

Cortical signatures of noun and verb production

Kevin A. Shapiro[†], Lauren R. Moo^{†‡}, and Alfonso Caramazza^{†§}

[†]Department of Psychology, Harvard University, 33 Kirkland Street, Cambridge, MA 02138; and [‡]Department of Neurology, Massachusetts General Hospital, 55 Fruit Street, Boston, MA 02114

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Categories like “noun” and “verb” represent the basic units of grammar in all human languages, and the retrieval of categorical information associated with words is an essential step in the production of grammatical speech. Studies of brain-damaged patients suggest that knowledge of nouns and verbs can be spared or impaired selectively; however, the neuroanatomical correlates of this dissociation are not well understood. We used event-related functional MRI to identify cortical regions that were active when English-speaking subjects produced nouns or verbs in the context of short phrases. Two regions, in the left prefrontal cortex and left superior parietal lobule, were selectively activated for verb trials compared with noun trials; one region in the left inferior temporal lobe was more active during noun production than verb production. We propose that these regions are involved in representing core conceptual properties of nouns and verbs.

actions | cortex | language | objects

Linguists since antiquity have classified words into two basic parts of speech, noun and verb (or equivalents thereof) (1, 2). These categories are universal across languages (3) and represent elemental building blocks for grammatical rules that combine single words into phrases and sentences, allowing us to distinguish, for example, well formed sentences (*the birds are singing*) from ungrammatical sentences (**the sings are birding*). Prototypically the class of nouns includes words that denote concrete objects, whereas verbs refer to imageable actions, but this semantic association is hardly restrictive: abstract concepts (*the idea*) and action words (*the kick*) can also be named by nouns, and not all verbs name actions (*to enjoy*) (4). Indeed, beginning at age 4 or 5 normal speakers can even assign grammatical categories to meaningless pseudowords, like *the wugs* and *he zibs* (5).

What cognitive and neural mechanisms underlie this extraordinary productivity? Some clues have come from the study of brain-damaged patients who appear to have selective difficulties in producing either nouns or verbs (6, 7). Patients with lesions in the left temporal cortex often present with deficits in noun production; left frontal lesions, on the other hand, are associated with impairments in producing verbs (8–11). However, the demonstration of such lesion-deficit patterns has relied, in most cases, on patients' abilities to name pictureable items of different types (objects and actions). This limitation has made it hard to ascertain whether such impairments are truly grammatical in nature, or more reflective of problems in accessing particular aspects of word meaning, like perceptual properties of objects or sensorimotor contingencies associated with actions.

Prior functional imaging studies of noun and verb processing (12–16) have been bedeviled by similar confounds. Although some of these experiments have used abstract as well as concrete word stimuli, thereby avoiding the simple conflation of semantic and grammatical categories, they have all nevertheless used tasks, like lexical decision (13–15) and word categorization (15, 16), that emphasize nongrammatical aspects of word retrieval. Interestingly, these studies have not turned up consistent differences in patterns of cortical activity related to noun and verb processing.

We have contended that true noun–verb differences should emerge in word production tasks in which on-line access to grammatical category information plays a crucial role (17, 18). For instance, we have shown that some patients with impairments in

noun or verb naming are also unable to use pseudowords as members of the impaired category; thus, a patient with a noun-naming deficit was able to say *he wugs*, but not *the wugs* (17, 19). Likewise, a study with repetitive transcranial magnetic stimulation showed that suppressing a portion of the left prefrontal cortex resulted in interference with the production of verbs and pseudowords used as verbs, but not nouns or pseudonouns (20).

These observations bolster the hypothesis that specific brain regions are engaged in processing nouns and verbs as members of distinct grammatical categories. Strictly speaking, however, such dissociations do not imply that categorically selective regions must subserve grammatical (that is, syntactic) processes. An area of cortex that is found to be sensitive to a word's grammatical status might indeed be one that is crucial for category-specific syntactic operations, like the production of inflectional morphemes. Alternately, such an area might represent the unique configuration of lexical properties that define a word's grammatical use (18). The former assumption would be favored if areas of selective activation for nouns and verbs were observed in a part of the brain known to be important for syntactic processing, such as the left posterior frontal cortex (18, 19).

In the present study we used event-related functional MRI (fMRI) to identify brain regions that were activated when subjects produced nouns and verbs in the context of short phrases or sentences, like *many doors* and *he weeps*. The manipulation of morphological inflections in this task (like the noun plural and verb agreement marker *-s*) ensured that subjects accessed grammatical category information. Moreover, this task differs from the tasks used in other functional imaging studies of word processing in that it required subjects to produce words aloud, making it more comparable to studies of production disorders in aphasic patients than are most earlier studies, which used comprehension tasks.

To control for the confounding of grammatical and semantic factors in word production, we divided the study into several experiments. Each of these experiments was performed by one group of subjects in the scanner, and by a separate group of subjects outside the scanner, to allow collection of reaction time data for the same stimuli. (For sample stimuli, see Table 2, which is published as supporting information on the PNAS web site) In Exp. 1, subjects produced nouns, verbs, and pseudowords used as nouns or verbs. Commonalities in patterns of cortical activation between real words and pseudowords of a given category could be taken to exclude areas responsive to specific perceptual or sensorimotor properties associated with word meaning, because pseudowords by definition have no stored semantic features.

