

# Processing Nouns and Verbs in the Left Frontal Cortex: A Transcranial Magnetic Stimulation Study

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## Abstract

■ Neuropsychological and neurophysiological studies suggest that the production of verbs in speech depends on cortical regions in the left frontal lobe. However, the precise topography of these regions, and their functional roles in verb production, remains matters of debate. In an earlier study with repetitive transcranial magnetic stimulation (rTMS), we showed that stimulation to the left anterior midfrontal gyrus disrupted verb production, but not noun production, in a task that required subjects to perform simple morphological alternations. This result raises a number of questions: for example, is the effect of stimulation focal and specific to that brain region? Is the behavioral effect limited to rule-based, regular transformations, or can it be generalized over the grammatical category? In the present study, we used rTMS to suppress the excitability of

distinct parts of the left prefrontal cortex to assess their role in producing regular and irregular verbs compared to nouns. We compared rTMS to sham stimulation and to stimulation of homologous areas in the right hemisphere. Response latencies increased for verbs, but were unaffected for nouns, following stimulation to the left anterior midfrontal gyrus. No significant interference specific for verbs resulted after stimulation to two other areas in the left frontal lobe, the posterior midfrontal gyrus and Broca's area. These results therefore reinforce the idea that the left anterior midfrontal cortex is critical for processing verbs. Moreover, none of the regions stimulated was preferentially engaged in the production of regular or irregular inflection, raising questions about the role of the frontal lobes in processing inflectional morphology. ■

## INTRODUCTION

Evidence from a variety of sources suggests that the language processing system includes at least some components that discriminate between nouns and verbs at the cortical level. For instance, electrophysiological studies have described different spatial and/or temporal patterns of event-related potentials (ERPs) evoked by noun and verb stimuli (e.g., Kellenbach, Wijers, Hovius, Mulder, & Mulder, 2002; Dehaene, 1995; Brown, Marsh, & Smith, 1973; Teyler, Roemer, Harrison, & Thompson, 1973). Some functional neuroimaging studies have also found cortical areas that respond more robustly to verbs than to nouns (Longe, Randall, Stamatakis, & Tyler, 2007; Shapiro, Moo, & Caramazza, 2006; Shapiro et al., 2005; Tyler, Bright, Fletcher, & Stamatakis, 2004; Perani et al., 1999) or vice-versa (Shapiro et al., 2005, 2006). Arguably, the most compelling source of evidence for the noun-verb dissociation, however, is the study of patients with focal ischemic lesions or neurodegenerative diseases who show either poorer performance in retrieving verbs than nouns, or the opposite pattern (e.g.,

Bates, Chen, Tzeng, Li, & Opie, 1991; Zingeser & Berndt, 1988, 1990; Miceli, Silveri, Villa, & Caramazza, 1984; see Shapiro & Caramazza, 2003c; Druks, 2002, for reviews).<sup>1</sup>

In general, verb deficits occur in patients with damage to the left frontal cortex, whereas noun deficits are associated with damage to the left temporal lobe (Tranel, Adolphs, Damasio, & Damasio, 2001; Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994; Damasio & Tranel, 1993; Miceli et al., 1984). Nevertheless, a number of patients not consistent with this pattern have been reported (Shapiro, Shelton, & Caramazza, 2000; Silveri & di Betta, 1997; De Renzi & di Pellegrino, 1995; Hillis & Caramazza, 1995), suggesting that several different patterns of brain damage can contribute to selective impairments in producing words of a given category. It may be that these various patterns are associated with functional impairments at different stages of word production, all of which lead to a behavioral dissociation in producing nouns and verbs.

Careful neuropsychological studies offer some support for this postulate. Case series by Crepaldi et al. (2006) and Berndt, Haendiges, and Burton (2002) have shown that dissociations in noun and verb production disappear for some patients, but not for others, when the imageability of target words is controlled across categories. Some single-case studies have reported patients

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whose deficits in noun and verb retrieval seem to reflect problems in accessing word meaning, while grammatical aspects of verb production remain intact (e.g., Laiacona & Caramazza, 2004; Shapiro & Caramazza, 2003a). In other cases, category-selective deficits have been linked to specific impairments in morphological processing (Laiacona & Caramazza, 2004; Shapiro & Caramazza, 2003b; Tsapkini, Jarema, & Kehayia, 2002; Shapiro et al., 2000). These patients have particular difficulty producing nouns or verbs in the context of sentences and, in some cases, are even impaired using pseudo-words as nouns (e.g., “many wugs”) or as verbs (e.g., “he wugs”).

Unfortunately, the patients that have been described have heterogeneous and sometimes diffuse patterns of brain injury, rendering problematic the association of particular functional deficits with precisely defined cortical areas. Functional neuroimaging studies are obviously better suited to answering questions about cerebral localization; nevertheless, even well-designed imaging studies present difficulties in interpretation, the most conspicuous of which is that they cannot establish a true causal relationship between areas of observed brain activation and the corresponding behavioral task. Transcranial magnetic stimulation is a valuable technique in this regard, complementing neuropsychology and neuroimaging in that it allows researchers to study the effects of modulating cortical function in a non-invasive fashion (Walsh & Pascual-Leone, 2003).

In an earlier study, we used repetitive transcranial magnetic stimulation (rTMS) in an attempt to determine whether a particular brain region was critical for processing verbs. Specifically, we targeted the anterior portion of the left middle frontal gyrus while subjects performed a task requiring the production of verbs or nouns in the context of short phrases (Shapiro, Pascual-Leone, Mottaghy, Gangitano, & Caramazza, 2001). The results showed that stimulation to this area induced a delay in producing verbs relative to nouns.

The task in the study by Shapiro et al. (2001) required subjects to manipulate the inflectional form of a stimulus word. For example, one trial presented the word *doors*, followed by a symbolic cue indicating the singular form; subjects were then required to say “door.” Interestingly, the same dissociation between nouns and verbs was found when the stimuli were meaningless pseudo-words, like *wug* and *narfs*. These data were taken as evidence that the targeted portion of the left prefrontal cortex is involved in processing grammatical properties of verbs, rather than properties related to verb meaning.

Several objections to this conclusion are immediately apparent. Perhaps the most important (and most contentious) of these relates to the problem of differentiating semantic from grammatical processing; we will take up this issue in the General Discussion. Aside from this theoretical challenge, there are a number of methodological concerns that confound the interpretation of

the experiments described in Shapiro et al. (2001). One is that rTMS was applied only to one area within the left frontal lobe; as a consequence, the study does not rule out the involvement of other parts of the left frontal cortex (or other parts of the brain generally) in verb processing. It is also possible that the targeted area itself was not crucial for verb processing, and that the observed effects were really attributable to the transsynaptic modulation of neighboring or distant cortical sites.

