactic–semantic role of a particular verb. Those dimensions were telicity, dynamicity, and subject agentivity. Telicity refers to the extent to which an action entails a natural endpoint: telic verbs such as *arrive* (someone is now at a location where she was not before) versus atelic verbs such as *walk* (it describes a way of walking without specifying any natural point at which there is a transition from walking to not walking); dynamicity refers to the expression of change or process: dynamic verbs such as *run* or *kill* versus static verbs such as *exist* or *sleep*; agentivity refers to an action intentionally performed by the subject: *agentive* verbs such as *kill* (the subject decides to perform the action) versus nonagentive verbs such as *like* (the subject involuntarily experiences the action). Controlling for these dimensions is of particular relevance because (a) transitive verbs tend to be telic (Levin & Rappaport Hovav, 2005; Levin, 1999; Dowty, 1991); (b) subject agentivity may also correlate with transitivity, because the subject of static actions (e.g., think, exist) tend to be nonintentional and intransitive; (c) Peelen et al. (2012) observed that the verb-specific region in the LTC responded more to states than dynamic actions. Note that, among all these dimensions, we hypothesize that predication is the property driving verb preference in the brain because of its role in binding the different arguments of a sentence—an exclusive role of verbs. Consider, for example, deverbal nouns (i.e., nouns derived from verbs) such as *destruction*. Despite its belonging to the grammatical category of nouns, this word carries semantic properties related to the verb it was derived from, namely, "destroy," which is telic, dynamic, and subject agentive. Thus, *destruction* expresses an event entailing a natural endpoint (something has been destroyed) that unfolded over time and was probably performed intentionally by a subject. However, in its grammatical quality of noun, *destruction* lacks the function of building a predication nexus like the one expressed by a verb in a sentence: Both "Alexander's destruction of the city" and "Alexander destroyed the city" refer to the same event, but only the latter expresses a full-fledged meaningful proposition. Nevertheless, because all verb-specific dimensions are interrelated, we also examine whether any verb-preferring region that responds to transitivity also represents some of these other syntactic–semantic dimensions related to verb processing.

METHODS

Participants

Fourteen right-handed healthy volunteers (10 women; mean age = 25 years, range = 18–38 years) took part in the lexical decision and the localizer experiments. All participants gave written informed consent for their participation. The experimental procedures were approved by the ethical committee for experiments involving humans at the University of Trento.

Functional Localizer

To identify cortical regions more sensitive to verb relative to noun processing, we used two runs (~8 min each) of a version of the paradigm used in Peelen et al. (2012). Stimuli consisted of 21 Italian verbs and 21 Italian nouns presented in two different syntactic contexts—as single words (e.g., *create*, *book*) or short phrases (e.g., *she creates*, *the book*). The two syntactic contexts were not analyzed separately in this study. Verbs were different from those included in the main experiment and referred to actions and events. Nouns referred to objects of different semantic categories with the exception of tools because they elicit action concepts, which activate portions of the LTC (e.g., Kemmerer et al., 2012; Kable et al., 2005). Verbs and nouns were matched for length in letters (verbs: 7.25, nouns: 7.38; $t(249) < 1$). Verbs had slightly higher logarithmic (log) lemma frequency values than nouns (verbs: 4.49, nouns: 4.32; $t(249) = 2.11$, $p < .036$). Note, however, that any potential verb-specific effect cannot be driven by difficulty confounds related to this difference in log frequency, because verbs were more frequent than nouns. Because the localizer was meant to replicate the typical verb-preferring findings reported in the literature—that is, regardless of transitivity effects—we did not control for verb transitivity. Participants indicated whether a memory probe was identical to one of the three previous stimuli by pressing the right/left buttons on a response pad. In an event-related design, each run consisted of 42 blocks. Each block consisted of four stimuli of one of the two conditions (nouns, verbs), with each condition occurring 21 times within a run in a random order. The fourth stimulus was the memory probe, which was presented in green instead of white. The first three stimuli were visually displayed for 1.5 sec, each followed by a 0.5-sec interval. After an extra 1.5-sec interval, the memory probe was presented for 1 sec, followed by an intertrial interval of 2.5 sec. For "identical" trials, the memory probe stimulus was randomly selected from one of the three preceding stimuli; for nonidentical trials, the memory probe stimulus was randomly selected from the remaining set of 18 stimuli.