Nevertheless, it could be argued that pseudowords like *the wug* and *he wugs* are automatically interpreted as naming unknown or generic objects or actions; therefore, activation during pseudoword trials could still reflect a process of retrieving information related

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Data deposition: The neuroimaging data have been deposited with the fMRI Data Center, www.fmridc.org (accession no. 2-2006-120NY).

[§]To whom correspondence should be addressed. E-mail: caram@wjh.harvard.edu.

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Table 1. Regions of activation associated selectively with noun or verb production

Region	Brodmann area	k	x	y	z
Nouns > verbs					
Left fusiform gyrus	20	36	-36	-42	-16
Left superior frontal gyrus*	10	17	-22	59	23
Right parahippocampal gyrus*	28	89	24	-17	-19
Verbs > nouns					
Left middle frontal gyrus/sulcus	9	17	-46	6	40
Left superior parietal lobule	7	23	-32	-57	64
Left superior temporal gyrus	22	39	-57	-40	9
Right inferior parietal lobule	40	166	38	-48	48

K, cluster extent in contiguous voxels. Talairach coordinate (x, y, z) refers to the center of activation within each region. Regions of significant activation were defined as clusters with $k \geq 12$ and voxelwise type I error rate equivalent to $P < 0.005$. With the cluster extent threshold method, regions with $k \geq 35$ have clusterwise type I error rates equivalent to $P < 0.05$ (corrected for multiple comparisons).

*These regions showed event-related decreases in activation.

to these semantic categories. To investigate this possibility, Exp. 2 comprised trials with both abstract and concrete nouns and verbs. It would seem less plausible that a brain region selectively active for concrete nouns, abstract nouns, and pseudonouns, for example, should be involved primarily in processing features of objects. We would rather conclude that such a region responds to properties shared by items of the grammatical category noun.

We also wanted to ensure that any such region, if it were found, did not merely reflect processing of some specific property shared by nouns in this task, but not necessarily diagnostic of category membership, like the presence or absence of the plural ending *-s* (or the third-person plural *-s* for verbs). In Exp. 3, subjects produced nouns and verbs with both regular inflectional endings (*ducks, played*) and irregular inflections (*geese, wrote*). If a region associated with noun production in both of the previous experiments responded equally to regular and irregular nouns (but not verbs of either type), it would further suggest that this region distinguishes nouns from verbs at a level before the specification of particular morphophonological transformations.

Results

Behavioral Results. The mean response latencies for each condition in the behavioral study are given in Table 2. There was no main effect of grammatical category on reaction time in either Exp. 1 or Exp. 2, nor were there any interactions between variables. In Exp. 1, response latencies to pseudowords were slightly longer on average than latencies to real words, although this difference did not reach statistical significance ($F_{\text{lex}} = 2.29, P < 0.15$). In Exp. 2, response latencies on trials with concrete words were significantly longer than on trials with abstract words ($F_{\text{con}} = 15.72, P < 0.002$). In neither experiment did we find main effects of morphological change. In other words, reaction times did not differ between trials in which subjects reproduced the stimulus word (e.g., *he thinks/he. . .*) and those in which a change in inflection was required (*he thinks/they. . .*). Although this is obviously a null result, it can be interpreted (with caution) as evidence that even the “no change” trials entail some morphological processing and do not merely involve retrieval of a lexical item from short-term memory.

In Exp. 3, three significant main effects emerged: response latencies were longer for verbs than for nouns ($F_{\text{cat}} = 50.38, P < 0.001$), longer for irregular words than for regular words ($F_{\text{reg}} = 14.92, P < 0.002$), and longer on trials that required no morphological change than on trials that did require change ($F_{\text{cng}} = 18.52, P < 0.001$). In addition, the discrepancy between regular and irregular items tended to be larger for verbs than for nouns ($F_{\text{cat} \times \text{reg}} = 2.26, P < 0.15$). No other interaction was significant.

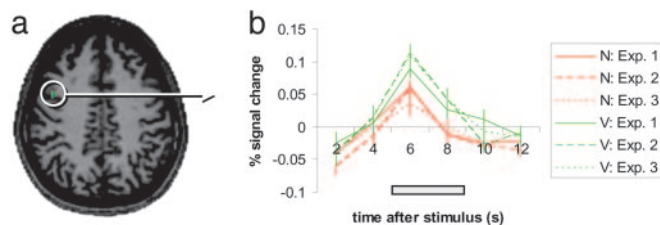


Fig. 1. Extraction of event-related time courses from regions of interest. (a) Regions of interest, such as the left middle frontal area depicted, were defined by contrasts between maps of event-related activation during noun and verb trials (displayed here on an anatomic image from a single subject, A.R.). (b) Subsequently, we extracted event-related activation time courses from each of these regions for all of the 24 experimental event types. For simplicity, each condition graphed here represents the mean of four event types within a grammatical category (N, noun; V, verb). Mean percent signal change relative to baseline at time points 6 and 8 s after stimulus onset was used as the dependent variable in post hoc statistical tests.

