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Spatiotemporal maps of past-tense verb inflection

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Abstract

Does the brain inflect verbs by applying rules, by associative retrieval of the inflected form, or both? We used whole-head magnetoencephalography to spatiotemporally map the brain response underlying verb past-tense inflection. Placing either regular or irregular verbs into the past tense sequentially modulates the bilateral visual, left inferotemporal, posterior superior temporal (Wernicke's area), left inferior prefrontal (Broca's area), and right prefrontal cortices. Although irregular and regular verb inflection evokes similar cortical response patterns, differences in specific frontotemporal regions are observed. At ~340 ms, irregular verbs evoke greater response modulation in left occipitotemporal cortex. This modulation occurs when widespread areas are simultaneously active, suggesting that it reflects associative activation necessary for generation of past-tense forms. Subsequently, regular verbs show increased response at ~470 ms within left inferior prefrontal regions associated with rule-based inflection. Increased right dorsolateral prefrontal response at ~570 ms may represent directed/effortful retrieval of irregular past-tense forms. Thus, the brain inflects verbs by dynamically modulating different functional divisions of an integrated language system.

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Introduction

The past tense of most English verbs can be generated by following the simple rule of adding “-ed” (e.g. walk-walked). Irregular verbs do not follow this rule, but nonetheless do tend to fall into categories (e.g., ring-rang, sing-sang), leading to models where all verbs are placed into the past tense using a limited number of rules (Halle and Mohanan, 1985). This view has been challenged by connectionist accounts, which do not require explicit rules for past-tense production, but may directly associate phonological input and output units (McClelland and Rumelhart, 1986). A third approach notes that regular and irregular verb inflection is differentially affected by brain lesions as well as developmental and psychological factors (Pinker, 1991;

Marslen-Wilson and Tyler, 1997; Patterson et al., 2001; Ullman, 2001). These data provide evidence against “single-mechanism” accounts and suggests instead a dual-mechanism model, where regular verbs are inflected using rules, and irregular verbs, via associative retrieval of the corresponding past-tense form (Pinker, 1999). The data have also led to the modification of earlier connectionist models to include semantic and other “hidden” modules (Joanisse and Seidenberg, 1999). These more recent models explain neuropsychological dissociations as owing to a greater reliance on word meaning by irregular verbs (Joanisse and Seidenberg, 1999; Patterson et al., 2001).

Since rule-based and associative mechanisms are posited to involve different brain structures, the dual-mechanism model predicts that the inflection of irregular versus regular verbs would activate different brain structures, whereas early single-mechanism models predict that they would activate the same brain structures, more specifically grammatical and/or phonological processing regions, to a similar

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degree. Thus, the uniformity of the brain activation evoked by inflection of irregular versus regular verbs has become a crucial point of evidence in this ongoing debate.

Brain activation during grammatical transformations has previously been imaged using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) (Indefrey et al., 1997). In one study (Jaeger et al., 1996), the left dorsolateral prefrontal cortex was activated during regular verb inflection while the left middle temporal gyrus was more active for irregular verbs, suggesting that a dual-mechanism account of verb inflection is most appropriate. This is further supported by other PET studies (Indefrey et al., 1997) and fMRI data demonstrating fronto-temporal processing dissociations (Ullman et al., 1997; Bergida et al., 1998). However, these studies continue to be debated on methodological and theoretical grounds (Jaeger et al., 1998; Seidenberg and Hoeffner, 1998; Indefrey, 2000).

Although PET and fMRI have good spatial localization, their temporal accuracy is poor (>1 s) in comparison to MEG and electroencephalography (EEG), which provide millisecond temporal resolution and adequate spatial resolution (Dale and Halgren, 2001). Several studies have demonstrated differential effects based on regularity for both nouns and verbs as modulation of a left anterior negativity (LAN) often occurring between ~ 200 and 600 ms after stimulus (Penke et al., 1997; Weyerts et al., 1997; Gross et al., 1998; Marslen-Wilson and Tyler, 1998; Newman et al., 1999). Additionally, priming studies showed that regular past-tense forms serve as more powerful primes for their corresponding stems than do irregulars, thus lending further support for dual-mechanism models (Weyerts et al., 1996; Munte et al., 1999).

These EEG effects, however, were evoked either by the perception of grammatical mistakes or by implicit cross-tense priming and are difficult to compare to the PET/fMRI activations evoked by the generation of correct grammatical forms. Furthermore, the cortical origins of the EEG effects are unclear. Two studies have used source modeling in an attempt to localize the cortical origins of EEG or magnetoencephalography (MEG) recorded during inflection of regular versus irregular verbs. Using a low-resolution inverse solution and 28 channels of EEG recorded during overt inflection, Lavric et al. (2001) inferred that irregular verbs evoked more current density at ~ 288 – 320 ms in the left posterior temporal and bilateral inferomedial frontal cortices, whereas regular verbs evoked more in the right temporal and frontal regions. An abstract by Rhee et al. (1999) reported the ability to model MEG patterns with left frontal dipoles to regular but not to irregular verbs, at ~ 320 ms after visual presentation onset. However, anatomical constraints from individual subjects were not applied in either study, nor were the differences between regular and irregular verbs presented within the context of the overall response common to both types. Thus, despite important find-

ings, the location as well as dynamics of cerebral processing underlying verb inflection remain to be established.