One of the runs was administered first, and the other last in the experimental session, with the main experiment in between.

Main Experiment

We used a lexical decision task (four runs of ~6 min). The experimental stimuli consisted of 200 Italian verbs, presented in the gerund or indicative mood with two separate runs for each grammatical mood—none of the verbal forms used could serve as both nouns and verbs. The two verb moods were not analyzed separately in this study. In addition, 100 pseudoverbs were created by replacing one letter in the stem of half of the experimental verbs. Participants indicated whether the letter string presented in each trial was an Italian verb or not by pressing the right/left buttons on a response pad. In an event-related design, letter strings were visually displayed for 1 sec followed by 1 sec of fixation cross (+). Thirty-eight null events consisting of a fixation cross for 2 sec were randomly interspersed with the letter strings. One hundred verbs and 50 pseudoverbs were randomly presented within each run. That is, the order in which participants were presented with verbs, pseudoverbs, and null events was left random. Each verb and pseudoverb was presented once within a run but twice across the whole experiment (once in gerund and once in one of six alternative forms of the indicative mood). Values for different variables were collected for the 200 experimental verbs. Except for length and number of senses, multiple decimal places were used. Imageability values were collected through 19 native Italian speakers rating whether each verb was easy to imagine or not and averaging their choices to obtain an imageability score ranging between 0 and 1, with higher values for highly imageable verbs—it is of note that, although a binary scale was used for this rating, variations in participants' judgments of the imageability of specific verbs yield an approximately uniform, continuous distribution in the imageability values used in this study. Log lemma frequency was estimated on the 1.5 billion-word *itWac corpus* (Baroni, Bernardini, Ferraresi, & Zanchetta, 2009). The number of senses of each verb was derived from the Italian *WordNet* (Pianta, Bentivogli, & Girardi, 2002). Values for telicity, dynamicity, and subject agentivity were collected through five linguists' ratings. Telicity values were obtained through a two-choice decision and ranged from 0 to 1, with higher values for telic verbs. Subject agentivity and dynamicity values were obtained through a three-choice decision, allowing the rating of few ambiguous cases and ranged from 1 to 3, with higher values for strongly nonintentional subject and strongly dynamic actions, respectively. The transitivity index was computed over the 325 million-word *La Repubblica Corpus*, using *LexIt* (Lenci, Lapesa, & Bonansinga, 2012) as A/A + B, where A refers to the number of times a given verb occurs with no other arguments besides the subject and B refers to the number of times the same verb occurs with a direct object. The transitivity score ranged from 0 to 1, with higher values for strongly intransitive verbs and lower values for strongly transitive ones.

Data Acquisition

Functional and structural data were collected with a Bruker BioSpin MedSpec 4T scanner (Bruker BioSpin GmbH, Rheinstetten, Germany) at the Center for Mind/Brain Sciences, University of Trento, Italy. Functional images were acquired using echo-planar T2*-weighted scans. We used 43 axial slices acquired in ascending interleaved order (repetition time = 2000 msec, echo time = 33 msec, flip angle = 73°, field of view = 192 mm, matrix = 64 × 64, voxel size = 3 × 3 × 3 mm), covering the whole cerebral cortex. Structural images were acquired with a T1-weighted 3-D MP-RAGE sequence (sagittal slice orientation, voxel resolution = 1 × 1 × 1 mm, field of view = 256 × 224, GRAPPA acquisition with acceleration factor of 2, repetition time = 2700 msec, inversion time = 1020 msec, flip angle = 7°).

Data Analysis

Data were analyzed using SPM8 software (www.fil.ion.ucl. ac.uk/spm/). After the first four volumes were discarded to avoid T1 saturation, functional data were slice time-corrected, realigned to the first volume, motion-corrected, normalized into standard stereotactic space using the Montreal Neurological Institute (MNI) template, and smoothed with a Gaussian kernel (6 mm FWHM). The time series were high-filtered to eliminate low-frequency components (filter 128 sec). Then the data were modeled based on a conventional general linear model (GLM) for each participant, convolving events with a canonical hemodynamic response function and including the motion parameters as regressors of no interest.