Moreover, even if the targeted area was uniquely crucial for performing the verb task used by Shapiro et al. (2001), the interpretation of this result would be constrained by the fact that the study investigated only the processing of regularly inflected nouns and verbs in specific morphological alternations, involving number (for nouns) and agreement (for verbs). It could be argued that the effect of rTMS on verb production in Shapiro et al. resulted from the different computational demands of these two operations—in particular, the greater complexity of subject–verb agreement.<sup>2</sup>

A related question concerns whether the area that was stimulated is important for the production of morphologically irregular verb forms, like *ran* and *bought*, which cannot be computed by adding or deleting an inflectional affix. Some authors have proposed that regular and irregular morphological transformations are subserved by distinct neural circuits (Tyler et al., 2004; Miozzo, 2003; Tyler, Russell, Fadili, & Moss, 2001; Marslen-Wilson & Tyler, 1997; Ullman, Corkin, et al., 1997), although this “dual-route” assumption has proven famously controversial (see, e.g., McClelland & Patterson, 2002; Bird, Howard, & Franklin, 2000; Joanisse & Seidenberg, 1999).

One version of the dual-route hypothesis holds that prefrontal brain regions are particularly important for rule-based or regular morphology (Ullman, Corkin, et al., 1997)—although neuroimaging studies have shown, if anything, the opposite association (Indefrey et al., 1997; Ullman, Bergida, & O’Craven, 1997). Consistent with the latter results, two neuropsychological studies have described patients with left prefrontal lesions who show an advantage for regular over irregular verbs, albeit in the context of a general deficit for verbs relative to nouns (Shapiro & Caramazza, 2003b, in an English-speaking patient; Balaguer, Costa, Sebastian-Galles, Juncadella, & Caramazza, 2004, in two Spanish–Catalan bilinguals). These findings do not necessarily call into question the differential role of the left prefrontal cortex in noun and verb processing, but they do raise the possibility that noun or verb effects may be modulated by an orthogonal dimension of regularity.

## Current Study

Here we report two new rTMS experiments that were designed to investigate the functional roles of different regions of the left frontal cortex in processing regular and irregular verbs and nouns. Aside from replicating

the effects reported in Shapiro et al. (2001), the experiments address at least two other important questions: first, whether any of the targeted areas in the prefrontal cortex is important in distinguishing regular from irregular morphological computations; and second, whether any role is played by other prefrontal cortical areas in grammatical processing of nouns and verbs.

The primary goal of the first experiment was to determine whether the area targeted in Shapiro et al. (2001) is important only for rule-based morphological transformations, or alternatively, whether it is involved in any computational process involving verbs, regardless of morphological type. In order to compare morphologically regular and irregular word forms, we modified the behavioral task, retaining the singular–plural alternation for nouns but using the present–past tense alternation for verbs. This change had the additional advantage of making the noun and verb tasks more comparable in terms of syntactic complexity because past tense verbs do not require the computation of an agreement relation with the external object of the verb phrase. As in our earlier study, rTMS was applied to a portion of the anterior midfrontal gyrus (aMFG) just anterior and superior to Broca’s area. We expected that this would again result in a delay in response latencies for verb trials (relative to a baseline), but no comparable delay for noun trials.

In the second experiment, we tried to determine whether the noun–verb difference obtained with stimulation to the left aMFG is specific to that region. To this end, we repeated the behavioral task in Experiment 1 with rTMS applied to two other regions in the frontal lobe: Broca’s area (inferior frontal gyrus, or IFG) and a more posterior portion of the midfrontal gyrus (pMFG). These sites were approximately equidistant from each other and from the aMFG with respect to the surface of the brain. If rTMS applied at these sites does not result in a verb–noun dissociation, this can be taken as evidence for the focality (if not the locality) of any effect of stimulation to the aMFG. To put it somewhat differently, this finding would support the conclusion that the aMFG—or some network to which the aMFG has a privileged connection (see General Discussion), is crucial for verb processing, but not for noun processing.

The IFG and the pMFG also serve as useful control areas from a functional perspective, as both have been implicated in verb production by some authors. A few neuroimaging studies have shown that verb processing induces greater activation in the left IFG than does noun processing (Tyler et al., 2004; Perani et al., 1999); in some studies this effect is specific to the processing of inflected words (Longe et al., 2007; Tyler et al., 2004). This dissociation may reflect the greater grammatical or morphological complexity of inflected verbs, compared to nouns.

On the other hand, it has been postulated that premotor brain regions are crucial for representing semantic features of verbs, by virtue of their role in storing

action schemata (Pulvermüller, 1999, 2001, 2005). Some neuroimaging studies have, indeed, shown activation in premotor regions during tasks involving the processing of verbs referring to imageable actions (Buccino et al., 2005; Tettamanti et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004). Interestingly, an fMRI study using a morphological alternation task identical to the one used here also showed increased activation for verbs compared to nouns in the left pMFG, regardless of whether the verbs were concrete or abstract (Shapiro et al., 2006). Thus, there are reasons to suspect that both the IFG and the pMFG might be more involved in verb production than in noun production, which would make the finding of an effect restricted to the aMFG theoretically more striking.

The current study incorporates several methodological improvements over the design used in Shapiro et al. (2001). In the previous study noun and verb trials were blocked, amplifying potential effects of practice, whereas in the current study, trials with words of each category were interleaved. Second, we replaced the iconic cues used by Shapiro et al. with more natural phrasal cues. Finally, in addition to sham TMS, we used real rTMS over homologous right hemisphere sites as a control for left-sided stimulation. In the previous experiments, we used only sham stimulation.

## METHODS

### Participants

Eight right-handed native speakers of English (4 men) aged 19 to 33 years (mean = 22.9 years) participated in Experiment 1. Twelve right-handed native speakers of English (5 men) aged 18 to 36 years (mean = 21.1 years) participated in Experiment 2. All subjects were healthy, with no history of neurological or psychiatric illness, and no contraindications to TMS as determined by the TMS safety screening questionnaire (Keel, Smith, & Wassermann, 2001). They were all screened for TMS exclusion criteria and gave their written informed consent before participating. This study was performed in close adherence to TMS safety guidelines (Wasserman, 1998) and was approved by institutional review boards at Harvard University and at Beth Israel Deaconess Medical Center. In Experiment 2, the same subjects were studied on two different days to minimize carryover effects.