The present study utilizes whole-head (204-channel) MEG and applies a distributed inverse solution normalized by estimated noise values to produce dynamic statistical parametric maps (Dale et al., 2000; Dhond et al., 2001). Sources are anatomically constrained to lie in the cortex (reconstructed from each subject's structural MRI), and activity is combined across subjects by aligning their cortical sulcal–gyral patterns. Spatiotemporal cortical activity maps of visual language processing made previously using this technique are highly consistent with activation patterns found in similar tasks with fMRI and intracranial EEG (Smith et al., 1986; Halgren et al., 1994a, 1994b, 2002; Dale et al., 2000; Dhond et al., 2001). These solutions are used to characterize the overall spatiotemporal pattern of cortical processing during past-tense generation, as well as the differences in brain activity when inflecting regular versus irregular verbs.

Methods

MEG recording

MEG was recorded using a Neuromag VectorView (Elektra AB, Stockholm, Sweden) with 204 gradiometer channels covering the entire scalp. MEG recordings took place within a magnetically-shielded room (Imedco, Hagnedorf, Switzerland). Signals were recorded continuously for the duration of the task and sampled at 601 Hz after filtering from 0.1 to 200 Hz. Separate averages of novel irregular and regular trials were constructed for each subject and then low-pass filtered at 20 Hz. Trials were rejected from analysis based on amplitude criteria supplemented by visual inspection to determine whether they were contaminated by artifacts (identified as peak-to-peak amplitude >500 fT/cm in any channel) or eyeblinks (>100 μ V in the EOG electrode). Head movement was minimized using a bite bar as well as chin strap and foam padding on the sides of the head.

Cortical surface reconstruction

A geometrical representation of the cortical surface of each subject was obtained using procedures described previously (Dale et al., 1999; Fischl et al., 1999a). First, high-resolution three-dimensional (3-D) T1-weighted structural images were acquired for each subject using a 1.5-T Picker Eclipse (Phillips Medical Systems, Netherlands). Then, the cortical white matter was segmented, and the estimated border between gray and white matter was tessellated, providing a topologically correct representation of the surface with about 150,000 vertices per hemisphere. For the inverse computation, the cortical surface is decimated to approximately 1700 dipoles per hemisphere, which is roughly equivalent to 1 dipole every 10 mm along the cortical

surface. Finally the folded surface tessellation was “inflated,” to unfold cortical sulci, thereby providing a convenient format for visualizing cortical response patterns (Dale et al., 1999; Fischl et al., 1999a). For purposes of intersubject averaging, the reconstructed surface for each subject was morphed into an average spherical representation, optimally aligning sulcal and gyral features across subjects while minimizing metric distortions and shear (Fischl et al., 1999a). Compared to volumetric morphing into Talairach (Collins et al., 1994) space, this method has been found to provide better alignment across subjects of functional activation in a verbal task (Fischl et al., 1999b). Furthermore, this method allows direct localization to regular gyri such as the inferior frontal gyrus, pars opercularis. Thus, while Talairach coordinates are reported here to facilitate comparison with other studies, it should be understood as a relatively indirect method for localizing activation. Functional activation is mapped on a representation of the average sulcal-gyral pattern across 35 subjects.

Forward solution

The boundary element method was used for calculating the signal expected at each MEG sensor, for each dipole location (deMunck, 1992; Oostendorp and Van Oosterom, 1992). The computation of the MEG forward solution has been shown to only require the inner skull boundary to achieve an accurate solution (Meijs et al., 1987; Meijs and Peters, 1987; Hamalainen and Sarvas, 1989). The same T1-weighted MRI described above was used for construction of the inner skull surface. The MEG sensor coordinate system was aligned with the MRI coordinate system using four head position (HPI) coils, attached to cardinal locations on the scalp (Hamalainen et al., 1993). The HPI coils generate weak magnetic signals, allowing them to be directly localized by the MEG sensors before and after the recording session. The positions of the HPI coils with respect to the subject’s head (and thus MRI) are determined by measuring ~80 points (including the HPI coils) around the head using a Polhemus FastTrack 3-D digitizer. These digitized points are later registered with the MRI image. Since the HPI coils are thus localized with respect to both the MEG sensors and the structural MRI, a common coordinate system is established allowing neural activity to be estimated for each cortical location.