Distinct Cortical Regions. As an initial approach to analyzing the fMRI results, we collapsed noun and verb trials across all three experiments and generated contrasts between event-related activation maps for trials of each category (i.e., noun – verb and verb – noun). These contrasts yielded five distinct cortical regions in which we observed a significantly greater event-related increase in activation for one category compared with the other (Table 1). Verb production was correlated with selective activation in part of the left middle frontal gyrus, the left superior temporal gyrus, and superior regions in the posterior parietal cortices bilaterally. Noun production, on the other hand, coincided with greater activation only in the left middle fusiform gyrus.[†]

We then examined each of these five regions by using ANOVAs on the event-related activity time courses (Fig. 1), to determine whether the observed noun–verb differences were consistent in the three experiments. In any of the regions described above, it was possible that a significant difference in activation between categories could have been driven by a strong dissociation in only one experiment, with no differences in the other experiments. That is, a difference could have been obtained within an experiment even if only one type of stimulus item had evoked a robust response (e.g., concrete or abstract words in Exp. 2). Such an explanation could be ruled out if a region showed a main effect of grammatical category that did not interact with experiment or other factors.

Activation Associated with Noun Production. One area within the left fusiform gyrus had consistently greater activation across all three experiments for noun trials than for verb trials (Fig. 2a). Analysis of variance in the event-related response measure ($R^2 = 0.83, P < 0.01$) revealed a main effect of grammatical category ($F_{\text{cat}} = 5.15, P < 0.05$), but no other significant effects. The results indicate that this area is selectively responsive during noun production, regardless of the semantic or morphological characteristics of the noun being produced.

Activation Associated with Verb Production. Of the four areas for which activation appeared to increase selectively during verb pro-

[†]Noun production was also correlated with decreases in activation of the left superior frontal gyrus and right parahippocampal gyrus. These decreases could reflect task-related inhibition for noun trials, a return to baseline of areas of unsuspected activation in other phases of the experiment (e.g., verb trials, stimulus phrase processing), or some other poorly understood modulation of cortical activity. In any case, we have no pretheoretical notions about the role of these two areas in lexical production. There is some evidence that the right parahippocampal gyrus specifically is involved in processing the spatial location or background context of perceived objects (21), and that damage to this area impairs visual-spatial memory without affecting object recognition (22). If this is true, perhaps right parahippocampal deactivation in noun production reflects an inhibition of context-specific object processing in favor of more “categorical” processes.

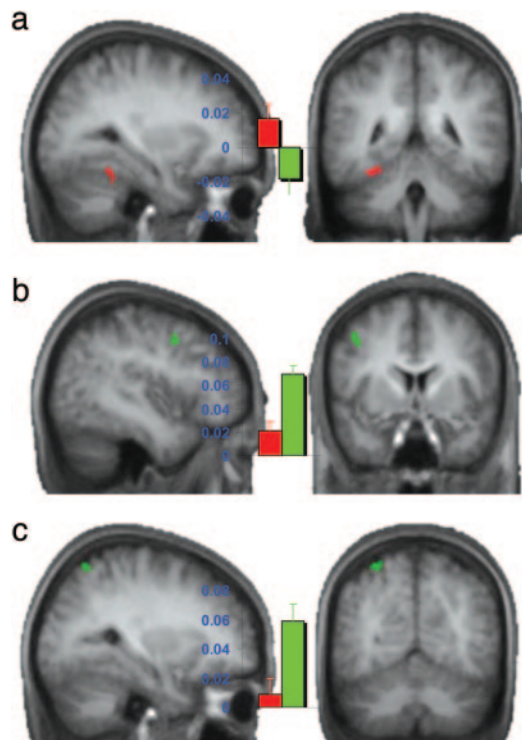


Fig. 2. Brain regions showing consistent patterns of selective event-related activation for nouns (red) and verbs (green) across all three experiments. (a) The middle/anterior portion (BA 20) of the left fusiform gyrus was active for noun trials. (b and c) The left middle frontal gyrus/sulcus (BA 9) (b) and the left superior parietal lobule (BA 7) (c) were active for verb trials. Bar graphs show category-specific event-related activation for each region collapsed across all three experiments, with mean percent signal change relative to baseline between 6 and 8 s poststimulus on the ordinate.

duction, two showed effects of grammatical category that did not differ across experiments, with no significant effects of any other variable. These regions were the left prefrontal cortex ($R^2 = 0.86$, $P < 0.001$; $F_{\text{cat}} = 18.59$, $P < 0.001$) and the left superior parietal cortex ($R^2 = 0.84$, $P < 0.01$; $F_{\text{cat}} = 8.65$, $P < 0.01$). Briefly put, these two areas seem to be activated more during verb trials than noun trials of all types (Fig. 2*b* and *c*). In a third region, the right inferior parietal lobule, the omnibus analysis did not reach significance ($R^2 = 0.77$, $P > 0.25$); therefore this region will not receive further consideration.

The fourth area of activation was in the left superior temporal lobe and displayed a more complex response profile across the three experiments. The initial analysis ($R^2 = 0.87$, $P < 0.0005$) revealed a highly significant main effect of grammatical category ($F_{\text{cat}} = 33.24$, $P < 0.0001$), but also a main effect of stimulus type ($F_{\text{typ}} = 3.71$, $P < 0.05$) and an interaction between these two factors ($F_{\text{cat} \times \text{typ}} = 4.84$, $P < 0.01$).

To determine which event types within each experiment were driving these effects in the left superior temporal lobe, we conducted additional analyses for each of the three experiments. Exps. 2 and 3 (but not Exp. 1) produced strong main effects of grammatical category in this region (Exp. 2: $R^2 = 0.41$, $P < 0.005$; $F_{\text{cat}} = 7.17$, $P < 0.01$; Exp. 3: $R^2 = 0.51$, $P < 0.0001$; $F_{\text{cat}} = 26.19$, $P < 0.0001$). These effects were modulated by concreteness in Exp. 2 ($F_{\text{cat} \times \text{con}} = 6.67$, $P < 0.02$) and by morphological regularity and the requirement for overt morphological change in Exp. 3 ($F_{\text{reg}} = 9.62$, $P < 0.005$; $F_{\text{cat} \times \text{reg}} = 5.50$, $P < 0.05$; $F_{\text{cat} \times \text{cng}} = 6.02$, $P < 0.02$).