Functional Localizer

Events were 2-sec long and consisted of each word and short phrase including memory probes. In the first-level analysis, each participant's GLMs were created to model single verbs, verb phrases, single nouns, and noun phrases separately. After estimating the model and extracting β-weights, contrasts against baseline were extracted for these four conditions. Then, a subject factor and the four conditions were included in a group-level flexible factorial design. We performed a whole-brain *F*-contrast to look for verb-specific clusters that allowed us to define the ROIs—the Verb > Noun contrast, collapsing single words and short phrases.

Verb-preferring ROIs

To define the ROIs, we first considered the group-level clusters significantly activated for the Verbs > Nouns

Table 1. Verb-preferring Regions

Brain Region	BA	Cluster Size	Cluster, p_{FWE}	Voxel Z	MNI Coordinates x	y	z
L MTG	22	265	.0001	5.4	−48	−43	4
	21			4.87	−54	−28	−2
L superior frontal/bilateral cingulate gyrus	32	246	.0001	5.03	−6	17	40
	32			4.35	9	20	40
	6			4.23	−6	8	55
	6			3.37	−6	11	64
L IFG	44	160	.001	4.53	−54	17	19
	44			3.8	−51	14	4
	47			3.79	−48	32	−2
	44			3.64	−54	17	1
MFG	6			4.3	−36	−1	34
	6			4.3	−39	2	37
	6			4.19	−45	5	40

Regions more active for verbs than nouns in a whole-brain analysis of the localizer experiment.

BA = Brodmann's area; Cluster, p_{FWE} = cluster-level, $p < .05$ FWE-corrected. Subregions denote local maxima; Voxel Z = peak voxel Z score.

contrast of the localizer experiment using a voxelwise threshold of $p < .001$ (uncorrected) and a clusterwise threshold of $p < .05$ (family-wise error [FWE]-corrected). There were four clusters showing a greater response to verbs than to nouns. Those clusters included the left MTG (BA 21 and BA 22), the left superior frontal gyrus extending into the bilateral cingulate gyri (BA 6 and BA 32), the left IFG (BA 44 and 47), and the left MFG (BA 6; see Table 1). Because the greater activation of left superior frontal regions does not seem to reflect grammatical class-specific processes (Willms et al., 2011) and the cingulate gyrus has not been reported as playing a role in the verb versus noun distinction, we did not consider those areas for the ROIs definition. This criterion reduced the probability of including ROIs where the higher activity for verbs relative to nouns is because of any potential confound unrelated to verb processing. Then, we defined six spheres of 7-mm radius around peak coordinates so that most of the cluster was included while avoiding ROIs overlapping. We only considered

Table 2. ROI Selection

Location of the Spheres	MNI Coordinates x	y	z	Verb > Baseline Contrast Value	T	SE	p
L MTG							
pMTG	−48	−43	4	1.45	3.78	0.384	.00024
midMTG	−54	−28	−2	1.03	3.07	0.336	.0026
L IFG							
supIFG	−54	17	19	1.46	3.36	0.435	.001
infIFG$_{(a)}$	−48	32	−2	0.15	0.48	0.313	.63
infIFG$_{(b)}$	−54	17	1	0.83	2.32	0.358	.022
L MFG	−45	5	40	2.84	6.69	0.425	.000001

We defined 7-mm spheres in three clusters showing greater response to verbs than to nouns in the localizer experiment. Spheres were defined around peak coordinates of those clusters avoiding overlap. Any sphere not showing greater response to the contrast verbs versus baseline in the main experiment ($p < .05$ uncorrected for multiple comparisons) was excluded as ROI (i.e., infIFG$_{(a)}$).

Table 3. Lexicality Effect

Brain Region	BA	Cluster Size	Cluster, p_{FWE}	Voxel Z	MNI Coordinates x	y	z
L angular gyrus/STG	39	120	.01	6.16	−48	−70	34
	39			5.10	−42	−58	31
L superior frontal gyrus/MFG	8	325	.0001	5.29	−15	38	46
	10			4.65	−6	62	7
	9			4.64	−6	56	25

Regions more active for verbs than pseudoverbs in a whole-brain analysis of the main experiment.