Inverse solution

To estimate the time courses of cortical response, we used the noise-normalized, anatomically constrained linear estimation approach described by Dale et al. (2000). This approach is similar to the generalized least-squares or weighted minimum norm solution (Hamalainen and Ilmoniemi, 1984), except that the active dipoles are constrained to lie in the cortical surface (as determined above) (Dale and Sereno, 1993), and the estimate is normalized for noise

sensitivity so that statistical significance rather than dipole strength is mapped (Dale et al., 2000). Noise normalization also has the effect of greatly reducing the variation in the point-spread function between locations (Liu et al., 2002). This approach provides statistical parametric maps of cortical activity, similar to the statistical maps typically generated using fMRI, or PET data, but with a temporal resolution of 5 ms or less.

Since in the current study, no a priori assumptions are made about the local dipole orientation, three components are required for each location. A sensitivity-normalized estimate of the local current dipole power (sum of squared dipole component strengths) at each source location is calculated (Dale and Sereno, 1993; Liu et al., 1998). For the irregular versus regular verb contrast, the waveforms of the individual conditions for each subject are subtracted prior to estimating the differential activity pattern. The nonsubtracted condition maps (Fig. 1) reflect the average probability that the generated signal is greater than the noise level; that is, the data are tested under the null hypothesis that the observed signal at each cortical source reflects the noise that had been measured at the same location. The subtracted condition maps (Fig. 2) show the average probability that the *difference* between the MEG conditions (irregular vs. regular) is greater than that expected randomly given the measured noise levels. The noise for all conditions is estimated from the baseline of the raw signals after all filtering is applied (about 160,000 time points per sensor are used to estimate sensor noise covariance). The significance of modulation at each site was calculated using an *F* test (Dale et al., 2000; Dhond et al., 2001). For the irregular and regular verb conditions, significance thresholds were set at $P < 10^{-8}$. Full red responses indicate a significance of $P < 10^{-15}$ and bright yellow $P < 10^{-23}$. In the statistical maps of the subtracted condition (irregular minus regular), significances were $P < 10^{-5}$, $P < 10^{-6}$, and $P < 10^{-7}$ for threshold, full red, and yellow, respectively. In interpreting these statistical thresholds it should be born in mind that they do not reflect any correction for the multiple comparisons that were made across sources and latencies. In summary, noise-sensitivity-normalized cortical surface constrained minimum norm inverse solutions were calculated every 5 ms for every condition and every individual. These movies were then averaged on the cortical surface across individuals after aligning their sulcal-gyral patterns. All activity in the figures is significant at $P < 10^{-5}$.

Verb inflection task

Data were collected from 12 normal right-handed native English-speaking males (18–30 years old, mean 27 years). Subjects were rejected if they had a history of mental or physical illness, head injuries, or drug/alcohol dependence/abuse. Subjects were screened for MEG artifacts owing to dental work or excessive eyeblinks. Strong right-handers