### Behavioral Task

Word production was cued by a simple completion task consisting of visually presented noun and verb phrases. Subjects were required to produce the singular and plural forms of regular and irregular nouns (e.g., *song/songs* or *child/children*), and the present or past tense forms of regular and irregular verbs (e.g., *walk/walked* or *sleep/slept*). In verb trials, subjects saw stimulus

phrases of the form “today I walk,” followed by cue phrases like “yesterday I...” (In this case, the subject was instructed to say *walked*). Noun trials consisted of stimulus phrases such as “one child,” followed by the cue “many...” (*children*).

The task was performed on a Dell PC using the DMDX package (Forster & Forster, 2003). Participants’ viewing distance from the computer monitor was about 0.5 m. Response latencies were recorded with a custom-built microphone connected to the computer through a pre-amplifier. Each trial began with a fixation cross, which appeared in the center of the screen for 500 msec. This was followed by a written stimulus phrase (e.g., “today I walk”), which appeared in the position of the fixation cross for 500 msec, followed for another 500 msec by the cue phrase (“yesterday I...”), indicating the morphological form in which the word in the stimulus phrase was to be produced aloud. Participants were instructed to supply appropriate single word responses immediately upon seeing the cue phrase. The next trial began 1500 msec after the offset of the cue phrase so that subjects had a maximum of 2000 msec to respond in each trial.

### Stimulus Preparation

Eighty words were used in the experiment, including 20 words of each of the following types: regular verbs, irregular verbs, regular nouns, and irregular nouns. We excluded verbs that can function as auxiliaries (*do*, *have*), verbs with syncretic past tense forms (*pleaded/pled*, *dreamed/dreamt*), and nouns with imported plural forms (*datum*, *octopus*). The four sets of words were matched as closely as possible for length in phonemes (average of inflected and unmarked forms), lemma frequency, and surface frequency of the relevant inflected forms (Kucera & Francis, 1982) (see Table 1). Bidirectional Student’s *t* tests showed no significant differences on these measures between nouns and verbs within each morphological type, or between regular and irregular words within each grammatical category ( $\alpha = 0.05$ , uncorrected for multiple comparisons).

Ratings of concreteness, imageability and familiarity on Likert scales of 1–7 were obtained from a group of 10 subjects at Harvard University, none of whom participated in the rTMS experiment (Shapiro et al., 2006). Confirmatory bidirectional *t* tests revealed no differences in imageability or familiarity within morphological types or grammatical categories. For both regular words [ $t(38) = 5.86$ ,  $p < .001$ ] and irregular words [ $t(38) = 5.82$ ,  $p < .001$ ], nouns were rated as significantly more concrete than verbs (although there was no difference between regular and irregular words of each grammatical category). The dissociation between imageability and concreteness in these stimuli is probably attributable to the fact that “concreteness” for verbs was defined as the extent to which they referred to actions. Some of the verbs in the stimulus set, such as *to sleep* and *to bleed*, may be considered highly imageable, but poor examples of actions.

The words were subsequently used to create eight lists of 160 trials each. In each list, every stimulus word appeared twice: once in a trial with a marked-form target (plural noun or past tense verb) and once in a trial with an unmarked-form target (singular noun or present tense verb). One of these trials required a morphological change relative to the cue phrase, whereas the other did not. Moreover, the lists were balanced so that each cue/stimulus pair appeared in exactly two lists. The order of trials in each list was pseudorandomized.

### Experimental Sessions

Experiment 1 was completed in a single session and included four blocks of trials, corresponding to four stimulation conditions (right hemisphere rTMS, left hemisphere rTMS, right hemisphere sham, and left hemisphere sham), as well as an initial practice block. In Experiment 2, subjects returned for two sessions, separated by at least 48 hr. In each session of the experiment, subjects completed a practice block and three blocks of trials (left hemisphere rTMS, right hemisphere rTMS, and either right or left hemisphere sham). Each block corresponded to one of the trial lists. Lists

**Table 1.** Psycholinguistic Characteristics of Words Included in the Experiment

Morphology	Category	$F_\lambda$	$F_{SZ}$	$F_{SI}$	Length	Concreteness	Imageability	Familiarity
Regular ( $n = 40$ )	Noun ( $n = 20$ )	93.1 (105.5)	53.1 (62.4)	30.1 (37.1)	3.6 (0.8)	6.1 (1.0)*	6.0 (1.3)	6.2 (0.6)
	Verb ( $n = 20$ )	115.2 (91.3)	35.4 (34.6)	34.5 (33.5)	3.5 (0.6)	4.5 (0.7)	5.3 (0.9)	6.3 (0.4)
Irregular ( $n = 40$ )	Noun ( $n = 20$ )	122.1 (218.8)	68.9 (157.0)	44.5 (95.8)	3.7 (0.8)	6.1 (0.8)*	5.9 (1.4)	6.1 (0.7)
	Verb ( $n = 20$ )	120.1 (86.9)	32.0 (28.4)	32.2 (34.2)	3.9 (0.6)	4.8 (0.6)	5.6 (0.8)	6.3 (0.3)

$F_\lambda$  = cumulative (lemma) frequency;  $F_{SZ}$  = surface frequency of unmarked form;  $F_{SI}$  = surface frequency of inflected form. Standard deviations are given in parentheses. Morphology refers to the marked form (plural for nouns, past tense for verbs). Frequency values are from Kucera and Francis (1982). Length refers to the mean length in phonemes of the inflected and unmarked forms, with diphthongs counted as two phonemes. Values for concreteness, imageability, and familiarity are mean ratings on Likert scales of 1–7 (see text).

\* $p < .001$ .



were assigned to blocks by subject in a Latin square fashion. In total, there were 640 trials in Experiment 1 and 960 trials in Experiment 2, excluding the practice trials. Data collected during the practice blocks were discarded.

The experimental blocks were completed immediately after each of the stimulation conditions in each session (right hemisphere rTMS, left hemisphere rTMS, and sham). A 30-min rest period followed the first non-practice block to allow any effect of rTMS to wash out. In both experiments, the order of the areas stimulated with rTMS was counterbalanced across subjects to avoid carryover effects. Similarly, the order of real rTMS and sham stimulation was counterbalanced across subjects. In Experiment 2, the two areas stimulated with rTMS in each session were never located in the same hemisphere and were never homologous.

### Areas Targeted with rTMS

Prior to the TMS experiments, each subject underwent a high-resolution structural MRI scan. Three-dimensional cortical surface maps were reconstructed from the MR images using theBrainsight neuronavigation system (Rogue Research, Montreal, Canada), and target sites for stimulation were marked on these maps.