Unlike the left prefrontal and superior parietal areas described above, the left superior temporal gyrus showed a pattern of activity that was highly variable across experiments. Interestingly, this

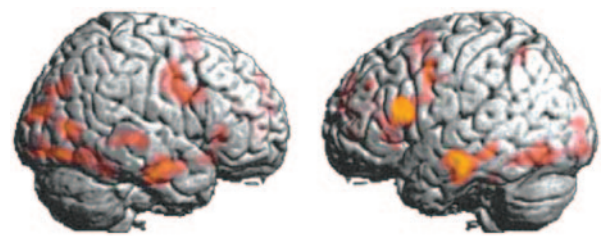


Fig. 3. Patterns of activation corresponding to the conjunction of noun and verb trials relative to fixation. Common areas of activation included the inferior frontal and middle temporal gyri bilaterally and other cortical areas. (Left) Right hemisphere projection; (Right) Left hemisphere projection.

variability seems to correlate with the differences in reaction time between trial types in the chronometric version of the experiments. Exp. 1 produced no significant differences either in reaction time chronometry or event-related activation within this region, Exp. 2 produced differences related to concreteness in both settings, and Exp. 3 produced differences related to regularity and morphological change in both settings. In all cases, more activation was observed within the superior temporal gyrus for trial types with longer mean response latencies. This relationship suggests that the left superior temporal gyrus may be sensitive to factors affecting the difficulty of retrieving a lexical item, but not specifically to an item's grammatical category.

Common Cortical Regions. Although our primary interest was in identifying regions that were active selectively for either nouns or verbs, it should be noted that the areas highlighted by these contrasts represent small, functionally distinct components of much larger networks engaged in word production. A majority of the cortical tissue activated for trials of each type undoubtedly is involved in both noun and verb processing. To illustrate this point, we computed the conjunction of activity for noun and verb trials relative to fixation (Fig. 3). Both noun and verb trials nonselectively engaged a number of brain regions known to be important for language processing, including areas within the inferior prefrontal and premotor cortex, middle temporal gyrus, and temporal-occipital junction (Table 3, which is published as supporting information on the PNAS web site).

Discussion

The experiments described here reveal four brain regions whose patterns of activation correlated selectively with the production of words of one grammatical category. We identified three regions in which significantly greater activity was associated with the production of verbs than nouns: the left prefrontal cortex, left superior parietal lobule, and left superior temporal gyrus. There was one area, the left anterior fusiform gyrus, in which activity for nouns was greater. For all but one of these areas (the left superior temporal gyrus), event-related responses were indistinguishable for real words and pseudowords, abstract and concrete words, and regular and irregular morphological transformations within a given category. Such consistent patterns of activation over words with different semantic and morphological properties can be taken as signatures of cognitive processes specific to noun and verb production.

On the other hand, activation in the left superior temporal gyrus was not consistent across experimental manipulations, but seemed to vary directly with the difficulty of producing words with different morphological and semantic properties. This observation is in keeping with the postulate that the superior temporal gyrus may be involved in lexical word form retrieval in production (23) and comprehension (24). By extension, it may be that grammatical category differences are evident in this region only when such differences covary with another dimension affecting lexical production. It is clear that computing the past-tense form of a verb, for

example, entails semantic, morphological, and phonological operations distinct from those involved in computing the plural form of a noun. The degree to which these two sets of operations differ in complexity may affect both the amount of time it takes speakers to produce words of each type and the amount of activation elicited in the left superior frontal gyrus during those acts of production.

It is worth noting again that none of the other cortical areas identified in this study were sensitive to probable “difficulty” effects (reflected in reaction times). Arguably, this fact reinforces our conclusion that these areas are specifically involved in computations related to the grammatical categories of noun and verb.

Comparison with Prior Neuroimaging Studies. Few neuroimaging studies to date have investigated noun and verb retrieval by using tasks with comparable processing demands across the two categories. Some experiments comparing nouns and verbs have used word generation paradigms (12, 25), which have been criticized for conflating processes involved in the production and retrieval of words of both categories (16, 26). Of the studies in which noun and verb tasks were better matched, two [one conducted in English (16) and one in Italian (13)] have reported areas of greater activation for verbs, but no areas in which nouns were more activated.

Both of these previous studies found that verbs, compared with nouns, selectively engaged parts of the left inferior prefrontal cortex, or Broca’s area. This activity has been interpreted as specifically reflecting the processing of inflected verbs, because experiments in which stimulus words bore no overt morphological marking did not find activity in the same area (16). As we have pointed out, however, the tasks for which verb processing correlated with left inferior prefrontal activity did not require access to grammatical information about stimulus words. Moreover, it is not even obvious that the “verb” stimuli in these studies should be interpreted unambiguously as verbs: both the English progressive form ending in *-ing* and the Italian infinitive, said to represent “inflected” verbs (16), are compatible with use as nouns in certain contexts (for example, *the singing*).