BA = Brodmann's area; Cluster, p_{FWE} = cluster-level, $p < .05$ FWE-corrected. Subregions denote local maxima; Voxel Z = peak voxel Z score.

as ROIs those spheres showing greater response to verbs versus baseline ($p < .05$, uncorrected for multiple comparisons) in the ROI analysis of the main experiment, using the same flexible factorial design by which we estimated linear increases in activation during verb processing as a function of the parametric modulators (see below; see Table 2). This criterion allowed us to include all ROIs that were at least minimally sensitive to verb processing during the lexical decision task, resulting in five final ROIs (see Results section).

Main Experiment

Events were 2-sec long and consisted of each verb presented during the experiment. Telicity, log lemma frequency, number of senses, imageability, length, response latencies (RTs), subject agentivity, event dynamicity, and transitivity were included as parametric modulators. Because parametric modulators are serially orthogonalized with respect to those previously entered in the GLM, the modulator of interest (i.e., transitivity) was entered last while the order of the remaining eight was left random. Pseudoverbs in the two grammatical moods and errors were modeled separately. β-weights estimated from each subject's GLM were used to create statistical maps of contrasts of interest. For verb processing-related activity, we contrasted verbs and pseudoverbs against baseline. The effect of lexicality was estimated in a group-level analysis by including a subject factor and a condition factor (verbs, pseudoverbs) in a flexible factorial design. We performed whole-brain F-contrast to assess the verb processing-related activity compared with that of pseudoverbs (i.e., the effect of lexicality) using a voxelwise threshold of $p < .001$ (uncorrected) and a clusterwise threshold of $p < .05$ (FWE-corrected). To estimate linear increases in activation during verb processing as a function of the parametric modulators, we contrasted each of them across baseline—contrasts were performed considering only verbs (i.e., verbs and pseudoverbs were never collapsed). All contrasts were combined in a group-level model based on a flexible factorial design that included a subject factor along with the "verb" condition as well as the nine para-

metric modulators. We used MarsBaR toolbox (Brett, Anton, Valabregue, & Poline, 2002) to obtain the mean parameter estimates at the group level for the contrasts of the nine parametric modulators within each of the five predefined ROIs. Results were considered at an α of 0.001, based on Bonferroni correction for multiple comparisons, taking into account 45 comparisons (5 ROIs, 8 control modulators, 1 parametric modulator of interest [transitivity], $p = .05/45$). Note that, because of the orthogonalization process, only the potential effect of the parametric modulator entered last in the GLM (i.e., transitivity) persists independently of any other modulator. In the case of the control modulators, however, any potential effect could be driven by the influence of any modulator entered later in the GLM. For the sake of completeness, in case any control modulator showed a significant linear correlation with activity in any ROI, we redid the analyses placing that modulator last.

RESULTS

Behavioral Results

Responses were faster and more accurate for verbs (820 msec, 93.8% correct) than pseudoverbs (927 msec, 84.2% correct; both $p < .0001$). Neither RT ($r = −.14, p < .296$) nor accuracy ($r = −.007, p < .591$) correlated with the parametric modulator of interest (i.e., transitivity).

Whole-brain Analysis

We observed an expected effect of lexicality reflected by greater neural activity for verbs relative to pseudoverbs in the left angular gyrus extending into the STG and the left superior frontal gyrus, including MFG areas (see Table 3). But no modulation of the neural activity as a function of transitivity was observed anywhere in the brain.

Verb-preferring ROIs

We were able to localize the most commonly reported verb-preferring region—the left LTC—that we divided

in two ROIs, the pMTG [−48 −43 4] and the middle MTG (midMTG) [−54 −28 −2]. Additionally, we also identified verb-preferring left frontal regions whose detectability has been rather elusive in previous functional neuroimaging studies. Those regions were the MFG [−45 5 40], infIFG [−54 17 1], and superior IFG (supIFG) [−54 17 19] (Figure 1A, B).

Are Verb-preferring ROIs Sensitive to Transitivity?

Once controlling for all other factors, we observed a clear linear increase of activity as a function of transitivity in one LTC ROI, the pMTG ($p < .000004$). The correlation between activity and transitivity also survived the threshold imposed by the correction for multiple comparisons ($p < .001$; see Methods) in one frontal ROI, the infIFG ($p < .0004$). The correlation between activity and transitivity reflected greater activity for strongly intransitive relative to strongly transitive verbs in these regions. No other verb-preferring ROI was influenced by transitivity (all $ps > .03$; Figure 1C).