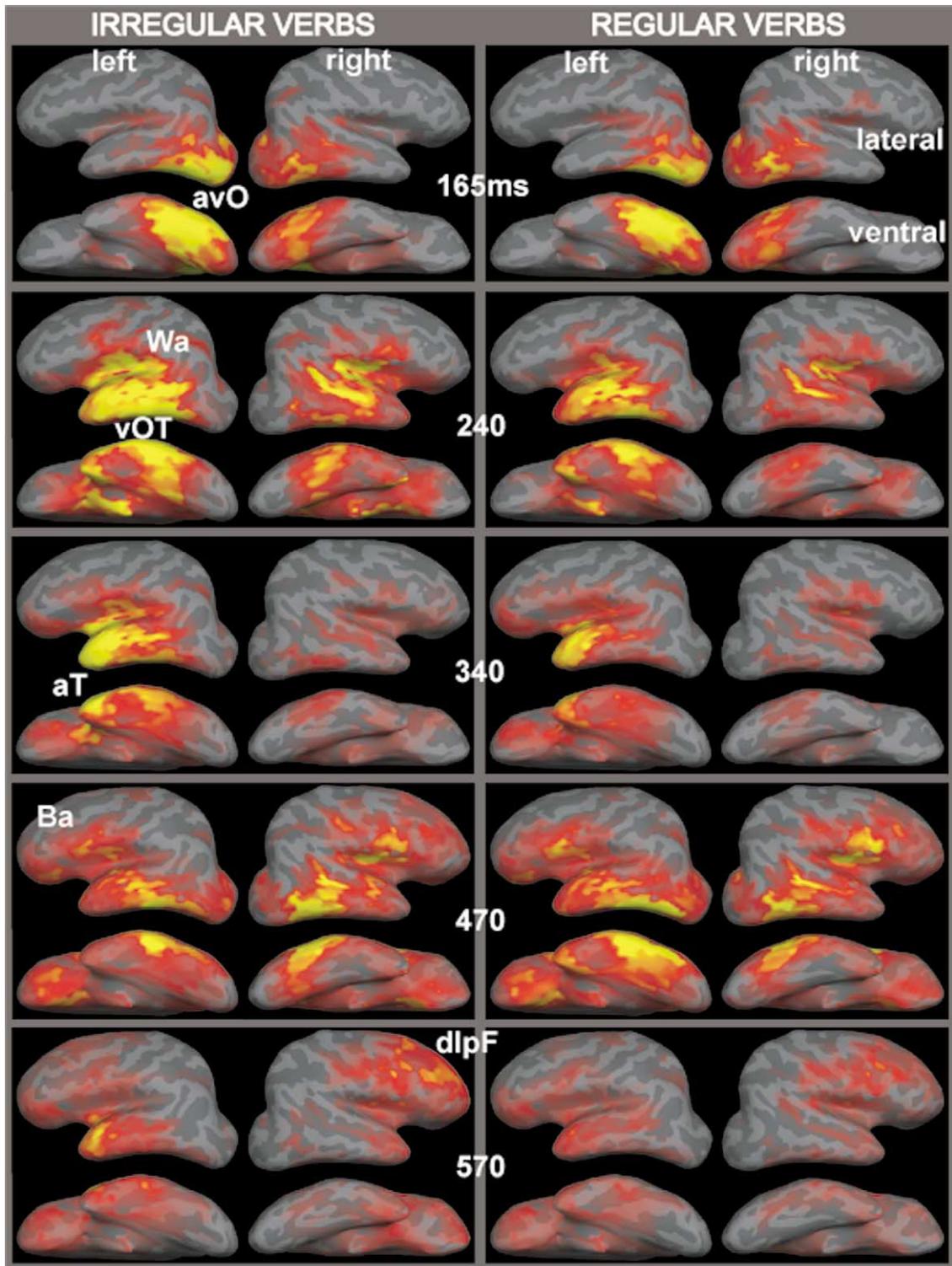


Fig. 1. Statistical parametric maps of spatiotemporal response patterns during the inflection of irregular and regular verbs. Activity begins in the occipital and progresses through the temporal and then prefrontal cortices, engaging successively areas involved in perceptive, lexical, semantic, grammatical, and strategic processing. Snapshots of significant response patterns at five latencies from 165 to 570 ms after word onset are shown for lateral and ventral views of the left and right hemispheres. Cortical activity begins in bilateral primary visual areas at ~ 100 ms (not shown) and quickly spreads to specialized form processing areas in the anteroventral occipital cortex (avO). This response peaks at ~ 165 ms and is strongly lateralized to the left (language dominant) hemisphere. By ~ 240 ms, activity has advanced further anteriorly to encompass Wernicke's area (Wa) and the surrounding cortex in the left superior temporal lobe associated with lexicophonemic representations, as well as ventral occipitotemporal (vOT) areas associated with lexicoiconic processing. By ~ 340 ms, activity is predominantly in the anterior temporal lobe (aT) including areas thought to contain multimodal semantic representations. Activity then shifts by ~ 470 ms to become more bilateral and frontal (including Broca's area, Ba), with a reactivation of the occipitotemporal areas. At ~ 570 ms activity is especially prominent in right dorsolateral prefrontal cortex (dlpF). Activity (significance threshold $P < 10^{-8}$) is estimated from MEG for each patch of cortex and averaged across 12 individuals. Cortical surfaces are inflated, with sulcal cortex in a darker shade of gray.