In the present study, with a production task constructed to rule out such grammatical ambiguities, the left inferior prefrontal cortex was activated for both noun and verb trials relative to baseline. Clearly, this region plays an important role in the processing of morphological inflection. Event-related selectivity for verb trials, however, was not observed, suggesting that Broca’s area may be important for morphosyntactic or morphophonological operations of a more general nature.

Prior findings of verb-related activation in the left inferior prefrontal cortex may have been driven by some factor not directly related to the retrieval of grammatical category information, such as the greater lexical and contextual ambiguity of verb stimuli (27). Even in a recent study where an attempt was made to control for word form ambiguity, the stimuli included more than twice as many unambiguous nouns as verbs (16).

Functional Significance of Noun and Verb Activation Patterns. We anticipated that the task used in this study would illuminate cortical areas involved in grammatical aspects of noun and verb production. We allow that this particular paradigm may not fully engage the cognitive machinery for lexical access; for example, it is not obvious that words must be retrieved afresh from the lexicon on every trial. Nevertheless, the task is clearly productive in the sense that it requires subjects to retrieve and produce word forms with different inflectional properties.

Based on prior investigations of the morphological manipulation of nouns and verbs by patients with category-specific production deficits (17, 19), we have predicted elsewhere that brain regions crucial for this kind of task are likely to be found in the left prefrontal cortex (18). Our results, however, do not fully bear out this expectation. Although the finding of verb-related activity in the left prefrontal cortex is consistent with the hypothesis that this

region is engaged in the manipulation of verbs as grammatical objects (7, 19, 20), the prior likelihood that the other activated areas are critical for morphological processing seems rather low. Instead, the foci of activation we observed for nouns and verbs seem more closely to correlate with areas that have been associated with the processing of words for artifacts (28, 29) and actions (30), respectively. The question, then, remains: precisely what kind of processing is reflected in these patterns of cortical activity?

One possibility is that these areas are sensitive to distributional information that correlates with the grammatical categories noun and verb. For example, in English nouns tend to appear in certain positions within sentences and to co-occur with the plural marking and the definite determiner *the* (among other morphemes), whereas verbs are compatible with past-tense marking, agreement marking, and other syntactic alternations. It has been postulated that such correlated networks of morphological and positional properties underpin the acquisition of grammatical categories by children (31, 32), and they may comprise the syntactic features (or “nodes”) that determine the discrete assignment of words to one grammatical category or the other (17, 33).

On this hypothesis, the cortical localization of category-specific distributional feature networks might be expected to hew closely to areas involved in the semantic representation of the first words over which categorical inductions are made (34). For example, the noun network could take root in the left anterior fusiform gyrus because of its proximity to more posterior fusiform regions involved in object recognition and classification (35–38). Likewise, verb nodes might colocalize with areas important for the representation and selection of motor schemata associated with prototypical action verbs, like the left prefrontal cortex (30, 39, 40), or with left parietal regions that may contribute to “motor attention” (40) or integrate limb positions to construct complex representations of action postures (30, 39, 40). Note that we do not mean to imply that the grammatical processing of nouns and verbs (including abstract items) somehow involves object or action recognition *per se*. Rather, this account offers one explanation for the seemingly puzzling observation that a grammatical task produces activation in areas close to those thought to be important for semantic processes.

A distinct, but related, possibility is that the areas highlighted in the present study are involved in representing semantic information of a very abstract nature, corresponding to the “core” conceptual properties of nouns and verbs. For example, it has been proposed that all nouns refer to entities that can be “individuated,” that is, distinguished from other items of the same type (41). This includes not only nouns naming concrete objects, but also mass nouns (*this butter*), abstract nouns (*these truths*), and nominalizations (*the kick*). The classification of a concept as an individuable thing, therefore, may govern its assignment to the grammatical category noun. In this light it is notable that regions within the fusiform gyrus bilaterally are thought to play a critical role in the individuation of items within a homogeneous class (42, 43).

For verbs, the criterial semantic feature is thought to be reference to an “event” (a phenomenon that is situated in time) (41). Although it is not well understood what brain regions may be involved in processing eventhood, there is some evidence from both neuropsychology (44) and functional neuroimaging (45) that parts of the left prefrontal cortex and posterior parietal cortex are critical for temporal discrimination, but not for other kinds of sensory discrimination. Electrophysiological studies with normal and brain-damaged patients additionally suggest that prefrontal and posterior parietal cortical regions are critical in mediating attention to novel events (46). Finally, it has been shown that patients with damage to the prefrontal cortex are impaired in detecting boundaries and transitions between actions (47).

Of course, there may be still other explanations for the divergent patterns of activation elicited by noun and verb trials. In the experiments described here, nouns and verbs were produced within the context of phrases, which had different syntactic properties; for

example, the verb phrases were sentential, whereas the noun phrases were not. One could therefore speculate that some or all of the observed differences in activation were attributable to differences in syntactic construction. The latter, however, stem directly from the intrinsic grammatical properties of nouns and verbs, such as the fact that verbs obligate external arguments (at least in English); such properties may in turn derive from the referential cores of noun and verb meaning (41). Careful research will be required to distinguish brain regions that generate categorical distinctions from those that are galvanized by their sequelae.