Effect of Variables Other than Transitivity

Neural activity was not modulated by any other semantic–syntactic property of verbs (i.e., telicity, dynamicity, and subject agentivity) in any verb-preferring region. However, the activity in the two verb-preferring ROIs sensitive to transitivity also showed influence of RT (pMTG and infIFG), imageability (infIFG), and length (infIFG; Figure 1C). When redoing the analyses placing each of these variables as the last parametric modulator in the GLM (see Methods for details), we still observed the effects of RT and length in infIFG (and a marginal RT effect in pMTG), as well as effects of RT in other verb-preferring ROIs not sensitive to transitivity—the MFG and supIFG. In contrast, the effects of imageability in infIFG vanished and were not observed in any other ROI (see Table 4).

DISCUSSION

This study was designed to explore which verb property is encoded (relative to nouns) in verb-preferring regions. We hypothesized that the fundamental syntactic–semantic distinction between verbs and nouns—predication—is what drives the widely observed verb-preferring activity. Because the predication-building function is limited to verbs, this question can only be addressed by testing whether verb-preferring regions distinguish between verbs with different predicative properties. To test this hypothesis, we first replicated previous studies showing
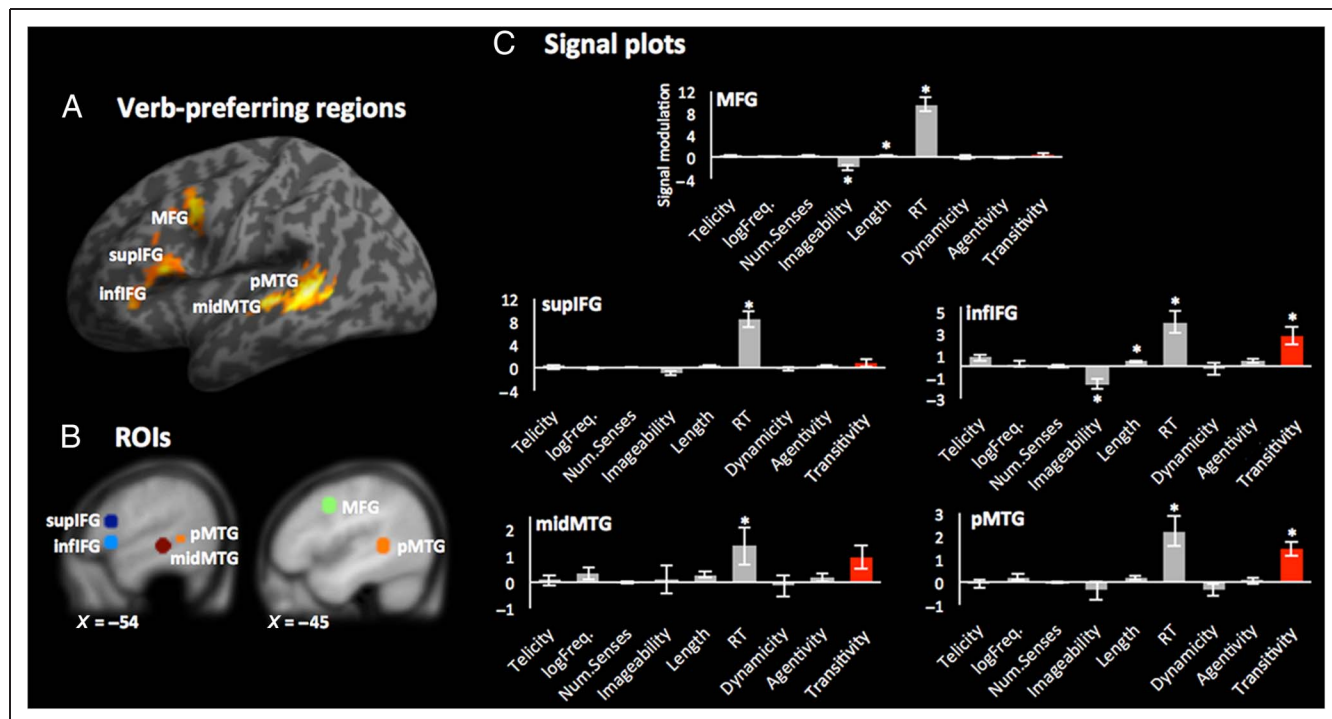