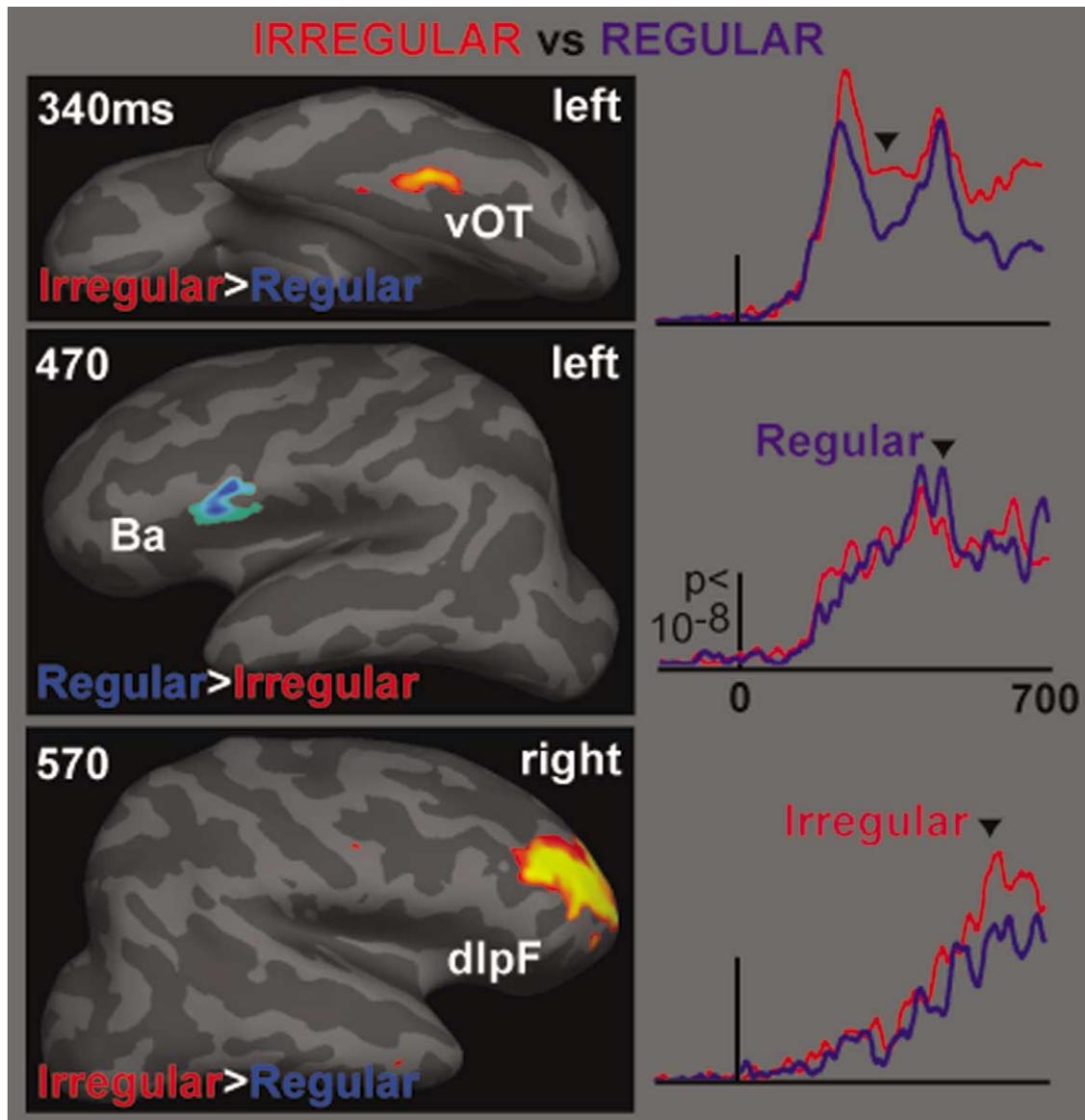


Fig. 2. Significant differences in brain response patterns to irregular versus regular verbs. At ~ 340 ms irregular verbs evoke greater activity in the left ventral occipitotemporal cortex (vOT), an area where lexico-iconic representations are thought to be stored or accessed. At ~ 470 ms, regular verbs evoke greater activity in Broca's area (Ba), a location classically associated with rule-based grammatical transformations. At ~ 570 ms response modulation again increases to irregular verbs, this time in the right anterior dorsolateral prefrontal cortex (dlpF), an area associated with controlled retrieval and other strategic processes. Approximate Talairach (Collins et al., 1994) coordinates at the centers of the activations are vOT $-47, -44, -10$; Ba $-54, 13, 7$; and dlpF $27, 58, 13$. The statistical significance threshold is $P < 10^{-5}$, with red/yellow indicating greater activity to irregular verbs, and blue to regular. To the right of each brain is the estimated time course of the response, for irregular and regular verbs considered individually, with an arrow at the latency of the image at left and the height of the y-axis at a significance level of $P < 10^{-8}$.

were selected as subjects using the Edinburgh inventory (Oldfield, 1971).

During the verb inflection task, stimuli were projected through an opening in the wall of the shielded room (which was covered with transparent plexiglass) onto a screen located within the room. Using MacProbe software (Hunt, 1994) word stimuli were presented in Geneva font as white letters on a black background. Subjects were shown 80 novel (presented only once) regular verbs, 80 novel irregular verbs, 5 repeated regular verbs (repeated 16 times each),

and 5 repeated irregular verbs, for a total of 320 trials. Regular/irregular and novel/repeated trials were fully crossed and randomly intermixed. Verbs were presented in the central 5% of visual angle for 250 ms in the infinitive form. Stimulus onset asynchrony was 2.3 s. Irregular and regular verbs were matched for word frequency (average 234 for irregular and 240 for regular, $P > 0.5$; Francis and Kucera, 1982) and number of letters (5.4 for both verb types). Subjects were instructed to silently generate the past-tense form, and fixated on a central "+" sign between

words. Practice consisted of past-tense generation to four repetitions of each of the 10 repeated verbs.