In Experiment 1 we targeted the inferior portion of the left aMFG and its right hemisphere homologue. To localize this area in each hemisphere, we initially identified the middle frontal gyrus in the 3-D anatomical brain reconstruction, and then marked the anterior part of the gyrus near the intersection of the inferior and superior frontal sulci and above the frontal pole. Sham stimulation was applied at the same sites as real rTMS.

In Experiment 2, three different stimulation sites were identified in each hemisphere. The first site of interest was the superior posterior third of the midfrontal gyrus (pMFG), near the precentral and superior frontal sulci and above the opercular part of the IFG. In functional terms, this corresponds to the premotor cortex. The second site was within the triangular part of the IFG, corresponding to the anterior portion of Broca's area in the left hemisphere. We targeted an area near the anterior ascending rami, roughly at the midpoint between the lateral sulcus (Sylvian fissure) and the inferior frontal sulcus. A third, intermediate site was marked in each hemisphere for sham stimulation.

### Stereotactic Guidance and Application of rTMS

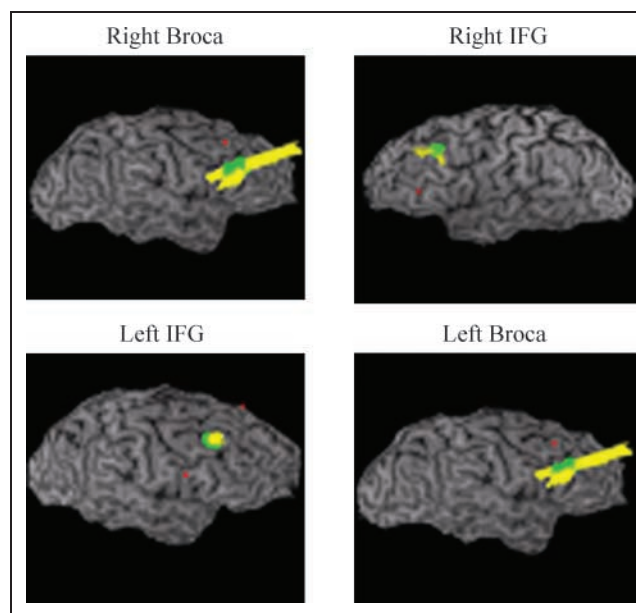
The application of rTMS during the experiments was guided with frameless stereotaxy using theBrainsight system and a Polaris infrared camera. Subjects wore tightly fitting elastic headbands with infrared-reflective trackers. At the beginning of each experimental session, surface anatomical landmarks were registered to the reconstructed MR images using a pointing device. A reflective tracker was also affixed to the TMS coil so that the

position and orientation of the coil with respect to the marked TMS target sites could be monitored on-line.

rTMS was applied using aMagstim Rapid Rate stimulator (Magstim, UK) and a focal eight-shaped coil with wings each measuring 70 mm in outer diameter. Stimulation was applied at a frequency of 1 Hz over 12 min for a total of 720 pulses. Figure 1 illustrates where TMS was delivered in each of the four target brain areas in a representative subject. Although many rTMS studies (including those reported inShapiro et al., 2001) tailor the intensity of stimulation to the motor threshold in individual subjects, this approach is problematic inasmuch as cortical excitability may vary across different brain areas (Robertson, Theoret, & Pascual-Leone, 2003). We therefore opted to use a fixed intensity of stimulation across subjects, corresponding to 65% of the maximum stimulator output. For sham stimulation, we used a specially designed coil that induces no magnetic field, but produces an acoustic artifact and a tapping sensation on the scalp similar to real TMS ([www.magstim.com](http://www.magstim.com)). Using this sham coil, TMS-naïve subjects are truly blinded to the sham nature of the stimulation (unpublished data).

### Data Analysis

Individual trials were excluded from the dataset when subjects responded incorrectly, self-corrected, or hesitated,



**Figure 1.** Sites and targeting of rTMS and sham stimulation. In Experiments 1 and 2, the order of stimulation conditions was fully counterbalanced across subjects. Yellow lines illustrate an example of where stimulation was applied during an entire 10-min rTMS train in a representative subject for each of the four stimulation positions; the green dots correspond to the point on the scalp where each TMS pulse was delivered. The stimulation coil rested tangentially on the subject's scalp and the handle pointing posteriorly parallel to the subject's midsagittal plane as calculated by the frameless stereotactic.

when no response was recorded, and when recorded reaction times (RTs) were less than 200 msec. Using these criteria, 3.8% and 3.5% of the total number of responses were counted as errors in Experiments 1 and 2, respectively. Visual inspection of histograms of the remaining data confirmed that RTs were approximately normally distributed. Experimental conditions in which real stimulation was applied were compared to conditions in which sham stimulation was applied. RTs following left- and right-sided sham stimulation were averaged. We used Fisher's LSD correction for multiple comparisons, and statistical significance refers to a two-tailed  $p$  value  $< .05$ .

## EXPERIMENTS

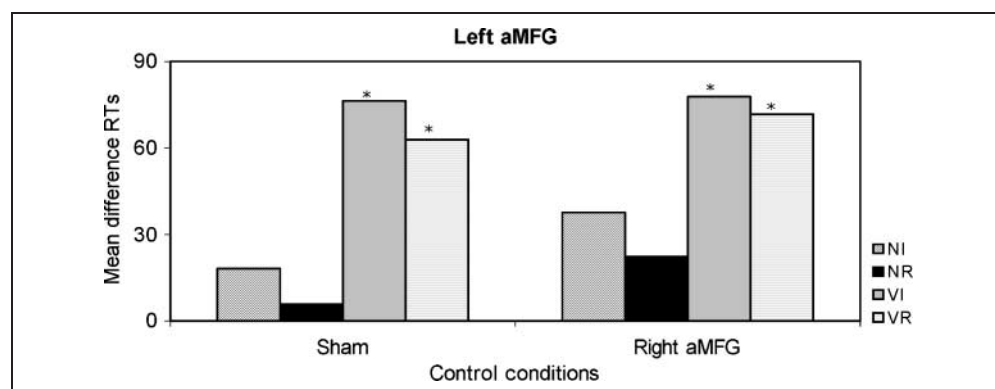
### Experiment 1: Stimulation to Left and Right Anterior Midfrontal Regions (aMFG)

Our first experiment was designed to replicate and extend the study by Shapiro et al. (2001), with two specific aims: (1) to determine whether the left aMFG is critical for processing both regular and irregular verbs—or, conversely, whether the effect of rTMS on this region is modulated by the morphological regularity of the words to be produced; and (2) to investigate the role of the homologous midfrontal area in the right hemisphere. We reasoned that if the left aMFG is critical for processing verbs irrespective of their morphological features, rTMS should equally affect regular and irregular verbs. Moreover, if verb processing critically depends on the left aMFG, we predicted that no specific impairment in performance should follow stimulation to the right aMFG.