Methods

Participants. Ten right-handed participants (five males) aged 19–25 years were enrolled in the fMRI experiments (average = 21.6 ± 0.73 years). All were native speakers of English with normal or corrected-to-normal visual acuity, at least 14 years of education, and no history of neurological or psychiatric illness. A separate group of 18 right-handed participants (eight males), all undergraduates at Harvard University, performed the same tasks outside the scanner, allowing the collection of chronometric data that could not be acquired concomitantly with fMRI. The protocols for these experiments were approved by both the Harvard University and Massachusetts General Hospital institutional review boards.

Stimulus Construction. The stimuli in Exp. 1 consisted of 40 nouns, 40 verbs, and 40 pseudowords matched in length and syllabic structure to the real words. In Exps. 2 and 3, 80 different stimulus words (40 nouns and 40 verbs per experiment) were used. Nouns and verbs were divided evenly into two stimulus types (A and B) orthogonal to grammatical category, such that in each experiment there were four sets of stimuli (20 noun A, 20 noun B, 20 verb A, 20 verb B). The A and B types for Exp. 2 corresponded to concrete words and abstract words; for Exp. 3, they corresponded to regular words and irregular words. Qualitative and quantitative characteristics of the real word stimuli are described in *Supporting Text* and Table 4, which are published as supporting information on the PNAS web site.

Task. Each real stimulus word appeared once within Exp. 1, whereas each pseudoword item appeared twice (once as a noun, once as a verb). Each stimulus word appeared twice within Exps. 2 and 3, resulting in 160 trials per experiment. Six different trial orders were produced for each experiment. (Each participant was assigned to one of these orders.) In three orders, trials were ordered by a random number generator, with the constraint that two trials of the same type never appeared in immediate succession. The remaining orders were produced by reversing the sequences in the first three orders. The 160 trials in each order were divided into two runs of 80 trials apiece. Intertrial intervals varied between 2 and 10 s and were determined by a simulation designed to optimize jitter within runs, such that the total length of each run was 648 s.

Each trial consisted of a stimulus phrase (1 s) followed by a cue phrase (1 s). In Exps. 1 and 2, the stimulus phrase always contained a (pseudo-)noun or (pseudo-)verb with either overt or null inflection (e.g., *one idea, many ideas, he thinks, they think*), whereas the cue phrase contained only a quantifier or a pronoun (*one. . . , many. . . , he. . . , they. . .*; see Fig. 4, which is published as supporting information on the PNAS web site). The same was true in Exp. 3, but with different stimulus and cue phrases on verb trials (*today I think, yesterday I. . .*). All of the phrases were grammatically licit.

Half (80 trials) of the trials in each experiment required subjects to change the morphological form of the stimulus word; in the other half, the subjects were required to produce the stimulus word in the same form. Stimuli with and without overt change were randomly interleaved. This manipulation was intended to ensure that subjects could not perform the task by simply changing the form of the

stimulus word; instead, the cue word was meant to signal a new noun or verb phrase.[†]

Subjects were instructed to produce the words presented in the stimulus phrases in forms appropriate to the subsequent cue phrases. Before the fMRI experiments, subjects were trained to respond aloud, but without moving their heads, as if they were practicing ventriloquy. This method minimizes head-movement artifacts that emerge when subjects produce spoken responses inside the scanner. The training session used a set of words that did not occur in any of the experiments. During the scanning session, subjects were monitored by intercom to ensure that they produced vocal responses.

Chronometric Data Collection and Analysis. In the behavioral study conducted outside the scanner, subjects sat comfortably in front of computer screens in dimly lit testing rooms and were asked to produce responses by speaking into a microphone. The trial conditions were identical to those used in the fMRI experiments. Response latencies were measured by voice key.

Trials on which the voice key failed to register a response were discarded (0.3% of the data set), as were trials with a recorded response latency <100 ms (0.2%). The remaining data for each experiment were entered into ANOVA models with grammatical category (two levels), stimulus type (two levels), and morphological change (two levels) as within-subjects repeated measures.

Image Acquisition and Preprocessing. Images were acquired by using a 3-Tesla Siemens (Iselin, NJ) Allegra MRI scanner. A multiplanar rapidly acquired gradient echo sequence was used to acquire high-resolution anatomic volumes [repetition time (TR) = 30 ms, echo time (TE) = 3.3 ms, 128 slices, $1 \times 1 \times 1.33$ -mm resolution], and a T2*-weighted echo planar imaging sequence was used for functional imaging (TR = 2 s, TE = 30 ms, 64×64 acquisition matrix, 30 slices, 4.5-mm isotropic resolution). Stimuli were projected by a collimating lens onto a screen at the rostral end of the scanner bore and were viewed through an angled mirror affixed to the head coil. All participants completed a single anatomic scan and six experimental runs (two runs per experiment), preceded by three short practice trials conducted outside the scanner.

Preprocessing and data analysis were conducted by using SPM99 (Wellcome Department of Cognitive Neurology, University College London). Functional images were slice-time-corrected and motion-corrected for each subject. Despite the task requirement for vocal responses, attributed motion artifact was well within the customary range for fMRI studies. Subsequently all runs were concatenated by using custom software written in MATLAB (Mathworks, Natick, MA). The images were then transformed into a standard space, including resampling at 2-mm isotropic resolution, and were spatially smoothed by using a Gaussian kernel (full width at half maximum = 9 mm). Anatomic images were transformed into a standard space, and a mean anatomic image (based on individual images from all 10 subjects) was generated for purposes of display.

fMRI Data Analysis. Event-related analysis was conducted by using a random-effect general linear model approach. For each participant, square waves representing onsets and durations for each of the event types were convolved with a canonical hemodynamic response function. In total there were 24 event types of 2-s duration (three experiments \times two grammatical categories \times two stimulus types per experiment \times two conditions of morphological change), plus fixation, which was modeled as a separate event with variable duration. The activation time course for each voxel was fit to

[†]It could be argued that no change trials can be performed by relying on working memory, rather than by truly engaging operations involved in word production. We believe that this is unlikely in the present task, because the context demands syntactic analysis at the phrase level on every trial. However, we are mindful of this objection, and therefore we report any differences in the behavioral or physiologic response to change and no-change trials.

hemodynamic response models constructed for the 12 noun and 12 verb event types across all three experiments, producing β -weights (model amplitudes) associated with trials of each event type.