Overt production was not used since it is often associated with small head movements that change the exact spatial relation of the cortex to the MEG sensors, resulting in inaccurate source localization. To monitor task performance accuracy and speed, subjects were instructed to lift their left index finger if, after silently generating the past-tense form, they found that it ended in “-ED.” This instruction was used because most subjects were not familiar with linguistic terminology such as “irregular” and “regular” (using such jargon may lead to confusion), and the “ED” ending is common to all regular verbs. Since three different phonological realizations of the -ED affix (/t/, /d/, /ed/) exist among regular verbs, both the practice run and the actual experiment contained regular verbs that varied in the phonological ending required for correct inflection. This implicitly instructed the subjects to categorize verbs based on the regularity of their past-tense inflection, rather than their precise phonology. In any case, this decision must occur *after* generation of the past-tense form of the verb and is not likely to invoke orthographic systems during the initial process of inflection.

During the task, repetition strongly decreased the response in the left anteroventral temporal and posteroventral prefrontal cortices, maximal at ~400 ms, as has been reported elsewhere for other verbal tasks (Dale et al., 2000; Dhond et al., 2001). All data reported here are to novel words. Response latencies were measured using a fiberoptic keypad triggered upon finger lift. For novel words, response latencies ranged from 760 to 1196 ms across subjects (mean 928 ± 119 ms), with $95.7 \pm 4.1\%$ correct. As subject performance in this task was very high, incorrect trials were not rejected from averages. Response times similar to those seen here were also found in studies of verb inflection requiring overt verbal responses (Seidenberg, 1992; Jaeger et al., 1996). Analysis was terminated at 670 ms (i.e., 100 ms prior to the most rapid subject’s reaction time) to avoid interpretive confounds arising from the fact that only regular verbs evoked an overt behavioral response.

Results

Inflection of both irregular and regular verbs evoked a posterior to anterior sequence of cortical recruitment (Fig. 1), consistent with classical models of language processing (Benson, 1979). The earliest significant brain response occurs at ~100 ms after stimulus in the primary visual cortex at the occipital pole. Activity spreads rapidly to anteroventral occipital cortex where by ~165 ms it is strongly lateralized to the language-dominant left hemisphere. Furthermore, it is centered within an area thought to be engaged in the encoding of letter strings and other word-like stimuli (Nobre et al., 1994). Subsequently, activity moves forward to left temporal regions by ~240 ms. A strong response is

present within the superior posterolateral temporal cortex encompassing classical Wernicke’s and occipitotemporal areas implicated in lexicophonemic and semantic processing (Benson, 1979; Caplan, 1990; Price, 2000). Overlapping activity is also present in ventral occipitotemporal cortex associated with lexico-iconic encoding (Dhond et al., 2001) as well as anterotemporal regions associated with lexicosemantic processing (Hodges et al., 1992; Damasio et al., 1996; Mummery et al., 2000). Thus, at an early latency, verbs activate areas that may encode them iconically, phonemically, and semantically.

The dominant focus of cortical response continues to move forward and by ~340 ms increasingly includes left anterotemporal cortex along with significant recruitment of inferior prefrontal regions. The prefrontal response increases over the next 100 ms, peaking at ~440 ms with a strong left lateralization. The cortical distribution and timing of this response, as well as its attenuation with repetition priming, are similar to those of the N400 as measured by MEG (Dale et al., 2000; Dhond et al., 2001; Halgren et al., 2002) and intracranial EEG (Smith et al., 1986; Halgren et al., 1994a, 1994b). Shortly thereafter, by ~470 ms, activity becomes more bilateral and spreads posteriorly to again involve occipitotemporal regions. Frontotemporal activity continues until the end of the epoch, with prefrontal areas showing their greatest activity at the longest latencies. These areas include classical Broca’s area and surrounding regions in the left ventroposterior prefrontal cortex (Benson, 1979), as well as the right dorsolateral prefrontal cortex often activated during memory retrieval (Buckner and Koutstaal, 1998).

Significant differential processing between verb types was evaluated by mapping the difference in the magnetic fields evoked by inflecting irregular versus regular verbs in each subject. An average dynamic statistical parametric map was made for this subtracted condition, and response modulation at times when differences occurred are shown in Fig. 2. Statistically significant differences did not occur until >300 ms, that is, after all elements of the widespread network invoked by this task (with the exception of right dorsolateral prefrontal cortex), had been engaged. Since inadvertent low-level lexical and sensory differences between conditions, as well as strategic expectations owing to nonrandom condition order, would be expected to produce differences in early responses, the lack of such differences increases the likelihood that later differences are actually due to the verb type.