#### Results

We initially tested for effects of stimulation using a  $4 \times 3$  repeated measures analysis of variance (ANOVA) on mean RTs by subject, with trial types (regular and irregular verbs and nouns) and conditions of stimulation (left aMFG, right aMFG, and sham) as factors. When appropriate, post hoc  $t$  tests were carried out to compare specific conditions to their respective controls.

**Figure 2.** Effects of rTMS in Experiment 1. Difference in average response times (RTs) between left aMFG and sham stimulation (left columns) and left aMFG and right aMFG (right columns).



Following real stimulation, mean response latencies differed significantly between the sham condition (643 msec), stimulation to the right aMFG (645 msec), and stimulation to the left aMFG [697 msec; main effect of stimulation condition,  $F(2, 14) = 6.23$ ,  $p < .02$ ]. However, the effect of stimulation differed across trial types [ $F(3, 21) = 6.03$ ,  $p < .005$ ], and a significant two-factor interaction [ $F(6, 42) = 2.56$ ,  $p < .05$ ] emerged.<sup>3</sup>

Post hoc comparisons showed that RTs increased following rTMS to the left aMFG, compared to sham stimulation, only for regular and irregular verb production [ $t(7) = -2.61$ ,  $p < .02$  and  $t(7) = -2.14$ ,  $p < .005$ , respectively], but not for the production of regular or irregular nouns [ $t(7) = -0.358$  and  $t(7) = -1.28$ ,  $ns$ , respectively; see Figure 2].

Similar findings were obtained when the effect of stimulation to the left aMFG was contrasted with the effect of stimulation to the right aMFG (rather than to sham). A significant increase in RTs was observed for verbs [regular:  $t(7) = 3.56$ ,  $p < .01$ ; irregular:  $t(7) = 4.29$ ,  $p < .005$ ], but not for nouns [regular:  $t(7) = 0.094$ ,  $ns$ ; irregular:  $t(7) = 1.91$ ,  $ns$ ]. No significant effects or trends ( $.05 < p < .10$ ) were found when we compared RTs after stimulation to the right aMFG with RTs after sham stimulation.

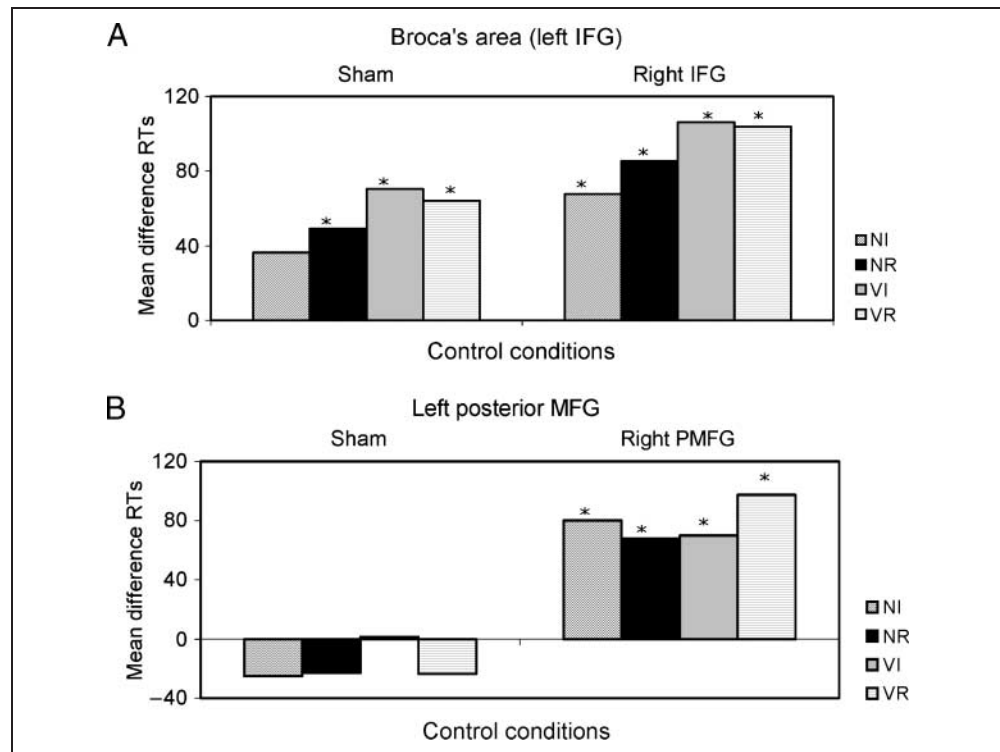
#### Summary and Interim Discussion

These findings indicate that the left aMFG appears to be more strongly involved in the morphological processing of verbs than nouns. The data are consistent with the results obtained by Shapiro et al. (2001), and extend the conclusions of that study in two ways.

First, the results show that the effect of stimulation on response latency applies to both regular and irregular morphological transformations with verbs. Just as importantly, the effect was replicated with a different set of inflectional features—in this case, tense rather than agreement. This suggests that the computation carried out by the left aMFG (or the network to which it is immediately connected) operates at a level more general than those at which either morphophonological features



**Figure 3.** Effects of rTMS in Experiment 2. (A) Difference in average response times (RTs) between left Broca's areas and sham stimulation (left columns) and left and right Broca's areas (right columns). (B) Difference in average RTs between the left posterior IMG and sham stimulation (left columns) and the left and right posterior IMG (right columns).



General Discussion, below). Moreover, in the case of verb processing, the effects of stimulation were significantly different in the aMFG compared to the other two regions in the left hemisphere.

There was no change in error rate following stimulation to any area in the left or right hemisphere. This is consistent with findings from other TMS studies, which have shown that TMS produces an increase in mean RTs, but not an increase in error rates, for tasks performed at a high level of accuracy (e.g., Cappelletti, Barth, Fregni, Pascual-Leone, & Spelke, 2007; Alexander et al., 2005; Ashbridge et al., 1997).