In the second level of analysis, a one-tailed paired t test was used to compute contrasts between β -weight maps associated with all noun and all verb events (or between events of either category and fixation) across all subjects. Consequently, only voxels with β -weight differences that were statistically consistent across subjects were considered active. Each β -weight map in these second-level contrasts reflected activation from 240 individual events.^{††}

Contrasts Between Noun and Verb Trials. Regions of interest were defined as clusters of 12 or more voxels in which individual voxel activity was significant to $P < 0.005$. The minimum cluster extent was determined by calculating the number of resampled (2 mm isotropic) voxels equal in volume to one original (4.5 mm isotropic) voxel. The cluster extent threshold procedure (48, 49) was used to establish corresponding clusterwise type I error rates (corrected for multiple comparisons), taking into account the imaging parameters used in this study.

Event-related activity time courses for each event type were extracted from each region of interest by using custom software written in MATLAB (49). Time courses were baseline-corrected to produce a null average signal change from 0 to 4 s before stimulus onset and were subject to linear trend removal. Prior convolution analyses have determined that the maximum hemodynamic response should occur between 6 and 8 s after stimulus onset for event durations on the order of 2 s (49). For two regions of interest, time courses showed decreases in activity relative to baseline. Because there is considerable uncertainty about the interpretation of task-related deactivations, we did not analyze these regions further. For

time courses extracted from the remaining regions, mean percent signal change between 6 and 8 s was used as the dependent variable in post hoc statistical tests (Fig. 1b).

For the noun–verb contrast, activation in each region of interest was assessed with a multifactorial ANOVA model by using partial sums of squares. The model included experiment (three levels) as a between-subjects factor, subjects within experiments as the between-subjects error term, and grammatical category (two levels), stimulus type (see *Stimulus Construction*; six levels), and morphological change (two levels) as within-subjects repeated measures. When a main effect of stimulus type was found, we conducted follow-up ANOVAs for each experiment with grammatical category (two levels), stimulus type (two levels), and morphological change (two levels) as within-subjects repeated measures. All statistical analyses were performed by using STATA 7.0.

Conjunction of Noun and Verb Trials. To calculate the conjunction of the contrasts (noun – fixation) and (verb – fixation), the former contrast was computed first to define regions of interest that comprised at least 23 contiguous voxels with a voxelwise significance threshold $P_1 < 0.01$. The resulting statistical parametric map was then applied as a mask for the second contrast, which was computed by using the same parameters ($k = 23$ voxels, $P_2 < 0.01$). According to Fisher's equation (50),

$$\chi^2 = -2 \ln(P_1 P_2);$$

this procedure yields a joint probability of $P < 0.001$ for individual voxel activity, assuming $2 \times n = 4^\circ$ of freedom.

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^{††}A separate analysis was conducted with only the change trials. In this model, there were 12 event types; all other parameters were the same. Patterns of activation for the contrasts (noun – verb) and (verb – noun) were congruent with those obtained in the larger analysis, allowing for some variability attributable to decreased power (increased random error). Because the results of these two analyses were similar, we report only the more powerful model.