Differential processing between irregular and regular verb inflection is first seen at ~340 ms in left ventral occipitotemporal cortex where it is greater to irregular verbs. Shortly thereafter, at ~470 ms after stimulus, inflection of regular verbs demonstrates an increased response modulation with the left inferior prefrontal cortex (classical Broca’s area). Finally, irregular verb inflection again shows more activity than regular verb inflection within right dorsolateral prefrontal regions at longer latencies, ~570 ms.

Discussion

Verb past-tense inflection results in widespread cortical activity

Spatiotemporal brain mapping with MEG demonstrates that after ~200 ms, verb inflection simultaneously modulates a large number of areas in multiple lobes. Activity is concentrated in language areas that are highly similar to those observed in other visual-verbal tasks using PET or fMRI (Wise et al., 1991; Fiez and Petersen, 1998; Cabeza and Nyberg, 2000). The timing and location of this activity strongly resemble that observed with MEG during semantic judgments on nouns (Dale et al., 2000), sentence-reading (Halgren et al., 2002), and word-stem completion (Dhond et al., 2001). Intracranial EEG recordings have demonstrated locally generated potentials in these areas during word recognition (Smith et al., 1986; Halgren et al., 1994a, 1994b). Activity is especially prominent in anteroventral temporal and inferior prefrontal areas implicated in semantic processing (Wagner et al., 1998; Mummery et al., 2000) and at a latency (~400 ms) when responses are strongly modulated by contextual and semantic factors (Kutas and Federmeier, 2000). However, activity is also present in areas associated with phonological and orthographic processing. Activity in all of these areas begins at a relatively early latency (<240 ms) and is sustained through the end of the analysis epoch. In contrast to this widespread and powerful overall response, significant changes related to verb regularity are relatively brief, small, and local. The overall response provides the physiological context for verb inflection and suggests that it may draw on multiple simultaneously active networks not specifically related to verb inflection, calling into question early connectionist theories suggesting that verb inflection proceeds solely by phonological associations (McClelland and Rumelhart, 1986) or purely by application of rules (Chomsky and Halle, 1968).

Verb regularity affects early processing in the left ventral temporal and later processing in left and right prefrontal regions

The first significant differential response modulation between irregular and regular verb inflection is seen in the left ventral occipitotemporal cortex, centered on the fusiform gyrus. A previous study using EEG also inferred greater left posterior temporal activity while inflecting irregular verbs in about the same latency range (Lavric et al., 2001). A variety of data suggest that the left fusiform area is engaged in lexico-iconic or “word-form” encoding (Halgren et al., 1994a, 2002; Nobre et al., 1994; Salmelin et al., 2000; Dhond et al., 2001; Dehaene et al., 2002). Specifically, it may help link the feature level with the lexical level and thus contribute to an early form of direct lexical access (Humphreys and Evett, 1985). In these studies, the initial responses specific for letter strings begin in this area at

~180 ms, and in the current study, responses in this area had become highly lateralized to the dominant hemisphere by the same latency. However, the irregular/regular difference does not reach significance until considerably later, at ~335 ms after stimulus, when irregular verbs evoke greater activation. This more sustained modulation and increased response to irregular verbs may reflect the fact that their past-tense forms have more varied orthography, thus requiring more sustained processing. The dual-mechanism model states that while a separate lexical representation for the past tense is necessary for irregular verbs, it is in most cases unnecessary and unlikely for regular verbs (Pinker, 1999). Thus, this model predicts that irregular verbs would evoke a more extended modulation of the locations involved in accessing lexical representations. The increased left ventral occipitotemporal response at ~340 ms to irregular verbs is consistent with that prediction. Alternatively, this activity may represent feature-based orthographic analysis of the past-tense form, which is more sustained for irregular forms owing to their greater variability. Note that the irregular/regular difference seen here does not appear until widespread frontotemporal language circuits have been engaged for >100 ms. These more anterolateral frontotemporal circuits also show a nonsignificant tendency to be more responsive at ~340 ms to irregular words. This suggests that the differential modulation within ventral occipitotemporal regions may actually be the nexus of a more widely distributed brain response.

The next location showing significantly different response modulation was Broca’s area, where activity was larger to regular verbs, maximal at ~470 ms. Classical studies of agrammaticism, as well as modern neuroimaging studies, suggest that this area participates in rule-based past-tense generation, syntactic parsing, and grammar (Caplan, 1990; Just et al., 1996; Clahsen, 1999; Indefrey et al., 2001). This finding suggests that rule-based syntactic processing may be greater for regular verbs and, thus, is also consistent with the dual-mechanism model (Pinker, 1999). Frontotemporal dissociations, providing further support for dual-mechanism approaches, were also noted in an early hemodynamic study of verb inflection (Jaeger et al., 1996).