## GENERAL DISCUSSION

In this study we used rTMS to explore the role of frontal cortical regions in processing regular and irregular verbs and nouns. We found greater interference for verb production than noun production when stimulation was applied to the left aMFG, but not to the right aMFG (Experiment 1) or to two other areas in the frontal lobes that are hypothesized to play important roles in verb processing (Experiment 2).

Three important conclusions can be drawn from these data. First, they strengthen the evidence that rTMS applied to the anterior portion of the left midfrontal gyrus interferes with the ability to produce verbs, but not nouns, in agreement with the results obtained by Shapiro et al. (2001). Second, they extend the previous results by showing that rTMS affects the production of both regular and irregular verb forms, suggesting that

this area is involved in processing at a level of computation that does not discriminate between rule-based and irregular morphophonological transformations. Indeed, we found no such distinction, for either nouns or verbs, at any of the cortical sites targeted with rTMS.

Third, the current results demonstrate that the effects of rTMS on verb processing are specific to the left aMFG; no category-specific interference effects were observed when rTMS was applied to the left pMFG and to Broca's area. Instead, stimulation to these areas seemed to result in generic interference with both noun and verb trials, suggesting that they may be engaged in production processes that do not discriminate between words of different grammatical categories. This is in contradistinction to results from functional neuroimaging studies, which have revealed noun-verb differences in both the IFG (Longe et al., 2007; Tyler et al., 2004; Perani et al., 1999) and the pMFG (Shapiro & Caramazza, 2006).

### Verb Processing in the Left Anterior Midfrontal Gyrus: Functional Considerations

Observations of language deficits in brain-damaged patients suggest that the production of nouns and verbs in speech can be differentially impaired (e.g., Daniele et al., 1994; Miozzo, Soardi, & Cappa, 1994; Damasio & Tranel, 1993; Caramazza & Hillis, 1991; Miceli et al., 1984; see Shapiro & Caramazza, 2003c; Druks, 2002, for reviews). These behavioral dissociations have been taken as evidence that distinct cortical areas are involved in noun and verb production. The most common anatomical



correlate of verb impairment involves damage to the left frontal lobe. The association between verb production and frontal regions has been replicated, albeit inconsistently, by some neuroimaging studies, which have shown that verb processing is associated with increased activation in prefrontal regions (Shapiro et al., 2005, 2006; Tyler et al., 2001, 2004; Perani et al., 1999; Herholz et al., 1996; Warburton et al., 1996; Crivello et al., 1995).

However, limited evidence has so far been provided as to whether frontal brain regions are really critical for the production of verbs as defined by their grammatical role—as opposed, for example, to the processing of words specifying concrete actions (Pulvermüller, 1999, 2001, 2005; Cappa, Sandrini, Rossini, Sosta, & Miniussi, 2002; Neiningner & Pulvermüller, 1997), or of words that happen to be poorly imageable (Bird et al., 2000). Some patient studies have attempted to address this problem by using real word and pseudoword stimuli in tasks that explicitly emphasize morphosyntactic transformation (Laiacina & Caramazza, 2004; Shapiro & Caramazza, 2003c; Shapiro et al., 2000), on the assumption that category-selective deficits in this context are difficult to interpret as anything other than grammatical impairments. The same logic was used in our earlier rTMS study, which showed that suppression of the left aMFG can be used to dissociate the processing of real words and pseudowords as nouns and verbs in unimpaired subjects.

The results of the current experiments show that stimulation to the aMFG, and not to other frontal regions, results in temporary interference with verb production, but not noun production, thus reinforcing the idea that the left aMFG, in particular, plays a critical role in verb processing. Using the same logic that was applied in our earlier studies, we have argued that this effect arises because the left aMFG is critical for processing certain kinds of grammatical operations—specifically, morphosyntactic operations that call for the application of inflectional morphemes restricted to the category of verbs. This, of course, is not the only possible interpretation of our results. We have not definitively ruled out an explanation on the basis of the different kinds of semantic features of nouns and verbs.

In the present study, groups of noun and verb stimuli were not matched for concreteness, although they did not differ significantly in imageability, a correlated semantic variable that has more often been invoked to account for specific verb deficits in aphasia (Crepaldi et al., 2006; Luzzatti et al., 2002; Bird et al., 2000). It is therefore possible that what we have called a noun–verb dissociation in the left aMFG could be attributable to this factor. We believe, however, that this is improbable for several reasons. To begin with, an effect of concreteness would more naturally be expected in premotor cortical regions, where no noun–verb effects were found (Pulvermüller, 1999, 2001, 2005). An explanation in terms of concreteness is also unparsimonious on the

basis of past results, including the pseudoword data in Shapiro et al. (2001).

One could argue that the effects with pseudowords were also “semantic,” but this would require one to qualify what is meant by “semantics.” In this context, it might be supposed that the postulated verbal semantic features are so abstract as to apply even to words with no specific meaning, which would divorce verb semantics from a notion of concreteness that reflects the activation of action schemata. This was essentially the argument we adopted in Shapiro et al. (2006), in which we proposed that a different cortical region activated in fMRI may have a role in representing the “core” or generic semantics of eventhood (but see below for a novel interpretation of that study). Alternatively, it may be that subjects adopted a strategy of associating pseudowords (like *wug*) with particular actions (like *wag*). It is unclear, however, why this additional, meta-cognitive assumption should be preferred to a simple explanation in terms of grammatical processing.

### Verb Processing in the Left Frontal Cortex: Anatomical Considerations

The area that we stimulated in the left aMFG is included wholly or partially in the lesions observed in several patients with selective verb deficits, including one patient who had analogous difficulties in producing verbs and pseudowords in the context of a morphological alternation task (Shapiro & Caramazza, 2003b). It may also correspond to the brain region implicated in so-called dynamic aphasia, which was characterized in part as involving a selective deficit in predication—that is, in using verbs in their natural syntactic context (Luria & Tsvetkova, 1967).

It must be said, however, that it is difficult to make more precise claims about the degree of anatomical similarity between the area targeted in this study and cortical regions damaged in patients or activated in functional neuroimaging studies. Even if we are mindful of concerns about the reliability of anatomical localization in functional neuroimaging (Brett, Johnsrude, & Owen, 2002), it is notable that patterns of frontal activation for verb production have varied widely, including almost every major division of the frontal lobes (in both hemispheres) in one study or another.