- Lyons, J. (1968) *Introduction to Theoretical Linguistics* (Cambridge Univ. Press, Cambridge, U.K.).
- Robins, R. (1979) *A Short History of Linguistics* (Indiana Univ. Press, Bloomington).
- Robins, R. (1952) *Language* **28**, 289–298.
- Hopper, P. J. & Thompson, S. A. (1984) *Language* **60**, 703–752.
- Gleason, J. B. (1958) *Word* **14**, 150–177.
- Caramazza, A. & Hillis, A. E. (1991) *Nature* **349**, 788–790.
- Liaconna, M. & Caramazza, A. (2004) *Cognit. Neuropsychol.* **21**, 103–124.
- Miceli, G., Silveri, M. C., Villa, G. & Caramazza, A. (1984) *Cortex* **20**, 207–220.
- Damasio, A. R. & Tranel, D. (1993) *Proc. Natl. Acad. Sci. USA* **90**, 4957–4960.
- Daniele, A., Giustolisi, L., Silveri, M. C., Colosimo, C. & Gainotti, G. (1994) *Neuropsychologia* **32**, 1325–1341.
- Tranel, D., Adolphs, R., Damasio, H. & Damasio, A. R. (2001) *Cognit. Neuropsychol.* **18**, 655–674.
- Warburton, E., Wise, R., Price, C., Weiller, C., Hadar, U. & Ramsay, S. (1996) *Brain* **119**, 159–179.
- Perani, D., Cappa, S. F., Schnur, T., Tettamanti, M., Collina, S., Rosa, M. M. & Fazio, F. (1999) *Brain* **122**, 2337–2344.
- Fujimaki, N., Miyauchi, S., Putz, B., Sasaki, Y., Takino, R., Sakai, K. & Tamada, T. (1999) *Hum. Brain Mapp.* **8**, 44–59.
- Tyler, L. K., Russell, R., Fadili, J. & Moss, H. E. (2001) *Brain* **124**, 1619–1634.
- Tyler, L. K., Bright, P., Fletcher, P. & Stamatakis, E. A. (2004) *Neuropsychologia* **42**, 512–523.
- Shapiro, K., Shelton, J. & Caramazza, A. (2000) *Cognit. Neuropsychol.* **17**, 665–682.
- Shapiro, K. & Caramazza, A. (2003) *Trends Cognit. Sci.* **7**, 201–206.
- Shapiro, K. & Caramazza, A. (2003) *Neuropsychologia* **41**, 1189–1198.
- Shapiro, K. A., Pascual-Leone, A., Mottaghy, F. M., Gangitano, M. & Caramazza, A. (2001) *J. Cognit. Neurosci.* **13**, 713–720.
- Johnsrude, I. S., Owen, A. M., Crane, J., Milner, B. & Evans, A. C. (1999) *Neuropsychologia* **37**, 829–841.
- Habib, M. & Sirigu, A. (1987) *Cortex* **23**, 73–85.
- Indefrey, P. & Levelt, W. J. M. (2000) in *The New Cognitive Neurosciences*, ed. Gazzaniga, M. (MIT Press, Cambridge, MA), pp. 845–866.
- Demonet, J. F., Chollet, F., Ramsay, S., Cardebat, D., Nespoulous, J. L., Wise, R., Rascol, A. & Franckowiak, R. S. (1992) *Brain* **115**, 1753–1768.
- Buckner, R., Koutstaal, W., Schacter, D. & Rosen, B. (2000) *Brain* **123**, 620–640.
- Fiez, J. A. (1997) *Hum. Brain Mapp.* **5**, 79–83.
- Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K. & Farah, M. J. (1999) *Proc. Natl. Acad. Sci. USA* **94**, 14792–14797.
- Tranel, D., Damasio, H. & Damasio, A. R. (1997) *Neuropsychologia* **35**, 1319–1327.
- Damasio, H., Grabowski, T. J., Tranel, D., Hichwa, R. D. & Damasio, A. R. (1996) *Nature* **380**, 499–505.
- Tranel, D., Kemmerer, D., Adolphs, R., Damasio, H. & Damasio, A. R. (2003) *Cognit. Neuropsychol.* **20**, 409–432.
- Maratsos, M. & Chalkley, M. A. (1981) in *Children's Language*, ed. Nelson, K. (Gardner Press, New York), pp. 127–214.
- Braine, M. (1987) in *Mechanisms of Language Acquisition*, ed. MacWhinney, B. (Erlbaum, New York), pp. 65–87.
- Caramazza, A. (1997) *Cognit. Neuropsychol.* **14**, 177–208.
- Caramazza, A. (1994) *Philos. Trans. R. Soc. London Ser. B* **346**, 121–127.
- Tyler, L. K., Stamatakis, E. A., Bright, P., Acres, K., Abdallah, S., Rodd, J. M. & Moss, H. E. (2004) *J. Cognit. Neurosci.* **16**, 351–362.
- Simons, J. S., Koutstaal, W., Prince, S., Wagner, A. D. & Schacter, D. L. (2003) *NeuroImage* **19**, 613–626.
- Chao, L. L., Haxby, J. V. & Martin, A. (1999) *Nat. Neurosci.* **2**, 913–919.
- Martin, A., Haxby, J. V., Lalonde, F. M., Wiggs, C. L. & Ungerleider, L. G. (1995) *Science* **270**, 102–105.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. H. & Rizzolatti, G. (2004) *Neuron* **42**, 323–324.
- Rushworth, M. F., Johansen-Berg, H., Gobel, S. M. & Devlin, J. T. (2003) *NeuroImage* **20**, S89–100.
- O'Grady, W. (1997) *Syntactic Development* (University of Chicago, Chicago).
- Gauthier, I., Tarr, M. J., Anderson, A. W., Skudlarski, P. & Gore, J. C. (1999) *Nat. Neurosci.* **2**, 568–573.
- Tarr, M. J. & Cheng, Y. D. (2003) *Trends Cognit. Sci.* **7**, 23–30.
- Lacruz, F., Artieda, J., Pastor, M. A. & Obeso, J. A. (1991) *J. Neurol. Neurosurg. Psychiatry* **54**, 1077–1081.
- Pastor, M. A., Day, B. L., Macaluso, E., Friston, K. J. & Franckowiak, R. S. (2004) *J. Neurosci.* **24**, 2585–2591.
- Daffner, K. R., Scinto, L. F., Weitzman, A. M., Faust, R., Rentz, D. M., Budson, A. E. & Holcomb, P. J. (2003) *J. Cognit. Neurosci.* **15**, 294–313.
- Zalla, T., Pradat-Diehl, P. & Sirigu, A. (2003) *Neuropsychologia* **41**, 1616–1627.
- Slotnick, S. D., Moo, L. R., Segal, J. B. & Hart, J. (2003) *Cognit. Brain Res.* **17**, 75–82.
- Slotnick, S. D. & Schacter, D. (2004) *Nat. Neurosci.* **7**, 664–672.
- Fisher, R. A. (1973) *Statistical Methods for Research Workers* (Hafner, New York).