Figure 1. (A) Verb-preferring clusters resulting from contrasting verbs with nouns in the localizer experiment that were considered for ROI definition. (B) Verb-preferring ROIs defined as 7-mm spheres around peak coordinates of the clusters shown in A. (C) Signal plots for the modulation of the BOLD response as a function of transitivity (red bars) and all control modulators (gray bars). Note: Because of the serial orthogonalization of the modulators in the GLM, they were entered in the order (left to right) that is shown in the plots—leaving transitivity last to make sure its effects persisted independently of any control modulator (see Methods; see Table 4 for the results of the complementary analyses in which we placed last in the GLM those control modulators showing here a significant linear correlation with activity). Error bars represent the *SEM*. *p value fulfills correction for multiple comparisons ($p < .001$; see Methods).

Table 4. Effect of Variables Other than Transitivity

ROI	Variable	Signal	T	SE	p
MFG	RT	9.8	6.76	1.45	.000001[a]
	Length	0.26	2.61	0.1	.01
	Imageability	−0.97	−1.66	0.584	.099
supIFG	RT	8.51	6.44	1.321	.000001[a]
	Length	0.18	1.85	0.097	.06
	Imageability	−0.12	−0.21	0.571	.83
infIFG	RT	3.9	3.99	0.977	.0001[a]
	Length	0.42	3.6	0.117	.00045[a]
	Imageability	−1.16	−1.14	1.018	.25
midMFG	RT	1.55	1.94	0.799	.054
	Length	0.25	2.6	0.096	.01
	Imageability	0.37	0.47	0.787	.64
pMTG	RT	2.41	3.29	0.733	.0013
	Length	0.15	1.97	0.076	.05
	Imageability	0.03	0.05	0.6	.96

We re-did the analysis three times, each placing last one of the three parametric modulators of no interest that showed a significant linear correlation with activity in any ROI in the first analysis (i.e., RT, length, imageability). Because of the orthogonalization process (see Methods), this action allowed us to examine the effects of these three variables unaffected by any other modulator.

[a]Region survives correction for multiple comparisons ($p < .001$; see Methods).

verb-preferring responsivity in the left LTC and in the less-consistently observed frontal regions by contrasting verbs with nouns in a localizer experiment. Then we examined whether different ROIs within those verb-preferring regions (LTC: pMTG, midMTG; frontal regions: MFG, infIFG, supIFG) were sensitive to the property of predication by seeking effects of verb transitivity (here defined as a gradient contrast between transitive and intransitive verbs) on neural activity. The results showed that, after controlling for relevant intrinsic properties of words and task difficulty, the activity in two verb-preferring ROIs—pMTG and infIFG—showed a positive correlation with transitivity. No other semantic–syntactic property of verbs (i.e., telicity, dynamicity, and subject agentivity) independently modulated activity in any ROI.

To the extent that (in)transitivity is a core aspect of predication structures defined by verbs, the correlation between transitivity and activity in pMTG and infIFG indicates that the role of verbs as "predication builders"—a role that nouns do not take—drives the grammatical class distinction in those regions. This hypothesis is silent on the specific direction of the effect: It does not speak to why neural activity increased for intransitive relative to transitive verbs (see also Assadollahi et al., 2009; den Ouden et al., 2009; Assadollahi & Rockstroh, 2008). Nonetheless, as

argued in the Introduction, the correlation between transitivity and neural activity may be tentatively interpreted in terms of verb prototypicality. The lower neural activity in pMTG and infIFG for transitive versus intransitive verbs would reflect the fact that verbs binding agents and objects (transitive) are easier to process in those regions because of their higher prototypicality compared with verbs that do not take a direct object (intransitive).