#### *Role of the Posterior Middle Frontal Gyrus*

In a recent fMRI study we conducted, using a behavioral paradigm identical in important respects to the task used here, the contrast between verb production and noun production isolated three areas that seemed to be more engaged for verb trials, including one area in the left frontal cortex (Shapiro et al., 2006). However, this area is anatomically more comparable to the pMFG region in this study—where TMS produced no differential

effects across categories—than to the aMFG area where category-specific suppression was found. Other functional neuroimaging studies have also shown that verb production activates parts of the left posterior prefrontal cortex (Herholz et al., 1996; Crivello et al., 1995). The implications of this apparent discrepancy between TMS and fMRI/PET results are unclear.

One possibility is that the stages of cognitive processing illuminated by functional neuroimaging and suppressed by rTMS are not entirely isomorphic. In the case at hand, it may be that the various neuroimaging studies revealed an area which is activated by the “core” semantic properties of verb stimuli (O’Grady, 1997), but which is not necessarily critical for the production of verbal morphology. If we grant that the fMRI study conducted by Shapiro et al. (2006) did *not* reveal areas engaged in morphological processing, it may be that this insensitivity resulted from the massive repetition of the specific morphological alternations, with adaptation in the blood oxygenation level-dependent (BOLD) response to the aspects of the task relevant to grammatical processing. The residual significant BOLD response may have been more sensitive to semantic features of the noun and verb stimuli, which were obviously repeated less often than the morphological cues. By contrast, rTMS interferes directly with cortical activity so the effects induced by rTMS may be less affected by repetition in a task.

### *Role of the Inferior Frontal Gyrus*

As we mentioned earlier, some functional imaging studies have also reported increased activation in the left IFG for verbs compared to nouns (Longe et al., 2007; Tyler et al., 2004; Perani et al., 1999). This effect has been attributed to the processing of inflectional morphology for verbs, which is assumed to be computationally more demanding than processing nominal morphology (Longe et al., 2007; Tyler et al., 2004). A full discussion of the problems raised by this account is beyond the scope of the present article. One question that is pertinent, however, is how much of this postulated computational disparity can be credited to task-specific or even stimulus-specific differences in various experiments. In the most recent and probably the best controlled of the above-mentioned studies (Longe et al., 2007), subjects performed a lexical decision task on unambiguous plural nouns (*bullets*) and third-person singular verbs (*sings*). It is probably reasonable to argue that the syntactic functions signaled by these inflections are mismatched in complexity—indeed, this is, in part, what motivated us to use the past/unmarked alternation for verbs in the present study (see Introduction).

Moreover, the presentation of English nouns and verbs as single words, outside of a phrasal context, is much less natural for verbs, which do not occur in many inflectional forms without an accompanying subject

(consider *What are these? Bullets.* vs. *What does he do? \*Sings.*) It is not even obvious how one should construe the English /s/ suffix without contextual cues. If grammatical category information is not encoded in the representation of lexical roots, as some theorists have argued (Marantz, 1997; Halle & Marantz, 1993), then part of the lexical decision process might involve rejecting the construals that are unlikely or prohibited on semantic or thematic grounds. This decision, in turn, could interact with factors like the relative frequency of the distinct /s/ morphemes. Because of these numerous uncertainties, it may be difficult to interpret the presence or absence of grammatical category effects in paradigms that do not explicitly involve grammatical processing (Shapiro & Caramazza, 2003c).

In the present study, we did not observe any categorical dissociation following stimulation to the left IFG. Instead, stimulation of Broca’s area resulted in an increase in response latencies for both noun and verb trials, suggesting that this part of the brain subserves category-general aspects of morphological production. Such a pattern of performance is in agreement with a large corpus of neuropsychological studies showing that damage to Broca’s area results in impaired processing of inflectional morphology for both nouns and verbs (Menn & Obler, 1990; Miceli et al., 1984). Further evidence along these lines comes from a TMS study by Sakai, Noguchi, Takeuchi, and Watanabe (2002), who showed that stimulation of Broca’s area results in selective impairment in a task that involves the detection of anomalous morphemes (Japanese case markers, which are postnominal clitics).

The result could also be compatible with the idea that Broca’s area is engaged in a way that is proportional to the difficulty of the computation required, or the number of alternative responses that exist (if not in the context of the task, then in the language as a whole). On the other hand, a number of prior studies using both functional neuroimaging and TMS have suggested that Broca’s area may in fact be parcellated into functionally distinct subregions (see Devlin & Watkins, 2007, for a review). Although this work has focused primarily on the difference between semantic and phonological processing, finer-grained distinctions may exist, suggesting that the region targeted here is not representative of the IFG as a whole. We ourselves have predicted elsewhere that part of Broca’s area might be important for processing of nouns (Shapiro & Caramazza, 2003b), based on the observation of a patient who had a left suprasylvian lesion that was accompanied by noun production difficulties (Shapiro et al., 2000). The present results offer no support for this prediction, although of course it may be that the processing of nouns depends on some other region within Broca’s area or elsewhere in the left frontal cortex that was not targeted in the present study.

Finally, we should reiterate the possibility raised elsewhere in this article that the effects of stimulation

to the left aMFG are not attributable to the disruption of the left aMFG per se, but are rather attributable to the transsynaptic suppression of some other cortical region or regions. If this is true, the distant site is presumably not one of those stimulated in Experiment 2, nor one to which either of those areas is connected very strongly. Therefore, a conservative conclusion would be that the effects arise either at the aMFG itself, or in a region or network to which the left aMFG has what we have called a “privileged” connection.

### Processing of Other Grammatical Categories

The experiments reported here were aimed, in part, at clarifying the role of a part of the left prefrontal cortex that is known from prior studies to be engaged in verb processing. We did not explicitly aim to target areas that might be involved in the processing of other grammatical categories, although as we have noted, we found no support for a prior prediction that the IFG might be engaged selectively in noun processing (Shapiro & Caramazza, 2003b). At present, there are no data that point to any particular brain region that might be engaged specifically in the grammatical processing of nouns or words of other categories (e.g., adjectives). The available data from neuropsychology (Daniele et al., 1994; Damasio & Tranel, 1993) and neuroimaging (Shapiro et al., 2006) suggest that lexical–semantic processing of nouns relies on portions of the left temporal lobe that, unfortunately, are largely inaccessible to TMS. Therefore, any attempt to demonstrate a double dissociation in processing between verbs and another category using TMS, however desirable this might be from a theoretical perspective, should await further advances in empirical knowledge about the anatomy of lexical processing.

### Processing Regular and Irregular Morphological Inflection

The contrast between regular and irregular nouns and verbs in Experiments 1 and 2 allowed us to assess the level at which category-specific effects arise in the left aMFG. In other words, we tested whether repeated stimulation interferes with the production of words of a specific category (verbs), words undergoing a specific morphological process (regular morphological inflection), or some interaction between these two dimensions. We showed that rTMS applied to the left aMFG interferes equally with the production of regularly and irregularly inflected verbs, and does not interfere with the production of either regular or irregular nouns. Moreover, no regularity effect was observed following stimulation to the pMFG or Broca’s area.