In addition to syntactic processing, left prefrontal activation has been found in a wide variety of tasks, including semantic encoding (Demb et al., 1995; Buckner and Koutstaal, 1998; Wagner et al., 1998), verbal working memory (Fiez et al., 1996; Gabrieli et al., 1998), and response selection (Thompson-Schill et al., 1999; Rowe et al., 2000). In the present study, incidental semantic encoding should be equal between conditions, and the anterior temporal areas also implicated in this process showed only nonsignificant increases in favor of *irregular* verbs at this latency. Working memory demands should be greater for irregular verbs, which take longer to inflect (Seidenberg and Hoeffner, 1998; Pinker, 1999). Similarly, irregular verbs by definition have a variety of endings that might be considered as response alternatives, whereas regular verbs have only one

morphological ending. Thus, it seems unlikely that increased response modulation within left inferior prefrontal cortex, centered on Broca's area, to regular verbs would be due to semantic encoding, working memory, or selection from multiple response alternatives, as these functions are expected to be more strongly engaged by irregular verbs.

The third location where a significantly different response was found between irregular and regular verb inflection is the right dorsolateral prefrontal cortex. This difference peaked at ~570 ms, and modulation was greater to irregular verbs. Several neuroimaging studies have found activation in this area to subserve controlled, effortful retrieval processes (Rugg et al., 1997; Buckner and Koutstaal, 1998; Duzel et al., 1999). Again, this activation is consistent with predictions of the dual-mechanism model, as underlying the intentional recollection of the irregular past-tense verb forms (whereas the earlier inferotemporal activation may reflect automatic spread of activation to multiple lexical representations). Lavric et al. (2001) also inferred differential EEG source activity in right dorsolateral prefrontal cortex between verb types, but this difference was in an earlier time period (~320 ms) and was greater to regular verbs. Greater prefrontal activity to irregular verbs was confined to the inferomedial prefrontal cortex, bilaterally, again during this earlier period. These differences between our results and those of Lavric et al. (2001) are likely due to differences in sensitivity between EEG and MEG, in sampling density, and/or in source estimation procedures.

A serious potential confound is that irregular verbs are overrepresented among the most common English verbs (to be, go, have, run, . . .). The verbs in the current study were carefully chosen to balance word frequency between those in the regular and irregular groups, according to standard norms (Francis and Kucera, 1982). In addition, we compared the differences obtained in this study to those obtained in another MEG study using the same localization technique, but where word frequency was intentionally manipulated (Halgren et al., 2002). In Halgren et al. (2002), low- versus high-frequency (15 vs. 381 words per million) content words were presented in intermediate sentence positions. The effects of this large manipulation were only marginally significant and were located mainly in the left temporal pole, unlike the more posterior occipitotemporal and more anterior prefrontal differential responses associated with irregular versus regular verbs, reported in this study.

Single-mechanism versus dual-mechanism accounts of verb past-tense inflection

Double dissociations in processing such as those seen here are unlikely to result from nonspecific factors such as differences in difficulty and thus provide good evidence for localization of processing across conditions, that is, for dual-mechanism models. However, it may be possible to obtain such dissociations within a single-process connec-

tionist model by positing separate (but interacting) network modules for verb inflection and semantic associations, that is, a single mechanism operating across two or more modules (Joanisse and Seidenberg, 1999). Our results, however, lack any significant spatiotemporal response differences in favor of irregular verbs within semantic processing regions at the appropriate latencies. Dual-mechanism models may also include parallel activation in multiple processing areas that modulate each other as intermediate results are obtained. In such models, verbs do not arrive with a tag specifying that they are regular or irregular, automatically directing them to areas specialized for rule application or lexical retrieval; rather, they are processed by both mechanisms until lexical retrieval either finds a past-tense form or definitively fails. Furthermore, associative activation of the irregular past-tense form is hypothesized to inhibit rule-based inflection (Pinker, 1999). The differential spatiotemporal dynamics when inflecting regular versus irregular verbs are consistent with this proposal; increased inferotemporal response to irregular verbs at ~340 ms may inhibit the left inferior prefrontal (Broca's area) response to the same stimuli at ~470 ms.

Conclusion

In summary, these data demonstrate a progression of brain responses during inflection of visually presented verbs, from areas associated with basic visual processing to those associated with word form, then phonological, and finally semantic and syntactic processing. Within the context of a largely identical overall spatiotemporal response pattern evoked by irregular versus regular verbs, significant differences between these stimuli suggest verb inflection is a dynamic process where specialized language areas interact over an extended period. Our data thus suggest that both kinds of models may capture important aspects of past-tense inflection. Further comparison of the models may be facilitated if proposed models specified in greater detail how inflection occurs as an overall process, as well as where processing differences may occur based on verb type.

Acknowledgments

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