A question that arises when interpreting the role of pMTG in representing a word's predication property is how this hypothesis fits with previous data implicating this region in processing semantic information of actions (e.g., Kemmerer et al., 2012; Kalénine et al., 2010; Noppeney et al., 2005; Tranel et al., 2003; Martin et al., 1995). However, as already noted, we have found in several studies (Bedny et al., 2008, 2012; Peelen et al., 2012; Shapiro et al., 2006) that the verb-preferring regions do not show greater preference for action verbs over other verb types. Indeed, if anything, state verbs and abstract verbs, more generally, produce greater activation in these regions (Peelen et al., 2012). The latter results are consistent with a broader characterization of the role of pMTG in the representation of verbs. The predication function of verbs does not merely consist in linking arguments within a sentence but also in determining the roles and relations that arguments (typically nouns) take—verbs inform about what an agent does (e.g., *John runs*), its properties (e.g., *John stinks*), or what it does *to* or *with* something else (e.g., *John rides the bike*). This makes predication a semantic–syntactic interface where semantic information is crucial to determine that, for instance, the syntactic structure "*The boy likes*" is not felicitous because the verb "like" needs an object "to be liked." It is then plausible that the pMTG, as a region involved in representing word meaning, provides the relevant neural substrate for the representation of the semantic–syntactic interface captured by a verb's predication role.

Transitivity is related to the number of arguments required by a verb. However, verbs are not the only category that can project an argument structure. An interesting question that follows from our results is whether the pMTG and infIFG would respond more to those nouns that also express argument structure to some degree (e.g., Alexiadou & Grimshaw, 2008). Consider, for example, *father* (e.g., *John's father*—where *father* expresses a relationship between two agents; in this context, it is interesting to note that, in some languages, kinship relations are expressed by verbs; Evans, 2000), *author* (e.g., *John is the author of a best seller*—where *author* embeds the concept of an agent writing something), or *killer* (e.g., *The killer of the man*—where *killer* is a deverbal noun derived from the verb *kill*). It is worth considering for future research whether brain regions sensitive to the predicative role of verbs respond differentially to nouns with or without argument structure. Alternatively, it is possible that those regions only respond to predication in the narrower sense that we suggested in the Introduction— the possibility of creating propositional expressions of

some state of affairs that can be true or false (e.g., *The man was killed*)—which is exclusively reserved to verbs. For instance, the noun phrase *The killer of the man* contains a predicative noun, but it does not express a state of affairs, because it only refers to an entity. Instead, the sentence *The man was killed* is a statement that can be true or false. Moreover, it is worth stressing that the direct object of the transitive verb *kill* is obligatory (*The soldier killed the man* vs. **The soldier killed*), whereas the argument of the corresponding deverbal noun is fully optional.

Both the pMTG (marginally) and infIFG were also sensitive to RT, and the infIFG was also sensitive to length. However, because the effect of predication survived after regressing out both RT and word length, we may confidently conclude that the observed transitivity effect in these regions is not because intransitive verbs are associated with higher RTs or length. In addition, other verb-preferring regions not sensitive to transitivity also showed sensitivity to RT (see Table 4), indicating that the presence or absence of the transitivity effect was independent of whether the ROIs also responded to other variables. In any case, the orthogonalization process used in this experiment (see Methods for details) was designed precisely to ensure that any surviving factor, such as transitivity, cannot be explained as the influence of a control modulator.

Finally, the contrast verbs versus nouns in the localizer experiment also gave significant verb-preferring activity in three other ROIs (midMTG, MFG, and supIFG). No effect of transitivity or any other verb-specific property (i.e., telicity, dynamicity, and subject agentivity) was observed in these regions. Therefore, at present, we do not have enough information to assess what grammatical distinction, if any, these regions might capture, leaving the question of what role these areas might play in determining their verb specificity to future research.

In short, we have observed that two verb-preferring regions—the left pMTG and infIFG—are sensitive to transitivity as a measure of the verb-specific predication function. Following the rationale that verbs' fundamental role is that of predication whereas nouns lack this property, we can conclude that verb preference in these regions is driven by this syntactic–semantic function. These results represent the first positive evidence on the question of what grammatical class distinctions are captured in the brain. In addition, our results reveal that, at least in the posterior LTC and inferior frontal cortex, these distinctions reflect the representation of grammatical (verbs vs. nouns) and not semantic properties associated with action concepts (e.g., dynamicity). Further research is needed to shed light into how other verb-preferring regions capture the distinction between verbs and nouns.

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