These results do not seem to support the view that regular and irregular forms are processed by two distinct and neuroanatomically segregated mechanisms, with

regularly inflected forms relying on the left inferior frontal cortex (e.g., Tyler et al., 2001, 2004; Ullman, Corkin, et al., 1997). At none of the three sites of stimulation in the left frontal cortex (nor at any of their right hemisphere homologues) did we observe a specific effect on the production of regular words.

Two explanations may be suggested to account for our results. First, failure to detect any difference between regular and irregular form processing may support the view that these forms are implemented by a single cognitive mechanism (McClelland & Patterson, 2002; Joanisse & Seidenberg, 1999). This view holds that inflectional processes arise from a single integrated system, namely, that both regular and irregular verb inflection emerge from one distinct mechanism. However, some recent neuropsychological cases of selective impairment of irregular verb forms (e.g., Miozzo, 2003) seem problematic for the single-mechanism account and require further explanations.

An alternative account is that regular and irregular forms are processed, at some level, by distinct neural circuits, but that this distinction is not reflected in the organization of the cortical regions targeted in our experiments. We have proposed that the area targeted in the left aMFG is crucial for morphosyntactic processes that apply to the grammatical category of verbs (cf. also Shapiro et al., 2001). Such processes could, in principle, operate over rather abstract kinds of representations; for example, a morphosyntactic rule might mark a lexical representation to be produced with the tense feature [+PAST], without specifying the phonological consequences of that feature setting. This would then require some other system to cash out abstract morphosyntactic features in phonological terms (e.g., the suffix /ed/ for regular verbs, or an internal vowel change like ablaut for some irregular verbs). Our results do not speak to the question of whether some brain regions might be more crucial for the morphophonological computation of regular or irregular forms for nouns or verbs, except to say that the areas we stimulated in the frontal lobes do not seem to encode any such distinction. It may be the case that portions of Broca’s area caudal to the region stimulated here, which are thought to be engaged in phonological processing (see Devlin & Watkins, 2007), are important for this kind of morphophonological process.

### Right Hemisphere Effects

For each condition in which an area in the left frontal cortex was targeted with rTMS, there were two controls: sham stimulation and rTMS to the homologous area in the right hemisphere. We reasoned that if any area in the left hemisphere was found to be critical for verb or noun processing, it would be unlikely that a similarly specific impairment in performance should be observed after stimulation to right hemisphere areas. Indeed,

Experiment 1 confirmed this prediction: Verb processing was delayed following left aMFG stimulation, but not after sham stimulation or stimulation to the right aMFG.

Interestingly, however, the overall effects of stimulating the right aMFG were not the same as the effects of sham stimulation. The difference in RTs for every trial type was greater when left hemisphere rTMS was compared to right hemisphere rTMS than when left hemisphere rTMS was compared to sham stimulation. In Experiment 2, this trend was more pronounced: The difference between left rTMS and right rTMS was greater than the difference between left rTMS and sham for all trial types in both areas that were stimulated (pMFG and IFG). In other words, stimulation to the right hemisphere seemed to result in a relative facilitation of responses across categories.

We should reiterate that this facilitation effect did not seem to be stimulus-specific; the only specific effect observed in either experiment was the delay in verb processing following stimulation to the left aMFG. Having said this, two interesting aspects of the left–right pattern deserve comment. One is that the facilitatory effect of stimulation to the right hemisphere (compared to sham) appeared to increase in an anterior-to-posterior direction. The second is that the absolute difference between stimulation to the left and right appeared to be relatively constant, especially for the IFG and the pMFG. Although the importance of these results is not obvious, they suggest that right hemisphere cortical areas may modulate the activity of homologous areas in the left hemisphere that are engaged in language production. This kind of interhemispheric interaction is believed to be mediated by callosal fibers, and has been described in areas such as the motor cortex and parietal lobes in both neurologically healthy subjects and in patients with stroke (Mansur et al., 2005; Naeser et al., 2005a, 2005b; Kobayashi, Hutchinson, Theoret, Schlaug, & Pascual-Leone, 2004; Theoret, Kobayashi, Valero-Cabre, & Pascual-Leone, 2003; Hilgetag, Theoret, & Pascual-Leone, 2001). The present results suggest that transcallosal inhibition may also be extended to lexical processing.

## CONCLUSION

We have previously suggested that verbs are processed by distinct cortical circuits that can be identified by targeted suppression of the left prefrontal cortex (Shapiro et al., 2001). In the present investigation, with the use of more sophisticated methods and an improved experimental design, we confirmed this hypothesis, at least insofar as it applies to the contrast between verbs and nouns. In addition, we have drawn three other important conclusions: (1) the left aMFG is equally involved in processing regular and irregular verbs, as no difference in response latencies emerged between them following rTMS; (2) the effect of rTMS on the left aMFG is relatively specific and focal, as no interference resulted

after stimulating the left pMFG; (3) rTMS applied to Broca's area did not specifically interfere with verb production, but seemed to result in category-general interference with word production.

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## Notes

1. Other word classes, like adjectives, may also be associated with distinct neural circuits, but the status of categories other than nouns and verbs has not been well studied. There are, however, a number of more principled reasons for focusing on nouns and verbs, including the consensus among linguists that nouns and verbs (but no other categories) are distinguished in every human language (Evans, 2000; Jacobsen, 1979; Robins, 1952; Sapir, 1921). In this article, the phrases “category-specific,” “selective,” and the like refer only to the categories of nouns and verbs.
2. In Shapiro et al., we attempted to address this concern by showing that the effects of rTMS were not greater for trials with longer reaction times at baseline; indeed, *less* interference was observed for more difficult trials within a category.
3. A similar ANOVA on error rates showed no significant main effect of stimulation condition [ $F(2, 14) = 0.173, ns$ ] or of trial types [ $F(3, 21) = 1.745, ns$ ], and no significant interaction [ $F(6, 42) = 0.901, ns$ ].
4. A similar ANOVA on error rates showed no significant main effect of stimulation condition [ $F(4, 44) = 0.167, p < .95, ns$ ] and of stimulus [ $F(3, 33) = 1.507, p < .23, ns$ ] and no significant Condition  $\times$  Stimulus interaction [ $F(12, 132) = 0.950, p = .5, ns$ ].

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